COURTS AND SEASONAL ACTIVITIES AT THEM BY MALE TOOTH-BILLED BOWERBIRDS, *SCENOPOEETES DENTIROSTRIS* (PTILONORHYNCHIDAE)

CLIFFORD B. FRITH AND DAWN W. FRITH

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Court seasonality and maintenance of male Tooth-billed Bowerbirds *Scenopoeetes dentirostris* were studied over the display seasons of 1978, 79 and 80 in a 50ha upland rainforest study area on the Paluma Range, north Queensland. Seasonality of court establishment was also recorded during nine subsequent seasons. Initial court establishment varied from season to season, the abundance of fruit in the study area having a greater influence than temperature and/or rainfall. Lack of rain and associated higher temperatures and fruit crop size influenced court decoration and maintenance levels at established courts during the display season. The onset of the wet season usually terminated court activity but significant dry spells thereafter caused a brief return to courts and their maintenance. Excessively dry, seasonally abnormal conditions caused a cessation of court activity altogther. The size of the cleared court area of more established courts of older males varied greatly, the largest being 2.75 X 1.95m and the smallest 1.0 X 0.8m. Partly established, temporary, courts of presumed younger males were smaller. Mean number of leaves on courts during peak display activity was 69. Of newly placed fresh leaves 79% were removed from courts within a week. During peak display activity a mean of 6.3 leaves were placed on courts/day and a mean of 6.9 removed. The turnover of leaves as court decorations was highest during hot dry spells. Leaves of *Polyscias australiana* were conspicuously favoured as court decoration by older males and the vast majority of leaves stolen from courts were of this plant. That leaves of a given tree species favoured by males as court decorations varied between age classes of males and geographical areas suggests the influence of local tradition based on imitive learning, as has been recorded in males of other polygynous bower-building bowerbirds. Results of leaf-marking experiments lend some support to the hypothesis that a male social hierarchy is established and maintained within groups of more densely dispersed and possibly older males, by leaf stealing. Leaf stealing was most frequent between immediate neighbours, more so between those with smallest nearest neighbour distance.

Attendance levels and behaviours of male Tooth-billed Bowerbirds at their courts were monitored throughout display seasons 1979, 80 and 89. Males spent an average 64% (range 52-79%) of daylight period 0600-1800 at their courts during peak display activity. Duration of a court visit averaged 23mins, most of which (96%) was spent singing from favoured court perches, the remaining time being spent decorating/maintaining the court (1.2% of total time) or displaying (<1% of total time). Males adopted a static posture when an unidentified intra- or inter-specific bird visited their court. Males performed loud and prolonged advertisement song followed by quiet and brief display vocalisations at courts. Advertisement song included a large proportion of avian mimicry the repertoire of which was added to opportunistically. Loud and complex vocalisations appear to substitute for epigamic plumage and a sophisticated bower in this cryptically-plumaged sexually monomorphic, simplistic court-clearing polygynous bowerbird. This represents an atypical set of evolutionary adaptations to polygyny in the bowerbirds that is, however, paralleled in several similarly atypical members of the evolutionary convergent but non-bower-building polygynous Cotingas (Passeriformes, Cotingidae) of the neotropics. ☐ *Court seasonality, leaf decoration, leaf turnover rates, leaf theft, male attendance, court behaviour, court vocalisations, Queensland, Australia, Tooth-billed Bowerbird, Scenopoeetes dentirostris.*

Clifford B. Frith & Dawn. W. Frith, Honorary Research Fellows of the Queensland Museum, 'Prionodura', P.O. Box 581, Malanda, Queensland 4885, Australia; 21 February 1994.

The Tooth-billed Bowerbird *Scenopoeetes dentirostris* lives in upland rainforests at 600-1400m above mean sea level, from Mt Amos (15°42'S, 145°18'E) southward to Mt Elliot (19°30'S, 146°57'E) just south of Townsville (Frith & Frith, 1985a; Nix & Switzer, 1991). The Tooth-bill is an atypical bowerbird in that although males are promiscuous and females uniparental, it is cryptically plumaged, sexually monomorphic (Gilliard 1969, Donaghey et al., 1985; Frith & Frith, 1985a, 1989, 1990a,b, 1993, 1994) and males form exploded leks (Frith, 1993).

Unlike males of other polygynous bowerbird species, male Tooth-bills do not construct stick bowers but instead clear leaf litter from an area on the forest floor (Borgia, 1986). This 'court' encompasses the trunk of at least one 'display tree'. The males place leaves, with their paler sides uppermost, onto the cleared area and perform courtship displays upon it (Frith & Frith, 1993). The court location is advertised by loud male vocalisations that deter rivals and attract potential mates, and the arrival of a female Tooth-bill stimulates the male to drop onto his court and display (Marshall, 1954; Warham, 1962; Frith & Frith, 1993). It is assumed that females assess male quality on the basis of vocalisations, displays, courts, decorations and perhaps male attendance (time investment) before soliciting and mating. Outside the display season Tooth-bills are mostly silent and secretive inhabitants of the forest canopy.

That male bowerbirds steal decorations from the bowers of rival males, with a preference for particular colours and items, has long been known (Marshall 1951, 1954 & references therein), but has been only briefly alluded to with the Tooth-bill (Frith & Frith, 1993). In recent years bower decoration theft has been studied intensively and it has been demonstrated that males steal predominantly from immediate neighbours (Borgia, 1985a), preferentially steal items rare in the birds' environment (Borgia & Gore, 1986; Frith & Frith, 1990c) and that the greater numbers of more favoured or stolen decorations on a bower positively influenced relative male mating success (Borgia, 1985a,b; Pruett-Jones & Pruett-Jones, 1993).

Frith & Frith (in press) found that 71% of individually-marked (n = 24) male Tooth-bills attended only one court site, that mean annual survival rate averaged 88% and mean expectancy of further life after banding was 8.1 years. Courts of Tooth-bills have been known to persist at one site for 16 years (Frith & Frith, in press), those of the Satin Bowerbird *Ptilonorhynchus violaceus* for up to 30 years (Vellenga, 1980), and those of the Great Bowerbird *Chlamydera nuchalis* and Golden-Bowerbird *Prionodura newtoniana* for more than 20 years (Frith & Frith, unpubl. data).

Temporal and spatial animal distributions are considered indicative of environmental pressures and the presence/absence of conspecifics (Brown & Orians, 1970). Whilst studies of bowers and/or bird activities at bowers are numerous, no study has fully documented male bower maintainance seasonality over one or more seasons and attempted to relate the so defined 'bower' or 'display' season to environmental factors such as climate and food resources. Marshall (1951) noted that the Tooth-bill display season varied from year to year. Vellenga (1970) observed that male Satin Bowerbirds in New South Wales had a display season of early August to late October, and that year to year variations possibly related to the irregular flowering of banksias and eucalypts and summer bushfires 'which affected food supplies'. No studies have attempted to relate such seasonality to the temporal availability of females which, in the case of the sexually monomorphic and secretive Tooth-bill, would be extremely difficult.

The display season of the male Tooth-bill starts with calling and court clearance. On the Paluma Range the season started in September or early October (Frith & Frith, 1993). The display season continues through to January or early February. Adult males perch above or adjacent to their court where they are conspicuously vocal, incorporating fine mimicry of other bird calls, and other sounds, into their repertoire (Frith & Frith, in press). All bowerbirds regularly attending and vocalizing at bowers have proved to be male (Marshall, 1954; Vellenga, 1980; Gilliard, 1969; Cooper & Forshaw, 1977; Frith & Frith, 1993). As there is no evidence that female bowerbirds attend and vocalize at bowers for any length of time we assume that all Tooth-bills doing so were male. The results of our long-term observations of Tooth-bills support this assumption (Frith & Frith, in press).

Male Tooth-bills spend most time at their courts performing loud and prolonged court-advertisement vocalisations, including avian mimicry, from several favoured perches immediately above or adjacent to the court (Marshall, 1954; Cooper & Forshaw, 1977; Warham, 1962). Remaining time at courts is spent maintaining and/or decorating the court or displaying. Most displays are performed on the court, are started at the base of a display tree, and are accompanied by a complex 'subsong' of avian mimicry (Frith & Frith, 1993). As interspecific mimicking by Tooth-bills has long been noted or denied in the literature (Frith & Frith, 1993) we provide both qualitative and quantitative data of it.

Males of other polygynous passerines that attend and maintain a traditional courting perch(es) or area, to which they attract females by vocalisations, have been found to be predomiantly frugivorous or nectarivorous and, as a consequence, have been able to devote a high proportion of daylight hours to attending and advertising their traditional location (Snow, 1962, 1976, 1982; Snow & Snow, 1988). For some predominantly insectivorous polygynous passerines, however, see Beehler (1989).

In this paper we describe the characteristics of Tooth-bill courts with reference to leaf decorations, leaf turnover rates and inter-court leaf theft rates and patterns. Court seasonality and maintenance over three display seasons (1978-80) are discussed in relation to fruit crop, rainfall and temperature. Seasonality of court establishment was also recorded during nine subsequent seasons. Male attendance levels, behaviours and vocalisations were monitored over three display seasons (1979, 80 and 89).

METHODS

Study Area, Climate and Phenology

The study was performed in 50ha of upland tropical rainforest, altitude c. 875m, on the Paluma Range (19°00'S, 146°10'E), NE Queensland, 7km from Paluma Township and 80km north of Townsville. The rainforest, classified as simple notophyll vine forest by Tracey (1982), occurs at c.600-1000m altitude. Because the Queensland Forestry Department selectively logged the study area c.1938, the canopy was uneven and disturbed, varying from c.17.5-25m high, with taller emergents. The understorey was dominated by lawyer palms, *Calamus* spp., terrestrial ferns including *Cyathea* spp., and saplings. Medium-sized woody lianes and climbing pandans, *Freycinetia* spp., were common.

The 1 × 0.5km forested study area (Fig. 1) was permanently gridded using compass, measuring tape and metal stakes, 25ha into 25 × 25m squares and the remainder into 25 × 50m rectangles. Topography to the north of the road was a flattish ridge c.30-50m wide and 600m long with a discrete knoll (= Tooth-bill Hill). Other terrain to the north was steep and dissected by gullies. Of the area to the south of the road, that to the NE was flat with less dense forest interspersed with disturbed patches of *Calamus*-dominated undergrowth. The central southern area sloped gently from the road into a system of creeks, with a few low ridges. The west end was another rise, less discrete than Tooth-bill Hill, contiguous with a flattish c.75m wide ridge sloping down toward the southern corner of the area.

Annual rainfall and temperature show marked seasonality. The dry season extends from April-November with June-August being the driest and coldest months. The hotter wet season is from December-March. Rainfall figures were provided by the Paluma meteorological substation for the years 1978-1990. Mean annual rainfall was 2379mm during the study period. Maximum-minimum temperatures were recorded in a standard screen located 20m from the edge of the rainforest from 1 August 1978-February 1981. To obtain fruiting phenology data we examined 602 trees from September 1978-April 1979, and thereafter c.500 of these trees at six-weekly (July 1979-August 1980) or eight-weekly (November 1980-February 1981) intervals. Only trees with a girth at breast height of >32cm were examined in two sample plots, each measuring 500 × 5m, along ridges inhabited by court-owning Tooth-bills.

Definitions

We refer to a display season by the year in which it started. By 'court' we mean a cleared terrestrial area and 'site' describes the location of a court or its immediately adjacent replacement court(s). A 'traditional' court site was one attended in the same location for at least two years. A 'traditional court owner' was an individually marked court-attending bird known to attend that court in a previous season(s). A 'court tree' is any tree or sapling rooted within the cleared court area and a 'display tree' is an individual tree or sapling trunk rooted within a court area that is used by a male in initial display activity (Frith & Frith, 1993). Attendance refers to known, individually marked, males perching, calling, displaying or maintaining their own court. Thus a male visiting the court of another to steal a leaf was not attending it. As we could see only the male during most displays we refer to them only as 'displays' as distinct from 'courtship displays'.

