Molecular information on bowerbird phylogeny and the evolution of exaggerated male characteristics

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Abstract

Mitochondrial DNA cytochrome b sequences of 849 base pairs are reported from eight species of Australian bowerbirds. These sequences are used with three from the literature (Edwards et al., 1991) to investigate bowerbird phylogeny using maximum parsimony and maximum likelihood methods. With respect to the three outgroup species, bowerbirds are shown to be monophyletic with high confidence using the bootstrap. The monogamous *Ailuroedus crassirostris* (which does not clear display courts) is indicated as the sister group to other bowerbirds. The maypole-builders (*Amblyornis macgregoriae* and *Prionodura newtoniana*) are significantly supported as a clade indicating a common origin for maypole type bowers, despite large differences in the design of these species' bowers. The avenue-builders (*Sericulus chrysocephalus*, *Ptilonorhynchus violaceus*, *Chlamydera maculata* and *C. nuchalis*) are also monophyletic. The pattern of divergence in avenue builders accords with the predictions of Gilliard's (1956, 1963) "transferral effect". The transference hypothesis is not supported by evidence suggesting that the dull plumage of *Scenopoeetes* is an ancestral condition in bowerbirds. The use of sticks to build bowers could have had a single evolutionary origin and been secondarily lost in *Scenopoeetes*, or evolved independently in the avenue and maypole builders.

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Introduction

Since Darwin (1871) discussed the evolution of the elaborated tails of male peafowl, biologists have tried to understand the evolution of extreme, sex-limited male display characters. These extreme male display characters have evolved at least 9 times among birds (Gilliard, 1963) and similar patterns are shown in other taxa (e.g. Eberhard, 1987). Males with extreme display traits typically provide nothing to females or offspring except sperm, yet females often show preference for a limited set of males (e.g. Scott, 1942; Buechner and Roth, 1974; Robet, 1966; Borgia, 1985a; Hoglund and Lundburg, 1987 and references in Bradbury and Gibson, 1983). Theories of sexual selection have focused on female choice as a force shaping the evolution of these traits (e.g. Fisher, 1930; Zahavi, 1975; Trivers, 1972; Emlen and Oring, 1977; Hamilton and Zuk, 1982; Andersson, 1982; Lande, 1981; Kirkpatrick, 1985, 1986).

Historical information about display trait evolution can be critical to understanding sexual selection. The phylogenetic analysis of such traits was first attempted by Darwin (1871) when he traced the evolution of eye spots on feathers in pheasants related to peafowl. In modern terms phylogenetic information can be used to determine if mechanisms of sexual selection dictate particular evolutionary patterns. Gilliard (1956, 1963) noted that there appeared to be a trade off between bower and plumage characters in bowerbirds. More recently, the widely-discussed runaway model (e.g. Lande, 1981) proposes very rapid evolution of highly elaborated male display traits and suggests a highly variable degree of elaboration of male traits among closely related species. The degree to which these variable patterns exist has never been tested.

The recent development of methods for direct sequencing of mitochondrial DNA (mtDNA) has opened new possibilities for studies of systematic relationships. The use of DNA sequences for estimating phylogenetic relationships is of particular value because it allows relationships to be investigated independently of gross phenotypic characters, and because it affords numerous relatively independent characters for analysis. This independence is critical when attempting to evaluate the role of common evolutionary history in determining phenotypic similarity.

Here we apply these methods to study relationship among the bowerbirds (Family: Ptilonorhynchidae) in an effort to evaluate the role of sexual selection in shaping male display traits. Birds in this family are unique in that males have evolved to build display courts with associated stick structures called bowers (Marshall, 1954b; Gilliard, 1969) and bowers are decorated with colored objects. The display traits of bowerbirds (Tab. 1) are of special interest both because of their uniqueness relative to other species and because of the large variation among species in the types and degree of elaboration of display characters (Marshall, 1954a, b, c; Mayr and Jennings, 1952; Gilliard, 1969).

There are 15 species that build bowers or clear courts (Marshall, 1954b; Cooper and Forshaw, 1977). Most species fall into one of two major groups that build either "avenue" (8 species, 3 genera) or "maypole" (5 species, 2 genera) bowers. The remaining species (2 in 2 genera) are not obviously associated with either of these categories (Borgia, 1986). These species clear courts, but do not build bowers.

Table 1. Classification of bowerbird display traits[1]

Species	Bower type	Court clearing	Decoration	Showey plumage	Polygyny	Lek	Interactive calls	Crest	Study site
Green Catbird *Ailuroedus crassirostris*	No bower	no	no	no	no	no	no	no	no	Wallaby Creek, Urbenville, N.S.W., Australia

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Green Catbird *Ailuroedus crassirostris*	No bower	no	no	no	no	no	no	no	Wallaby Creek, Urbenville, N.S.W., Australia
Macgregor's Bowerbird *Amblyornis macgregoriae*	Maypole	yes	yes	yes	yes	no	no	yes	Snove, Central Province, P.N.G.
Spotted Bowerbird *Chlamydera maculata*	Avenue (modified)	yes	yes	no	yes	no	no	yes	Bullamon Plains, Thallon, Australia
Great Bowerbird *Chlamydera nuchalis*	Avenue	yes	yes	no	yes	no	no	yes	Curraghmore, Mt. Carbine, Qld, Australia
Golden Bowerbird *Prionodura newtoniana*	Maypole (two spires)	no	yes	yes	yes	no	no	no	Atherton, Qld., Australia
Satin Bowerbird *Ptilinorhynchus violaceus*	Avenue	yes	yes	yes	yes	no	no	no	Wallaby Creek, Urbenville, N.S.W., Australia
Toothbill Bowerbird *Scenopoeetes dentirostris*	No bower	yes	yes	no	yes	yes	yes	no	Atherton, Qld., Australia
Regent Bowerbird *Sericulus chrysocephalus*	Avenue	yes	yes	yes	yes	no	no	no	Wallaby Creek, Urbenville, N.S.W., Australia.

[1] From Marshall (1954).

