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DISPERSION, SIZE AND ORIENTATION OF BOWERS OF THE GREAT BOWERBIRD *Chlamydera nuchalis* (PTILONORHYNCHIDAE) IN TOWNSVILLE CITY, TROPICAL QUEENSLAND

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Eighty active Great Bowerbird *Chlamydera nuchalis* bowers were examined of which 54 were measured and 61 plotted in the suburbs of Townsville City, tropical E. Queensland, where the species was reported by earlier authors to be absent or uncommon. The average number of years a bower was known to have been in use at 54 sites was 4.4 (range 1–13, SD = 3.3) and seven of them were known to be so for more than a decade. Mean nearest neighbour distance of 45 bowers was 790 m (range 300–1 875, SD = 378.4). Of 54 bowers examined only four had a structure(s) additional to the two parallel walls that constitute the avenue bower typical of this species. Bower shape, quality and size are described and discussed. Compass orientation of the bower avenue was strongly biased toward a NNW–SSE alignment, and 76% of bowers were orientated within 45° either side of the N–S axis. While only 32% were within 45° either side of the E–W axis. The main display platform was to the E half of the compass in 60% of 54 bowers. Sixty-three per cent of bowers had their main display platform orientated within the quarter of the compass centred on the NNW–SSE axis. Compass orientation of bower avenue and main display platform are discussed with respect to previously observed biases and these findings are compared with data for other avenue bower-building bowerbird species. A plausible explanation for observed orientations is that males orientate their bowers to maximize advantageous illumination of their display decorations and postures during mornings of the annual peak courtship season, but further studies are required.

INTRODUCTION

The Great Bowerbird *Chlamydera nuchalis* is the largest of the 19 bowerbird species (Ptilonorhynchidae), and belongs to the only genus adapted to relatively dry, sparsely-vegetated habitats. It is endemic to tropical Australia, where it frequents riverine woodlands and vine thickets, eucalyptus and melaleuca woodlands, open savannah woodlands and well-foliaged suburbia. Broadbent (1910) described the species as being common 'out from Townsville' on the east coast of tropical Queensland, implying that it was absent from or uncommon in that city. Hopkins and Lavery (1963) described it as uncommon and only occasionally seen there. It is now common within Townsville and its suburbs (Garnett 1983; Wieneke 1992).

Eleven bowerbird species are known to reproduce polygynously (Diamond 1986; Coates 1990; Frith and Frith 1990a,c, 1993) and five (*Sericulus aureus, S. bakeri* and three *Amblyornis* spp.) are assumed to do so, the promiscuous males attempting to mate with many females each breeding season and taking no part in nesting duties. Three bowerbird species known as catbirds, *Ailuroedus* spp., are monogamous (pair-bonding birds in which both sexes share nesting duties). In the 16 apparently polygynous species,

males clear a court, accumulate fern fronds on the forest floor or construct structures of sticks, known as bowers, which they decorate with objects such as stones, bleached bones, fruits, snail shells, etc. These bowers are cleared, built, decorated and maintained, as externalized secondary sexual characters, by males to attract females for mating (Borgia 1986).

Bowerbirds' bowers are of four distinct, basic types. The only cleared 'court' type is that of the Tooth-billed Bowerbird *Scenopoeetes dentirostris*, which clears an area of forest floor and places fresh leaves upon it (Frith and Frith 1993, 1994b). The only 'mat' type is that of Archbold's Bowerbird *Archboldia papuensis,* which accumulates fern fronds on the forest floor beneath decorated perches and places decorations upon the 'mat' (Frith and Frith 1990b, 1991, 1994a; Frith *et al.* 1996). Far more complex 'maypole' bowers of sticks are constructed by the New Guinea gardener bowerbirds *Amblyornis* spp. (Cooper and Forshaw 1977) and the Golden Bowerbird *Prionodura newtoniana* of tropical north-eastern Australia (Frith 1989 and unpubl. data). The 'avenue' bower builders comprise the three 'regent' bowerbirds *Sericulus* spp. of New Guinea and eastern Australia, the Satin Bowerbird *Ptilonorhynchus violaceus* of eastern Australia and the 'grey' bowerbirds *Chlamydera* spp. of tropical Australasia (Gilliard 1969; Cooper and Forshaw 1977). Avenue bowers typically consist of two parallel walls of sticks placed upright into a foundation platform of sticks and/or the cleared ground. Almost invariably the area of sticks upon the ground and/or the cleared area to one end of the bower avenue is larger and more prolifically decorated than that of the other end. This larger area is presumably more often frequented by the bower-owning male and we refer to it here as the main bower or display platform.