Court Seasonality and Maintenance

Intensive fieldwork was performed from 1 August 1978-28 February 1981, apart from 1 May-18 July 1979 when we were absent. This included the three display seasons 1978, 79 and 80 and non-display months March-April 1979 and March-August 1980. We divided the display seasons 78, 79 and 80 into three periods based on the degree and kind of activity at courts. 'Pre-

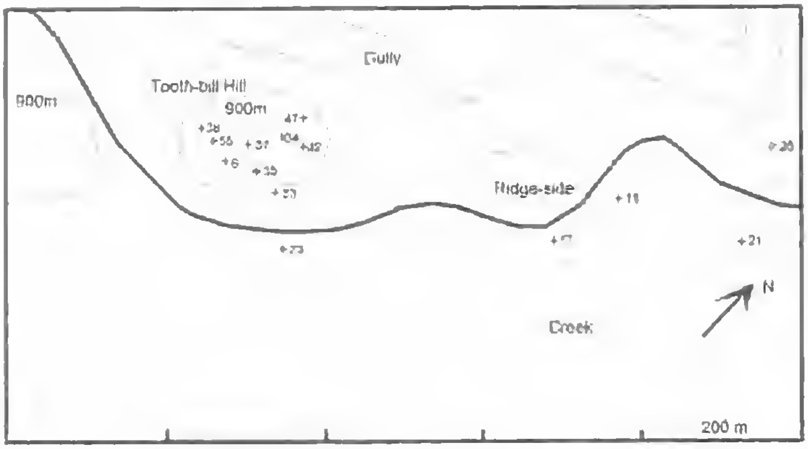

FIG. 1. The fifty hectare study area on the Paluma Range. Note: + = location and reference number of court sites examined for leaf turnover rates, inter-court theft and/or male attendance at courts. See Frith & Frith (in press) for locations of all court sites within the study area. Solid black line = road.

peak' was the period of court establishment, commencing with the first sign of litter clearance and decoration (courts partly established) and concluded when they were cleared and decorated (well-established). We examined courts as they were established and recorded the extent of clearance and number of leaf decorations. 'Peak' activity was the period of regular court maintenance and attendance, commencing when courts were well established and continuing until courts began to deteriorate. 'Post-peak' activity was the period of declining court maintenance and attendance, when decoration leaves rotted and courts became covered by fallen leaves.

Court maintenance levels were assessed by counting leaves on five adjacent courts, initally chosen at random, every seven to 12 days throughout the peak and post-peak periods of 79 and 80. Court attendance levels by males were assessed in two ways. Faeces were collected at weekly intervals during peak and post-peak periods from fine black mesh traps suspended beneath favoured perches that were above or immediately adjacent to ten courts. In addition, court attendance levels were monitored by direct observations, by use of a tape-recorder, or both.

Court Characteristics and Decorations

All courts were measured during 1989, from the cleared court edge, directly behind the display tree, to the opposite court perimeter and at right angles to this across the widest part of the court. To rank court sizes we multiplied these two measurements. The relative position of display trees and their diameter at breast height and the location of court trees and lawyer canes, *Calamus* spp., within the court were noted. Numbers of leaves in use as decorations were counted over several consecutive days during the earlier part of peak activity of seasons 79, 80 and 81 and during the late peak activity in 86 and 89. Leaves were identified to species when possible.

Leaf Turnover Rates and Theft

Decoration leaves were counted on five adjacent courts (sites 6, 32, 33, 35, 37) on Tooth-bill Hill and adjacent slopes (Fig. 1). Counts were made during peak and post-peak activity at seven day intervals during 79 and at 7-12 days (mean = 9) during 80 (see Fig. 4 for dates). Each court was attended throughout this period by only one individually marked bird. Unmarked court leaves were marked with the court number and date on their natural upper surface, using an oil-based felt-tipped pen. Previously marked leaves, including those moved from one court to another, were re-dated and re-numbered.

Numbers of leaves newly brought to the five courts (= decoration rate) were compared with numbers removed from them (= removal rate); the data are expressed as mean number of leaves per day. Leaf thefts were also monitored at two additional courts (sites 23, 34) during 79 and four additional courts (sites 34, 38, 47, 55) during 80. Leaf movement between a pair of courts was counted as one stealing event, distances between the courts being noted.

Male Attendance Levels, Behaviour and Vocalisations at Courts

Males were mist-netted at or near courts banded with a metal band and a unique two colour band combination (= marked) and released immediately. Observations of marked males did not start until at least a full week after their release.

We established cryptic canvas hides six metres from each court two weeks before starting observations each season. Each observation lasted three hours, during 0600-0900, 0900-1200, 1200-1500 or 1500-1800h, over peak activity. Male attendance levels at courts were monitored during 7-28 November of peak activity and 8 December of post-peak activity during season 1979, and between 1 October-28 December of peak activity and 29 January-14 February of post-peak activity during season 80. The same eight court sites were monitored during both seasons, six of the eight males attending the same court throughout. The other two males were unmarked during 79 but were possibly the same birds we individually marked at their courts in 80. During seasons 79 and 80 male attendance was monitored simultaneously at two courts, at one by direct observation by DWF from a hide while tape-recording sound, and at another by tape recording sound only. The microphone was placed at the perimeter of the court and camouflaged with leaf litter. DWF started each three hour direct observation ten minutes after being put in the hide by CBF, but earlier if the male returned to his court and behaved normally. When a twelve hour cycle (i.e. 0600-1800h) was completed at a pair of courts we repeated it, but then making the direct observation at the court previously only tape recorded. Thus both calling and silent behaviours of all males were observed, as a control in order to enable us to interpret audio-recordings made in our absence. A total of 96 and 220h of sound were audio-recorded at eight courts during peak activity of seasons 79 and 80 respectively, of which 48 and 110h respectively were accompanied by direct observations. A total of 6 and 18h of audio-recordings were made during post-peak activity of seasons 79 (during 1200-1500h) and 80 (0900-1200h) respectively.

During peak activity (17 October-22 December) of season 89 four males were monitored at their courts by direct observation by DWF during three hour watches for a total of 119 hours. One site (35) was attended by the same individual that had attended it during 79 and 80, a different male attended site 33, and the other two sites were not previously examined. Each male was radio-tagged with a 4 Biotrack single stage radio- transmitter (SS-1), using a tail mount, and was radio-tracked by G. Moore using a Telonics (U.S.A.) Tr-2 receiver with a Yagi antenna (Custom Electronics, U.S.A.). This enabled us to determine whether a silent male, unseen by the observer in the hide, was in fact present above his court.

Male activities at courts were classed into advertisement song, court maintenance, display, and silence, each being monitored. The number of court perches used for advertisement song by the same four marked males (at sites 18, 28, 33 & 35; Table 3) during 79 and 80 were noted and time spent on each recorded during direct observation. Male vocalisations, including mimicry, performed at courts during 79 and 80 were analysed to determine whether they differed between individuals, seasons or years.

RESULTS

COURT SEASONALITY AND MAINTENANCE

The display season was started by males calling above uncleared or slightly cleared and decorated court sites. Initially only 1-5 leaves were placed on a site with little or no ground clearance. Placement of leaves and ground clearance subsequently increased simultaneously through pre-peak activity. Courts were well established by the third to fourth weeks of September during seasons 80, 83, 85, 87 and 88, and by the third to fourth week of October during seasons 78, 79, 81, 82, 84 and 89.

Detailed results from display seasons 79, 80 and 81 are summarised in Figure 2. Differences between those seasons may be related to differences in climate and phenology (Fig. 3) and these are discussed below.

Season 78. Males started calling on 27 September and pre-peak activity started between 29 September-5 October and lasted three weeks (Fig. 2). This period was dry (9mm of rain over five days of rain) and mean weekly temperatures were 20.9-21.8°C. Peak activity started 20-26 October with all courts well cleared and decorated with many leaves (mean = 73.1, SD = 34.7) and faecal samples accumulating. This phase lasted ten weeks, until 28 December, during which 441mm of rain fell over 43 rain days and mean weekly temperatures were 18.0-27.8°C (mean of means = 22.9°C). Post-peak activity lasted seven weeks. Courts deteriorated during heavy early January rains but some faeces indicated males were still attending, but were not maintaining, courts. During 19-25 January, the rain eased and courts were re-cleared, decorated and attended but this activity was brief and declined after a few subsequent days of increased rain. By 15 February all courts were derelict (Fig. 2).

Season 79. On 12 September some males were calling above 10 known but uncleared traditional sites. Court establishment began during 15-21 September and pre-peak activity lasted five weeks (Fig. 2). This period was dry (37mm of rain over nine rain days) and mean weekly temperatures were 19.1-20.9°C for three weeks, rising to

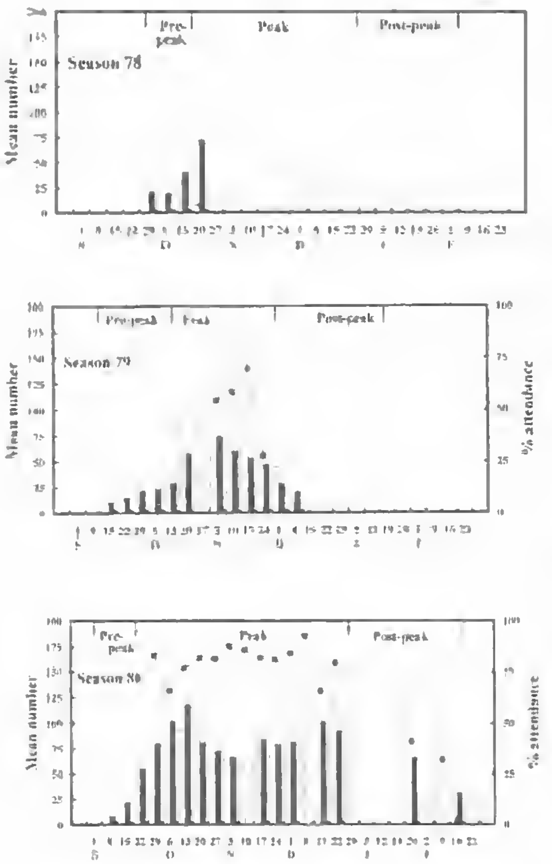

FIG. 2. Court maintenance and attendance by male Tooth-billed Bowerbirds at courts during pre-peak, peak and post-peak activity of display seasons 78, 79 and 80.Note: Solid column = mean number of court leaves (pre-peak n = 5-25 courts, peak & post-peak n = 5 courts); Clear column = mean number of defaecated seeds (pre-peak n = 5-10 courts,, peak & post-peak n = 10 courts); Line = % of time males attended courts (n = 8 males).

24.5°C. Peak activity started 20-26 October and lasted six weeks, until the end of November, whilst remaining extremely dry and hot (51mm of rain over 13 rain days) with mean weekly temperatures of 21.5-24.8°C (mean of means = 23.9°C). Leaf numbers peaked (mean = 75, SD = 31.0) between 3-9 November but had declined by the end of November. Male attendance levels remained high until 23 November. This suggests that while males were attending courts they were not maintaining them during these extremely dry conditions. There were significantly fewer leaves on courts when less rainfall preceded counts (r_s = 0.97, P<0.05) and mean weekly temperatures were higher (r_s = 0.92, P<0.05). Post-peak activity lasted eight weeks. During 1-21 December it remained extremely dry (0.2mm of rain) and hot with mean weekly temperatures of 24.6-28.3°C (mean of means = 26.2°C). Activity at courts rapidly declined and ceased by 21 December. Rain started on 25 December and on 8 January, when rain eased, there was a brief period of renewed court activity for two weeks, but courts subsequently became derelict with no further activity or calling during the extremely wet late January and February (Figs 2, 3B).

