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Notes on the Nesting Biology of the Great Bowerbird *Chlamydera nuchalis* (Ptilonorhynchidae)

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Summary

Two Great Bowerbird *Chlamydera nuchalis* nests were studied and their situations, location relative to an active bower, and egg measurements are described, discussed, and compared with those of congeners. Limited evidence for polygamous bowerbirds suggests that some females nest relatively close to an active bower. Results of 28.8 hours of observation of incubation and 63.5 hours of nestling feeding activity are presented. Levels of egg and nestling parental attendance are compared with other bowerbirds. Of 208 identifiable nestling meals 116 were animals and 92 were fruit. Of animal meals 54% were large grasshoppers (Acridoidea) and of fruit meals 44% were figs (*Ficus*). A single parent, presumably female, attended the nest. Vocal mimicry at the nest by females and at the bower by males, particularly of predatory bird calls, is discussed. Egg laying, nesting season, clutch size and nestling period are reviewed.

Introduction

The Great Bowerbird *Chlamydera nuchalis* is the largest of the Ptilonorhynchidae, and belongs to the only bowerbird genus adapted to dry, sparsely vegetated habitats. It is endemic to tropical Australia where it frequents riverine woodlands and vine thickets, eucalypt and melaleuca woodlands, open savannah woodlands and well-foliaged suburbia.

The sexes of the Great Bowerbird, and of its four congeners, are almost identical as described by Gilliard (1969), Cooper & Forshaw (1977), Schodde & Tidemann (1986) and others. Males build a substantial 'avenue' type bower (Marshall 1956, Gilliard 1969, Borgia 1986, Donaghey et al. 1985, Frith 1985), which they decorate with numerous objects, and at which they court and mate females (Cooper & Forshaw 1977, pers. obs.). By marking males and bower decorations during 1983 Stephen Garnett (pers. comm.) demonstrated that male Great Bowerbirds steal each other's decorations, which are thus moved from bower to bower. The courtship behaviour of male *Chlamydera* bowerbirds is indicative of a promiscuous male mating system, in which females are known or assumed to raise offspring unaided (Gilliard 1969, Cooper & Forshaw 1977, Donaghey et al. 1985, Diamond 1986, Borgia 1986). Little nesting information is available other than egg collection dates and no parental activity has been reported. For this reason it was important to confirm whether only a single parent attended the nest during this study. The nest is described as a bulky, shallow saucer or cup shape, loosely constructed of twigs, sometimes lined with finer twigs, built between 0.3 and 10.0 m above ground (Campbell 1901, North 1902, Gilliard 1969, Cooper & Forshaw 1977, Beruldsen 1980).

Peckover (1969) noted Fawn-breasted Bowerbird *Chlamydera cerviniventris* nests 'well clear of bower sites, at least 150 m distant'. H.J. Frith (1976), repeated by Beruldsen (1980) and Schodde & Tidemann (1986), reported Great Bowerbird nests 'far from bowers'. Warham (1962), however, found a nest of this species c. 46 m from an active bower. The location of nesting females relative to active bowers may prove important to understanding the significance of bower sites, which may be used over decades by successive males, female choice of males over successive nesting seasons and relations, if any, between nesting females and conspecifics.

Methods

On 21 September 1984 an empty Great Bowerbird nest (nest 1) was examined 8.5 m high in the upper, outer foliage of a *Caesalpinia ferrea* tree on the James Cook University campus, Townsville, Queensland. It contained one egg on 25 September, still present at 1100 h on 26 September. Observations of incubation activity were made at this nest from 1-4 October inclusive, from the ground nearby, until the egg remains were found below the nest on 9 October. A second nest (nest 2) containing two eggs typical of the species was discovered at 1630 h on 28 September, 5.2 m high and built in a *Jasminium racemosum* vine tangle suspended from hanging canopy foliage of a *Eucalyptus alba* tree. Both nests were typical of those described for the species. An active Great Bowerbird bower was 50 m from nest 2. We did not search for other bowers closer to nest 1, but in view of our work and that of S. Garnett in the area it is considered unlikely another existed.