Although gross variation in architecture and construction may be apparent between individual bowers of gardener and Golden Bowerbirds (Diamond 1986; Frith 1989), the bowers of avenue bower builders usually appear similar, although subtle differences in the 'quality' of sticks and their placement do exist (Borgia 1985; Lenz, unpubl. data). Some architectural additions to avenue bowers are, however, known in several species. These usually take the form of a small to average-sized third, rarely a fourth (Chaffer 1959, 1984), wall that may be parallel to the original normal two walls or at an angle to them. In some abnormal Satin bowers a third wall may be at right angles to, and at one end of, the parallel avenue walls, as are the normal end walls in bowers of the Yellow-breasted Bowerbird *C. lauterbachi* of New Guinea which builds the most elaborate of avenue bowers. Such irregular bowers are known for Satin (Hyem 1968; Chaffer 1959, 1984), Great and Spotted *C. maculata* Bowerbirds (Chaffer 1984; Frith *et al.* 1994; C. and D. Frith, unpubl. data).

Interspecific differences in bower form and the location and colour of decorations are thought to be functional but few have been demonstrated to be so (Borgia 1995). One conspicuous character of bowers within the species of avenue builders is that most are typically compass-orientated, mostly about the north–south (N–S) axis. A widely accepted explanation for this is that this results in illumination of the bower, its decorations and/or the owner in a manner most advantageous to the male (Marshall 1954; Gilliard 1969; Peckover 1970).

Bower dispersion in any *Chlamydera* species has previously been studied for only a relatively small number of bowers of individual males: see Table 2 for these and comparative data on other bowerbird genera.

During 12 years of residence near Townsville City (19°15′S, 146°48′E), Clifford Frith (CBF) and Dawn Frith (DWF) found the Great Bowerbird widespread and common there. They carried out some preliminary studies of aspects of nesting biology (Frith and Frith 1990a) and bower structure with Jo Wieneke (JW) (Frith *et al.* 1994). The Townsville population provides an ideal opportunity to examine density and dispersion of males at their actively-attended bowers over the extensive suburbs, as city features facilitate more accurate mapping than might be possible in a similar area of natural habitat. This study sought to take advantage of these circumstances and to examine variation in bower size, structure and orientation of the avenue and main display platform, in the light of existing literature and explanations of observed variations, with the aim of stimulating further studies. A primary aim of this preliminary study is to stimulate further investigation into these aspects of avenue bower-building bowerbirds.

METHODS

In order to maximize the number of active Great Bowerbird bowers that could be studied in Townsville a publicity campaign of interviews with radio stations and Townsville newspapers was performed by JW during the 1992 courtship season (July–November). As a result of this more than 151 reports from different individuals were received, involving some 64 bowers over *c.* 113 km^2. Because more than a single report (and up to 12) was received for most (49) bowers, we are more than reasonably confident that almost all active bowers within suburban Townsville were located by this means and by searching by JW who was resident in Townsville throughout the study.

A total of 80 bowers became known to us by the end of this study. Of these, 61 occurred within the study area (Fig. 1). Fifty-four bowers were adequately described and measured during the period 1 November–12 December 1993 for analysis of variation in structure and orientation. Many people reporting bowers were able to indicate a minimum period of years during which they and/or their family or friends were aware of a bower being present in the same spot or immediate area (within 20 m radius). In defining the minimum number of years an active bower was at a specific location (bower site), we have been most conservative and cite periods only when corroborated by more than one source or known from our own experience.

A standard data sheet was used that incorporated a schematic sketch plan and profile of a bower to ensure that all required scores, measurements and bearings were systematically recorded at each bower visit. To minimize disturbance, observations were made by JW during early afternoons, when bowers are least attended by birds (pers. obs.) The relative quality of bower geometry was subjectively scored on a scale of 1 (= poor) to 5 (= superb), the comparative height, length and width of the two avenue walls and the relative evenness of the avenue width throughout its length being particularly noted. Bower quality was similarly scored on a scale of 1 to 5 by noting the relative compactness and quality of stick placement and alignment over the bower as a whole and the relative smoothness of finish of the inner avenue walls. Quantity of bower decoration was scored from 1 (= few) to 5 (= numerous) and a sketch plan of decoration placements, types, colours and approximate quantities was drawn on the back of each bower data sheet by JW. It was noted at which end of the bower avenue the larger, or main, display platform was located with reference to the nearest 16 cardinal compass bearings.

