Courts and courtship behaviour of Archbold's Bowerbird Archboldia papuensis in Papua New Guinea

CLIFFORD B. FRITH¹, GERALD BORGIA² & DAWN W. FRITH¹

¹ "Prionodura", PO Box 581, Malanda, Queensland, Australia, 4885

² Department of Zoology, University of Maryland at College Park, Maryland 20742-4415, USA

Twelve bowers of Archbold's Bowerbird Archboldia papuensis in the Tari Gap, Southern Highlands, Papua New Guinea, are described. Incomplete courtship displays at four bowers were observed directly and videotaped, and 13 courtship displays culminating in copulation at five bowers were videotaped automatically. Bowers and male advertisement and courtship vocalizations and visual displays are described. Vocalizations included the mimicry of numerous sympatric bird species, calls like those of other bowerbird genera found elsewhere and inanimate sounds of the habitat. Courtships involved two phases. In the first, the male repeatedly chased the female while moving low, close to the surface of the display court. In the second phase, the male prostrated himself below the female and the yellow crest of adult males was presented to females as the male shook and repeatedly raised and lowered his head. Contrary to a previous report, the courtship display of the male Archbold's Bowerbird was assertive and the low position of the male appeared to function in threat reduction.

Archbold's Bowerbird Archboldia papuensis was the last bowerbird species to be discovered (Rand 1940). The two subspecies are patchily distributed on the central ranges of the island of New Guinea, Archboldia papuensis papuensis in Irian Jaya and Archboldia papuensis sanfordi in Papua New Guinea (Frith et al. 1995). Monotypic Archboldia occupies coniferous and mixed beech forest at altitudes of 1800–2900 m a.s.l. (Beehler et al. 1986, Coates 1990). At 37 cm in length, it is the second largest bowerbird. Both sexes are black with a small, yellow-brown wing patch, and adult males are adorned with a crest of elongate bright yellow feathers streaked with black.

Archbold's Bowerbird has been considered rare, and little is known about its behaviour, save for some descriptions of courts and a single observation of an adult male display (Gilliard 1959, Collar 1986). Archbold's Bowerbird is the only "mat" builder; all other polygynous species build a stick and/or grass "maypole" (Prionodura, Amblyornis spp.) or "avenue" (Ptilonorhynchus, Chlamydera, Sericulus spp.) bower structure except the Tooth-billed Bowerbird Scenopoeetes dentirostris, which clears a forest floor court that encompasses a display tree (Borgia 1986, Frith & Frith 1993a, 1994a). Males accumulate a mat of fern fronds laid upon several square metres of forest floor beneath a number of horizontal and/or sloping branches and decorated with snail shells, beetle elytra, fruits, fungus, tree resin (Gilliard 1969, Peckover & Filewood 1976), feathers of the King of Saxony Bird of Paradise Pteridophora alberti (Frith & Frith 1990) and other objects. The branches directly above the mat (=decorated branches) are conspicuously draped with myriad stems of epiphytic orchids (Gilliard 1969, Frith & Frith 1991, 1994b).

2

In July 1956, Gilliard (1959) watched an adult male display to a female-plumaged conspecific perched upon the decorated branches. He described the male as appearing "submissive and begging in the extreme" as it "crawled like a wounded animal, body pressed to the ferns, wing half open, their under surfaces against the ferns". This single observation of what appears a unique and intriguing male court-ship display in bowerbirds has interested ornithologists ever since (Gilliard 1963, 1969, Peckover & Filewood 1976, Schodde 1976, Collar 1986, Coates 1990, Frith & Frith 1991). Courtship displays by males of other polygynous bowerbird species are, for the most part, typically aggressive (Borgia 1986, 1995, in press a,b, Frith & Frith 1993a).

Female Archbold's Bowerbirds nest build, incubate and raise their single nestling alone (Frith & Frith 1988, 1994b). As some other court-attending bowerbird species are known to breed polygynously, polygyny is assumed for Archbold's Bowerbird. For detailed descriptions and illustrations of Archbold's Bowerbird and its bowers, nests, eggs and general biology see Gilliard (1969), Cooper and Forshaw (1977), Coates (1990) and Frith and Frith (1988, 1991, 1994b).