Some bowerbird species show highly elaborated bowers and display courts and the cause of this elaboration is not known (Marshall, 1954b; Gilliard, 1969; Cooper and Forshaw, 1977; Borgia et al., 1985; Diamond, 1987). Even within categories there are large differences in the shape, size and decoration of bowers (Marshall, 1954b; Gilliard, 1969; Diamond, 1986), extent and color of plumage dimorphism, and acoustical displays (personal observation). Species vary in the extent to which they share common types of display and, as in the case of crests and bowers, it is not clear if similarities occur because of common origin or because of convergent evolution.

Gilliard (1956, 1963) hypothesized that male bowerbirds may have reduced the costs of display by the transfer of costly plumage display traits to bower decorations (Gilliard, 1969, p. 396). Various sexual selection models have focused on the costs of male display and some authors consider them as critical in allowing truthful advertising (Zahavi, 1975; Andersson, 1982; Kodrick-Brown and Brown, 1985). Thus indications of selection for reduced male cost of display would be relevant to evaluating these models. Gilliard's hypothesis is based on the observation of an inverse relation between male plumage brightness and the degree of bower elaboration (Gilliard, 1956). Phylogenetic information would be useful in testing his prediction that bright plumage represents the ancestral condition in bowerbirds.

Elsewhere, it has been suggested that runaway sexual selection can cause rapid and unexpected divergence in sexually selected traits (Lande, 1981; Arnold, 1983). Phylogenetic information on bowerbirds could help address this question by indicating the extent and speed with which novel display traits emerge within groups.

The form of bowers and other display traits has been important in the construction of the currently available phylogenies (see Marshall, 1954; Gilliard, 1963, 1969). Here we present our initial evidence on the phylogenetic relationships among 8 species of bowerbirds that represent 7 of 8 genera and which include all major bower types and mating systems in the Ptilonorhynchidae. Phylogenetic relationships inferred from mtDNA sequence data are then used to construe patterns of character trait evolution and the extent to which extreme elaborations of species traits are dependent on common evolutionary origin. DNA hybridization studies have provided limited information about bowerbird relationships (Sibley and Ahlquist, 1987; Sibley et al., 1987), but because representatives of only three genera were included general evolutionary relationships could not be deduced.

Materials and methods

Species

In total, eleven species were considered in the phylogenetic analyses. The sequence data for eight of these were obtained in our laboratories: Spotted Bowerbird, *Chlamydera maculata*; Great Bowerbird, *Chlamydera nuchalis*; Satin Bowerbird, *Ptilonorhynchus violaceus*; Regent Bowerbird, *Sericulus chrysocephalus*; Golden Bowerbird, *Prionodura newtoniana*; Tooth-billed Bowerbird, *Scenopoeetes*

dentirostris; Green Catbird, *paradiseus*. In addition the s Edwards et al. (1991): Mac tailed Sicklebill, *Epimachus* Together these species repre from New Guinea (*A. mac* paradise (*E. albertisii* and *P.*

Preparation of DNA

DNA was isolated from extracted following Crozier e extracted according to a moc was ground to a fine powde solution (100 mM Tris-HCl with SDS (10%, 50 μl) and p hours at 55° C. The prepa phenol:chloroform:isoamyl ethanol (2 volumes) and 5 (10 mM Tris-HCl, 0.1 mM

Polymerase chain reaction ar

Sequence was obtained fe cytochrome b (Fig. 1) were of Kocher et al. (1989) and

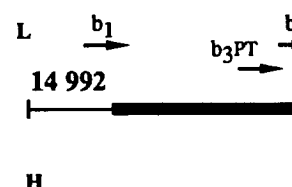**Fig. 1.** Primer orientation for the a delimits the region presented in thi

b₁.	L14990	5′-CCATCCAAC
b₂.	H15298	5′-AAACTGCAG
b₃PT.	L15218	5′-CGAGGGGTT
b₃.	L15272	5′-ATCCTCCTT
b₆.	L15567	5′-AAATCCCAT
b₇.	H15695	5′-AATAGGAA
b₁₀.	H15916	5′-ATGAAGGG

Letters L and H refer to light and at the 3′ end of the primer accordi 1990).

dentirostris; Green Catbird, *Ailuroedus crassirostris* and Paradise Riflebird, *Ptiloris paradiseus*. In addition the sequence data for three other species were taken from ▸Edwards et al. (1991): MacGregor's Bowerbird, *Amblyornis macgregoriae*; Buff-tailed Sicklebill, *Epimachus albertisii* and Australian Magpie, *Gymnorhina tibicen*. Together these species represent all genera of Australian bowerbirds, one genus from New Guinea (*A. macgregoriae*) and two putative outgroups; the birds of paradise (*E. albertisii* and *P. paradiseus*) and the corvids (*G. tibicen*).

Preparation of DNA

DNA was isolated from liver, heart, or muscle tissue. Crude mtDNA was extracted following Crozier et al. (1989) with minor modifications. Total DNA was extracted according to a modification of Hillis and Davis (1986). 0.1–0.3 g of tissue was ground to a fine powder in liquid nitrogen and added to 300 μl of digestion solution (100 mM Tris-HCl pH8, 1 mM EDTA, 100 mM NaCl). Cells were lysed with SDS (10%, 50 μl) and proteins degraded with Proteinase K (25 mg/ml) for 1.5 hours at 55° C. The preparation was extracted twice with equal volumes of phenol : chloroform : isoamyl alcohol (25 : 24 : 1). DNA was precipitated with 95% ethanol (2 volumes) and 5 M NaCl (0.1 volumes) and resuspended in 100 μl TE (10 mM Tris-HCl, 0.1 mM EDTA).