Season 80. Pre-peak activity was early, starting on 27 August when a Tooth-bill was calling above an uncleared traditional site. No traditional sites (n = 10) were cleared on 1 September but between 8-14 September a few were partly established and within two weeks, during which no rain fell and mean weekly temperatures were 21.3-24.4°C, courts were well established (Fig. 2). Peak activity started 22-28 September and lasted 14 weeks, to 28 December, during which 298 mm of rain fell over 20 rain days and mean weekly temperatures were 21.2-25.2°C (mean of means = 23.0°C). Leaf numbers reached a maximum (mean = 119.4, SD = 50.1; Fig. 2) between 13-19 October. During the next three weeks the numbers of leaves on courts declined, although court attendance levels remained high. Leaf numbers increased again during mid-December. There were more leaves on courts when male attendance levels were relatively lower and this correlation was significant (r_s = 0.32, P<0.1). There were significantly fewer leaves when less rainfall preceded counts (r_s = 0.72, P<0.01) and when temperatures were higher (r_s = 0.54, P<0.05). Courts were still maintained and attended at the end of December, but all activity stopped when torrential January rains started (Fig. 3B). Post-peak activity lasted nine weeks. Courts became waterlogged, leaves rotted in situ, and no attendance or maintenance took place. Between 26 January-1 February courts were re-cleared and decorated as rain eased (Figs 2, 3B). During February, when it again rained heavily (Fig. 3B), courts deteriorated, few leaves were added, and whilst some faeces were collected, court attendance levels were low. This indicated that males were seldom maintaining, or perching at, their courts.

Non-display seasons. We heard Tooth-bills calling above traditional court sites during March and/or April of seasons 78, 79, 80, 81 and 83, after wet season rains eased. During March 1980 we found 15 traditional court sites to be uncleared, or slightly cleared, but decorated (<12 leaves).

Males then called above court sites with much mimicry. We identified one male as the marked traditional site owner but two birds, at sites usually occupied by traditional marked males, were unbanded 'intruders'. On 11 June, we heard a bird calling above an uncleared, undecorated, traditional court site. Between 19-23 June we examined ten traditional sites to find six uncleared or slightly cleared and decorated (< nine leaves) and males calling infrequently above them. All courts were derelict by 3 July. During five other winter seasons no similar activity was observed. The observed winter activity may have related to an abundant fruit crop at that time (Fig. 3C).

Court Characteristics and Decorations

Size and form. Of 59 courts attended in peak activity of season 89, 54 were well established and five partly so (see below). Of the 54 well established courts, three were almost circular and 51 were oval. The largest oval court measured 2.75 × 1.95m (we have seen one 3.65 × 2.1m elsewhere) and the smallest 1.0 × 0.8m. Mean length of the longer oval court axis was 1.96m (SD = 0.35, n = 51), and of the shorter 1.31m (SD = 0.34, n = 51). One extremely elongate court measured 2.64 × 0.75m. Large courts tended to have more leaves but there was no significant correlation between court size/leaf numbers (r_s = 0.03, P>0.05) during peak activity of season 89.

Of the 54 well established courts 50 had a tree rooted just within their cleared area. The ground to at least one side of this display tree was clean of floor litter and leaf decorations. The remaining four courts had two display trees, the ground around part of both being cleared. The display tree on most (90%) oval-shaped courts was located near one end of the longer axis. Display trees varied in size from a large sapling to a substantial tree (mean diameter at breast height = 113.6mm (SD = 1.4, range 30-340mm, n = 53). Twenty one of the 54 courts were flat, the rest being on sloping ground. The display tree on sloping courts was usually (91%) at the higher end. Twenty of the 54 courts had lawyer canes, *Calamus* spp., growing on them. A few to 10 saplings of <30mm diameter were growing on 54% of courts. One or two heaps of germinating seeds beneath commonly-used singing perches were found on many courts.

The five partly established courts were all small. One was a 1.4 × 0.75m oval and the others were circular, of <1m diameter. Two of these encompassed a, centrally located, display tree.

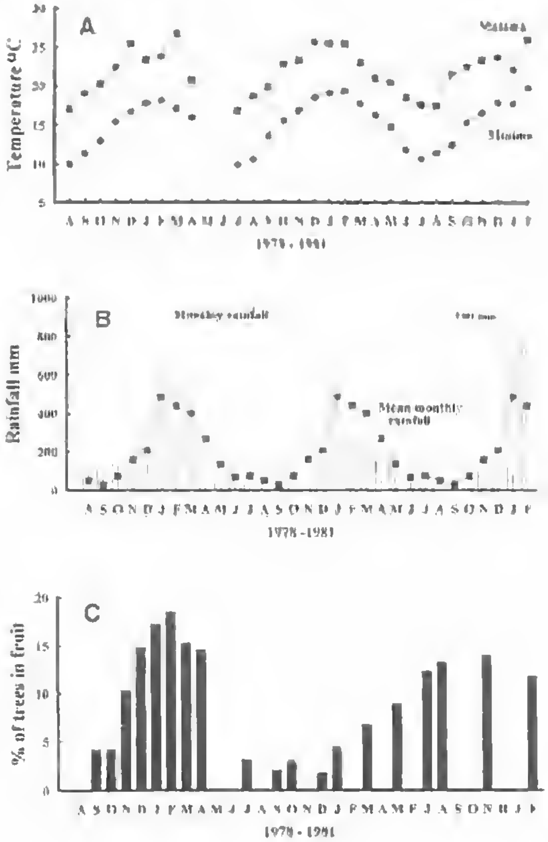

FIG. 3. Mean monthly temperature (a), mean monthly rainfall (1978-1990) (b), and monthly percentage of sampled trees in fruit (c) on the Paluma Range, north Queensland.

Leaf numbers and types. The mean number of leaves on courts during peak activity of seasons 79, 80, 81, 86 and 89 varied from 60-78 (mean of means = 69, Table 1). There were more leaves on courts during 79, 80 and 81 than during 86 and 89 but differences were not significant (χ^2 = 4.45, P>0.30). Variations between seasons were possibly due to the dates counts were made during peak activity (see Table 1).

The most abundant decoration leaf species (mean = 92%, Table 1) was *Polyscias australiana*, Araliaceae (= *Polyscias* in the following). Other leaves often used as decoration included *Sloanea langii* (Elaeocarpaceae), *Cryptocarya hypospodia*, *C. mackinnoniana*, *C. putida*, *Neolitsea dealbata*, *Litsea bindoniana* (Lauraceae), *Symplocos cochinchinensis* (Symplocaceae), *Alphitonia whitei* (Rhamnaceae), *Commersonia bartramea* (Ster-

TABLE 1. Mean number of leaves and percentage of them that were *Polyscias* on male Tooth-billed Bowerbird courts during peak activity of five display seasons. (Months are indicated by their first capital letter).

	Seasons				
Courts and leaves	79 (20O-9N)	80 (22S-26O)	81 (27O-9N)	86 (15-21D)	89 (17-30N)
Number of well established courts	21	36	17	46	53
Mean number of leaves a court	70.0	75.2	78.2	59.5	59.4
Range	20-120	19-179	44-150	19-108	20-120
SD	28.3	34.2	25.9	22.3	22.8
% of total leaves that were Polyscias	97	98	90	91	83
Number of courts with >90%	20	34	12	34	21
70-90%	1	2	4	7	20
< 70% Polyscias	0	0	1	5	12
Number of new court sites	3	6	1	5	7
Number of partly established courts	1	2	2	2	5
Mean number of leaves a court		16.5	24.5	31.0	19.8
% of total leaves that were Polyscias		64	73	69	52
Number of new court sites	1	2	2	2	3
Court sites (n = 6) with one owner					
Mean number of leaves a court	79.6	92.8	79.2	61.0	45.5
% of total leaves that were Polyscias	99	97	88	94	73
Courts sites with 2 (n = 3) or 3 (n = 4) owners					
Mean number of leaves a court	75.0	69.4	81.0	59.4	65.9
% of total leaves that were Polyscias	99	98	98	98.0	92.0

culiaceae), *Smilax australis, S. glyciphylla* (Smilacaceae) and *Rubus moluccanus* (Rosaceae). Leaves of *Asplenium* and *Alpinia* spp. were used seldom.

The percentage of *Polyscias* leaves on well established courts during 79 and 80 was higher than during other seasons, but these differences were not significant ($\chi^2 = 1.62$, P>0.80). A lower proportion (83%) of *Polyscias* were used as decoration during 89, the remaining proportion consisting mostly (12%) of *Cryptocarya* spp.. During seasons 78 and 79, 95% of courts were decorated with >90% *Polyscias*. During seasons 81, 86 and 89, 85% of courts were decorated with >70% *Polyscias*. Seventeen courts over these five seasons had <70% *Polyscias* (range = 30-65%), and another had only 10%. Of 21 newly established sites over these five seasons, five were decorated with 70-90% and three had <70% *Polyscias* (Table 1).

The numbers of leaves on traditional courts attended by the same male during the five seasons averaged 71.6 (SD = 18.8, n = 6) and was similar (mean = 70.1, SD = 8.3, n = 7) to the numbers on traditional courts attended by two or three males over the period (Table 1). These courts were all mostly decorated with *Polyscias*.

Twelve courts were only ever partly established, during the peak activity of the five seasons. These were decorated with fewer leaves and a smaller proportion of *Polyscias* (Table 1). Ten of the 12 were at new court sites and the other two (season 89) were on traditional sites of nine and 11 seasons standing. The latter site had been attended by the same individual male during the previous 11 seasons, but during 89 was attended by an unmarked male who cleared three small separate areas < 1m apart and decorated each with a few leaves.

LEAF TURNOVER RATES

Season 79. The total number of leaves on adjacent courts (sites 6, 32, 33, 35 and 37; see Fig. 1 and 5) were counted four times over 21 days (mean sampling interval = 7 days) during peak activity and 871 newly-placed leaves were marked on them. Of these leaves, 79% were removed from courts within 7 days, 18% (1% of which had been moved from one court to another) between 7-13 days and 3% between 14-20 days. The mean number of days an initially fresh leaf remained on a court was 6.1.

There was an average of 59 leaves on each court during peak activity, courts 35 and 37 having most (Table 2). Mean numbers of leaves brought

TABLE 2. Court decoration and leaf turnover rates by the same five male Tooth-billed Bowerbirds during peak activity of display seasons 79 and 80.

		Court reference number					
Season	Decoration and removal rates *	6	32	33	35	37	Mean of means
79	Mean number of total leaves	13.5	68.5	46.0	87.8	79.5	59.1
	Mean number of new leaves a day	1.1	6.8	3.8	9.9	8.1	5.9
	Mean number of leaves removed a day	2.1	7.0	6.2	11.2	9.8	7.3
80	Mean number of total leaves	63.3	82.1	66.8	103.6	106.8	84.5
	Mean number of new leaves a day	6.3	6.7	5.6	7.8	7.7	6.8
	Mean number of leaves removed a day	6.1	5.8	5.2	7.4	7.7	6.4
	% of Polyscias leaves	91	100	99	99	85	95

* = Mean numbers are for over 21 days in 79 and 97 days in 80.

to the five courts per day during peak activity varied considerably (range 1.1-9.9, SE = 1.57), as did the daily removal of old leaves (range 2.1-11.2, SE = 1.58). Daily decoration and removal rates were significantly correlated during peak activity (r = 1.33, P<0.001).

Decoration and removal rates on the five courts declined as peak activity progressed, mean numbers of leaves placed on courts declining from 51 to 24 and leaves removed from 66 to 30 (Fig. 4). Peak activity ended at the end of November. During the first two weeks of December (= post-peak activity) few new leaves were placed on courts and none were removed. Decline in decoration placement and removal rates this season were associated with extremely dry conditions. Only one of the five sample courts was, slightly, re-cleared and decorated during a brief period of renewed post-peak activity following January rains.

Season 80. The total number of leaves on the five adjacent courts used in season 79 was counted twelve times over 97 days (mean sampling interval = 9 days) during peak activity and 3219 newly-placed leaves were marked on them. Of these 53% were removed from courts within 9 days, 42.9% (2.5% of which were moved from one court to another) were removed between 9-17 days, 4% (0.3% of which were moved from one court to another) between 18-26 days and 0.1% between 27-34 days. The mean number of days an initially fresh leaf remained on a court was 5.9.