Observations of incubation of the two eggs in nest 2 were made from 1-4 October inclusive, and of nestling care from 16-19 and on 25, 26, 30, 31 October and 1 November inclusive from a hide atop a scaffold tower, 2.5 m from the nest. We could identify the idividual attending nest 2 throughout our study, because this bird had dried fruit remains sticking to feathering of the anterior left malar region; these had gone on 16 October, but left the area conspicuously bare. The attendant bird at each nest lacked a nuchal crest, as do most females and some immature males. On many occasions we were able to continually watch the nesting bird leave the nest, forage, and then return to feed young.

Egg and nestling measurements were taken with vernier calipers and a stopped wing rule, and weights with 50, 100 and 300 g Pesola balances as appropriate. Wing measurement was the maximum, flattened, length. First primary length was from the feather's point of entry into the skin to its tip. Total head length (THL) was the maximum distance from bill tip to back of skull. Nest 2 nestlings were banded with Australian Bird and Bat Banding Scheme bands.

Mean monthly Townsville rainfall figures (mm) for January to December during 1940 to 1986 inclusive are 297, 300, 212, 62, 36, 21, 14, 13, 11, 25, 54 & 116; and for July to December 1984 inclusive are 59, 6, 21, 20, 39 & 48. Thus, mean Townsville rainfall for July-September inclusive is 38 mm whereas for the same months during our study year it was 86 mm.

Results

Incubation

The nest 2 eggs measured 38.1 x 27.9 and 38.1 x 27.4 mm and weighed 14.7 and 14.5 g respectively, c. 14 days before hatching. They were viewed daily at 0730 h until 11 October. When next examined, at 1600 h on 12 October, one hatchling with long, dense, grey down and one egg were present. At 1000 h on 13 October two nestlings were present.

A total of 28 hours 50 minutes of incubation activity was observed, 11 hours 30 minutes at nest 1 and 17 hours 20 minutes at nest 2 (Table 1). We assume an incubation period of c. 21 days in view of data for other bowerbirds (see Discussion). A total of 77.5% of observation time was spent incubating (including 1.3% of time perched on nest rim); the mean length of incubation bouts was 24 mins 51 secs. The mean number of incubating bouts per hour was 2; mean bout duration was almost 25 minutes. A mean of 46 mins 24 secs was spent incubating each hour.

Table 1
Maternal Great Bowerbird incubation activity at two nests. F = female.

Nest #	*Approx. age of 1st egg (days)*	*Time watch commenced*	*# mins per watch*	*% watch F incubating*	*$\bar{x}$ incubation bout time (mins/secs)*	*$\bar{x}$ time F absent (mins/secs)*
1	9	14.30	210	82.9	24.51	5.30
1	10	15.00	180	75.2	19.20	6.50
1	11	7.00	210	79.5	20.53	6.50
1	12	7.20	90	69.9	12.35	6.00
2	10	14.45	210	76.7	26.51	9.27
2	11	15.00	180	82.6	29.44	7.38
2	12	7.00	300	78.0	33.27	12.36
2	12	15.53	90	75.7	22.43	9.54
2	13	7.10	260	76.7	33.13	12.07
—	—	—	1,730	77.5	24.51	8.33

Table 2
Maternal Great Bowerbird nestling care activity at nest 2. F = female.