All active bowers of the 1992 season, plus some additional ones found during the 1993 season, were plotted onto a detailed 1:25 000 Townsville City street map and the nearest neighbour distances (NND) of all simultaneously-active bowers were calculated to the nearest 25 m from these plots. A detailed copy of this map (summarized in Fig. 1), which includes the number given to each bower is available from CBF upon request.

Spearman rank correlation (r_s, corrected for ties) was used for statistical comparisons.

RESULTS

Bower structure scores, measurements, calculations of NND, minimum number of years each bower was known at a particular bower site and avenue compass orientations appear in Table 1. One resident of >70 years informed us that a

TABLE 1

Details of 54 Great Bowerbird bowers actively in use in Townsville City, north Queensland during the 1993 courtship season.

	Mean	n	SD	Min.	Max.
Years known at site	4.4	54	3.3	1	13
Nearest neighbour distance (m)	788	46	376.7	300	1 875
Compass bearing (°) of larger display platform	153	54	106.6	0	338
Bearing (°) of bower avenue	256	54	123.4	2	360
Bower length (mm)	611	54	105.7	310	900
Bower width (mm)	507	54	72.1	350	690
Average inner bower avenue width at entrances (mm)	135	54	16.6	100	175
Avenue floor height above ground (mm)	89	54	41.8	20	180
Maximum bower height (mm)	523	54	80.4	350	645
Average bower height (mm)	371	54	55.7	240	480
Average bower wall thickness (mm)	188	54	34.2	120	280
Overall bower size*	1 486	54	162.7	1 070	1 825

*bower length × width × height.