There was an average of 85 leaves on each court during peak activity, courts 35 and 37 having the most (Table 2). Mean numbers of leaves brought to a court per day throughout peak activity by each of the five males were similar (range 5.6-7.7, SE = 0.42), as were the daily removal of old leaves (range 5.2-7.7, SE = 0.48). Daily decoration and removal rates were significantly correlated during peak activity (r = 0.96, P<0.01).

Decoration and removal rates on the five courts varied considerably during peak activity. The mean number of new leaves on courts at each inspection ranged from 49-85 and of leaves removed from 24-91. Decoration and removal rates were highest during the early peak activity. Males brought more leaves to courts per day during the first seven weeks of peak activity (mean = 7.8, SE = 0.57) than during the later seven weeks (mean = 5.9, SE = 0.4), and the difference was significant (Mann Whitney U = 1,

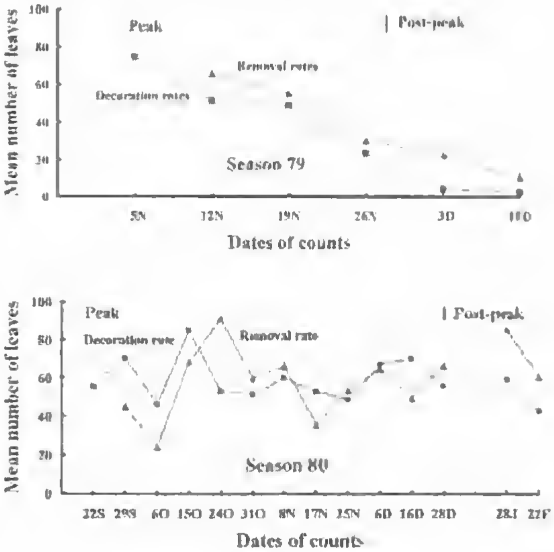

FIG. 4. Mean number of leaf decorations brought to (= decoration rate) or removed from (=removal rate) courts by the same five male Tooth-billed Bowerbirds during display seasons 79 and 80. Months are indicated by their capital letter.

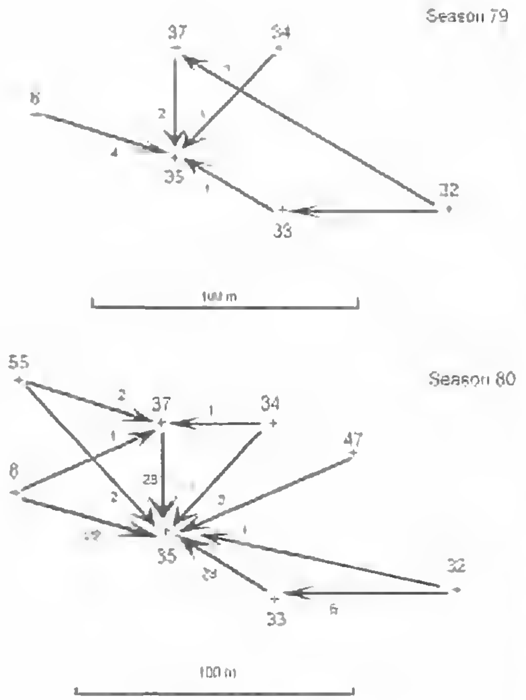

FIG. 5. Inter-court leaf theft by six (season 79) and eight (season 80) adjacent male Tooth-billed Bowerbirds on Tooth-bill Hill and slopes. Note: Large-type number by court site (+) = site number; Arrows indicate direction of leaf theft with total number of leaves involved indicated by smaller-type number beside the line.

p = 0.008). Similarly, more leaves were removed per day during the first half (mean = 7.4, SE = 0.67) than during the latter half (mean = 5.4, SE = 0.38) of peak activity, the difference being significant (Mann Whitney U = 1, p = 0.008). Immediately after January rains eased males removed all old leaves from courts and placed new ones on them (Fig. 4).

More *Polyscias* leaves (mean = 98%, range 93-100%) were used on these courts during the first half of peak activity than during the latter half of it (mean = 90%, range 72-93%). Fewer (mean of means = 61%) *Polyscias* leaves were used as decoration during post-peak activity.

LEAF THEFT

Season 79. Of 871 leaves marked on six adjacent courts during peak activity, ten (1%) were subsequently found on neighbouring courts. All were stolen within 7 days of being marked. Three of the six male court owners were thieves, males at courts 33 and 37 each stealing one leaf, and the male at court 35 stealing a total of eight leaves from three neighbouring courts (Fig. 5). Daily theft rate was 0.38 leaves/day/male.

Season 80. Of 3219 leaves marked on nine adjacent courts during peak activity, 93 (3%) were subsequently found on neighbouring courts. Of stolen leaves 88% were taken within a mean of 9 days of being marked and the remainder were moved >9 days after they had been marked on the victim's court. More leaves were stolen during the first half (63% of thefts) than the latter half of peak activity. Three of the nine male court owners were thieves, these being the same individuals found to be thieves in season 79 (Fig. 5). Daily theft rate was 0.88 leaves/day/male. Most (97%) leaves stolen were *Polyscias*.

The male at court 33 stole six leaves from one neighbour, and the male at court 37 stole four leaves from three neighbours (Fig. 5). The male at court 35 was never stolen from but stole a total of 85 leaves from seven neighbouring courts (mean inter-court distance = 60.3, SD = 21.5m, range 36-95m). There was a significant correlation between number of thefts by the court 35 male and the distance he travelled to a victim's court (r_s = 0.97, P<0.01). He stole more leaves from closer neighbours (Fig. 5) but did not steal from another neighbour, at court 38, 105m distant. Court 34, from which a single leaf was stolen, was excluded from this analysis as it was not established until the last two weeks of peak activity. Neighbouring males usually stole leaves during a court owner's absence. On four occasions, however, we watched the bird from site 35 remove a leaf from site 33 whilst the owner continued singing above it.

MALE ATTENDANCE LEVELS AT COURTS

Seasonal variation. During peak activity of seasons 79, 80 and 89 males spent an average of 52, 79 and 61% respectively of time attending courts. The proportion of total time individual males spent at courts during peak activity (Table 3) varied significantly during season 79 (χ^2 = 26.5, P<0.001) but not during 80 (χ^2 = 2.25, P>0.90) or 89 (χ^2 = 2.81, P>0.30). Males spent an average of 25 (range 18-31, SE = 1.58), 22 (range 17-27, SE = 1.18) and 21 (range 20-25, SE = 1.03) mins at the court per presence during seasons 79, 80 and 89 respectively (Table 3). Thus, despite lower attendance levels during season 79 and, to lesser extent, during 89, once males were at their courts the duration of each visit was similar. Mean duration per absence from

TABLE 3. Court attendance levels by individual male Tooth-billed Bowerbirds during peak activity of display seasons 79, 80 and 89.

		HOURS		ABSENCE		PRESENCE	
Season	Site number	Audio-recordings	Observations	Mean mins @ absence	% of total time absent	Mean mins @ presence	% of total time present
79	18 *	12	12	23.5	55.5	18.9	44.5
	28 *	12	12	15.0	35.4	25.8	64.6
	33 *	12	12	32.4	67.6	18.0	32.4
	35 *	12	12	23.5	45.6	28.0	54.4
	6 *	12		37.4	62.4	24.6	37.6
	17	12		16.0	37.7	28.0	62.3
	21	12		13.0	27.2	30.9	72.8
	32 *	12		24.0	53.1	24.1	47.0
Total / Mean / %		**96**	**48**	**22.5**	**48.0**	**24.9**	**52.0**
80	18 *	27	12	8.2	22.6	25.6	77.4
	28 *	26	17	5.1	16.0	23.8	84.0
	33 *	30	18	7.6	25.7	20.6	74.3
	35 *	27	21	5.3	21.1	20.0	78.9
	6 *	27	6	7.9	29.6	17.0	70.4
	17	27	15	4.9	17.9	21.8	82.1
	21	26	9	5.3	15.1	27.1	84.9
	32 *	30	12	4.7	17.1	19.9	82.9
Total / Mean / %		**220**	**110**	**6.1**	**20.7**	**21.6**	**79.3**
89	33	23	23	16.9	44.1	20.3	54.3 (1.6) **
	35 *	24	24	17.7	39.2	24.7	58.4 (2.4)
	23	36	36	13.6	37.9	20.4	59.4 (2.7)
	37	36	36	8.4	27.0	21.6	71.9 (1.1)
Total / Mean / %		**119**	**119**	**13.1**	**36.0**	**21.5**	**62.0 (2.0)**

* = same male owner each season
** in parenthesis = % total time males were present but detected only by radio-tracking.

courts during season 80 was much briefer and far less variable between individual males (range 5-8mins, SE = 0.53) than during 79 (range 13-37mins, SE = 3.02) or 89 (range 8-18mins, SE = 2.11).

During season 89 transmitters on the four radio-tagged males enabled us to learn that they spent 1.1-2.7% (mean = 2) of time silently in the forest canopy above their court, this figure being similar during different months of peak activity, and times of day. Thus, figures for absence of other males, lacking radio-tags, during seasons 79-80 (Tables 3-5) could include an error of up to 3% and figures for time present could be higher by up to 3%. This potential error was not taken into account in time-budgeted court activity data presented for season 89 (Tables 6-8).

Monthly variation. Peak activity lasted six weeks (20 October-30 November) during season 79, 14 weeks (22 September-28 December) during 80 (Fig. 2), and 11 weeks (13 October-28 December) during 89. Season 79 was excessively dry and, although December rainfall was near average, it did not start raining until 25 Decem-

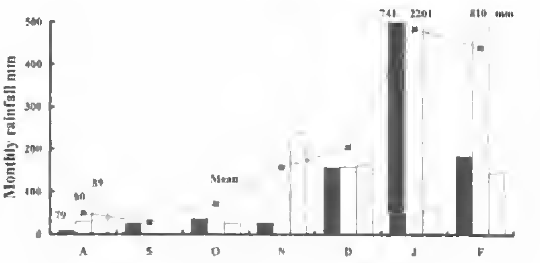

FIG. 6. Monthly rainfall during display seasons 79, 80 and 89 and mean monthly (= ■) for 1978-1990 on the Paluma Range, north Queensland.

TABLE 4. Monthly court attendance levels by male Tooth-billed Bowerbirds during peak (seasons 79, 80 & 89) and post-peak (79 and 80) activity.*

			ABSENCE		PRESENCE	
Season	Months	Hours of audio-recordings	Mean mins @ absence	% of total time absent	Mean mins @ presence	% of total time present
79						
Peak	November	96	22.5	48.0	24.9*	52.0
Post-peak	December	6		100.0		
80						
Peak	October	78	6.4	23.0	19.3	77.0
	November	81	4.9	16.8	22.2	83.4
	December	61	7.5	23.2	24.5	76.8
Post-peak	February	18	27.4	66.0	15.3	34.0
89						
Peak	October	47	13.4	34.1	23.6	63.6 (2.3) **
	November	36	9.7	28.6	22.8	69.7 (1.7)
	December	36	16.3	46.0	17.6	52.0 (1.9)

* = court sites and sample sizes as in Table 3
** in parenthesis = % total time males were present but detected only by radio-tracking

ber. Little or no rain fell during September 80 or 89, and October rainfall of those seasons was below average, November 79 was dry, and November 89 wet (Fig. 6).

Court attendance levels were higher during each month of season 80 than during each corresponding month of 79 and 89. Attendance levels reached a peak in November of seasons 80 and 89. Court attendance levels were lowest during November 79 and December 89. Mean duration per presence at courts varied little between the respective months of each season. Mean duration per absence from courts was notably low during all months of the 80 season. During the extremely dry early December 79 court attendance stopped. During season 80 there was a brief return to post-peak activity when torrential January rains stopped but attendance levels were low, males spending little time at courts each visit (Table 4).

Daytime variation. Court attendance levels were always highest during the period 0600-0900h. During season 79 attendance declined during the latter part of the day (Table 5). During season 80 court attendance levels remained high throughout the day. Mean duration per presence at courts did not vary greatly at differing times of the day over each season (Table 5).