Polymerase chain reaction and direct sequencing

Sequence was obtained for a segment of the cytochrome b gene. Primers for cytochrome b (Fig. 1) were designed by slight modification of the primer sequences of Kocher et al. (1989) and Edwards et al. (1991).
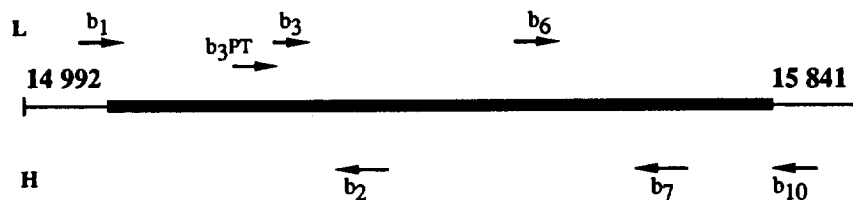

Fig. 1. Primer orientation for the amplification and sequencing of the cytochrome b gene. The thick line delimits the region presented in this paper. The primer sequences are:

b_1	L14990	5'-CCATCCAACATCTCAGCATGATGAA-3'
b_2	H15298	5'AAACTGCAGCCCCTCAGAATGATATTTGTCCTCA-3'
b_3PT	L15218	5'-CGAGGGTTCTATTACGGCTCATACCT-3'
b_3	L15272	5'-ATCCTCCTTCTAACCCTAATAGCAAC-3'
b_6	L15567	5'-AAATCCCATTCCACCCATACTAC-3'
b_7	H15695	5'-AATAGGAAGTATCATTCGGGTTTAATG-3'
b_{10}	H15916	5'-ATGAAGGGATGTTCTACTGGTTG-3'

Letters L and H refer to light and heavy strands respectively. Numbers refer to the position of the base at the 3' end of the primer according to the chicken mitochondrial sequence (Desjardins and Morais, 1990).

Samples were amplified with Taq polymerase (United States Biochemical Corporation) in an Inovonics™ thermal cycler using the following parameters: denaturing: 92° C, 1 min; annealing: 53° C, 1 min; extension: 72° C, 1 min (35 cycles). Double stranded amplification products were phenol extracted, precipitated with 95% ethanol (2.5 volumes) and 3 M sodium acetate (0.1 volumes) and resuspended in 40 µl TE. Single primer amplification (Kessing et al., 1989) was performed on double stranded products using the same cycling parameters (but using 40 cycles). Products were phenol/chloroform extracted and precipitated with 7 M ammonium acetate (0.33 volumes) and 95% ethanol (1.33 volumes). Single stranded DNA was resuspended in 16 µl TE buffer and subjected to direct sequencing according to Kessing et al. (1989).

Cloning and sequencing cloned products

Double stranded products amplified with cytb1 and cytb2 primers were cloned into M_{13} mp18. Briefly, M_{13} mp18 (2.75 mg) was digested with Sma1 (16 units) and a double blunt end ligation performed using between 1.5 and 6.5 units of DNA ligase, 0.5 mg of digested vector and approximately 0.25 mg of double stranded fragment. Cloned inserts were sequenced by the dideoxy chain terminating procedure of Sanger et al. (1979) using Sequenase® T7 DNA polymerase.

Tree building programs and analyses

Trees were generated using Apple Macintosh computers under maximum parsimony using Swofford's (1989) package PAUP or under maximum likelihood using program DNAML +3.31 in the PHYLIP package of programs (Felsenstein, 1990). Under maximum likelihood the values of the transition/transversion ratio, and the relative evolutionary rates for codon positions 1, 2, and 3 were optimised using trial trees and maximising the likelihood. Having optimised these parameters, data was input to a global maximum likelihood search and the tree of maximum likelihood recovered.

The weights to be applied to the different codon positions in parsimony analyses should be based on the absolute evolutionary rates of the codon positions (Felsenstein, 1981), but these absolute rates are hard to determine in practice. It is clear however that the third codon positions are liable to evolve much more rapidly than the other two, and so changes at the third position should be devalued relative to changes at the other two. We therefore followed two weighting schemes for parsimony: weight the third positions to zero while weighting the others equally, and using the reciprocals of the relative evolutionary rates determined from the maximum likelihood analyses. A variety of transition/transversion rates, based on the likelihood results, were used in conjunction with various character weights.

Parsimony trees were obtained either by heuristic or branch and bound methods. Support for nodes was determined by bootstrapping the data set 1000 times. Significance of a grouping may be regarded as established at the 95% level if 95% of the bootstrap replicates contain this group in the case of a priori expectation, or $(100 - 5/(n - 2))$% (where n = no. of species) of them for expectations generated by the analyses themselves (Felsenstein, 1985). Trees retained under parsimony

were compared under maxi
(1983) test (Kishino and Ha
a tree across sequence positi

Results and discussion

The sequence data are gi
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characterized sites 187 prov
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Likelihood was maximised
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Amblyornis and Prionodura
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Scenopoeetes with maypole
bowerbirds are not so stro
require further testing.
Trees derived from parsin
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were found to be significar
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indicate that the Kishino-H

General patterns

Our results show that bov
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were compared under maximum likelihood using a modification of Templeton's (1983) test (Kishino and Hasegawa, 1989), which uses the variance of support for a tree across sequence positions.

Results and discussion

The sequence data are given in Fig. 2. The 60 sites at which character state information was missing were not included in parsimony analyses. Of the fully characterized sites 187 proved informative (were shared, derived) according to parsimony. Only these sites were used in parsimony reconstructions.

Likelihood was maximised for the set of all mtDNA sequences with a transition/transversion ratio of 3.1 and relative evolutionary rates of 2, 1 and 17 for codon positions, one, two, and three respectively.

The bootstrap parsimony result for all species is shown in Fig. 3, obtained using a transition/transversion ratio of 3.1 and reciprocal weights. Similar results were obtained when all codon positions were weighted equally, when third positions were weighted to zero, or a transition/transversion ratio of 2.0 was used. The maximum likelihood tree has the same topology and was used to determine the branch lengths for Fig. 3.

The bootstrap results give strong support at the 95% level for bowerbird monophyly (separation of the outgroups from the bowerbirds), as shown by the 98% occurrence of this prior expectation in the bootstrap replicates. The 100% occurrence of a bird of paradise grouping also accords with prior expectation. There is significant support for the monophyly of the two maypole builders, *Amblyornis* and *Prionodura* and for the monophyly of the avenue builders. Within the avenue builders there is significant support for the hypothesis that *Ptilinorhynchus* is the sister group of the *Chlamydera* genus. The nodes grouping *Scenopoeetes* with maypole builders and that separating *Ailuroedus* from other bowerbirds are not so strongly supported and indicate those relationships that require further testing.