Approx. age of older young (days)	*Time watch commenced*	*# mins per watch*	*% watch F spent brooding*	*% watch F feeding young*	*$\bar{x}$ brooding bouts per hour*	*$\bar{x}$ brooding bout time (mins/secs)*	*$\bar{x}$ length of F absence (mins/secs)*
5	13.00	300	15.1	5.3	1.8	5.02	15.43
6	7.00	660	12.3	5.7	1.3	5.46	13.56
7	7.00	600	13.4	6.7	1.0	8.01	12.37
8	8.00	420	12.2	7.4	0.9	8.31	12.23
14	11.00	420	7.4	7.0	0.1	31.10	13.60
15	7.30	510	—	7.1	—	—	15.48
19	16.00	60	—	2.0	—	—	12.10
20	7.00	600	—	7.7	—	—	10.33
21	10.40	240	—	3.7	—	—	15.25
—	—	3,810	6.7	5.8	0.6	6.30	13.31

Brooding and feeding

Table 2 summarises 63 hours 30 minutes of time-budgeting of parent attentiveness to nest 2 nestlings, 16 October-1 November inclusive. Of total observation time 6.7% was spent brooding young, involving 0.6 brooding bouts per hour and a mean of 6 mins 30 secs duration per bout. A mean of 3.6 nest visits were made per hour, mostly to feed young; the mean length of each feeding visit was 59 secs (range 35-75 secs). Feeding young occupied 5.8% of observation time, although the parent spent a total of 12.4% of the time at the nest (including perching on nest rim and preening itself/the nestlings there etc.).

Food and nestling growth

The hide proximity to nest 2 enabled us to closely observe feeding of young (Plate 38). Of 254 meals delivered by the parent, 208 could be identified as animal or fruit. Food brought in the adult's bill represented a meal, thus several figs and/or other fruits or several different animals brought at once constituted a meal. Forty-six smaller meals were not identified.

Of 208 identified meals 115 (55%) contained animals, 91 (44%) fruit and 2 (1%) were of both animal and fruit. Of 115 animal meals 62 (54%) were of large grasshoppers,

almost all being stripped of head, legs and wings (see photograph in Dwyer et al. 1988); 4 (3.5%) of large lepidopteran caterpillars; 15 (13%) of large crickets; 8 (7%) of mantids; 4 (3.5%) of large huntsman spiders; 3 (2.6%) of medium-sized beetles; 2 of mole crickets, 2 of large moths, 1 of a katydid, 1 of a large horse fly, 1 of a cockroach, 10 of unidentified insects, 1 of a slug or snail and 1 of a skink.

Of 91 fruit meals, 40 (44%) were of fig(s) or fig pieces, predominantly *Ficus microcarpa* of which a large fruiting individual was c. 100 m from the nest; 14 (15.4%) were of the exotic Brazilian Cherry *Eugenia uniflora* and 37 (40.6%) were of unidentified fruit(s) or fruit pieces. Two meals of both animal and fruit components consisted of a medium-sized beetle with a single fruit.

Nestling meals were carried between the parent's mandibles, but if of several fruits one or two were in the back of the mouth, clearly visible in the open bill. None was regurgitated to the young. Nestling faeces were eaten by the parent, as were those of the fledgling in the nest tree canopy on 1 November. Nestlings' growth measurements appear in Table 3.

Table 3
Growth and development of Great Bowerbird brood of two nestlings in nest 2.

Date/time	*Approximate age of young (days)*	*Weight (g)*	*Wing length (mm)*	*First 1Y length (mm)*	*THL (mm)*	*Eyes*
14.10/0930	3	23.1	—	—	29.2	jo
	2	15.6	—	—	26.2	c
17.10/1800	6	50.2	30	—	—	o
	5	29.3	18	—	—	c
18.10/1700	7	55.9	35	15	37.4	o
	6	34.9	22	7	32.7	o
19.10/1515	8	67.8	42	20	38.7	
	7	37.3	26	9	34.3	
21.10/0900	10	85.2	57	—	—	
	9	55.8	44	—	—	
24.10/0900	13	98.3	76	—	—	
	12	77.2	61	—	—	
26.10/1615	15	114.8	87	60	47.9	
	14	103.8	72	48	44.6	
31.10/0825	20	older young fledged				
	19					
1.11/1900	21	older young in nest tree crown, younger being brooded				
	20					
2.11/1100	22	both young in nest tree crown				
	21					
21.1/1000		an adult-looking banded young feeding alone on fruits 150 m from nest tree				