MALE BEHAVIOUR AT COURTS

Advertisement song. Male Tooth-bills spent most (mean of means = 95.7%) of their time at courts giving loud advertisement song from favoured perches. This was similar for all males (range 90-98%) during each season, each month of peak activity and different times of day (Tables 6-8).

Mean duration of advertisment song periods was similar during seasons 79 (range 19-30mins, SE = 1.46), 80 (range 17-27mins, SE = 1.18) and 89 (range 20-27mins, SE = 1.31, Table 6). Mean duration of song periods was similar each month of peak activity except during December 89 when seasonal activity declined. It was also much lower during post-peak activity of season 80 (Table 7).

TABLE 5. Variation in daytime court attendance levels by male Tooth-billed Bowerbirds during peak activity of display seasons 79, 80 and 89. *

			ABSENCE		PRESENCE	
Season	Time	Hours	Mean mins @ absence	% of total time absent	Mean mins @ presence	% of total time present
79	0600-0900	24	14.6	35.5	25.8	64.5
	0900-1200	24	20.0	48.6	20.6	51.4
	1200-1500	24	21.8	45.5	27.1	54.5
	1500-1800	24	39.2	62.6	28.4	37.4
80	0600-0900	48	4.4	16.2	20.8	83.8
	0900-1200	60	7.0	23.2	21.6	76.8
	1200-1500	60	6.7	22.7	20.6	77.3
	1500-1800	52	6.1	19.7	23.9	80.3
89	0600-0900	29	8.2	27.4	19.5	70.7 (1.9) **
	0900-1200	30	18.1	40.1	21.8	58.1 (1.8)
	1200-1500	30	15.1	41.9	20.0	55.5 (2.8)
	1500-1800	30	14.1	34.5	25.6	63.9 (1.6)

* = court sites and sample sizes as in Table 3
** in parenthesis = % total time males were present but detected only by radio-tracking.

TABLE 6. Time-budgeted activities performed by individial male Tooth-billed Bowerbirds at courts during peak activity of display seasons 79, 80 and 89. *

		ADVERTISEMENT SONG		MAINTENANCE		DISPLAY		SILENCE **		TOTAL TIME PRESENT
Season	Court site number	Mean mins @ song period	% of time present singing	Mean mins @ maintenance period	% of time present maintaining	Mean mins @ display period	% of time present displaying	Mean mins @ silence period	% of time present spent silent	(mins)
79	18 *	19.4	96.9	1.3	1.9	1.4	0.9	1.0	0.3	321
	28 *	25.3	98.4	0.8	0.8	1.9	0.4	1.0	0.4	465
	33 *	19.0	89.6	2.0	1.7	1.8	3.9	3.7	4.8	233
	35 *	26.5	94.7	2.3	1.2	0.0	0.0	2.0	4.1	392
	6 *	26.1	96.1	1.0	0.4	1.1	1.8	1.3	1.9	271
	17	29.2	97.6	2.8	1.3	1.6	0.7	0.9	0.4	449
	21	30.4	98.4	1.4	0.5	1.6	0.9	0.5	0.2	525
	32 *	23.8	98.4	1.4	0.8	0.0	0.0	0.9	0.8	330
Total / Mean / %		**25.2**	**96.7**	**1.3**	**1.0**	**1.5**	**0.8**	**1.7**	**1.4**	**2993**
80	18 *	25.1	98.2	1.7	0.7	1.4	0.3	0.9	0.8	1253
	28 *	24.1	97.4	1.3	0.6	1.4	1.0	0.8	0.9	1311
	33 *	23.7	94.0	1.5	2.1	1.7	1.9	1.3	2.0	1338
	35 *	19.8	92.8	2.0	2.7	1.8	0.7	1.2	3.8	1278
	6 *	16.8	94.1	1.5	3.0	1.3	1.2	0.9	1.7	1141
	17	23.1	95.6	1.7	2.4	1.5	0.4	1.0	1.6	1330
	21	26.7	98.7	0.9	0.4	1.5	0.2	0.9	0.7	1325
	32 *	19.5	95.1	2.1	2.4	2.0	0.9	1.0	1.0	1493
Total / Mean / %		**22.0**	**95.8**	**1.6**	**1.8**	**1.6**	**0.6**	**1.1**	**1.8**	**10469**
89										
	33	20.4	92.6	1.0	1.2	2.0	0.8	1.5	5.4	750
	35 *	26.6	94.8	0.9	0.6	2.2	0.5	2.2	4.0	840
	23	22.3	93.9	1.0	0.8	1.6	0.2	1.8	5.1	1282
	37	23.9	95.4	1.2	1.1	1.5	0.4	1.3	3.1	1552
Total / Mean / %		**23.2**	**94.4**	**1.2**	**0.8**	**1.8**	**0.4**	**1.6**	**4.3**	**4424**

* = same male owner each season

** = silent periods of > 30 seconds duration (see Results), but excluding maintenance time.

Mean duration of song periods did not vary greatly during different times of the day over each season (Table 8).

Almost all (>99%) advertisement song was given from perches immediately above or about courts, males only rarely (<1%) singing loudly on the ground at the base of the display tree, prior to the distinctly different display subsong. Males usually sang from more than one perch during a court visit (mean = 1.9), spending an average of 13mins on each (Table 9).

Song perches were high above the court (high perches), adjacent to it (adjacent perches) or just above the court (court perches). High perches were >5m above the ground in the understorey or lower canopy, and up to 8m horizontally from the court location. Most males had two high perches (mean = 1.9). Adjacent court perches were mostly horizontal or sloping sapling or small tree branches, 3-5m above ground and between 1-5m from the court perimeter. Males used 1-4 adjacent perches (mean = 1.8). Court perches were horizontal branches of saplings and, less commonly, vines or fallen branches lying across the court at 0.3-3.0m (mean = 1.4) above the cleared ground or within a metre radius of its perimeter. More court perches were used during season 80 (mean = 8.3, range 5-12) than during 79 (mean = 4.8, range 4-7).

Males spent an average of 21, 11 and 68% of total song time singing on high, adjacent and court perches respectively, spending more time singing on high and adjacent perches during season 79 than 80 (Table 9). High perch singing decreased as season 80 progressed, from 22% of October song time to 13% of November and 4% of December song time. High perches were mostly used (90% of occasions frequented) for singing when males first returned to their court area, birds subsequently flying down to their adjacent and/or court perches. Returning males sometimes flew directly to an adjacent perch and sang there before moving to a court perch or returned directly to a court perch (Table 9). Of returns to a court perch 37% were, however, via the court to place a newly-aquired leaf there.

During 0600-0900, 0900-1200, 1200-1500 and 1500-1800h males sang from high perches for 12, 19, 19 and 8% of total song time respectively. Thus, males spent more time singing on high perches during the hotter, brighter, part of the day.

Of 31 perches used by four males at court sites 18, 28, 33 and 35 during season 79, 84% were still

TABLE 7. Monthly time-budgeted activities performed by male Tooth-billed Bowerbirds at courts during peak (seasons 79, 80 and 89) and post peak (80) activity. *

Season	Months	ADVERTISEMENT SONG Mean mins @ song period	% of time present singing	MAINTENANCE Mean mins @ maintenance period	% of time present maintaining	DISPLAY Mean mins @ display period	% of time present displaying	SILENCE ** Mean means @ silence period	% of time present spent silent	TOTAL TIME PRESENT (mins)
79										
Peak	November	25.2	93.7	1.3	1.6	1.5	0.3	1.7	1.4	2993
80										
Peak	October	20.3	96.4	1.3	2.2	1.5	0.3	1.1	1.1	3604
	November	22.0	96.2	1.2	1.3	1.5	1.1	1.2	1.4	4054
	December	24.5	94.2	1.8	2.0	1.6	1.2	1.0	2.6	2811
Post-peak	February	13.9	91.8	0.8	1.5	1.5	4.5	3.6	2.6	367
89										
Peak	October	25.7	94.4	1.3	1.5	1.7	0.5	1.3	3.6	1794
	November	26.7	95.6	1.0	0.6	1.7	0.4	2.0	3.4	1506
	December	17.4	92.9	1.1	0.5	2.3	0.1	1.7	6.5	1124

* court sites and sample sizes as in Table 3
** = silent periods of > 30 seconds duration (see Results), but excluding maintenance time

in use by the same males during 80. Of six perches used by the site 35 male during 79, all were in use during 80 and he was still using three of them during 89.

Maintenance. Male Tooth-bills spent a mean of only 1.2% of total time actually on courts and maintaining them. This figure was similar for all males each season, during different months of peak activity and different times of day (Tables 6-8). Mean length of court maintenance periods varied between males but was never >2.8mins (Table 6).

Of 104 observed court maintenance periods, 95 immediately followed a male's arrival with a leaf and nine occurred during or after singing or display and involved court clearing only. After placing a new leaf and/or performing court maintenence males hopped up to a perch to sing (72% of arrivals) or simply flew away from the court.

Number of new leaf decorations brought to the court in each three hour period was higher during season 80 (mean = 1.3) than 79 (mean = 0.8) or 89 (mean = 0.7). More leaves (60%) were brought to courts during 0600-1200hrs than during the rest of the day. Once a male had placed a new leaf on his court he usually tidied or re-arranged his fresher leaves and removed old or fallen ones to beyond the court perimeter. Males were usually silent when maintaining courts, only occasionally giving a single 'chuck' note.

Displays. Upon first noticing a conspecific near his court a male would drop to the base of his display tree to give quieter, more intense, advertisement song or, more often, would immediately commence display 'subsong' vocalisations. On a few occasions a male adopted a static 'frozen' sleeked posture prior to subsong and display (see below). Display vocalisations and posturing are described elsewhere (Frith & Frith, 1993). Most times (83%) males performed only one display, but on a few occasions they performed a sequence of two to four immediately repeated ones.

During peak activity males spent <1% of their total time at courts displaying, the mean duration of a display (including subsong) ranging from 1.1-2.2mins (mean = 1.6, Table 6). Number of displays per three hour period was greater during the peak activity of seasons 80 (mean = 0.8) than during 79 (mean = 0.5) and 89 (mean = 0.3). The total time males spent displaying was greatest during the peak activity month of November (1.5 displays/display period) and December (0.9 displays per three hours, Table 7). Most displays were performed during 0600-0900h of seasons 79 and 80 and least during 1500-1800h (Table 8). Males continued to display during post-peak (court maintenance) activity (Table 7), in fact spending relatively more time displaying then. We could not sex birds seen to be displayed to by their appearance or behaviour. No mating was seen.

Silence. The proportion of total court attendance time males spent silently (= >30secs without calling), other than during court maintenance periods, was greater during season 89 (4.3%) than 79 (1.4%) or 80 (1.6%, Table 6). These higher 89 figures were reflected during each month of peak activity (Table 7) and different times of day (Table 8), notwithstanding up

TABLE 8. Variation in daytime-budgeted court activities by male Tooth-billed Bowerbirds during peak activity of display seasons 79, 80 and 80. *

		ADVERTISEMENT SONG		MAINTENANCE		DISPLAY		SILENCE **		TOTAL TIME PRESENT
Season	Time	Mean mins @ song period	% of time present singing	Mean mins @ maintenance period	% of time present maintaining	Mean mins @ display period	% of time present displaying	Mean mins @ silence period	% of time present spent silent	(mins)
79	0600-0900	25.1	97.4	1.0	1.1	1.6	1.1	1.1	0.5	928
	0900-1200	21.6	96.3	1.5	2.0	2.0	1.0	1.2	0.7	741
	1200-1500	27.9	95.9	1.0	0.1	1.5	1.0	2.1	3.0	766
	1500-1800	27.6	97.3	1.8	1.0	1.1	0.2	1.6	1.5	539
80	0600-0900	20.3	95.6	1.3	1.8	1.4	1.2	1.2	1.4	2414
	0900-1200	22.8	96.3	1.4	1.4	1.7	1.0	1.1	1.3	2765
	1200-1500	21.2	95.0	1.9	1.9	1.7	1.0	1.0	2.1	2785
	1500-1800	24.1	96.1	1.9	2.1	1.6	0.3	1.0	1.5	2506
89	0600-0900	21.7	95.4	1.0	1.1	1.4	0.1	1.1	3.4	1229
	0900-1200	25.4	94.8	1.2	0.6	0.0	0.0	1.6	4.6	1046
	1200-1500	20.6	94.6	1.5	1.0	1.8	0.8	2.0	3.4	998
	1500-1800	26.1	92.9	1.3	1.0	1.6	0.8	2.0	5.3	1150

* court sites and sample sizes as in Table 3

** = silent periods of > 30 seconds duration (see Results), but excluding maintenance time

to an additional 3% silence of potential, but undetected, presence (see Table 3). The possibility that the movements of two people radio-tracking in the area might have caused relatively longer silent periods during season 80 is considered unlikely but cannot be dismissed. There were more silent periods over 1200-1500h during 79 and 80 than at other times of day (Table 8).