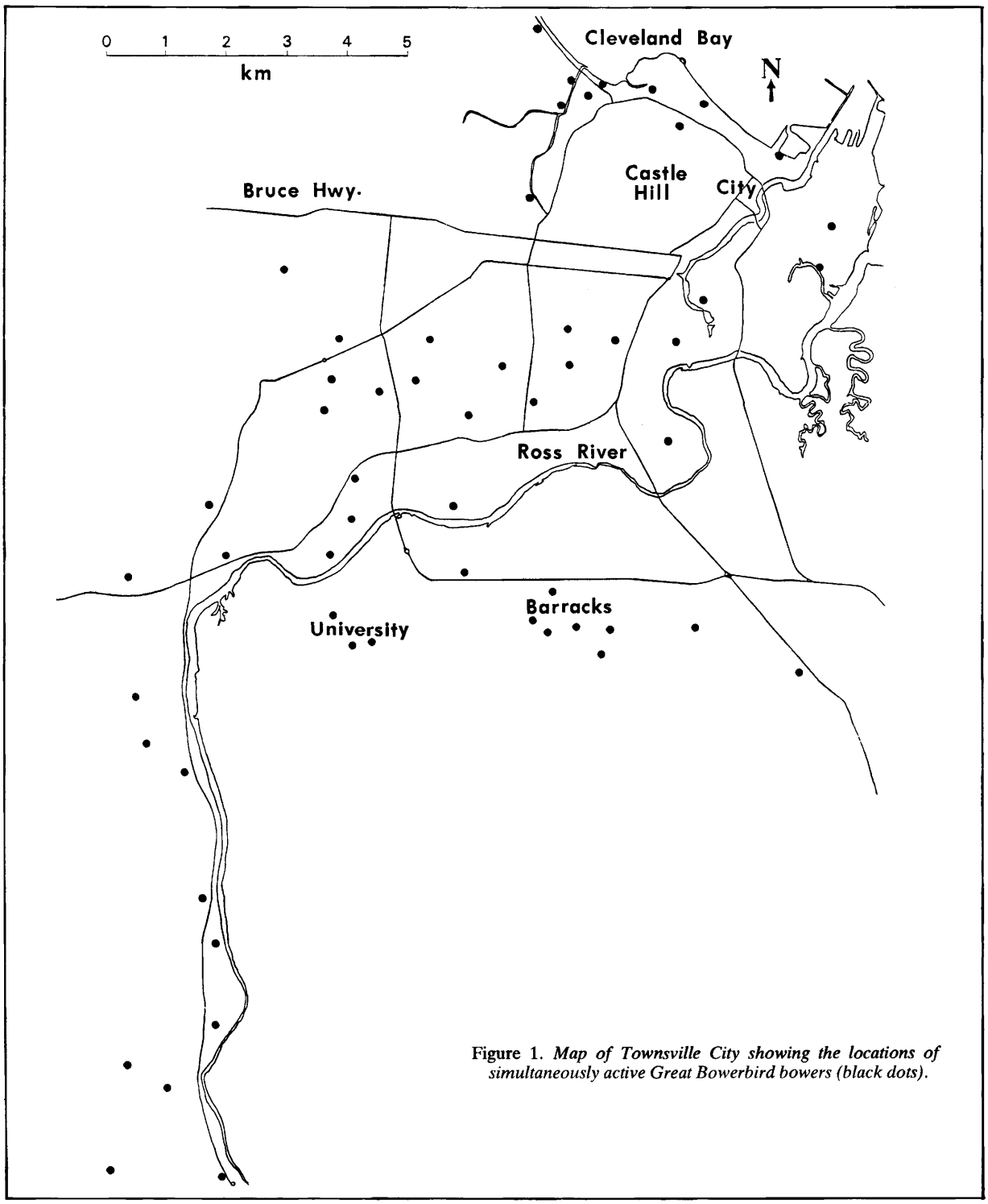

Figure 1. *Map of Townsville City showing the locations of simultaneously active Great Bowerbird bowers (black dots).*

bower had been near a local cemetery for as long as he could recall. Reference to two bowers in Hopkins (1974) and Chaffer (1984) appear to involve sites where bowers were found by us. Thus the average of 4.4 years that bowers persisted at a site is probably most conservative.

Bower locations, sites and nearest neighbour distances

All bowers were partly to well covered by the canopy of a densely-foliaged shrub(s) and/or tree(s) but if these were low there was also a tall tree(s) immediately adjacent, used by the bower owner to perch and call from and to depart from and arrive at the bower area. Bower sites were almost always immediately adjacent to an expansive open area, such as a road, larger open garden or park. Thus, they were usually only a few metres from the edge of where a well-vegetated microhabitat abutted open habitat. Males at five bowers also placed decorations around the base of a tree trunk adjacent to the bower and litter about this was cleared by the bird's movements (see Frith *et al.* 1994). The 46 bower sites (i.e. not including replacement bowers built close to a previous one) plotted within the inner city and suburbs (Fig. 1) had a mean NND of *c* 790 (range 300–1 875) m (Fig. 1, Tables 1 and 2). Most bowers were found within the areas of densest, well vegetated, housing immediately to the north and west of Ross River. Those to the south of the river were within the developed university and army barracks complexes. All bowers found during 1992 were revisited in 1993, some poorer 1992 bowers not being rebuilt, replaced, or attended in 1993.

Bower size, shape, quality and decoration

Table 1 summarizes the measurements of 54 Townsville Great Bowerbirds' bowers, and provides a significant basis for comparative observations of bower size and proportions with those of populations elsewhere. Larger overall bower size correlated well ($r_s = 0.40$, $p < 0.0025$) with overall bower quality (bower geometry + quality + decoration). Five of six adjacent bowers within the Lavarack Barracks grounds (Fig. 1) were larger than average.

TABLE 2

Dispersion of bowers or courts of males of nine bowerbird species — from the literature.

Genus and species	Nearest Neighbour Distance (m) Mean	Range	Bower sample size	Area studied	Habitat	Source
Chlamydera guttata	>2 000	1 000–2 000	8	*c* 78 km²	Arid open woodland	Bradley 1987
maculata	*c* 1 830	*c* 860–2 600	12	*c* 100 km²	Semi-arid open woodland	Borgia and Mueller 1992
	870	645–1 170	9	*c* 7 km²	Open woodland	Frith *et al.* 1995
nuchalis	*c* 790	300–1 875	45	*c* 113 km²	City suburbs	This study
cervinventris	*c* 490	*c* 425–600	10	*c* 6 km²	Woodland savannah	Peckover 1969
Ptilonorhynchus violaceus	311	135–694	13 & 15	*c* 3.3 km²	Woodland	Donaghey 1981
	c 300	*c* 100–975	17	*c* 6 km²	Woodland and suburbia	Vellenga 1980
	284	109–583	10 & 14	*c* 2.0 km²	Rainforest	Donaghey 1981
Sericulus chrysocephalus	195 ± 112 (sd)	—	8	44.4 ha	Rainforest	Lenz 1993
Amblyornis macgregoriae	169	75–348	42	*c* 8 km²	Rainforest	Pruett-Jones and Pruett-Jones 1982
Scenopoeetes dentirostris	61 ± 25 (sd)	24–142	55	50 ha	Rainforest	Frith and Frith 1995

Note: Sample sizes for bowers are of unspecified age male owners except in the *P. violaceus* studied by Donaghey (1981) which are for adult-plumaged males only. Mean Nearest Neighbour Distance for the studies of Vellenga, Borgia and Mueller, Bradley and Peckover have been calculated by measurements made, to the nearest 25 m, from maps therein.