Notes: 14.10 the older nestling had 20 mm long dense grey down
17.10 both nestlings with mid-grey down, skin dark flesh, inside mouth bright yellow, gape whitish, egg-tooth white, legs blue-grey
26.10 egg-tooth on both nestlings still obvious
1Y = primary, THL = total head length or bill + skull
jo = just open, c = closed, o = open

Nest and nestling defence and vocal mimicry

On 2 October, the incubating parent left the nest to chase a conspecific out of, and well away from, a neighbouring tree; but on 3 October permitted a Helmeted Friarbird *Philemon buceroides* to perch and forage within 1 m.

From 12 October, after the first egg hatching, the parent invariably performed vocal mimicry during our nest examinations, or as one of us was escorted into the hide. This was given by the parent from uppermost foliage of the nest tree, or an immediately adjacent tree, as long as one of us was visible by the nest. During incubation the parent was silent, but as from our first observation of nestling care (16 October) it often gave vocal mimicry of predators' calls as approaching, or perching in, the nest tree.

This mimicry always included some calls of the potential predators: Whistling Kite *Haliastur sphenurus*, Black Kite *Milvus migrans*, Pacific Baza *Aviceda subcristata* and what sounded exactly like a cat *Felis catus*. A distraction display was not performed as a result of our presence. On 1 November, however, CBF was in the hide when the parent performed a frantic distraction display, hopping about the immediate nest area with tightly sleeked plumage and drooped wings giving vocal mimicry of potential predator calls. The cause of this became apparent as a Common Tree Snake *Dendrelaphis punctulatus* entered the hide!

At 0825 h on 31 October one nestling hopped and fluttered upward from the nest into the nest tree crown, where it remained until at least 1900 h, after dark, on 1 November when the parent was brooding the remaining nestling. At 1100 h on 2 November both young were in the nest tree crown, where the parent fed them. On 21 January 1985 one of the banded young was feeding itself on fruits c. 150 m from the nest tree.

The active Great Bowerbird bower found was 50 m from nest 2 and c. 270 m from nest 1, and was known to be within a few metres of its location for at least 10 years by university staff, and by us for 7 years.

Discussion

Nest location

Whereas Peckover (1969), Vellenga (1980) and more recent popular literature (Chaffer 1984 p. 75, Schodde & Tidemann 1986) give the impression that bowerbird nests are typically located not 'close' to or are 'well clear', 'far', 'well away', 'distant' or 'a considerable distance' from bowers, this is often not the case; nests are often relatively close to bowers (see Donaghey 1981 and in Trounson & Trounson 1987, Pruett-Jones & Pruett-Jones 1983, Frith & Frith 1989 and in prep.).

Most active nests of bower-building species we have examined (Frith & Frith 1985, 1988, 1989 and in prep.) have been within hearing of a conspecific male at his bower or court. Green (1977) studied a female Satin Bowerbird's nest 'only a few hundred yards from the bower of the male'. Vellenga (in litt. 3 May 1989) believes that female Satin Bowerbirds avoid nesting 'within the territory of a male'. Rand (1942) examined a Fawn-breasted Bowerbird's nest, containing a young, 'about 150 yards' (137 m) from a bower. Mayr & Gilliard (1954) reported that of two Lauterbach's Bowerbird *Chlamydera lauterbachi* nests one was 400 yards (366 m) from an occupied bower and the other 15 feet (4.6 m) from a deserted bower. Of three active Western Bowerbird *C. guttata* nests examined by Kolichis (1979), one was c. 250 m from an active bower, one did not appear to have a bower in the area, and the area about the third was not searched. Jackson (1912) wrote of an active Spotted Bowerbird nest 'an old bower was not far away'; and of a new nest 'about 400 yards from', a nest with an egg '300 yards from' and of seven old nests 'a few hundred yards from' an active bower! Marshall

(1954) stated that the Spotted Bowerbird nests 'within a few hundred yards of the bower'. Pruett-Jones & Pruett-Jones (1982) found that all six active Macgregor's Bowerbird *Amblyornis macgregoriae* nests they found were approximately midway between adjacent active bowers, a mean of 116 m (range 69-130 m) from the nearest bower. Donaghey (1981) plotted Satin Bowerbird nests over four years in a study area including six active bowers, and found that of 14 nests, 11 were restricted to the two interspaces between 3 adjacent bowers, and 3 were immediately adjacent to two active bowers. Schodde & Tidemann (1986) stated that Regent Bowerbirds may often nest within 20 m of a bower.