STUDY AREA AND METHODS

This paper summarizes observations by two groups of researchers in different years at the same study site. The site is located in montane cloud forest at 2460–2800 m a.s.l. in the Tari Gap (5°57′N, 143°10′E), Papua New Guinea. C.B.F. and D.W.F. studied birds at this site from 8 September to 29 October 1986 and 14 October to 5 December 1987. A group organized by G.B. intensively studied courts and their owners at the same site from 20 October to 10 December 1992.

C.B.F. and D.W.F. were responsible for the initial discovery of 24 courts within an area of approximately 1000 ha (see Frith & Frith 1994b). The longest and widest axes of 12 bower mats were measured, six small ones and six large ones. Six males were mist-netted near bowers and given unique combinations of two colour rings and an Australian Bird and Bat Banding Scheme metal numbered ring (Frith & Frith 1993b) at least 1 week prior to observations being made of them from hides. Observations were made from cryptic canvas hides placed approximately 5 m from bowers that were erected at least a week prior to observations being made. Over 30 h of direct observation of male activity at four large well-established bowers were made, of which 1 h 45 min were of courtship display (male displaying to female-plumaged, presumed female, bird). Over 10 min of directly observed male activity was also videotaped, of which 7 min 45 s was of courtship display at two bowers. Also available was a video copy of 15 min 26 s of 16-mm film of male behaviour (of which 4 min 56 s was of courtship display) at a third bower during November 1991 (made by Robert Brown for Television New Zealand).

In 1992, G.B. and his group relocated display courts using maps provided by C.B.F. and D.W.F. and with the help of Mediu Medea. They erected video cameras controlled by infrared sensors that recorded male behaviour on 11 courts (see Borgia in press a). This contribution contains information from 22 min of videotape of 13 courtships that led to copulations. Videotapes were viewed repeatedly in order to analyse display vocalizations, postures and movements. Recordings of 8.5 h of male vocalizations, almost exclusively advertisement calls, made from hides at one bower by Andrée Griffin on 11, 12 and 21 October 1986 were analysed.

RESULTS

Courts

The six smaller mats, with few orchids on the decorated branches, measured between 1.2 m \times 1.0 m and 2.6 m \times 2.2 m (mean = 1.8 m \times 1.03 m) and totally lacked snail shells, beetle elytra and bird of paradise plumes. The six larger mats were well decorated with numerous snail shells, beetle elytra and some King of Saxony Bird of Paradise plumes, fruits, fungus, charcoal and tree resin and had myriad orchid stems on the decorated perches (Fig. 1). These mats measured between 3.2 m \times 2.3 m and 5.8 m \times 5.0 m (mean = 4.0 m \times 3.4 m). Two courts, located 1–2 km from the nearest road, had broken pieces of brown beerbottle glass on their mats. The larger courts had decorated branches heavily draped with orchid stems to a height of up

to 3.5 m above the fern mat. Decorated branches varied greatly in number, size, height above the mat and tree/vine type. All decorated branches were draped exclusively with orchid stems and were decorated with varying quantities of the kind of objects noted by Gilliard (1959, 1969).

The largest mat covered 29 m² of forest floor area. As this court had orchid-draped branches up to 2.6 m above the mat, it occupied almost 75 m³, although decorated perches were not draped above all extremities of the mat. Some of the uppermost orchid stems on each decorated branch were in flower, most flowers were white or off-white but some were dull red or purple. The longer, thick, ribbonlike fronds used to form the mat were up to 1 m long. While some upper mat fronds were fresh and green, the majority had become brownish and gave the overall mat a darker colour and tone which was in marked contrast to the surrounding lush green, living forest floor plants. Males also brought to the mat longer and larger fern fronds that were already brown. They often picked up an orchid stem, fallen from decorated branches onto the mat, and replaced it on branches. Beetle elytra decorations (Fig. 2) were from members of the family Passalidae and almost certainly of the subfamily Macrolininae, common log-frequenting beetles, the remains of which could be found in leaf litter near infested logs (G. Monteith in litt.).

Orchid species found draped on bower perches that were identifiable included Bulbophyllum sesaile, Bulbophyllum piudensis, Glossorhyncha amblicaulis, Glossorhyncha aff. duteobrunnea, Glossorhyncha caespitosa, Glossorhyncha keysseri, Glossorhyncha tortuosa, Giulianettia diffusa and a Grastidium sp.