Most (92%) silent periods occurred immediately before, or during, advertisement song when birds preened, changed perches, turned on their perch to face the opposite direction, or when they stopped singing to apparently listen to neighbours' calls. Having apparently noted a neighbouring male was not calling, a court owner flew immediately in the direction of the presumably unattended court to steal a leaf.

The other 8% of silent periods occurred when males adopted a sleeked 'frozen' posture. We recorded the frozen posture 34 times (mean duration = 1.1mins), 28 of which were performed in response to a conspecific flying toward the court. On nine of these latter occasions the male immediately followed the frozen posture with display. On the 19 other occasions he chased the conspecific, which we assume to have been a neighbouring male (sometimes confirmed by band colours). Court owners sometimes chased off potential thieves without first adopting a frozen posture, the latter usually being performed by birds apparently initially unaware of the identity or sex of the visitor. Four frozen postures occurred when we heard, but could not see, a bird land high above the Tooth-bill at its court and two were given when a Grey-headed Robin *Poecilodryas albispecularis*, flew directly to a court. This behaviour appears typical of male Tooth-bills surprised by the appearance or sound

TABLE 9. Perch type used for advertisement song by the same four male Tooth-billed Bowerbirds at courts during peak activity of display seasons 79 and 80.

	HIGH PERCHES (> 5 m)			ADJACENT PERCHES (3-5 m)			COURT PERCHES (< 3 m)			GROUND	TOTAL SONG TIME*
Season	Mean mins @ perch	% of total song time	% of times used on arrival	Mean mins @ perch	% of total song time	% of times used on arrival	Mean mins @ perch	% of total song time	% of times used on arrival	% of total song time	(mins)
79	11.2	26	90	21.5	14	56	14.7	59.9	49	0.1	1349
80	8.9	16	89	11.1	8	50	10.5	75.4	37	0.6	2878

* = direct observation watches only at court sites 18,26,33,&35; see Table 3.

TABLE 10. Analysis of advertisement song given by male Tooth-billed Bowerbirds at eight courts during peak activity of display seasons 79 and 80.* Court sites as in Table 3.

Season	SQUEAL		CHUCK		CHUCK + BABBLE		CHUCK + MIMICRY		BABBLE		BABBLE + MIMICRY		MIMICRY		TOTAL SONG TIME (mins)
	Mean mins @ phase	% of total song time	Mean mins @ phase	% of total song time	Mean mins @ phase	% of total song time	Mean mins @ phase	% of total song time	Mean mins @ phase	% of total song time	Mean mins @ phase	% of total song time	Mean mins @ phase	% of total song time	
79	2.9	1.7	2.6	5.8	2.2	1.2	3.1	4.1	17.9	23.4	11.7	56.5	5.1	7.3	2788
80	1.8	1.7	1.9	5.4	2.0	3.3	2.2	2.9	7.7	36.7	8.0	40.1	4.2	8.9	5637

of an incoming bird as we often saw Grey-headed Robins, Chowchillas *Orthonyx spaldingii*, Eastern Whipbirds *Psophodes olivaceus*, Yellow-throated Scrub-wrens *Sericornis citreogularis*, Brush-turkeys *Alectura lathami* and Spotted Catbirds *Ailuroedus melanotis* foraging toward a court without concerning the Tooth-bill owner.

We did not witness a single aggressive encounter between Tooth-bills at a court other than an owning bird chasing off another. On a few occasions we did note two birds confronting each other in a food (fruiting) tree by facing each other with sleeked plumage and agitated vocalisations.

MALE VOCALISATIONS AT COURTS

Advertisement song content was similar in seasons 79 and 80. We could divide song into seven component calls: 'squeal', 'chuck', 'chuck + babble', 'chuck + mimicry', 'babble', 'babble + mimicry', and exclusively pure 'mimicry', changes from one to another usually being quite obvious. Calls were given in phases, a male performing a phase of 'chuck' calls, following this with a phase of 'chuck + mimicry' and so on. Each song period (= a court visit) consisted of several to many phases. Each phase lasted an average of 8 and 5mins during seasons 78 and 80 respectively. The relative time spent giving each call component and mean length of each phase was similar each season (Table 10).

'Squeals' were squeal-like screetchy notes. Phases of 'squeals' represented 1.7% of total song time and were brief (Table 10). 'Squeals' were mostly (64%) given first by returning birds or as second phase calls (19%) that usually followed 'chucks' (Table 11). Occasionally 'squeals' were again given, briefly, when a male changed perches.

'Chucks' consisted of a repeated 'chuck' note, represented 6% of total song time, and were brief (Table10). 'Chucks' were mostly (72%) given first by returning birds (Table 11), but also followed 'squeals'. Males sometimes briefly reverted to 'chucks' after changing perches.

'Chuck + babble' and 'chuck + mimicry' were dominated by 'chuck' notes interspersed with occasional 'babble or mimicry'. These calls represented < 4% of total song time and phase duration was brief (Table 10). Males sometimes gave these calls having just returned to their court instead of a 'chuck' call, but mostly they were given as second phase calls (Table11) following 'squeals' and/or 'chucks'.

'Babble' and 'babble + mimicry', often including occasional 'chucks', were the most common calls and represented 30 and 49% of total song time respectively with long phase duration (see Table 10). Males sometimes first gave these calls upon returning to the court, but mostly they were given as second, third or fourth phase calls (Table 11) following 'chuck', 'chuck + babble' and/or 'chuck + mimicry'. Some males continuously alternated between 'babble, babble + mimicry' and/or 'mimicry'. Males gave more intense and quieter advertisement song, of 'babble' or 'babble + mimicry', immediately prior to display of a mean duration of 20.9mins (range 0-65).

Exclusive mimicry was performed by all males, represented a mean of 8% of total song time, and each phase lasted an average of 4.7mins (Table 10). A far larger proportion (60%) of song time involved mimicry, however, when 'mimicry', 'chuck + mimicry' and 'babble + mimicry' were combined. Mimicry usually followed 'chuck + mimicry' or 'babble + mimicry'. Cicadas, crickets, frogs, dripping water and 27 bird species were identified as models for mimicry.

We audio-recorded 1074mins of exclusive mimicry during advertisement song over seasons 79 and 80. Of total 'mimicry' time, 43% was of Bower's Shrike-thrush *Colluricincla boweri* and 30% of medleys of various bird calls mostly dominated by that species. Mimicry of Bower's Shrike-thrush also dominated 'chuck + mimicry' and 'babble + mimicry'.

King Parrots *Alisterus scapularis* were also commonly mimicked (11% of 'mimicry'). Other bird species mimicked for a combined total of

TABLE 11. Phase sequence of each call component of advertisement song given by male Tooth-billed Bowerbirds at eight courts during peak activity of display seasons 79 and 80. * Data are expressed as % of total number of phases of each call component.**

	Phase sequence										
Call component	1	2	3	4	5	6	7	8	9	10	11-18
Squeal	64.0	19.4	5.6	5.6	0.9	1.8	0.9	0.9	0.9	0.0	0.0
Chuck	72.4	7.1	6.7	4.3	2.6	2.6	1.0	1.5	0.2	0.5	1.0
Chuck + babble	17.1	44.2	12.2	9.4	5.5	3.3	1.1	0.6	3.7	0.6	2.3
Chuck + mimicry	19.4	39.4	14.7	7.6	5.3	4.0	2.4	3.0	0.6	1.2	2.4
Babble	11.3	21.7	16.9	17.3	12.5	6.7	4.8	3.5	1.0	1.2	3.1
Babble + mimicry	9.3	18.3	21.6	17.3	10.7	7.9	5.8	2.6	1.9	1.8	2.8
Mimicry	7.7	19.8	27.2	15.4	10.5	6.5	4.1	2.8	2.8	1.2	2.0
Display subsong	8.3	3.3	15.0	23.4	15.0	8.3	8.3	10.0	5.0	0.0	3.4

* = court sites as in Table 3
** = data for seasons 79 & 80 combined. See Table 10 for total song time.

13% of 'mimicry' time were: Fan-tailed Cuckoo *Cuculus flabelliformis*, Yellow-eyed Cuckoo-shrike *Coracina lineata*, Grey-headed Robin, Golden Whistler *Pachycephala pectoralis*, Chowchilla, Eastern Whipbird, Yellow-throated Scrub-wren, Little Treecreeper *Climacteris minor*, Bridled Honeyeater *Lichenostomus frenatus* and Golden Bowerbird *Prionodura newtoniana*. Bird species mimicked less frequently (combined total = 3% of 'mimicry') included: Pale-yellow Robin *Tregellasia capito*, Black-faced Monarch *Monarcha melanopsis*, Spectacled Monarch *M. trivirgatus*, Rufous Fantail *Rhipidura rufifrons*, Grey Fantail *R. fuliginosa*, Australian Fernwren *Crateroscelis gutterlais*, Large-billed Scrub-wren *S. magnirostris*, Brown Gerygone *Gerygone mouki* and Mountain Thornbill *Acanthiza katherina*.

Tooth-bills mimicked several distinct calls of a given bird species. For example, they commonly mimicked both the whistled single note song and the 'chee-chee' greeting calls of Grey-headed Robins, both whip-crack song and the 'chip-chop' calls of Eastern Whipbirds and both squeals and rattle calls of Golden Bowerbirds. Mimicry was sometimes given opportunistically, in immediate response to calling birds, such as those of a passing flock of Crimson Rosellas *Platycercus elegans*, lorikeets *Trichoglossus* spp. or, less frequently, Sulphur-crested Cockatoos *Cacatua gelerita* or Red-tailed Black-Cockatoos *Calyptorhynchus magnificus*.

Tooth-bills sometimes 'duetted' with other species including King Parrot, Grey-headed Robin, Golden Whistler, Bower's Shrike-thrush, Eastern Whipbird, Yellow-throated Scrub-wren, Little Treecreeper and Bridled Honeyeater. Neighbouring Tooth-bills also appeared to instantaneously copy each others 'mimicry', 'chuck' or 'babble' calls.

Tooth-bill mimicry models changed seasonally. For example, during season 79 Fan-tailed Cuckoos were extremely vocal in the study area and their calls were mimicked by all eight males (12% of 'mimicry'). During season 80 we heard fewer Fan-tailed Cuckoos and less (1%) 'mimicry' of them. The proportion of 'mimicry' incorporated into song did not differ greatly over the three peak activity months of season 80 (October = 7%, November = 9%, December = 10% of total song time), although increasing towards peak mating time and falling to an average of 6% in post-peak activity. Moreover, it did not differ much throughout the day. During the periods 0600-0900, 0900-1200, 1200-1500, and 1500-1800h males performed 'mimicry' for 6, 10, 8 and 10% of total song time respectively over seasons 79 and 80.

Bird species that regularly called in the study area during Tooth-bill display seasons but were not, or only rarely, mimicked included the Noisy Pitta *Pitta versicolor*, Victoria's Riflebird *Ptiloris victoriae* and the Spotted Catbird. The whistled bower advertisement call of male Satin Bowerbirds and the sound of dripping water was mimicked by Tooth-bills in display subsong but not during advertisement singing.