The proximity of the Great Bowerbird nests in this study to an active bower agrees with observations by Warham (1962), who found an active nest in Townsville on 24 November 'about 50 yards from the bower', and wrote of this species and the Spotted Bowerbird 'its nest is built not very far from the bower'. Stephen Garnett (pers. comm.) observed a Great Bowerbird nest-building c. 60 m from an active Townsville bower in September 1987. It is possible, therefore, that these female bowerbirds nest closer to active bowers (? of the male of their choice) than elsewhere (Frith & Frith 1989). The possibility that earlier or more dominant females may nest in suitable sites closest to the male they mated each season might also be considered.

Laying & nesting season, clutch size, incubation & nestling period and growth

The literature indicates that most Great Bowerbird egg laying is September to December (Campbell 1901, North 1902, Marshall 1954, Frith & Davies 1961). Clutches have, however, been recorded during late July (Shilling 1948), in August (Campbell 1901, Olive in North 1902) and late January (North 1902). The record of a bird just moulting into immature body plumage on 16 September at Darwin is also indicative of an early egg laying (Hall 1974). The RAOU Nest Record Scheme contains records by L. Vernon of a 3 m high nest containing an egg on 23 September to 11 October but a nestling on 13 October 1986; and an approximately 8 m high nest with a well-feathered young found on the ground beneath it on 20 March 1987; both on Koolan Island, Western Australia.

It has been suggested that the commencement of Great Bowerbird nesting is closely associated with rainfall (North 1902, Marshall 1954, Gilliard 1969), as several early collectors obtained clutches during a wetter than usual July or August. Moreover, Marshall (1954) suggested that the initial rain of the annual tropical monsoon brings about an abundance of insect foods for nestlings, which stimulates nesting in both Great and Spotted Bowerbirds. Marshall presented Townsville rainfall data and suggested that Great Bowerbird nest building generally occurs there in October, although conceding that eggs are frequently laid in September. He further stated that because seasonal rainfall 'generally begins in September, and more than doubles the August precipitation in October, it could be suggested that this increase, in a very dry environment, is probably sufficient to stimulate the birds towards the end processes of display and perhaps to nidification and ovulation'. Townsville nesting data remain limited but do indicate that egg laying may commence in the, on average, driest month of September (see Methods); but it must be noted that July rainfall preceding this study was more than four times the monthly mean.

Lavery's (1986) inclusion of February among months during which clutches are started is for a two-egg clutch recorded by D. Seton at Swan's Lagoon, Millaroo, lower Burdekin River basin. Various authors have defined the breeding or nesting season (which we assume alludes to the period when eggs or young are in the nest) as September to February (Mathews 1925-27, Gilliard 1969), September or October to

Great Bowerbird *Chlamydera nuchalis* **nestling approx. 19 days old stretching.**
Plate 37 Photo: C. & D. Frith

January or February (Beruldsen 1980), August to February (Schodde & Tidemann 1986), October to January (Chaffer 1984) and July to February (C. Frith 1986 p. 337). The Great Bowerbird, like most 'frugivorous and insectivorous landbirds' (Lavery 1986) in north-eastern Australia, lays eggs predominantly during September to January.

Published clutch sizes are one or two eggs, with a single-egg clutch suggested as being more common by Olive (in North 1902), but clutch size may vary geographically or with the seasonality of climate and/or food abundance (Lack 1968). Seton (in litt. to H. Lavery, pers. comm.) examined a three-egg clutch at Swan's Lagoon on 1 December 1961.

