Labile evolution of display traits in bowerbirds indicates reduced effects of phylogenetic constraint

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SUMMARY

Bowerbirds (Ptilonorhynchidae) have among the most exaggerated sets of display traits known, including bowers, decorated display courts and bright plumage, that differ greatly in form and degree of elaboration among species. Mapping bower and plumage traits on an independently derived phylogeny constructed from mitochondrial cytochrome *b* sequences revealed large differences in display traits between closely related species and convergences in both morphological and behavioural traits. Plumage characters showed no effect of phylogenetic inertia, although bowers exhibited some constraint at the more fundamental level of design, but above which they appeared free of constraint. Bowers and plumage characters, therefore, are poor indicators of phylogenetic relationship in this group. Testing Gilliard's (1969) transferral hypothesis indicated some support for the idea that the focus of display has shifted from bird to bower in avenue-building species, but not in maypole-builders or in bowerbirds as a whole.

1. INTRODUCTION

Bowerbirds (Ptilonorhynchidae) form a monophyletic family (Kusmierski *et al.* 1993) (eight genera, 19 species) endemic to Australia and New Guinea, and are unique in the bird world in constructing and using a bower in male courtship display. A bower is a stick structure built on or adjacent to a display court that is entered by one or both sexes during courtship and mating. It has been suggested that morphological and behavioural characters may be as useful as molecular characters in reconstructing evolutionary history (de Queiroz & Wimberger 1993), but this hypothesis has rarely been tested with characters under extreme sexual selection. Bowerbirds are an ideal group in which to test this hypothesis as they appear to be subject to strong sexual selection and exhibit great variation among species in the form and elaborateness of exaggerated, sex-limited display characters, including bowers, bright plumage and decorated display courts.

Bowerbirds have traditionally been divided into three groups based primarily on presumed homologies in bower design (Schodde 1976). The catbirds (*Ailuroedus*, three spp.) do not construct bowers or display courts (table 1), are the only monogamous bowerbirds, and have been associated with the drably plumed, monomorphic *Scenopoeetes*, which clears a display court decorated with upturned leaves. The sexually dimorphic, yellow-crested *Archboldia* builds a mat of dried ferns and feathers, but no stick bower. Overhanging branches are draped with orchid vines resulting in a 'curtain' that divides the court. The maypole-builders (*Amblyornis*, four spp.; *Prionodura*) include the orange-crested males of *A. macgregoriae*, which decorate a sapling with horizontally interwoven sticks. The dull-coloured, monomorphic *A. inornatus* of western Irian Jaya (Arfak and Wandamen mountains) and the orange-crested, dimorphic *A. subalaris* of eastern New Guinea both build elaborate maypoles with hut-like roofs. Recently, some disjunct populations of *A. inornatus* (Fak Fak and Kumawa Mountains) have been found with hutless, spire-type bowers (Diamond 1986, 1987). *Prionodura* is sexually dimorphic, males having bright yellow head, nape, chest and tail feathers, but no extendible crest. Males construct a large bower with a raised display perch built on a branch spanning two stick-covered, decorated maypoles. The avenue-builders (*Chlamydera*, four spp.; *Sericulus*, three spp.; *Ptilonorhynchus*) have bowers with a central avenue enclosed by at least two stick walls. Most avenue bowers are generally similar, with the most dramatic variants being *C. maculata*'s use of straw instead of sticks in a bower with widely spaced see-through walls in contrast to the very thick stick walls of *C. nuchalis*. *Chlamydera lauterbachii* and *C. cerviniventris* both have avenue bowers built on raised stick platforms, the former further differentiated by having two additional walls perpendicular and partially enclosing the walls defining the central avenue. The Satin Bowerbird, *Ptilonorhyncus violaceus*, and the Regent Bowerbird, *Sericulus chrysocephalus*, differ from *Chlamydera* spp. in building simpler avenue bowers and exhibiting brilliant body plumage dimorphism. Among the drably plumed *Chlamydera*, male *C. maculata* and