Trees derived from parsimony analyses were used to test particular results from the bootstrapped parsimony analyses. These tests, in general, did not yield significance at the 95% level according to the Kishino-Hasegawa-Templeton test, even though the differences in likelihood were generally large. The exceptions were those trees in which bowerbird or avenue builder monophyly was disrupted. Such trees were found to be significantly worse than the tree of maximum likelihood (ln likelihood = -3971.01611). The failure to obtain the same level of support for other nodes impels further caution about the parsimony results, but may also indicate that the Kishino-Hasegawa-Templeton test is over-conservative.

General patterns

Our results show that bowerbirds are monophyletic and divergent from birds of paradise as has been suggested by Sibley and Ahlquist (1987), and indicates a common origin for all currently known bower building species after the divergence

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                15000
           TTTGGATCAC TACTAGGCAT CTGCCTAGTA ACACAAATCA TCACAGGCCT ACTACTTGCT ACACATTACA CACCAGATAC CAACCTAGCC TTCGCTTCCG TCGCTCACAC ATGCCGAAAC
Macg       .......... .......... .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
Green      .......... ..C....... .......... .......... .......... .......A.C .......... ..T....... .......... ..C.A..... .A.T.T.T.. ...G......
Golden     .......... ..T....... .CT....... .TC....... ......T... .......... .......... .......C.. ......T... .T.C...... .......... ..........
Great      .......C.. ..C....... T..T...... .......... ......C... ....T.G... ...C...... ......C... ...G....T. .T.C...... .A..C..... ..........
Regent     .......C.. ..C....... .......... .....T..TG ......C... ....C.T... .......... ......C... .......... .T.C...... .A..C..... ..........
Satin      .......... ..C....... .T........ .......... ....C.T... .C.T...... .......... ......C... .......... .......... .A..C..T.. ....T....T
Spotted    .......... ..C...CT.. T..T...... .....T..G. ......C... .T.G...... .......... ......C... ..G.G..... .A..C..... .A..C..... ..........
Toothbill  .......... ....CG.... .T.....C.. ......T... ....T.C... ....C.TG.C ...C...... ......C... .......... .T..C..... .ATC...... ..........
Sicklebill .......CG. .T.....A.. T.....A.C. ......T... .......... ...C..A.A. .......... ......C... ..T....... ..TAGC.... .A..C....T ...G......
Paradise   .......... ..C....... .T........ ...A....C. ......A... ...G.A.A.G ...C...... ......C... .......... ..TC...... .A..C..... .G........
Magpie     .......... ..T....... .....CA... ......T... ....A..... ...A.T.... .......... ......C... .......... .T.C...... .A..C..... .A..T....T

                15150
           GTGCAGTTTG GGTGACTAAT CCGAAACTTA CATGCAAACG GAGCCTCATT CTTCTTTATC TGCATCTACC TACACATCGG ACGAGGAATT TACTACGGCT CATACTTGAA CAAAGAAACC
Macg       .......... .......... .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
Green      .A........ .T..T..... .........C .......... ....T..... .......C.. ......G... .......... ......C... ......C... ......C.C. ..A.G.....
Golden     .......... ..A....... .......... .......... .......... .......C.. .......... .......... .....G..C. .......... ......C.C. ..........
Great      .A........ .A...T.... .........C .......... ......... .......C.. ......G... .......... ........C. ....T..... ......T.CA ..........
Regent     .A........ ..A..C.... .......... .......... .......G.. .......... .......... ......T... .......... .....T.T.. ..T.A.T.CA .........T
Satin      .A.A...C.. ..A..C.... .......T.. .......... .......... .......C.. ......G... .......... .......... .....T..A. .......C.A ..........
Spotted    .A...A..C. ..A..C.... .......... .......... .......... .......C.. .......T.. .......... ........C. .........T ...T.TC.A. ..........
Toothbill  .......... ..A....... ..G....... .......... .......... .......C.. ....T..C.. .......... ......G.T. ..T....... .T.TC.A... .G........
Sickle     .C.A..C... .T.....A.. .......C.. .......... .......... ...T.TC... ......A... .......... ......GT.C ...C...... ......C.C. ..G.......
Paradise   .C.A..C... .A.....A.C .......C.G .......... .......... .......CA. ......CG.T .......T.. .......... ...C...... ......GT.C ..........
Magpie     .C.A...... ..C....T.. .......C.G .......... ......T... .......... .......... .......... .......CT. .......... ......C.A. ..G.G.....

                15250
           TGAAACACCG GAGTGATCCT CCTTCTAACC CTAATAGCAA CTGCTTTCGT AGGGTACGTC CTCCCCTGAG GACAAATATC GTTCTGAGGG GCTACAGTAA TCACAAACCT ATTCTCAGCC
Macg       .......... .......... A.A..GCT.. .......... .......... .......... ..C..NNNN. .......... .......... .A........ .T.C...... .........T
Green      ....TT.... ..A....... .......... .......... .......... .G......T. ..C..NNNN. .......... .......... .......... .T.C...... ..........
Golden     .....TGT.. ..AC.T.... .......... .......... .......... .......... ......G... .......... .......... .......... ..NN...... .........N
Great      .....TGT.. ..A...T... ....A..G.. .......T.. ....C.C... .......A.. ......T... ..A..T.... ..A.T..C.. .......... .....T.... ..........
Regent     ......TA.. .G........ ....C..... .......... ....C.C... ....A..... .......... ..A....... ..A.T..C.. .......... ........C. ..........
Satin      .....TGT.. .......... ...C....T. .......... ....C.C.T. ....A..... .......... ..A....... ..A.T..C.. .........A .......C.. ..........
Spotted    ..G.TGT... .A........ T.C....... .......... ....C.C.T. ....A..... .......... ..A..A.... ..A.T..A.. .......... .......C.. ..........
Toothbill  .G........ .......... T.A....... .......G.. ....C.C... .......... ..C..T..A. .......... .......... .G........ ...A...... ..........
Sickle     ....T..... ..A....T.. .......C.G ......A.C. ....T.A..T ....A..T.. .T.A...T.. .......... ..C..T.A.. .......... ...C....C. ..........
Paradise   .....GTT.. ..A....... .......A.. ......A.T. ....C.A..T ....A..T.. .C.A...T.. .......... ..T.......T .......... ...T...T.. ...C...A.A
Magpie     ....T.T... ..A....T.. A.CA.C.... ......G..T ....C.C.T. ....A.A.T. .A.A...... .......... ..A....... .......... ...T.C..C. ....T....A