Incubation periods for the Green Catbird *Ailuroedus crassirostris* and Satin Bowerbird *Ptilonorhynchus violaceus* are 23-24 and 21-22 days respectively (Donaghey 1981, Marchant 1980), and 21 days for a captive Regent Bowerbird *Sericulus chrysocephalus* (Brown 1956), and in view of their hatching dates we assume a nest 2 incubation period of c. 21 days, the eggs being at least a week old when found. The first egg to hatch in nest 2 did so at least 15 days after it was first seen. Using methods reviewed by Marchant (1980) for recording nestling periods, we conclude that the second nestling to hatch fledged at 20 days 8 hours 30 minutes $\pm$ 10 hours 30 minutes, in view of its presence in the nest at 1900 h on 1 November and assuming it left the nest between 0800 and 1100 h the following day. This compares with nestling periods for other avenue bower-building species of c. 22 days in the Fawn-breasted Bowerbird (Menzies 1976), and c. 19 (Hyem 1968, Pratt 1974, Vellenga 1980) to 20 days 12 h $\pm$ 12 h (Donaghey 1981) in the Satin Bowerbird.

Growth of the nest 2 nestlings differed conspicuously for their first week (Table 3), suggesting a more asynchronous hatching than expected in a clutch of two laid at an interval of 24 hours; but this may be explained by a long laying interval reported

in the Satin Bowerbird by Marchant (1986) who suggested that the Ptilonorhynchidae may have long laying periods. Vellenga (1980) observed a brood of two nestlings fledge 9 h 30 mins apart in severe weather on the same day. Donaghey's (1981) record of a brood of two fledging over alternate days may, therefore, also be indicative of a long laying interval.

Parental care

Studies of marked male avenue bower-building Satin Bowerbirds confirm that males are promiscuous (Vellenga 1970, Donaghey 1981, Borgia 1985) and much circumstantial evidence has led authors to assume that males of other avenue bower-building species are likewise (Gilliard 1969, Cooper & Forshaw 1977, Borgia 1985, Loffredo & Borgia 1986, Borgia & Gore 1986, Diamond 1986). Schodde & Tidemann (1986) stated that male Great and Spotted Bowerbirds mate with several females in the breeding season, as did Diamond (1986) for the Great Bowerbird but, although this is almost certainly true, there is no evidence.

Vellenga (1980) and Donaghey (1981) demonstrated that only female Satin Bowerbirds nest, and several casual studies have indicated this is the case in the Regent Bowerbird (Bell 1960, Threlfo 1983, Chaffer 1984). In these sexually dimorphic bowerbirds it is clear that only the female attends the nest, and this is widely assumed to be so in other bower-building species. Although our observations do not conclusively prove this is so in the Great Bowerbird only the most sceptical would doubt it, and we therefore refer hereafter to the nesting bird as female.

Writing of the Fawn-breasted Bowerbird, Peckover (1969) and Schodde & Tidemann (1986) stated, without evidence, that males do not participate in nesting. We have, however, presented circumstantial evidence supporting this assumption at one nest (Frith & Frith 1989). Forshaw (in Cooper & Forshaw 1977) followed previous authors in assuming that only female Great and Spotted Bowerbirds attend the nest. In addition to evidence presented here for the Great Bowerbird we have recently confirmed single parental, presumed female, nest attendance at one Spotted Bowerbird nest (Frith & Frith in prep.). Our results provide the first conclusive evidence that the, presumed female, single parent Great Bowerbird incubates and provisions young unaided.