Table 1. *Classification of bowerbird display traits*

species	bower form	court	crest/colour	body plumage	habitat
Archboldia papuensis	no bower/orchid-draped branches	thick fern mat under draped branches	yellow, short, non-retractile	black	moss forest
Amblyornis inornatus (Arfak Mts)	hut-covered maypole	moss court at bower entrance, downhill side	no crest	drab	rainforest
Amblyornis inornatus (Fak Fak Mts)	uncovered maypole	circular moss court	no crest	drab	rainforest
Amblyornis macgregoriae	uncovered maypole with rim	circular moss court	yellow/orange, long, retractile	drab	moss forest
Amblyornis subalaris	hut-covered maypole	cleared ground with stick wall behind, on downhill side	no crest, yellow tuft	drab	rainforest
Prionodura newtoniana	two spires with raised perch	no ground court	yellow/orange, medium length, retractile	bright yellow and dark brown	rainforest
Scenopoeetes dentirostris	no bower	cleared ground	no crest	drab	rainforest
Sericulus chrysocephalus	simple avenue	no outside court, decorations in bower	no crest	bright yellow/orange and black	rainforest
Ptilonorhynchus violaceus	simple avenue	straw covered, at north bower entrance	no crest	irridescent blue	rain and wet sclerophyll forest
Chlamydera lauterbachii	avenue, four walls, upturned lip at front and back	two small courts on raised stick platform	no crest	drab	semi-open woodland and riverine forest
Chlamydera cerviniventris	avenue on raised stick platform	two courts on raised stick platform, at E and W entrances	no crest	drab	semi-open woodland and riverine forest
Chlamydera nuchalis	avenue, elongate, thick walls, raised avenue base	two courts, at N and S entrances, on ground or pebble base	lilac, rounded and retractile	drab	open woodland
Chlamydera maculata	wide avenue, see-through, straw walls	two courts, N and S, on ground with widely spread decorations	lilac, short and flattened, retractile	drab	open woodland
Ailuroedus melanotis	no bower	no court	no crest	drab	rainforest
Ailuroedus crassirostris	no bower	no court	no crest	drab	rainforest

C. nuchalis possess a lilac retractile crest. The most fully resolved set of relationships in this family are based on presumed homologies in the bower and other display characters (table 1), but mitochondrial and allozyme studies on smaller numbers of species have shown the catbirds to be ancestral to polygynous bowerbirds and support separation of the two other bower-building clades (Sibley & Ahlquist 1985; Christidis & Schodde 1992; Kusmierski *et al.* 1993).

Here we explore two aspects of bowerbird display evolution. First we examine the utility of bowers in defining relationships among bowerbirds. There has been a recent resurgence in the use of behavioural characters to construct phylogenies (e.g. McLennan *et al.* 1988; Prum 1990), and concordance between molecular and behavioural phylogenies based on nest design has been demonstrated in swallows (Winkler & Sheldon 1993), but not so in swiftlets (Lee *et al.* 1996). Exaggerated, sex-limited display traits differ from

other behavioural and morphological traits in being subject to the strong and often fluctuating forces of sexual selection that may reduce their ability to act as phylogenetic markers. Previous studies of bowerbirds (Kusmierski *et al.* 1993) have suggested that bower characters can make useful phylogenetic markers, but several critical species were unavailable for examination at that time.

We also test Gilliard's (1969) hypothesis regarding the relationship between plumage dimorphism and bower complexity in bowerbirds. It has been suggested that in the course of display trait evolution in bowerbirds there has been a shift of the focus of display from the bird to the bower, presumably in response to the cost to males in maintaining bright plumage (Gilliard 1969; Borgia *et al.* 1985; Diamond 1986). Developed to explain an apparent inverse relationship between plumage brightness and degree of bower elaboration in the genus *Amblyornis*, and in avenue-

building species, the hypothesis assumes an ancestral condition of brightly coloured males and small, undecorated bowers. Gilliard proposed that plumage traits were transferred to bowers leading to a derived condition of dull, monomorphic plumage and extremely elaborate, decorated bowers.

By mapping plumage and bower characters on an independently derived phylogeny it is possible to reconstruct the evolutionary history of bower and plumage traits, identify convergence in the form of parallelisms and reversals, determine the impact of phylogenetic constraint in observed patterns of display trait distribution and test Gilliard's transferral hypothesis of display evolution in bowerbirds.