                15400
           ATCCCATACA TCGGCCAAAC CCTCGTAGAA TGGGCATGAG AGTAGACAAC CCAACATTAA CCCGGTTCTT AGTAGAGATC CCCGGTTCTT TGCTCTCGCAC TTCCTTCTCC CGTTGTAAT CGCAGGAATC
Macg       .......... .......... .......... .......... .......... .G...C.G.. .......... .......... .......... C.C.A..... .......... ..A....... CC........
Green      .......... ...A...... A..T...... .......... .......... .......... ...A...... .C........ .......... C.C.A..... .......... .A..T..... ..CC......
Golden     .....G.... ..T.A..... A.T....... .......... .......... .......... .......... .G........ .......... C.C.A..... .......... .A..C.C... .CC.T.....
Great      .......... .....T.... A..T...... .......... .A........ .......C.. .......... .G........ ....T..... C.C.A.T... .......C.. .A..C..... .CC.......
Regent     .......T.. ...T.A.... A..T...... .......T.. .......... .......C.. .......... .T........ .......T.. C.C.A.T... .......C.T .A..C..T.. T.T.CC.N..
Satin      .......... ...A..T... A..T...... .......... .......... .......C.. .A.T...... .G........ .......... C...A..... .......C.N .A..C..... .CC.N.....
Spotted    .......... ...A....C. A..T...... .......G.. .......... .......C.. .......... .G........ .......G.. C.C.C..... .......... .A..C..... CC........
Toothbill  ....T..... .T...T.G.. ....T..... .......... G......... .......C.. ......G... .G........ .......... C.C.C..... ......G... .A..C..... ..CC......
Sickle     .......... ...T...G.. A..T...... .......... .......... ..T..C.G.. .......... .T.C.G.... .......... C.C.T..... ....C.T... .A..C..... .A.CC.G...
Paradise   .......... ...A...... A..T...... .......... .......... ..T..C.... .......... .T.C...... .......... C.C.C..... ....C.T... .A..T..T.. .CC.C.....
Magpie     ....C..... .T.A...... A..T...... .......... .......... .C..GC.C.. .......... .C.C...... .......... C.A....... .......... .A..C..... .A.C.A....

                15550
           ACACTAGTCC ACCTAACCTT CCTGCATGAA ACTGGGTCAA ACAATCCACT AGGAATCCCA TCAGACTGCG ACAAAATCCC ATTCCACCCA TACTACTCCA TAAAAGACAT TCTAGGATTC
Macg       .......... .......... .......... .......... .......... .......... .......... .......... .......... .......... .......... ..........
Green      ......... .....T.A.. .T.A.C.... ...A.A.C.. ...C.N.... .......... ...C..T... ......N... .......... .....NNNN. .......... C.........
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                                                    15400
       ATCCCATACA TCGGCCAAAC CCTCGTAGAA TGGGCATGAG GTGGATTCTC AGTAGACAAC CCAACATTAA CCCGGTTCTT TGCTCTGCAC TTCCTTCTCC
                                                    15450
       CGTTTGTAAT CGCAGGAATC
Macg
Green      ......G... ...A...... A..T...... .A........ .C........ ........ .G...C.G. .........A .C.C..A... ....A....
                  .A....T... ......CC.
Golden     ......G... ..T.A..... A..T...... .A........ .G........ ...........C. ....A. ...C...A.. .........C  .A..C.G.
Great      .......... ...A...... A..T....:. .A...C.... .A........ ...........C. .C.C..A... .A...C....  A..C.C.
Regent     .........T ...A...... A..T...... .A..:..... .G...T.... .T...T... .C.NN .NNNNNNN. ..C..C.A..T ..C.T..  T.T..CC.T
Satin      .........T ..T.A..... A..T...... .A........ .G.......T ..........C. ..A.T. .C.C..A...  .A..C.C. ...CC.N
Spotted    ..T....... ..T.A.G... .....T.:.G .A...G.... .G........ .G.......... ...C..... .C.C..A. .A..C..  T...CC..
Toothbill  ..T...:... ...T.G.... ..T...T.:G .A........ .A........ ..........A. ...C...C.T .........G  .C..C..
Sickle     ..T....... ...T.G.... .......A.. .A..C..... .A...T.... ...T.C.G. ...C...C.. ...........A.  .A...CC.A
Paradise   ...C...... ...G...... ..A.T..... .A..T..... .A...T.... .T...C... ....A..... .C.C..C... ..C.T.  T.T..CC.G
Magple     .......... ..T.A..... .T.A...... .A..T..... .C..C..... .C.GC.C. .T.A...... ...C.C.T.T ...C..  A.T....C.A


                                                    15500
       ACACTAGTCC ACCTAACCTT CCTGCATGAA ACTGGGTCAA ACAATCCACT AGGAATCCCA TCAGACTGCG ACAAAATCCC ATTCCACCCA
                                                    15550
       TACTACTCCA TAAAAGACAT TCTAGGATTC
Macg
Green      ......... T.A.C..... A.A.A.C... .C..N. ..C.T.... ......... N.......... ...T......      NNNNN NNNNNNNNN.
Golden     ..G..T.. ...C..... T......... .A.....C. ..C..C.... ......... ...............  C......   C........G.
Great      ....T.... .C.A..... ...C...... ..A...C... .C..T..... ..C....... ..........  .A......   C.....T...
Regent     ...A..... T..C.A.... .G..A..C.. .A...C.... .C........ ...G..... ........T.  ..A.....   C........
Satin      ......... .T..C..A.. ..A.C...:. .A.A..C... .C..C..... .C.......  ..A......   C.....G...
Spotted    .......T. ...C..... ..A.A.C... .A.A.A.T.. .C..C..... ...C..T.. ..T....... .N........   .N.GN.N.. .T...G..T
Toothbill  ......... .T..C.... T.A.C..... .A.A...... .C..T.... ...C...... ........C  ..T....   C........
Sickle     ......T.. ..G..A.... ..A.A..... ..A.A..... ..C..T..... ..C..... ........  ..N..NN.   .N..N.  C.......
Magple     ..CT..... ....T..... ..A..C.... ..A.T.... ..C..C.... .C........ ..T....T.  ..T.A..   T.A..C.    .........T