Brooding and feeding young attendance was lower in Great Bowerbird nest 2 (12.4%) than in the Satin Bowerbird (16.4%, Donaghey 1981) and two Spotted Catbird pairs (44.4%, 30 hours pers. obs. at 2 nests with broods of 2) and Green Catbird pairs (37.8%, Donaghey 1981). The female Great Bowerbird's proportion of (a) time spent brooding, (b) mean length of each brooding bout, and (c) proportion of time a parent was at the nest with two nestlings was far less (see Table 2) than in the Spotted Catbird. Corresponding figures for two catbird pairs were (a) 29.8%, (b) 12 minutes and 57 seconds, and (c) 44.4% (pers. obs.). This comparatively lower nest attendance would be expected in a uniparental species nesting in a hot dry habitat. This agrees with differences in these investment levels observed between the monogamous, biparental, Spotted Catbird and the uniparental Golden Bowerbird *Prionodura newtoniana* and Tooth-billed Bowerbird *Scenopoeetes dentirostris* females tending broods of one (Frith & Frith 1985).

Feeding

All meals brought to the nest were carried in the bill and/or mouth, as is the case with Spotted Catbirds and the Tooth-billed, Macgregor's, Golden, Satin, Spotted and Lauterbach's Bowerbirds (Frith & Frith 1989, in prep. and pers. obs.). It is noteworthy that in all birds of paradise (Paradisaeidae) in which provisioning has been observed, nestling meals are regurgitated (pers. obs. and in prep.). In addition, nestlings and adults of at least some typical birds of paradise (Paradisaeinae) regurgitate fruit seeds and other indigestible matter whereas bowerbirds have not been reported doing so

Young Great Bowerbirds are raised on fruits, insects and spiders. They are fed by the female alone. First photo of female at nest.

Plate 38 Photo: C. & D. Frith

(C. Frith in prep. and pers. obs.). These differences are interesting in the light of the recent departure (Sibley et al. 1988) from the traditional view that these two groups are very closely related (Gilliard 1969, Schodde 1976, Cooper & Forshaw 1977).

The significance of figs in the diet, and to the distribution, of the Great, Spotted and Western Bowerbirds has been noted (Serventy & Whittell 1962, Marshall 1954, Gilliard 1969, Binsted 1977, Cooper & Forshaw 1977). Gaukrodger (1922), however, preceded this by recording grasshoppers, moths, caterpillars and berries as Spotted Bowerbird nestling foods. A noteworthy aspect of meals provided at nest 2 is the high proportion of the 115 animal meals consisting of large grasshoppers (53.9%), the vast majority of which were prepared by the removal of legs, wings and head. This preparation presumably requires experience, skill, and significant handling time, particularly as bowerbirds, unlike typical birds of paradise, do not use their feet to hold and manipulate food items (pers. obs. and in prep.). Donaghey (1981) showed that of 322 nestling Satin Bowerbird meals he saw delivered to the nest 95.3% consisted of insects: beetles, cicadas, grasshoppers, stick insects and others. The cicadas and phasmatids had their wings removed by the female. The Vellengas (1985) studied Satin Bowerbirds for over a decade and made some most significant observations concerning diet on the Upper Blue Mountains in New South Wales. They found that this bird ate mostly insects during spring and summer and that nesting females fed only large flying insects to their young and from which they removed the wings and legs. Moreover, the Vellengas noted that females did not breed during the two years of their study when large insects were in short supply. A study at one Spotted Bowerbird nest shows that this species also feeds predominantly 'stripped' grasshoppers to nestlings (Frith & Frith in. prep.).

It is possible that fig availability may dictate Great, Spotted and Western Bowerbird distribution in more arid areas, but population fluctuations of larger insects may influence their breeding seasons as they represent significantly large high-protein meals. Authors agree that the adult diet of this bird consists of fruits and insects but it would appear that all evidence for the latter foods is from stomach analysis only (Marshall 1954, Hall 1974).