2. MATERIALS AND METHODS

Mitochondrial cytochrome *b* sequences from five bowerbird species; *Amblyornis inornatus* (Fak Fak and Arfak mountain populations), *Am. subalaris*, *Archboldia papuensis*, *Chlamydera cerviniventris* and *Chlamydera lauterbachii* and a lyrebird, *Menura novaehollandiae*, were added to those obtained previously by us (Kusmierski *et al.* 1993) or published by others (*Am. macgregoriae*, Edwards *et al.* 1991; *Ailuroedus melanotis*, Helm-Bychowski & Cracraft 1993). We applied standard extraction, amplification and direct sequencing techniques (Kusmierski *et al.* 1993) to derive mitochondrial cytochrome *b* gene sequences using primers designed by, or modified from, Kocher *et al.* (1989) and Edwards *et al.* (1991), or designed independently in our laboratory.

Phylogenetic trees were inferred using parsimony as implemented by PAUP 3.1.1 (Swofford 1993), and by the maximum likelihood and neighbour-joining methods in PHYLIP 3.4 (Felsenstein 1991). Transition/transversion ratios were derived empirically by optimizing likelihood using trial trees. Analyses were performed on all equally weighted codon positions or on all sites weighted according to their empirically derived rates of substitution. Statistical confidence of nodes was estimated using 1000 bootstrap replicates (Felsenstein & Kishino 1993), and the Kishino–Hasegawa–Templeton test (Kishino & Hasegawa 1989) was used to compare alternative phylogenetic hypotheses. Steel *et al.*'s (1993) frequency-dependent significance test was used to determine if a biased base composition at third codon positions affected phylogenetic inference.

Reconstruction of discrete behavioural and morphological characters was performed using MacClade (Maddison & Maddison 1992), in which trait evolution is modelled and historical states assigned using the principal of parsimony. Bowers were coded according to two different schemes. In the more detailed coding we identified five bower states: (0) no stick/straw bower, (1) single wall or maypole, (2) single spire, (3) two spires, (4) hut over spire, (5) two walls, (6) four walls. A simpler coding of bowers was also used: (0) no stick/straw bower, (1) central maypole, (2) walled avenue. The three other display traits that were reconstructed on the phylogeny and their states are listed in table 1.

The extent to which phylogenetic constraints operate in bowerbird display traits was tested by generating 1000 random character sets using MacClade. In each of these sets characters were assigned randomly to species according to the observed frequency of the character state. To test for phylogenetic inertia, the resulting distribution of state transitions required to fit each of these randomly generated sets to our phylogeny was compared with the number of state transitions observed (Maddison & Slatkin 1991).

Maddison's concentrated changes test (Maddison 1990)

was used to test presumed instances of correlated character evolution between plumage dimorphism and large or complex bowers. Characters were coded as binary discrete states. Complex or large bowers were traced onto the phylogeny and the number of times plumage dimorphism was lost on these traced branches was noted. Observed numbers of losses or gains were then compared to expected values according to random assignment of character change.

3. RESULTS AND DISCUSSION

The inferred phylogeny of 14 bowerbird species (rooted with *Menura*) using data from a 924 bp region of the mitochondrial cytochrome *b* gene (Genbank accession numbers U10113, U10364, U10367, U10370–U10372, U76503-U76509, X60940, X74257) is shown in figure 1. This tree was returned by both parsimony and unweighted maximum likelihood methods. High levels of bootstrap support were obtained for most nodes, although earlier nodes had lower bootstrap values. The neighbour-joining tree differed from this topology in splitting *Chlamydera* species into two monophyletic groups: *C. maculata* and *C. lauterbachii*; and *C. cerviniventris* and *C.nuchalis*. When different relative rates (4, 1, 34) were applied to the three codon positions the maximum likelihood topology was altererd in some respects. The catbirds (*Ailuroedus* spp.) diverge after the avenue-builders and become the sister group to the maypole-building clade. Among *Chlamydera* species the positions of *C. maculata* and *C. lauterbachii* are reversed. No significant difference in likelihood was observed between these alternative topologies. The trees support early divergence of maypole- and avenue-builders, a common ancestry for *Scenopoeetes* and the maypole-builders and for avenue-building species. Trees constrained to reflect *Amblyornis* monophyly were significantly worse than the minimal length tree when compared using the Kishino–Hasegawa–Templeton test. Monophyly of hut-building species (*Am. subalaris* and *Am. inornatus*) was similarly rejected, as was that of *Scenopoeetes* and *Archboldia*. A biased base composition (index of compositional bias (Prager & Wilson 1988) = 0.4383) at third codon positions led us to check these conclusions using Steel *et al.*'s frequency-dependent test. We found further significant support for grouping *Am. inornatus* and *Archboldia* to the exclusion of *Am. subalaris* and *S. dentirostris* ($p < 0.01$). Our tree suggests a recent common ancestry for *Am. inornatus*, regarded as having the most elaborate of bowers, and *Ar. papuensis sanfordii*, a yellow-crested species that does not build a stick bower.