                                                    15600
       GCACTATTAT TCATTGCACT AGTCGCCATA GCCCTATTCT CACCAAACCT GCTAGGCGAC CCAGAAAACT TCACCCCAGC AAACCCACTA TCCACACCCC
                                                    15650                                           15700
       CTCACATTAA ACCCGAATGA
Macg
Green      ..T.A..... ...CCTT... ...T....G ...T...... C........ ...T.A.... ......... C........ C......NN   A..T.C...   ..A....G
Golden     ...C....:. ..G...... A.T.T.T.. ....T..... ..C.......  ......G. ........T ..C.T.T.N  .NNNN.. C..A.T.C.
Great      ..T.A..... ....CCTT.. ...T....G ..T...... C...T..A..  ..T.A....  ...T ..C..T.T.C   ...G.A.   .N.T.C.   AG....
Regent     .G..A..C ....CCT... ...T.G ......... ..C.T..T..  A.T.A...  T...T..C ..C..T.C    G.A.    .C..T...
Satin      ..T..A.GC .T.CCTT.. .........  ..T...... ..C......  A...A...   .NN... C..NN.CTNT   .ACNNNNNN NNNNN.
Spotted    ..T..A.GC .GCCCT.... ..A..C.G T.....:. ..C...... ..A..T.G.  T.T..... ..C.....T.C   ...NN.   C..T...
Toothbill  ..A..C .A...T.... C..A..C.G .T....... .T.....T..  .A...G.  C...T.... C....NN..   .C.T.   C..T.C.   ..A....G
Sickle     ..A..GC .A..A..... T.C.A..C.G A......... C........ .A......  C...T..C  C......T.   G.....T.   C..T.C.   .A....
Paradise   ..A..C .A.CCCTG.. ...C...T.. .A........ ..C..... AT....A..  C..T.C.. C...A....T   A....   T.C.   .A....
Magple     ..A..C .T..CT.... C.C.A.T... .T.......  ..C...... ...G....G  C...T...  ..G.C.C.   GT.T.T.   GT..T.T.   .C..T.
```
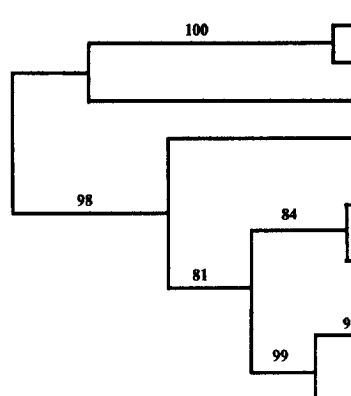
Fig. 3. Bootstrap parsimony tree f[or]
sequence data of Fig. 2 and using a[...]
inverse of the relative evolutionary ra[te...]
indicate the percentage of times a [...]
maximum likelihood tree was identic[al...]
recovered by PAUP (length 63 212, [...]
of *Ptilinorhyncus violaceus* and *Seric[...]*
longer, but was not significantly we[...]
scheme used such a difference is eq[...]
demonstrates monophyly of the b[...]
Topologically identical trees occur[...]
monophyly consistently statistically [...]
to those shown here.

of *Ailuroedus sp.*, the only g[...]
not exhibit bower building o[...]
of monogamy in birds lend[...]
represents an ancestral con[...]
clearing occurred after their [...]

The association of the ave[...]
major style of bower cons[...]
relationship is a good pred[...]
closely related species like t[...]
bowers are used in display ([...]

Another grouping consists [...]
show less obvious affinities[...]
Prionodura and *Amblyornis* b[...]
tendency to build bowers of[...]
1969). However, *Prionodura* [...]
bower construction compare[...]
putative claim of their close r[...]
of these genera revealed by b[...]
that the use of a sapling as [...]

Fig. 2. Sequences of an 849 base pair region of cytochrome b from eleven species. "N" indicates missing data. Dots indicate identity to Macgregor's bowerbird, used here as the reference sequence. Nucleotides are numbered according to the chicken mitochondrial sequence (Desjardins and Morais, 1990). Abbreviations are: Macg – Macgregor's bowerbird, Green – green catbird, Golden – golden bowerbird, Great – great bowerbird, Regent – regent bowerbird, Satin – satin bowerbird, Spotted – spotted bowerbird, Toothbill – toothbill bowerbird, Sickle – buff tailed sicklebill, Paradise – paradise riflebird, Magpie – magpie. Species names are listed in methods.
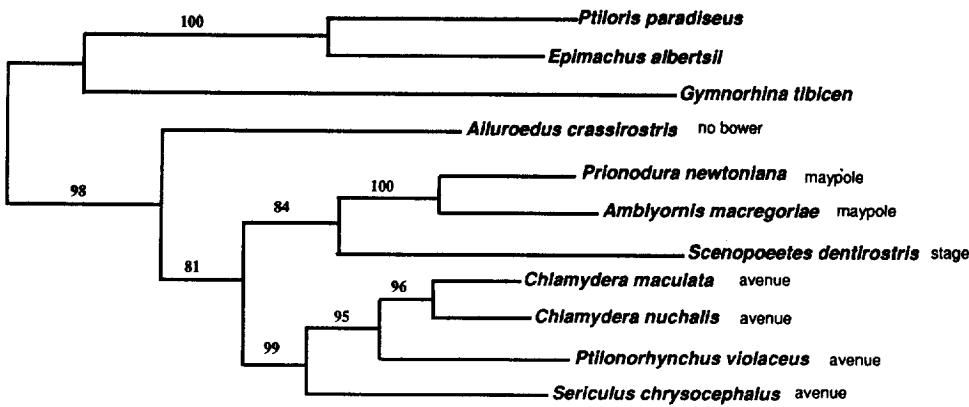
Fig. 3. Bootstrap parsimony tree for eight bowerbird and three outgroup species, inferred from the sequence data of Fig. 2 and using a transition/transversion ratio of 3.1 and weights calculated as the inverse of the relative evolutionary rates for codon positions 1, 2 and 3 (see methods). Numbers at nodes indicate the percentage of times a group occurred in 1000 bootstrap replicates. The topology of the maximum likelihood tree was identical and was used to infer branch lengths. The most parsimonious tree recovered by PAUP (length 63 212, tree not shown) differed from the above tree in the relative positions of *Ptilinorhyncus violaceus* and *Sericulus chrysocephalus*. The topology shown above was thirty four steps longer, but was not significantly worse according to the Kishino-Hasegawa test. Under the weighting scheme used such a difference is equivalent to one extra step at a second codon position. The result demonstrates monophyly of the bowerbird species and is indicative of intra-bowerbird affinities. Topologically identical trees occurred with a variety of other parameter values, with bower-bird monophyly consistently statistically significant and support for the other relationships of a similar order to those shown here.