Of the 54 active bowers included in the structural analysis, all but four consisted of an avenue of two parallel walls of sticks typical of the species. Bowers 1 and 5 had an additional, smaller avenue of two parallel walls immediately beside and almost parallel or parallel to them. Bower 1 remained like this over three years. Bower 19 had a previous avenue structure almost directly in line with it (decorations being placed between the two and at the extreme opposite end of each) plus a rudimentary small parallel wall, all of which was present for three years. Bower 24 had an additional area of sticks on one end of one wall (see Fig. 2).

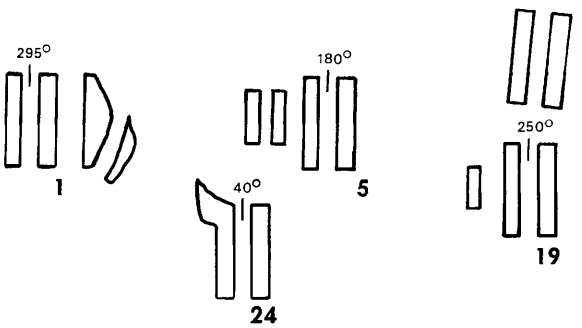

Figure 2. *Schematic plan, not to scale, of four active and numbered Townsville Great Bowerbird bowers with structures additional to the usual two parallel avenue walls of approximately equal length. Compass orientation of the avenue is indicated.*

Thirty per cent of bowers had the uppermost tips of most avenue wall sticks meeting above the centre of the avenue and another 30% had at least 10% of sticks doing so. In five bowers, this meeting of the two upper walls formed an arched 'roof'. One bower had one end of some long supple stems anchored into the outside base of one wall and extending up and over the top of the avenue, to be anchored into the outside base of the other wall.

Bower geometry score correlated significantly with decoration score ($r_s = 0.63$, $p < 0.0005$). A decoration quantity score of < 5 coincided with a bower geometry score of <5 in all but six of the 32 bowers involved. A bower quality score of <5 (n = 28) coincided with a bower geometry of <5 in all but three cases. In general, bower geometry score correlated positively with quality score ($r_s = 0.74$, $p < 0.0005$). Bower quality score also correlated positively with decoration score ($r_s = 0.77$, $p < 0.0005$).

Mean avenue floor height increased steadily with increasing overall bower quality score, from 52 mm for five bowers with a quality score of 2 to 98 mm for 27 bowers with a quality score of 5. Bowers with an avenue floor height of 50 mm or less were of overall poorer quality. A significant correlation was found between higher avenue floor height and bower quality ($r_s = 0.37$, $p < 0.005$). Generally poorly-constructed and little-decorated bowers were predominantly those with an ill-defined and poorly decorated circular depression within the central avenue.

At 42 better quality bowers, the location of red decorations was noted. They were placed about bowers, always represented a small proportion of total decoration numbers, and were never within the avenue or at the southern end of it. Red decorations were exclusively or very predominantly placed to the E of the avenue in 60% of bowers, equally to both E and W in 26%, mostly to the N in 7%. In only 7% of bowers were there no red decorations to the east. Nine bowers had multiple opaque white plastic bottle top rings hung upon sticks of the inner avenue walls.

Compass orientation of the bower avenue and main display platform

Figure 3 summarizes avenue orientation of 54 bowers. Sixty-eight per cent were orientated within 45° either side of the N–S axis and only 32% within 45° to either side of the E–W axis.

Thirteen (24%) bowers had their more extensively-decorated main platform located precisely N or S of the avenue. Of the remaining 41, 63% of bowers had their main platform to the E side of the compass and only 37% to the W side. Thirty-seven per cent of bowers had their main platform to the SE quarter of the compass, 31% to the NW, 22% to the NE and only 9% to the SW. Sixty-three per cent had their main platform on the 90° (= 25% of the compass circle) centred about the NNW-SSE axis (see Fig. 3).