Advertisement vocalizations

A male Archbold's Bowerbird advertised the location of his bower by loud vocalizations, usually from perches immediately above and about its bower and to a radius of c. 12–15 m from it. Court advertisement calls were extremely diverse and included mimicry of avian and inanimate sounds of the habitat. Some calls were clearly whistled whilst others were harsh, grating or churring notes. A characteristic note of the species, also given away from bowers, was a harsh loud waagh often immediately repeated once (Frith & Frith 1992).

The calls of the following sympatric bird species (Frith & Frith 1992, 1993b) were noted to be mimicked extremely well: New Guinea Harpy-eagle Harpyopsis novaeguineae, lorikeets Neopsitticus spp., Lesser Melampitta Melampitta lugubris, scrub-wrens Sericornis spp., Rufous-naped Whistler Pachycephala rufinucha, Black-throated Honeyeater Lichenostomus subfrenatus, Belford's Melidectes Melidectes belfordi, Crested Bird of Paradise Cnemophilus macgregorii, Brown Sicklebill Epimachus meyeri and King of Saxony Bird of Paradise. The powerful 'machine gun' call of the adult male Brown Sicklebill was reproduced perfectly, but the King of Saxony Bird of Paradise call mimicked was only that of immature males, which is quite different from the unique and complex call of adults. Doubtless the calls of many other



Figure 1. Archbold's Bowerbird bower 16, Tari Gap, Papua New Guinea. Wide view of entire bower. Note decorated branches, with "drapes" of epiphytic orchid stems hanging from them. Small round objects on ground in central foreground are snail shells c. 25–30 mm diameter.

bird species, which we were inadequately familiar with, were also mimicked. A sound commonly mimicked was that of bird wings being fluttered vigorously. On several occasions a male copied the call of another species immediately after it was given. Mimicry of characteristic inanimate habitat sounds included those of dead Pandanus Palm Pandanus cf. P. tectorius fronds rattling against each other and of a falling frond(s) hitting the ground.

Typical nonmimicry calls were a strange-sounding single, hollow, large, flutelike whooo note, a sharp, loud, clear whistled note, a dull hollow whukk, a loud and harsh arrgh and a drawn-out (c. 1 s), high-pitched, slightly rising and pleading, pathetic weeeeek note, which was often ended with a sharp click. A cicadalike call was also mimicked.

Males also made calls similar to other, geographically separated, bowerbird species, such as the odd mechanical-like buzzing interspersed with sharp clicking notes given by adult male Satin Bowerbirds *Ptilonorhynchus violaceus* in courtship display, the rattle "bower call" and a harsh "wolf whistle" call of the Golden Bowerbird *Prionodura newtoniana* (Frith 1989). The Satin and Golden Bowerbirds are confined to Australia. Churring, chugging and scolding notes, extremely similar to those given by the avenue bower-building *Chla-*

mydera species, and swishing, clicking and fluttering sounds, similar to those produced by male gardener bowerbirds Amblyornis spp., were also produced. Male vocalizations became more frequent and intense, and then softer, shortly prior to the discernible presence of a female-plumaged (presumed female) bird adjacent to or on decorated branches.

Courtship and associated vocalizations

By the time a female was on a decorated branch above the mat, the male had fluttered or dropped down onto the mat to start his display. When standing on the mat alone, the male appeared a large and stocky bird for a passerine (Fig. 3), in marked contrast to its appearance when displaying (Fig. 4). The courting male adopted a characteristic posture on the thick springy mat of fern fronds to face and approach the female. He lowered his elongated and sleeked body to prostrate himself on horizontal tarsi and pressed himself into the mat. The wings were held in close to the normal position, with the primary tips only slightly lowered to expose the rump. The crest was fanned, though not extensively, whilst the forecrown crest feathering was conspicuously erected and widely fanned. In this Prostrate Posture (Fig. 4) the male



Figure 1.—Archbold's Bowerbird bower 16, Tari Gap, Papus New Guinea. Wide view of entire bower. Note decorated branches, with "drapes" of epiphytic orchid stems hanging from them. Small round objects on ground in central foreground are small shells < 25–30 mm diameter.