Nest and nestling defence and vocal mimicry

Mimicry of potentially predatory bird calls by female bowerbirds at nests has been recorded in the Great, Spotted, Western, Fawn-breasted and Satin Bowerbirds (Gaukrodger 1922, Fleay 1943, Marshall 1954, Serventy & Whittell 1962, Warham 1962, Hyem 1968, Bell 1969, Peckover 1969, Hopkins 1974, Pratt 1974, Robinson 1974, Howard 1986), involving mimicry of at least the genera *Butorides, Aviceda, Milvus, Haliastur, Accipiter, Aquila, Falco, Dacelo, Cracticus, Gymnorhina* and *Corvus*. Calls of *Cacatua, Barnardius, Geopelia, Rhipidura, Philemon, Manorina, Lichenostomus, Coracina, Pomatostomus, Struthidea, Artamus* and other non-predatory genera have also been noted (Campbell 1901, North 1902, Warham 1962, Bell 1969, Hopkins 1974, Chaffer 1984, Bradley 1987), as well as the mimicry of non-avian sounds. Marshall (1954) considered such mimicry as 'distraction display'. Bower-owning male Great and Spotted Bowerbirds give vocal mimicry of predatory and other birds close to their bowers when disturbed by human presence (Marshall 1954, Robinson 1974, Howard 1986, Bradley 1987, pers. obs.). At both nests and bowers, Great, Spotted and Western Bowerbirds give a remarkably cat-like meowing cry, which Chisholm (1929) and Serventy & Whittell (1962) thought was, in the case of the Western and Spotted Bowerbirds respectively, 'probably its natural call'. Warham (1962) and Hopkins (1974), however, noted apparent cat mimicry at a nest and at bowers respectively but not away from them. Austin (in Mathews 1925-27) snared a Spotted Bowerbird in a bower which attracted six conspecifics which then gave mimicry of cat calls from the tree above. In view of the number of other potential nest predators these bowerbirds mimic, and the fact that the Spotted and Western Bowerbirds produce a similar call under similar circumstances (Frith & Frith in prep.), the possibility that the cat-like calls are mimicry of this introduced predator requires study and confirmation, notwithstanding doubts expressed by North (1902) and others.

Adult bowerbirds are certainly preyed upon: David Baker-Gabb (unpubl. data) has found the remains of a Great Bowerbird in two Red Goshawk *Erythrotriochis radiatus* nests. Butler (1977) published a photograph of a female Collared Sparrowhawk *Accipiter cirrhocephalus* taking a Western Bowerbird at a bower, and G. Czechura reports a Grey Goshawk *A. novaehollandiae* taking a Satin Bowerbird (S. Debus pers. comm.). In addition, we have examined one Spotted Bowerbird bower and several Tooth-billed Bowerbird courts with the remains of birds, presumably their owners, on them with evidence suggesting the former species was killed by a cat and the latter by a predatory bird (probably the Grey Goshawk).

Some speculative questions these facts raise are: Does vocal mimicry of predators by a bowerbird distract or deter a potential predator near the nest, bower, or fledgling (see Hopkins 1974)? Is a performer merely associating the perceived threat with the vocalisations of previously experienced predators or is it performing a learnt vocal repertoire used under the specific stress of a potential predator presence, evolved as a result of selective advantage?

Hyem (1968) and Robinson (1974, 1975) were of the view that the mimicry of predators' calls and the alarm notes of aggressive bird species is aggressive or territorial

in function. Vocal mimicry is unknown in the much-studied monogamous catbirds *Ailuroedus* spp. (Cooper & Forshaw 1977, Donaghey 1981, pers. obs.).

Nothwithstanding our regular inspection of nest 2, the female did not perform a physical distraction display. This could be attributable to her familiarity with constant human presence about her nest, but we have found a Spotted Bowerbird nesting remote from humans to behave identically (Frith & Frith in prep.), unlike Gaukrodger (1922) who witnessed an intense terrestrial distraction display by this species. The presence of a snake close to Great Bowerbird nest 2 immediately resulted, however, in frantic distraction display with vocal mimicry. Peckover (1969) and Bell (1969) reported nesting Fawn-breasted Bowerbirds performing a 'broken-wing' distraction display on the ground and a Tooth-billed Bowerbird performed this behaviour when its fledgling was handled by Warham (1962).

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