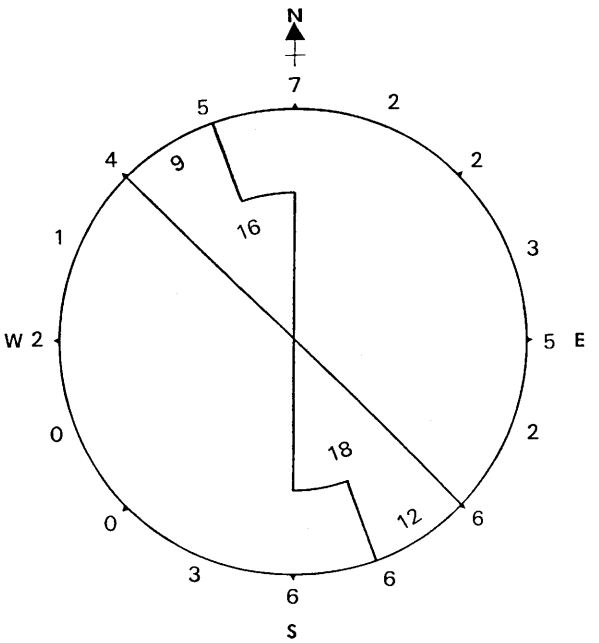

Figure 3. *Diagramatic summary of the compass orientation of the main display platform of bowers (numbers outside circle) plotted to nearest 16 cardinal compass bearings on 54 active Townsville Great Bowerbird bowers during the 1993 display season. Numbers within the circle show that 34 bowers had their main platform, and thus their avenue orientation, orientated to within 45° of the NNW–SSE axis and of these 21 bowers were within only 22.5° of the NNW–SSE axis.*

DISCUSSION

Bower locations, sites and nearest neighbour distances

As earlier literature indicates Great Bowerbirds were absent or rare about Townsville City (Broadbent 1910; Hopkins and Lavery 1963) it would seem that increasing vegetation and/or availability of water in this city has advantaged this bowerbird. Marshall (1954) and Blakers *et al.* (1984) stated that Great Bowerbirds' bowers are usually close to permanent water but many Townsville bowers were not particularly so.

The bowers of this study conformed to the 'woodland edge' location preference of the species. Great bowerbirds' bowers elsewhere are usually a few metres into riverine or other protective vegetation adjacent to an expanse of more open habitat (Warham 1962; Gilliard 1969; Veselovsky 1979) as is the case with most *Chlamydera* bowers. Lenz (1993) noted that inter-bower distances are greater in species of more open habitats (see Table 2). The Great Bowerbird mean NND of 790 m of this study fits this pattern, being less than the mean NND of 1 370 m for nine Great Bowerbird bowers in a more arid open area *c.* 100 km SSE of Charters Towers, northern Queensland (Frith *et al.* 1995).

Bower size, shape quality and decoration

Sedgwick (1946) considered 12 Northern Territory Great Bowerbird bowers to be 'fairly uniform' in size and gave the approximate average dimensions of 660 mm in length, 405 mm in width, 130 mm inside avenue width and 455 mm in height. Twenty-six bowers near Darwin, Northern Territory and 10 near Mt. Carbine, north-eastern Queensland averaged 10% and 4% shorter, 15% and 7% wider and had walls 19% and 27% thicker than those in Townsville respectively; and the average inner bower avenue width in Darwin was 133 mm, and at both Mt. Carbine and Townsville was 135 mm (Veselovsky 1979; Borgia 1995). Long-term studies are required to assess if any significance, such as male age and/or relative reproductive success might be attached to such findings that five adjacent bowers were all above average in size.

Comparative bower measurements show that less geometrically constructed bowers were numerically less decorated and lacked a high degree of compactness and of better stick placement or alignment. It is also clear that better built and decorated bowers, presumably those of older or more experienced males (Borgia 1986), tend to have a higher avenue floor. Substantially 'roofed' Great Bowerbird bower avenues, such as 9% of those in this study, have been recorded elsewhere, particularly in the Northern Territory (Sedgwick 1946) and on Cape York Peninsula (Hopkins 1974).

It has been stated that male Great Bowerbirds build a new bower each year (Veslevosky 1979; Blakers *et al.* 1984), but we observed that two bowers of a previous year were merely refurbished, the inner avenue walls of the structure being relined with new sticks. The clear preference for accumulating red decorations along the outside

of the length of the avenue and the slight preference given to placing these to the E of the bower had previously been noted in only a single bower. Hopkins (1953) noted as novel a Townsville bower having red decorations placed 'close to the side for its whole length'. This may relate to better lighting during mornings when most courtship occurs (see below). The significance and location of red bower decorations in this species is a topic worthy of further study. The decorating of inner avenue walls by hanging items from sticks in the way we observed is apparently unrecorded in this species. Male Fawn-breasted Bowerbirds *C. cerviniventris* typically hang bunches of small fruits atop and within the avenue walls (Peckover 1970).