of *Ailuroedus sp.*, the only genus within the family that is monogamous and does not exhibit bower building or court clearing behaviour. The widespread occurrence of monogamy in birds lends weight to the suggestion that the genus *Ailuroedus* represents an ancestral condition and that the transition to polygyny and court clearing occurred after their divergence.

The association of the avenue-building species and their ancestral sharing of one major style of bower construction suggests, for this group, that phylogenetic relationship is a good predictor of the general form of bowers. However, even closely related species like the two *Chlamydera* species can differ radically in how bowers are used in display (see Borgia and Mueller, 1991).

Another grouping consists of the genera *Prionodura* and *Amblyornis*. These species show less obvious affinities in bower construction than the avenue builders. *Prionodura* and *Amblyornis* have been associated by some because of their common tendency to build bowers of sticks around saplings (Marshall, 1954a, b; Gilliard, 1969). However, *Prionodura*'s use of two saplings and an associated cross branch in bower construction compared with *Amblyornis*' single sapling bower has made the putative claim of their close relationship open to question. The significant association of these genera revealed by bootstrapping indicates that these species are related and that the use of a sapling as part of a bower construction had a common origin.

Plumage characters appear less reliable than bower characters in predicting phylogenetic patterns. Both avenue and maypole building clades involve species with crests yet none of the phylogenetic patterns suggest a common origin for the crests. Three genera (*Sericulus*, *Chlamydera* and *Amblyornis*) include species with and without well developed crests. Plumage color shows similar but less severe variation. Both major clades include dimorphic and monomorphic species and one genus (*Amblyornis*) includes both types of species. Some major changes in plumage appear to be adaptive responses to environmental conditions (Borgia et al., 1985), however the possibility of display trait elaboration due to runaway sexual selection (see Kirkpatrick, 1986) or sensory exploitation (Burley, 1985; Ryan et al., 1990) cannot be ruled out.

Transference

The pattern of divergence seen among the avenue builders accords with Gilliard's suggestion about the pattern of plumage evolution. In his transfer effect model Gilliard suggests an ancestral condition in which brightly plumed species build simply decorated bowers and more recently derived species exhibit dull plumage and build elaborate bowers. Our results are consistent with this claim. The monomorphic and drably plumed *Chlamydera* species build the most elaborate and highly decorated of avenue bowers. This genus is more recently derived than *Sericulus* or *Ptilonorhynchus*, two genera in which the males are vividly plumed and the bowers simply constructed and decorated.

The different colored plumage seen among avenue building species (e.g. the orange and black plumage of *Sericulus* and the irridescent blue-black plumage of *Ptilonorhynchus*) may be independently derived. Alternatively, these bright plumages may represent modifications of an ancestral dimorphism that enhanced the signal quality of displays as these species moved into novel habitats (see Endler, 1990). In either case, Gilliard's simple model of character loss and replacement may have to be expanded to one that posits a general transfer of display functions from bird to bower, but which also allows for modification and replacement of plumage characters.

The evolution of bower building

The position of *Ailuroedus* in our phylogeny is consistent with the hypothesis that dull male plumage and the absence of bower building are ancestral traits. It is not clear, however, that the dull plumage and absence of a bower in *Scenopoeetes* are ancestral. Like other bowerbird species male *Scenopoeetes* are polygynous and clear and decorate display courts. Our phylogeny is consistent with two hypotheses: that bower building evolved twice, or that it evolved once and was lost in the lineage leading to *Scenopoeetes*. A comparison of the two most parsimonious pathways for bower evolution shows no difference in the number of character state changes needed to explain bower building (Fig. 4).