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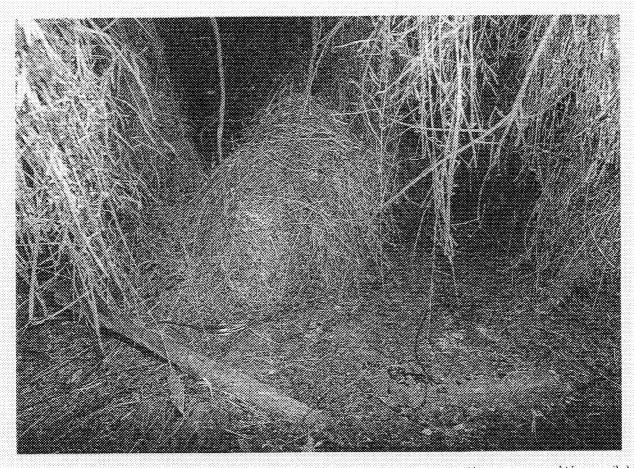


Figure 2. Archbold's Bowerfund bower 16, Tan Gap, Papua New Guinea. Detail of bower mat area. Note numerous orchid stems piled onto a central bower porch and discrete accumulation of shiny black beetle elytra placed on an exposed fallen branch on the ground.

uttered a continuous murmuring call, reminiscent of a quickly rotating, squeeky, small wheel. The relatively quiet sounds were made by rapidly vibrating the lower mandible up and down, which partly exposed the pale yellowish mouth colour. This sound was frequently interspersed with hissing.

chugging, spluttering and notes like the sound of dripping water and lip-smacking. Males mimicked the calls of other bird species also, as well as the sounds of whirring bird wings, fluttering vegetation and, once, the sound of a bush-knife cutting vegetation. The male occasionally shook its



Figure 3. Adult male Archbold's Bowerbird on hower mat in Normal Standing Posture.



Figure 4. Courting adult male Archhold's Bowerbird on bower mat in Prostrate Posture.



Figure 5. Courting adult male Archbold's Bowerbird on bower mat in initial leap forward of the Courtship Chase.

head sharply and rapidly from side-to-side through a miniscule arc, causing the yellow and black crest to vibrate into a blur, sometimes doing this as the bill was pushed down into the mat of fern fronds as if "nuzzling" it. This posture and associated behaviour continued, with the male occasionally raising his head to peer at the female, before he moved toward her.

The horizontally prostrate male shuffled over the mat of ferns toward the female using rapidly repeated, miniscule hops involving almost no vertically upward movement. The male's legs remained fully obscured by the body pressed into the fern mat (Fig. 4). His movements caused ferns in front of and beside his breast to vibrate. He sometimes turned to move away from the female, having reached a point directly beneath her. Throughout this behaviour the wings remained close to the normal position, as above. When moving from one part of the mat to another between prostrate displays, the male did so by light, bouncing hops with his tail raised to c. 45° and conspicuously swung through an arc to one side during each hop (Fig. 6a) before "belly-flopping" to adopt the Prostrate Posture (Fig. 4) again. Occasionally a male briefly adopted the Swinging Tail Posture (Fig. 6a) on a decorated branch.

When a female flew down from a decorated branch to stand on the mat, the displaying male's initial response was always (n=27, at three bowers) to rush at her with loud calls and chase her to or just beyond the edge of the mat. This Courtship Chase was always performed by the male rushing rapidly forward from his Prostrate Posture whilst remaining sleeked, elongated and close to the ground. The male's tarsi only momentarily extended downward as he vigorously "attacked" the female by rushing at her with, initially, fully but not expansively open and flapping wings (Fig. 5), instantly followed by stiffly fluttering, half-opened wings (infrequently one wing). The wings appeared as a blur and produced a whirring sound as the male continued to rush forward and simultaneously emitted vocal mimicry of vigorously fluttering bird wings.