Compass orientation of the bower avenue and main display platform

Marshall (1954) reported the orientation of 13 bowers on Cape York Peninsula to be within 45° either side of the N–S axis and the average deviation from due N–S to be only 16°. Three large bowers 21 km south of Musgrave, Cape York Peninsula were all orientated NNW–SSE (Len Robinson *in litt.* via W. T. Cooper). Of four bowers in Townsville three had their avenue orientated N–S and one NW–SE, and two at Gregory Downs, north-western Queensland were orientated NNE–SSW and NE–SW (Warham 1962). A bower near Mt. Garnet, northern Queensland was orientated N–S (Hore-Lacy 1962). Avenues of 10 bowers at Mt. Carbine, north-eastern Queensland were orientated at 359° ± 34° N–S (Borgia 1995). Warham (1957) described one bower near Darwin, Northern Territory as orientated NW–SE and all three active Northern Territory bowers found by Rix (1970) were orientated NNE–SSW. Also in the Northern Territory, 28 bowers were found to be similarly orientated, 62% being generally aligned to the NW–SE and 38% to the NE–SW axis (Veselovsky 1979). Three disused Great Bowerbird bowers at Kakadu, Northern Territory were noted to be orientated NW–SE, NE–SW and E–W by William T. Cooper (pers. comm.). Thus, judging from these data and results of the present study (Fig. 3), the species clearly favours a generally N–S bower orientation, with a strong bias to NNW–SSE.

All 54 bowers we examined had a display platform or 'court' at each end of the avenue, one being larger and better decorated (Table 1). During spring to early summer (August–November), when courtship and mating peaks, the sun rises and sets slightly to the north of due E and W respectively. Given this, the bower avenue alignment and location of the bower display platforms in most bowers studied suggests an orientation that provides best illumination of both display platforms during early morning and of the NNW display platform during the afternoon (Fig. 3).

It should be particularly noted that only 9% of bowers had the main display platform located within the 25% of the compass represented by due W to (but excluding) due S (Fig. 3) where morning illumination would be poorest during the courtship season, given an avenue orientation of NNE–SSW. Thus, few bowers had their main platform to the SW while the sun rises to the north of due E (peak display season) which would result in the most disadvantageous lighting. Given that most courtship display is probably performed on the (generally E-facing and predominantly the SE-facing) main bower platform, the highly favoured NNW–SSE avenue orientation would clearly be the best compromise. This is diagrammatically illustrated in Figure 4.

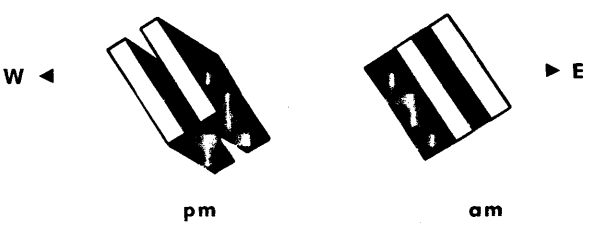

Figure 4. *Diagramatic representation of Great Bowerbird bower (white parallel bars) with a compass orientation of NNW–SSE to show approximate position of shadows (solid black) cast by morning sun at c. 0800–0900 hr (right) and afternoon sun at c. 1500–1600 hr (left) during the peak courtship period of July–November (see text).*

Males appear to display mostly during the morning (Sedgwick 1946; Warham 1957, 1962 and pers. obs.). Veselovsky (1979) watched activity of a male at a bower near Darwin for 12 hours for each of 14 days and found that the male displayed for approximately 50 mins during the morning

between 0845–1100 hrs, and for only half that time during afternoons, between 1700–1830 hrs. Thus by aligning their avenue to the east of due S and west of due N males ensure that the light of mid morning and, to a lesser extent, mid afternoon, remains as close as is possible to right angles to their bower axis (Fig. 4). Sunlight will then provide, on average, the best possible morning illumination of decorated display platforms, red decorations and the displaying male whilst placing the avenue interior, from which females usually view displays, in the strongest possible shadow.

To avoid the male having to look into the sun (*cf* Marshall 1954) during the mid morning and mid afternoon of mid-summer, an avenue alignment of N–S is needed, but (it is noteworthy that) given that the sun at the time of most courtship and mating travels the sky to the north of the E–W axis, an avenue orientation of due N–S would be disadvantageous because once the sun has gained limited altitude (i.e. *c.* 0700–1000 and 1500–1700 hrs) it might impinge upon the eye of the displaying or watching bird(s).