A cladistic analysis based on this character would suggest that these alternatives be considered equally likely. There are, however, several reasons to favour the second hypothesis. First, the evolution of bower building is a rare event, having
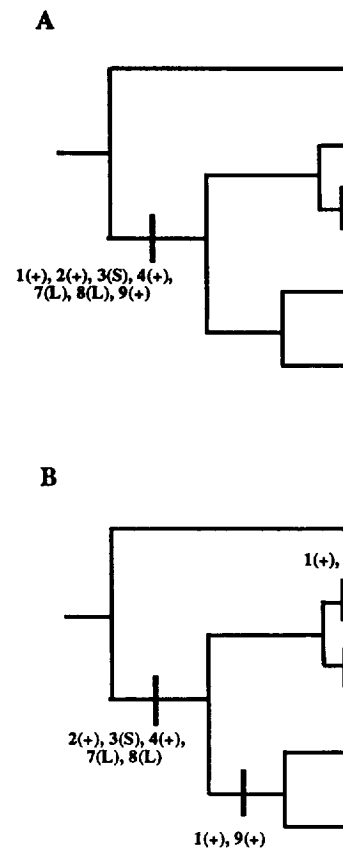
A

1(+), 2(+), 3(S), 4(+), 7(L), 8(L), 9(+)

B

1(+),

2(+), 3(S), 4(+), 7(L), 8(L)

1(+), 9(+)

Fig. 4. Two trees with display chara[cters]
sequences. The trees represent two [
1 = bower, 2 = court clearing, 3 = [
5 = lekking, 6 = continuous loud call[
courts (long(L) or short(S)), 9 = pl[
otherwise noted. The trees differ with[
which undergo a reversal in tree A [
association between traits thought t[
dimorphism, long courtships, brief co[
equivalents are replaced (e.g. bower[
tions on the lineage leading to *Scen[
episodes during which either one or [

occurred in only a single fa[
bowerbuilding, e.g. polygyn[
creased the likelihood of mul[
existed at the time the two m[
why the evolution of bower b[
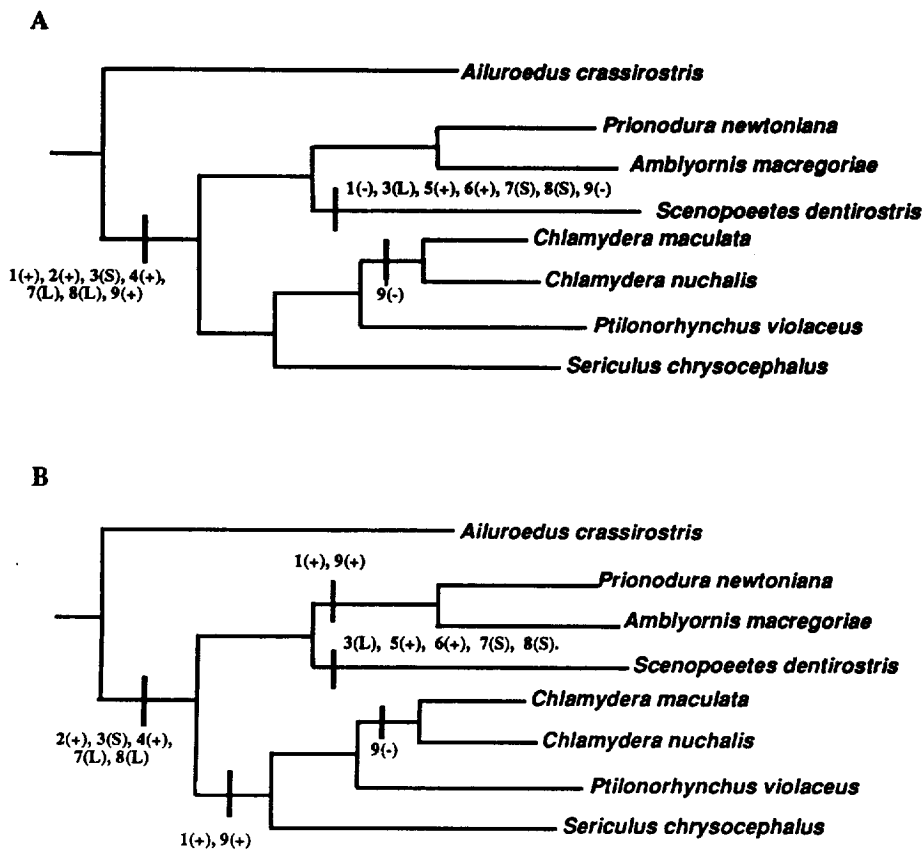maypole builders until after [

A

B

Fig. 4. Two trees with display characters mapped onto bootstrap parsimony tree derived from mtDNA sequences. The trees represent two equally parsimonious maps of display traits. Trait definitions are: 1 = bower, 2 = court clearing, 3 = decorations (absent(A), small(S), or large(L)), 4 = polygyny, 5 = lekking, 6 = continuous loud calls, 7 = copulations on court ((long(L) or short(S)), 8 = courtship on courts (long(L) or short(S)), 9 = plumage dimorphism. Presence (+) or absence (−) of trait unless otherwise noted. The trees differ with respect to traits 1 and 9, bowerbuilding and plumage dimorphism, which undergo a reversal in tree A and show parallelism in B. The trees also differ in the degree of association between traits thought to be functionally linked (e.g. bowers, small decorations, plumage dimorphism, long courtships, brief copulation), and in the extent to which traits thought to be functional equivalents are replaced (e.g. bowers and small decorations are replaced by lekking and large decorations on the lineage leading to *Scenopoeetes* in tree A). Tree A is preferred because it does not require episodes during which either one or another equivalent trait is not present.

occurred in only a single family of birds. Preadaptations for the evolution of bowerbuilding, e.g. polygyny, court clearing and court decoration may have increased the likelihood of multiple bower origins. If, however, these preadaptations existed at the time the two major clades of bower-builders separated, it is not clear why the evolution of bower building might be delayed in the lineage leading to the maypole builders until after the divergence of *Scenopoeetes*. In addition, if bowers

and lekking (and associated interactive vocal displays) have complementary functions related to female choice among court clearing bowerbirds (see Borgia, manuscript), then only the single origin hypothesis allows ancestral species to exhibit a fully developed male display and mate choice mechanism. The alternative would require that ancestral court clearers existed for a long period of their evolutionary history with incomplete displays and then independently evolved the final parts of their display. Given that bowers are central to much of the display of these species this pattern of trait evolution seems unlikely.

Genera not represented

One genus of bowerbird, *Archboldia*, is not represented in our study. *Archboldia*, like *Scenopoeetes*, builds a display court but fails to build a bower. The location of *Archboldia* in our phylogeny should help resolve some of the questions discussed above, e.g. is the absence of bower building ancestral in these lineages or the result of reversals. The occurrence of an orange head crest in *Archboldia* associated with the absence of a bower suggests the absence of compensatory change predicted by the transference hypothesis.

Acknowledgements

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Gene arrangement pl
species of the *Obscu*

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Department of Genetics, Un

Key words: Drosophila; obs

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