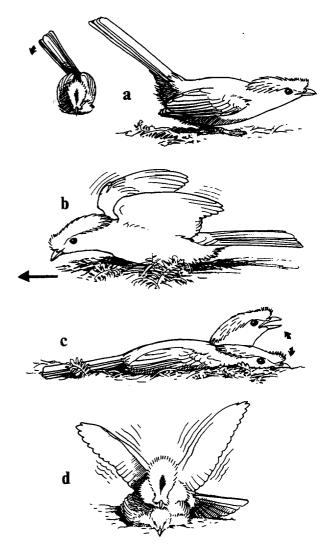


Figure 6. Some display postures performed by courting and mating male Archbold's Bowerbird at Tari Gap, Papua New Guinea. (a) The posture adopted during the Shuffle Side-hop or during sideways hops about the bower mat in the presence of a female. The bill is directed at the female, the raised tail swung up and widely in the direction of the hop (left) and the body kept rigid, sleeked and low to the mat until the Prostrate Posture is adopted or resumed (see Fig. 4); (b) The Courtship Chase posture. After the initial leap out of the Prostrate Posture (Fig. 5), the sleeked male continues to rush at the female with lowered bill and half-opened wings fluttering rapidly above the back from c. 45° (as illustrated) downward to about parallel with the ground; (c) The Head-lift & Shake precopulation display, performed as a female approaches and stands immediately beside or in front of the male (see text); (d) A copulating pair. Note that the male's forecrest feathers project conspicuously forward and either side of the bill (see text).

A Courtship Chase could take the male across the entire mat and back again if the female doubled back. The half-opened wings were usually fluttered stiffly and rapidly above the back during the chase, and the bill was held rigidly downward at c. 45° to present the forecrest to the female.



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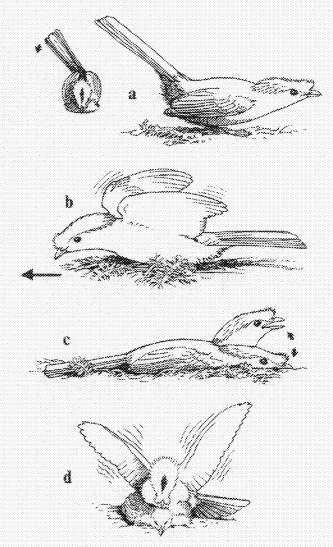


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A Courtship Chase could take the male across the entire mat and back again if the female doubled back. The halfopened wings were usually fluttered stiffly and rapidly above the back during the chase, and the hill was held rigidly downward at c. 45° to present the forecrest to the female. The legs remained, for the most part, obscured by the bird's body and the soft fern substrate, and the male's rapid forward motion and the stiffly fluttering wings gave the appearance (Fig. 6b) of a clockwork toy in motion. One male performed six such chases in 23 s, then spent 3 min 8 s prostrating himself and calling to entice the female back to the mat from the decorated branches, only to chase her eight more times in 38 s before she flew off altogether.

Another male performed the Courtship Chase across his mat several times in pursuit of a female-plumaged bird flying across the mat area a metre or so above it. Immediately following a chase, the male may rapidly flutter or vibrate his stiffly half-opened wings (but not like the slower "loose" fluttering of a begging young passerine) before reverting to the Prostrate Posture. It would appear that, subsequent to each consecutive chase, the prostrate and softly calling male permitted the nervous but apparently fascinated female to approach him more closely before his next chase. On two occasions the male merely shuffled rapidly toward the female in the Prostrate Posture with wings at his side (Fig. 4). Between Courtship Chases, the female perched above or stood at the opposite side of the mat and the male often performed a rapid and stiffly rigid series of (usually three) minute Shuffle Side-hops to one side, whilst conspicuously swinging the tail through a wide arc in the direction of the hops (Fig. 6a).

If a female persisted in remaining on decorated branches, the sleeked and displaying male usually hopped to the mat edge, his raised tail swinging through a wide arc to one side with each hop (Fig. 6a), and continued the prostrate display. Any head movements at this time to locate or follow the female were conspicuously jerky, thus enhancing the yellow crest in the dull light on the bower mat. Whilst prostrating himself to the perched female, the male occasionally raised his head and neck to perform a Shuffle Side-hop of two or three movements to one side whilst raising and swinging the tail through an arc as was typically performed at the end of a Courtship Chase. This apparently enticed the female to the central mat on most occasions, immediately following which she was displaced by a Courtship Chase.