DISCUSSION

COURT SEASONALITY AND MAINTENANCE

Male Tooth-bills started court clearing in September-October, approximately six to eight weeks before first known egg-laying (Marshall, 1951; Frith & Frith, 1985a, 1993) and increasingly attended courts from October-December (Fig.

2). Food resources are abundant at this time of year (Frith 1984; Frith & Frith, 1990, 1985b). Although Marshall (1951, 1954) suggested increasing daylight time, rising temperatures and decreasing humidity might instigate the seasonal sexual resurgence of male Tooth-bills our data do not reveal clear-cut relationships between weather patterns and variation in the initiation of pre-peak activity across years.

Pre-peak activity lasted three, five and two weeks during seasons 78, 79 and 80 respectively; interesting differences because whilst temperatures were seasonally increasing slightly, relative rainfall differed between seasons (Fig. 3a,b). Relative fruit crop, however, was poor during 79 and rich during 78 and 80 (Fig. 3c), and it is possible that this influenced these differing lengths of pre-peak activity.

Peak court activity lasted for ten, six and 14 weeks during seasons 78, 79 and 80 respectively. A prolific fruit crop became available in November 78, the 79 fruit crop failed and in season 80 peak activity was preceeded and accompanied by much fruit (Fig. 3c). Late peak court activity, and nesting coincided (November-February) with the months of relatively far greater beetle abundance at Paluma (Frith & Frith, 1985a,b), Coleoptera apparently being important in the nestling diet (Jackson, 1909; Marshall, 1951). Lapses in court decoration rates during the long period of peak court attendance in season 80 (Fig. 2) coincided with increasing temperatures during drier periods. At such times court decoration leaves dry and curl quickly and extremes in these conditions, such as during season 79, may cause birds to desert courts.

The start of post-peak activity is strongly associated with persistent heavy rains of wet season months January-February but during season 79 it preceeded this due to excessively dry conditions (Fig. 3b). Significant dry spells within the wet season rains stimulated a brief return to renewed court activity. Warham (1962) correctly thought the onset of the wet season caused cessation of court attendance and the start of moult.

During March-April of several seasons we observed some males calling and poorly clearing and decorating courts. This would appear to be a post-moult activity performed mostly by subadult males, as occurs in other bowerbird species (Frith & Frith, unpubl. data). Similar behaviour was also observed in June-July 1980, which may have related to an abundant winter fruit crop (Fig. 3c) that supported a subsequent early start to the 80 display season.

COURT CHARACTERISTICS AND DECORATION

Marshall (1954) found the average number of leaves on a Tooth-bill court to be c.40 and the maximum 103 whereas Schodde & Tidemann (1988) give an erroneously low 8-15 leaves/court. Grant & Laurance (1991) found an average of 23-95 leaves a court for their 27 September-17 December study and an average of 52 leaves to 15 October and only 37 thereafter. We recorded an average of between 60-78 per season and a largest number of 108-179 leaves per court over five seasons (Table 1). Chaffer (1984) gained the impression that fewer leaves were used if they were of larger size but this could not be tested in our study area where birds preferred plant species with smaller leaves.

Male Tooth-bills in this study decorated courts predominantly with *Polyscias* leaves (Table 1) and only infrequently with leaves of 14 other tree species. Jackson (1910) listed the 14 most commonly used leaves he found on Atherton Tableland courts but does not include *Polyscias*. Marshall (1954) lists identifications of 181 leaves from five Atherton Tableland courts and does not include *Polyscias* which are, however, used by Atherton Tableland birds (Frith & Frith, unpubl. data). Grant & Laurance (1991) found that decorations on 13 Atherton Tableland courts consisted of >90% *Schlefflera actinophylla* leaves. These facts suggest geographic variation in favoured court decorations, a situation found in bower decorations of the two Satin Bowerbird subspecies (Chaffer, 1984; Frith & Frith, unpubl. data) and between populations of the Vogelkop Bowerbird *Amblyornis inornatus*. Diamond (1986, 1987) considered this to be indicative of local tradition based on imitive learning.

Whilst traditional court-owning Tooth-bills at Paluma very predominantly used *Polyscias* leaves we noted that courts established at new sites or traditional sites that were only partly re-established during a season had fewer *Polyscias* leaves. This suggests to us that more *Polycias* was indicative of relative male experience as we consider males attempting to establish new sites or replacing traditional owners at their traditional sites to be younger birds (Frith & Frith, in press). In some cases where an unknown, unmarked, male took over the traditional court site of a traditional marked male at the start of a display season, we observed the presumed relatively inexperienced male to clear an inferior court and decorate it poorly. Such newly-aquired courts and their decoration improve over subsequent seasons. Thus, long established, older, court-owning males used mostly *Polyscias* leaves whereas younger and/or peripheral males used less. Older males also selectively stole *Polyscias* leaves from courts of peripheral, probably subdominant, neighbouring males. These conclusions are supported by the findings of Borgia (1985a, 1986) who found the ability of male Satin Bowerbirds to build better quality bowers and retain greater numbers of decorations to be a function of age.

The more significant bower decorations of some other bowerbird species are items rare in the birds' environment (Borgia & Gore, 1986; Frith, 1989; Frith & Frith, 1990c) and it appears that an abundance of such decorations on bowers improves the owners mating success (Borgia, 1986). Rare decorations might, thus, indicate something significant to rival males and to females about fitness, and possibly level of dominance, of the males acquiring and retaining them. It is doubtful, however, that *Polyscias* leaves are rare in the Tooth-bill's present environment for in considering this possibility the modification or degradation of Tooth-bill habitat must be kept in mind. Pioneering *Polyscias* in our study area were characteristic of disturbed forest edge and gaps. Prior to any upland rainforest disturbance (i.e. roads, snig tracks, logging etc.) this plant would certainly have been less abundant and more patchily distributed than it is today. This aside, however, it is possible that *Polyscias* presents a leaf that has a structure and moisture content that gives a long 'court-life' and provides a strikingly contrasting pale underside.

We were unable to study male mating success relative to court position, size, or number of leaf decorations. We observed that a display tree, at or within the court periphery, is fundamentally important to enable males to initiate courtship by hiding from the female behind (Frith & Frith, 1993). Whilst all long-term traditional courts had at least one display tree a number of small and temporary courts, apparently made by younger males early or late in the display season, lacked such a tree. As the initial clearing of the court of all litter and debris doubtless involves considerable effort by, and cost to, the male and, given the observed variation in the size of area cleared it is possible that court size may be of some significance to females in mate selection. It should be noted that Grant & Laurance (1991) did not discuss court-size but unfortunately used the term 'court size' to represent the number of leaves on a court.

Of 54 courts examined for the presence of lawyer cane plants growing within them 37% proved to have them, indicating that this is not a prerequisite for a court location as suggested (Jackson, 1910). All fruit remains found on courts, often in discrete piles beneath favoured perches, are excreted by birds and not 'cast or vomited' as suggested by Jackson (1910).

LEAF TURNOVER RATES AND THEFT

Courts examined for leaf numbers, species and evidence of leaf stealing were those of part of the dense population of males on Tooth-bill Hill and adjacent slopes. These were traditional court-owners, which we concluded consisted of older and more experienced individuals. In most cases, colour-banding proved this to be true (Frith & Frith, in press).

Most leaves remained on courts for two weeks or less but some did so for up to three (dry season 79) or four (season 80) weeks, leaf turnover rates being faster with drier conditions. These results agree with Grant & Laurance (1991) who found most leaves were removed at 13 courts after two weeks or less. We found leaf turnover rates to be significantly higher during hotter drier periods of peak activity and, given that leaves are presumably selected for contrasting paler undersides, large size, flat structure and moisture retention (anti-curling properties), this is predictable as dehydration renders leaves unsuitable decorations more quickly. We performed no experiments on relative dehydration and deterioration rates of various leaf species, but observed that leaves of other species dried, curled and discoloured quicker than did *Polyscias*.

We found a peak activity court decoration rate of 5.9 and 6.8 and a removal rate of 7.3 and 6.4 leaves/day in seasons 79 and 80 respectively. These rates are higher than the 4.05 and 3.96 leaves added and removed per day respectively observed by Grant & Laurance (1991). Differences in leaf decoration and removal rates between individual males may reflect relative differences in experience, and/or dominance within the population of adjacent males. Grant & Laurances' (1991) period of study, however, included pre-peak activity, which would have lowered the overall rate of observed leaf replacement.

There were more leaves on courts during early peak activity in season 80 with a greater proportion of them *Polyscias*. Relatively fewer *Polyscias* leaves were present during later peak activity (and fewer still during post-peak activity), which may suggest competition for favoured decorations is more intense initially each season, when males are establishing or re-establishing a social heirachy. More leaf thefts occurred during early peak activity, indicating greater inter-male competition, and these mostly involved *Polyscias*.

Movement of stolen leaves among several adjacent well-established marked males' courts indicated the possibility of a social hierarchy. That one of nine adjacent individuals proved to steal more leaves from more adjacent courts than did all eight other birds combined, and apparently inhibited all other males from stealing from him (Fig. 5), is indicative of a system similar to that operating in some other polygynous bowerbird species (Borgia, 1985a,b; Borgia & Mueller, 1992). It is possible that more acquisitively successful court-owning males might obtain most successful matings within the localised dense population of court-owning males, or exploded lek (Frith & Frith, in press).

Borgia (1985a) demonstrated that male Satin Bowerbirds restrict their bower decoration theft raids to immediate neighbours, their most likely sexual competitors, as we do in the Tooth-bill (Fig. 5). He found, moreover, a highly significant correlation between male social dominance of individuals at feeding sites, and the number of bower destructions performed by the individuals, thereby providing evidence in support of bower interference being an aggressive act by which more dominant males can detrimentally affect the quality of bowers of rival males. We obtained no empirical data to support our hypothesis but we think it possible that a relatively large number of fresh and appropriate leaves on the court of a male, within an exploded lek, reflects that male's experience among the local male population and perhaps also his relative dominance.

MALE ATTENDANCE LEVELS AT COURTS

Over the peak court activity of season 79, 80 and 89 males spent an average of 64% of time attending courts. By radio-tagging four males, we and G. Moore showed that a bird was potentially present but silent high above his court where he might have otherwise been overlooked by an observer within a hide for up to 3% of total time. Differing court attendance levels by males during seasons 79, 80 and 89 clearly reflect seasonal environmental differences, being lowest during 79 (52%) and highest during 80 (79%). This pattern was the same during each month of peak activity and at different times of day.

The time that individual male Tooth-bills spent at courts during season 79 was lower and more variable than during 80 and 89. Males took longer absences from courts both during different months of peak activity and times of day in season 79, than 80 and 89. During 79, peak activity lasted only six weeks and it would appear that the dry conditions and poor fruit crop prevailing during this season were detrimental. The exceptionally dry early December of season 79 combined with a poor fruit crop caused birds to quit courts (Figs 3 & 6).

Court attendance levels by all males was high during season 80 and mean duration of absences from their courts was 3.7 and 2.2 times briefer than during seasons 79 and 89 respectively (Table 3) which would seem attributable to relatively greater availability of fruit (Fig. 3c). While the period of early peak activity of season 80 was relatively dry, fruit was prolific throughout the prolonged peak activity of 14 weeks. The onset of wet season rains terminated court attendance and, while significantly dry spells thereafter brought birds briefly back to courts, court attendance was low during post-peak activity (Table 4). Peak activity lasted ten weeks in season 89 with attendance levels being intermediate between those of 79 and 80 (Table 3). That the early 89 peak activity period was relatively dry, the November wet (Fig. 6), and the fruit crop relatively poor (Moore, 1991) possibly accounts for this.

Most polygynously-breeding passerines are inhabitants of tropical rainforests that eat predominantly, if not exclusively, fruits which are abundant in space and time in that habitat and require, therefore, a small proportion of the day to harvest. It has been argued that these ecological factors favour the evolution of polygyny because seasonally abundant fruit resources enable males to devote most of their time to courtship and females are able to provision their offspring unaided by the promiscuous males (Snow, 1976, 1982; Snow & Snow, 1988; Beehler ,1989).