In view of the above it could be concluded that individual males displaying more often in the afternoon might be expected to construct a bower with the main display platform to the NW, but no data exist to test this. Warham (1962) made the observation, however, that males (number unrecorded) he observed normally displayed at the northerly end of their bowers 'where the larger collections of bone and other objects were placed'. It might also be predicted that a male displaying during the morning on a SSE display platform would be more likely to stand to the S side of the platform and a male doing so on a NNW platform would be more likely to stand to the N side of the platform in order to avoid placing his crested head in his own shadow and to thus best illuminate his lilac crest as he presents it to the female. This also remains to be tested.

The above facts do suggest that a generally N–S Great Bowerbird avenue orientation results in the best illumination of both display platforms and red decorations (to the E of the bower) and that, in Townsville bowers at least, the modification of this to the NNW-SSE axis maximizes optimal illumination during the courtship season (Figs 3 and 4).

Other bowerbirds: While the avenue bowers of the Satin and Great Bowerbirds are predominantly orientated to or close to a N–S axis, that of the Regent is less so, that of the Fawn-breasted is orientated E–W and that of the Spotted is possibly predominantly so (Jackson 1912; Robinson 1936; Chaffer 1945; Gaukrodger in Chaffer 1945; Marshall 1954; Warham 1962; Peckover 1970; Lenz 1993; Borgia 1995). The E–W avenue orientation of Spotted Bowerbirds' bowers is noteworthy as courting males atypically approach the bower (within which the female stands) toward the length of the outside of the northern wall, perpendicular to the avenue alignment (Borgia 1995). Thus, this diametrically opposed E–W avenue orientation and male display approach lends support to the conclusion that bower avenue orientation relates to optimal illumination of elements of bird/decoration display. Further studies of Spotted Bowerbird bowers and displays are required, however.

No typical bower orientation has been found for the Yellow-breasted Bowerbird's structure (Gilliard 1969; Frith and Frith 1989) and given its box-like form further study is most desirable. Most species of avenue bower-building bowerbirds that decorate an extensive area at both ends of the avenue more closely orientate their bowers to the N–S axis, which enhances illumination of their decorations and display plumage/postures (viewed by females from within the deeply shaded avenue). Lenz (1993) found that 44 Regent Bowerbird bower avenues on the Sarabah Range, SE Queensland had a mean deviation of 37.6° ±23.2° from due N–S and 12 Satin Bowerbird bowers a mean deviation of 14.6°±14.8°, those of Regents thus being significantly less close to N–S than those of the Satin Bowerbird. Lenz (1993) suggested that a N–S orientation may be less important to Regents because their bower sites, beneath the rainforest canopy and directly underneath vine tangles, dictate that diffused light comes mostly from above and not the sides. Moreover, he also found that Regent Bowerbirds place their bower decorations within the bower avenue and not spread predominantly about one end as in other avenue builders.

Quantitatively significant comparative studies of bower avenue and display platform orientation and of where, when and how males display to females relative to the position of the sun, their bower walls, decorations and that of the courted

female are required for all avenue-building bowerbird species before a comprehensive understanding of bower orientation can be gained. Such studies will need to consider variables such as where courtship display occurs relative to better-decorated bower areas and at what time of season and day. What influence(s) does bower shading by vegetation have on light, relative humidity, predators/predation and other factors? Is bower orientation in any way influenced by prevailing wind and what influence, if any, might potential fire have on bower site and orientation choice? These questions and possibilities require investigation. The abundance of resident bower-attending male Great Bowerbirds in and about tropical Australian centres of human population, such as Townsville and Darwin, make study populations comparatively easy to access.

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TERRITORIAL AND BREEDING BEHAVIOUR OF THE RUFOUS TREECREEPER (*Climacteris rufa*) IN THE STIRLING RANGES, WESTERN AUSTRALIA

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A population of colour-banded Rufous Treecreepers *Climacteris rufa* was studied in wandoo woodland in the Stirling Range National Park, 89 kilometres north of Albany, Western Australia, from June 1990 to January 1994. Five territories were studied and consisted of at least one adult female, one, two or three adult males and one to two juvenile birds. Breeding commenced in August and finished in February. Females layed up to two eggs per clutch and were capable of three broods per breeding season. Juveniles assisted in feeding young of the next brood. Only two of the juveniles banded in 93/94 stayed in the study area. Tree hollows only were used for nesting, while hollows in logs and trees were important sheltering areas for fledglings.

INTRODUCTION

Long-term studies of the White-throated Treecreeper *Climacteris leucophaea,* Red-browed Treecreeper *Climacteris erythrops* and Brown Treecreeper *Climacteris picumnus* have been undertaken by Noske (1980, 1984, 1985, 1991). However, no studies have been undertaken on the Rufous Treecreeper.