Persistent females eventually were not pursued with the Courtship Chase and, with some hesitation, approached the prostrate male to stand immediately or obliquely in front of (facing) him with the head obliquely beside, or parallel to, his. The male's vocalizations then became softer and were almost exclusively of the murmuring call reminiscent of a squeeky small wheel, with rapidly vibrated lower mandible. Should the prostrate male move his legs, his tail was sharply raised and lowered. Once the female was immediately in front of the prostrate male, he stopped moving his legs and tail and performed a highly stereotyped Head-lift & Shake display. This involved vibrating the head rapidly to either side through a very small arc as the yellow forecrest feathers were conspicuously erected and projected forward over the base of the upper mandible and then repeatedly lifting the head and bill from the bower mat to c. 25-35 mm above its surface. This head vibration caused the yellow crest to appear as a blur. This Head-lift & Shake (Fig. 6c) was repeated at about 1-s intervals, but, if the female remained in front of the displaying male, he progressively increased the tempo of the Head-lift & Shake. At this point the female usually "billed" or pecked at the male's crest feathers once or twice.

A female that remained beside a male giving the Headlift & Shake display and billing his vibrating crest adopted a plump body posture with contour feathers somewhat raised, the breast pushed forward and downward toward the bower mat and the wings held loosely but only slightly drooped at her sides. On two occasions at this point in the display, a male performed a Head-lift & Shake to "nuzzle" his vibrating bill into the female's flank feathers just below her wing primaries.

Suddenly, the last of the increasingly rapid head-lifts of the male was used to rapidly raise his entire body to hop onto the female's back to copulate, accompanied by rapidly and loudly fluttering open wings. Of the nine complete copulations that were timed, the average (±s.d.) duration was 5.8 ± 1.4 s. During copulation, the forepart of the female was vigorously driven forward and downward, causing her breast and bill to be pushed into the bower mat to retain her balance. The forecrest of the male was conspicuously bifurcated and projected well forward and appeared as a yellow tuft either side of and above the upper mandible base (Fig. 6d). His tail was initially fanned and swung from side to side as he sought to achieve copulation. The male held nothing in his bill during the display and mating but used his bill to "bill" or peck at the female's nape just prior to dismounting, possibly during ejaculation.

After copulation, the male hopped off the female's back, again adopted the Prostrate Posture immediately in front of her and performed Head-lift & Shake displays with soft murmuring vocalizations. At the end of 12 of the 13 copulations seen, the female immediately, vigorously and loudly fluttered her drooped and slightly opened wings at her sides for about 2 s, then hopped about the mat and/or decorated branches and repeated the wing-fluttering every few seconds, usually for at least 20–60 s, until she flew off or was chased off by the male with a Courtship Chase. In one case, the male pursued the mated female with a Courtship Chase five times before she left the mat and flew off.

DISCUSSION

Courts

Because access to its habitat was difficult to attain, the Archbold's Bowerbird's mat bower of "dried fern fronds, sticks, and grasses" (Mayr & Gilliard 1954, Gilliard 1959) and associated behaviour remained little known, despite attempts to investigate them. Gilliard (1969) described five bowers at Mt. Hagen. Their mats varied from 91 cm to 244 cm in diameter, and decorated branches were draped with "strands of living and dead climbing bamboo" and some were decorated with snail shells, fruits, seeds or charcoal.

None of the Tari Gap bowers involved sticks or grasses as

was the case on Mt. Hagen. The largest bower mat at Tari Gap was twice the size of the largest one Gillard (1969) examined. Tari Gap bower mats were variable in shape, some being oval or circular and others roughly rectangular, square or triangular. Bower decorations noted by Gilliard are typical of the species in Papua New Guinea, but the additional King of Saxony Bird of Paradise plumes may be highly significant as they were centrally located and on only large mats (Frith & Frith 1990). Glass on two bowers indicated that man-made objects were utilized.

Gilliard (1969) described decorated branches at Mt. Hagen as draped exclusively with strands of scrambling bamboo. Tari Gap bowers were draped only with epiphytic orchid stems, despite the availability of bamboo. It is possible that geographical variation in bower decoration exists in this species, as in Ambluornis spp. (Diamond 1986, 1987), Scenopoeetes and Ptilonorhynchus (Frith & Frith 1994a and unpubl. data). Gilliard may have misidentified the plant material, however, as his photographs (Gilliard 1959, 1969) suggest orchids. While Cooper (in Cooper & Forshaw 1977) did find bamboo on one Mt. Hagen bower, orchids were commonly used there (Coates 1990). Decorated branches and mat decoration plants did not consist exclusively of dead ones (cf. Schodde 1976, Coates 1990). Much vegetation was brought to the bower live and relatively fresh; some orchid stems were in flower. This vegetation dried and turned brown to give the decorated branch 'drapes' a yellow to pale brown appearance and the mat a contrasting brown colour.