Male Tooth-bills are almost exclusively frugivorous during their courtship and mating season (Frith & Frith, unpubl. data) and while nesting females are known to also feed insects to their young, the diet of the offspring is probably predominantly fruit (Frith & Frith, 1985a). Thus, this bowerbird fits well the ecological scenario common to most polygynous passerines. In the case of some neotropical polygynous passerines, males have been observed to spend as much as 87-90% of daylight hours attending display courts or perches (Snow & Snow, 1988). It is most noteworthy, therefore, that male Tooth-bills appear far more frugivorous than males of other bowerbird species and spend significantly longer at their courts than do males of other bowerbirds. This was emphasised because during this study, male Tooth-bills spent significantly longer at their courts during the season of highest fruit abundance.

Male Satin Bowerbirds, a species with a 67% fruit component of annual diet, spent an average of 73% of daytime within 50m of their bowers (Donaghey, 1981). Males of the predominantly frugivorous Macgregor's Bowerbird *Amblyornis macgregoriae* spent 54% of daylight at, or within 20m of, their bowers (Pruett-Jones & Pruett-Jones, 1982, 1985). A male Great Bowerbird, a species considered to be predominantly frugivorous (Diamond, 1986; Schodde & Tidemann, 1988) spent 47% of daylight hours at or near his bower (Veselovsky, 1978). The Regent Bowerbird's annual diet includes 81% fruit and yet males were found to spend a mere 3% of daytime at or near their bowers. The explanation for this exception is that regent bowerbirds *Sericulus* species represent an early stage in the evolution of bower-building, in which bowers have not yet replaced elaborate male nuptial plumage. Male Regent Bowerbirds *S. chrysocephalus* initiate courtship in the forest canopy before accompanying the female to the bower where a prolonged courtship display primarily presents colourful nuptial plumage, not the bower, to the female (Lenz, 1993).

MALE BEHAVIOUR AT COURTS

The length of time males spent at courts at each visit was similar for individual males during each season, different months of peak activity and at different times of the day (Tables 3-5). Once males started to attend courts the proportion of time they spent giving advertisement song, performing court maintenance or displaying was similar each season (Tables 6-8). Of their time at courts males invested 95.7% in performing loud advertisement song from favoured perches, 2.4% in silence, 1.2% in court maintainence and 0.7% in display.

Most (99%) advertisement song was performed by male Tooth-bills from favoured high, adjacent or court perches, males rarely singing on the ground prior to display subsong. Birds spent more time singing on high and adjacent perches during the drier and hotter 79 season than in 80 and spent more time on higher perches during the brighter and hotter time of day. During season 80, males spent more time on court perches as the season progressed. Most birds frequented only one or two, favoured, adjacent court perches, resulting in large accumulations of excreted fruit remains beneath them.

Male Tooth-bills spent a mean of 1.4mins maintaining courts. Given that males were present immediately above their courts for 64% of total time, the 1.2% of time spent in court maintenance is remarkably brief compared with mean proportion of time spent in bower maintenance by Macgregor's Bowerbirds (12%; Pruett-Jones & Pruett-Jones, 1982), Satin Bowerbirds (8%; Donaghey, 1981), Great Bowerbirds (Veselovsky, 1978), Western Bowerbirds *C. guttata* (Bradley, 1987) Spotted Bowerbirds *C. maculata*, Fawn-breasted Bowerbirds *C. cerviniventris* and Lauterbach's Bowerbirds *C. lauterbachi* (Frith & Frith, 1989, unpubl. data). It is similar, however, to that invested by the Regent Bowerbird which builds the most rudimentary and sparsely decorated of bowers (Lenz, 1993).

Male Tooth-bills do not spend much time on the court 'searching for insects and snails' as reported by Forshaw (in Cooper & Forshaw, 1977). The limited time they did spend on the cleared court area presumably merely reflects the low maintenance required once it is initially cleared and decorated. The cryptic morphology of males, their habit of remaining all but motionless when perched, of being silent when maintaining the court, the ventriloquistic quality of their calls, the extreme brevity of their courtship display (Frith & Frith, 1993), the adoption of a sleeked frozen posture when alarmed and the fact that they are not infrequently preyed on at their courts by goshawks *Accipiter* spp. (Frith & Frith, unpubl. data) all suggest that predation might have significantly influenced some or all of this behaviour. The fact that we witnessed not a single aggressive encounter between birds at a court other than owning birds chasing off another suggests such events are extremely rare.

MALE VOCALISATIONS AT COURTS

Bower-attending bowerbirds studied to date advertise the bower location with specific calls given relatively infrequently (Gilliard, 1969; Cooper & Forshaw, 1977; Veselosky, 1978; Donaghey, 1981; Frith & Frith, unpubl. data) and use a distinctly different, usually quieter and more complex, song in courtship display that in the case of the Satin Bowerbird (Loffredo & Borgia, 1986), the Regent Bowerbird (Lenz,

1993) and gardener bowerbirds *Amblyornis* spp. (Frith & Frith, 1993, Frith & Frith, unpubl. data) often includes avian mimicry. Tooth-bill, Satin, Macgregor's, Streaked Bowerbird *Amblyornis subalaris* and Archbold's Bowerbird *Archboldia papuensis* calls lack directional cues or have ventriloquistic qualities (Frith & Frith, unpubl. data). It has been suggested that this is a result of the enhanced risk of predation upon birds calling from long-term traditional locations (Robinson, 1974).

Advertisement song of Tooth-bills consisted of seven component calls. Phases of several to all of these calls were performed during each visit and usually followed a definite sequence. Thus males returning to courts invariably first gave a 'chuck', as noted by Chaffer (1984), or less frequently a squeal. 'Chuck' and 'squeal' calls were followed by 'chuck + babble' or 'chuck + mimicry'. These were followed by 'babble', 'babble + mimicry' and/or 'mimicry'. Display vocalisations (Frith & Frith, 1993) usually followed the latter three calls. Sometimes, but not often, the sequence of calls was broken when males changed position on a, or moved to another, perch. In these instances they often gave 'chuck' calls again. The 'chuck' appeared to us the loudest, most far-carrying, and most locatable call. This may explain why 'chuck' is used to recommence calling, as it clearly and quickly establishes the bird's presence and location. It is possible the 'chuck', which we here treat as a natural Tooth-bill call, is in fact mimicry of a similar note of Bower's Shrike Thrush, particularly as calls of this species dominated Tooth-bill mimicry. Of the total time males spent advertisement singing at their courts, at least 60% of vocalisations included elements of mimicry (Table 10).

Calling male Tooth-bills at locations remote from Paluma sound similar in general terms but incorporate some different avian model species into their mimicry and/or give different bias to different species (C. & D. Frith, unpubl. data) as is found in Satin Bowerbirds (Loffredo & Borgia, 1986) and lyrebirds *Menura* spp. (Smith, 1988) at different areas. This is indicative of the kind of 'culturally' transmitted behavior seen expressed in the bower architecture and decorations of bowers of geographically distinct populations of bowerbird species (Diamond, 1986, 1987).

While the loud song of the Tooth-bill presumably functions to indicate presence to rival males (Marshall, 1950) we think the conspicuous mimicry content may function to advertise court location and bird status to females (see below). Once a female shows serious interest in the court the male Tooth-bill performs a far softer 'subsong' exclusively of mimicry (Frith & Frith, 1993), as do male Satin Bowerbirds and Noisy Scrub-birds *Atrichornis clamosus* (Loffredo & Borgia, 1986; Robinson, 1974). We think it likely that this subsong is in fact more informative to females than advertisement song as it has been demonstrated that female Satin Bowerbirds use the quality of more intimate male mimicry to assess the relative merits of prospective mates (Loffredo & Borgia, 1986). Contrary to Robinson (1974), but consistent with Dobkin's (1979) interpretation that male bowerbird mimicry is given in precopulatory display (and in nest defence by females), the male Tooth-bill does specifically perform mimicry prior to and during courtship displays, as male Satin Bowerbirds appear to do (Loffredo & Borgia, 1986).

Loffredo & Borgia (1986) showed that among competing male Satin Bowerbirds, older males produced longer bouts of higher-quality avian vocal mimicry than younger males and as a consequence gained higher mating success. These authors also found that the male Satin Bowerbirds in their study area performed mimicry of only two bird species during courtship and that when both were given they were always performed in the same order. During subsong mimicry male Tooth-bills showed a strong tendency to perform their repertoire of approximately ten model species and other sounds in a particular order and within a minute (Frith & Frith, 1993).

The nature of male Tooth-bill vocalisations would suggest that females may make some general assessment of male experience from their loud court advertisement song prior to selecting individual males and/or courts for visitations. This initial loud 'broadcasting' of mimicry may reflect pressures of greater male competitor density. During the subsequent court visit females can assess the quantity and quality of the more stereotyped sub-song exclusively of mimicry (Frith & Frith, 1993). Thorpe (1985) stated that there is some evidence that variety in male bird song is attractive to females, and suggested that mimicry may simply be a way of increasing repertoire size.

The repertoire of singing male court owners was found to change, by other bird calls being opportunistically mimicked, thus incorporating novel characters into the song. Bourke & Austin (1947) also noted that males would stop calling to listen to other bird species and then immediately mimic the bird listened to. Goodwin (1986) reported several wild Jays *Garrulus gladarius* mimicking the call of the Grey Heron *Ardea cinereus* immediately upon seeing this species. Smith (1988) observed the same behaviour by mimicking, promiscuous male, lyrebirds. The significance of such individualistic call components is unknown. The idea that females may in fact select for novel secondary sexual characteristics has, however, recently been presented (Ten Cate & Bateson, 1988; Christidis & Schodde, 1993). It is possible this theory may have significance to the question of avian mimicry in addition to the finding of Loffredo & Borgia (1986) that male Satin Bowerbirds performing more and better mimicry were older individuals obtaining higher mating success.

Hoglund (1989) observed that in lekking birds all species that display on the ground have larger males than females, with the exception of the Great Snipe *Gallinago media*. He noted that the male Great Snipe uses vocalisations rather than nuptial plumage to enhance reproductive success. It is noteworthy, therefore, that the terrestrially-displaying Tooth-bill is cryptically monomorphic in plumage, nearly so in size, and that males use prolonged complex vocalisations but a markedly brief display (Frith & Frith, 1993) in courtship. Five adult male Macgregor's Bowerbirds, decorated only with an extensive orange crest, spent an average of 71% of court attendance time perched silently and 14% vocalising from traditional perches (Pruett-Jones & Pruett-Jones, 1982). Brilliantly-plumaged adult male Regent Bowerbirds spent a mere 1.01% of their total, brief, court attendance time vocalising (Lenz, 1993).

It is possible, therefore, that continuous loud complex vocalisations by male Tooth-bills, at least in part, compensates for the lack of visual secondary sexual characters by containing information that rival males and potential mates can use to assess male 'fitness'. It has been noted that in the evolutionarily convergent polygynous Cotingas (Passeriformes, Cotingidae) of the Neotropics, in which most species are conspicuously sexually dimorphic, the lekking males of the few species with much-reduced or no sexual dimorphism use vocal behaviour to attract and court females far more than their relatives. (Snow 1982). Male Tooth-bill fitness could be indicated by the amount of calling (time invested at the court) and/or its qualities and proportion of avian mimicry (reflecting male experience). Loffredo & Borgia (1986) found that female Satin Bowerbirds use male vocalisations, particularly the quality of mimicked bird calls, as an indication of relative male age. They found that older males perform better mimicry and that females selected for the ability in males to learn complicated songs.

Thus, while female Tooth-bills cannot simultaneously compare members of an 'exploded' aggregation (lek) of males displaying their vigor and plumage (as females in true leks can) they may be able to simultaneously assess court attendance levels as indicated by vocalization time and the quality of song content. By this means females could initially assess male age (cf. Loffredo & Borgia, 1986) from perches above or adajcent to areas of greater court densities that in effect form exploded leks (Frith & Frith, in press), prior to selecting a male(s) to visit.

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