Court dispersion appears to be relatively even and certainly not clumped into leks as suggested by Diamond (1982). Gilliard (1959) correctly considered males to be solitary, each maintaining a bower, as demonstrated by observations of two marked individuals over 2 and 4 years of this study.

Courtship displays

Contrary to Gilliard's assertion (1959, 1969) that "the female does not land on the ferns", females in our study frequently visited the bower mat and were courted there. We did not observe display in the absence of a conspecific. Although males were below the female during the "Grovel" display (cf. Gilliard 1959), it appeared that this was to reduce threat. There was no evidence of begging or submissiveness by males. Males did not hold their wings "half open" and away from the body with "their under surfaces against the ferns" or fan the forked tail during the "Grovel" display (contra Gilliard 1959). The crest was spread laterally, the bill was not opened widely and at no time did a courting or mating male hold a fern or anything else in the bill.

The low position of the male in the Prostrate and Headlift & Shake displays probably enhanced the likelihood that a female would land on the mat and approach the male. Females are potentially subject to various forms of threat from the male. In other bowerbird species, courtship commonly involved aggressive movements by the male combined with hiding and other threat reduction gestures that encouraged the female onto the court and appeared to reduce the likelihood that a female would leave (Gilliard 1969, Frith & Frith 1989, 1993a, Borgia & Mueller 1992, Lenz 1994, Borgia 1995, in press a,b). Females may benefit from threat reduction arising from the low position of displaying males because females are potential victims of attack by the courting male (Borgia & Mueller 1992, Borgia in press b) or because males are capable of forcing copulations before the female has decided to mate (Borgia 1995, in press a). In Archbold's Bowerbird the low position of males would enhance the ability of females to escape.

Charging the female by the courting male was performed by several bowerbird species (Borgia & Mueller 1992, Lenz 1994, Borgia in press b, C. Frith & D. Frith, pers. obs.). Males might charge females as part of a display of vigour that could enhance female willingness to mate, to permit males to assess the sex and readiness to mate of female-plumaged visitors or as a means of approaching females to engage in the later stages of courtship (Borgia 1995, in press a,b). Subsequent less aggressive behaviour, the Prostrate and Headlift & Shake displays in Archbold's Bowerbird, allows the female to approach the male for the last stages of assessment before she mates while still retaining the opportunity to escape if she detects undesirable male traits. The close attention of females to the yellow crest of adult males at this point could be an example of inspection of bright plumage to assess the male's value as a sire (e.g. Hamilton & Zuk 1982).

It is unlikely that the low position taken by the male during courtship was begging or infantile. First, males assumed this posture while actively chasing females. Second, the male failed to flutter his wings or show other behaviour common to begging young birds, such as gaping widely while vibrating the head. Gilliard (1959) alluded to fluttering wings like a young bird only in his summary, not in his display description. Our results do not support the regular occurrence of infantile-like wing fluttering.

Gilliard (1959) interpreted the female behaviour as "extremely aggressive" because a presumed female perched and flew over a displaying male with loudly "thrashing" wings. He discussed the "reversal of the usual roles of courtship between males and females" and the female as "always occupying dominating positions in the bower" (perched upon decorated branches). We interpret perching by a visiting bird (regardless of sex) as simply adopting a safe position from which to view the male's displays. All birds we considered to be female (mated by males) watched the display passively from a decorated branch and dropped onto the mat repeatedly to be chased immediately by the male. One bird that flew from perch to perch followed by the displaying male below did not drop onto the mat. This bird, and perhaps the one seen by Gilliard (1959, 1969), was likely a subadult male.

The crest of the adult male Archbold's Bowerbird is significant in courtship (contra Gilliard 1969), and the pecking of it by females prior to copulation emphasized this. Other than this behaviour, the females we observed did not take an active role in courtship. Contrary to Gilliard's (1959, 1969) interpretation, male courtship is aggressive in nature

and, whilst predominantly different, is not unique but includes some calls, postures and movements like those of other bowerbirds. To what extent these result from convergent evolution or a common ancestry remains unclear.

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