Bower evolution has 12 equally parsimonious reconstructions under the detailed coding scheme (figure 2*a*), however, under both this and the simpler coding bowers arose twice, once in avenue-builders and again after the divergence of *Scenopoeetes*. If we further simplify bower coding to stick structure or no stick structure then the origin of bower-building becomes ambiguous with single or dual origins possible. Plumage characters also had ambiguous evolutionary histories. Crests have three equally parsimonious reconstructions, each of five steps. Brilliant body plumage dimorphism has two
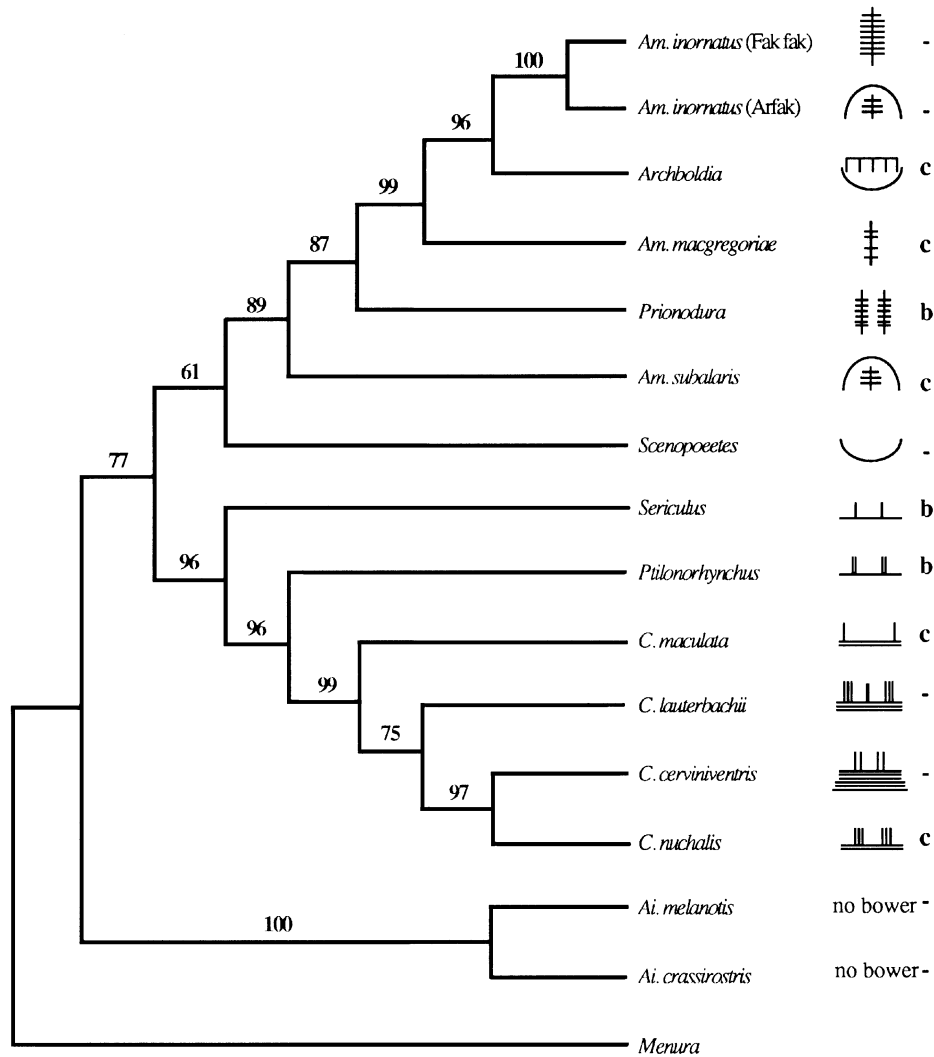
Figure 1. Bootstrap parsimony tree of 14 bowerbird species, rooted with the superb lyrebird, *Menura novaehollandiae*. Numbers at nodes reflect the percentage of times clades were returned from 1000 bootstrap replicates. Key to symbols is as follows:

⬠ hut bower ⬚ single spire ⬚ twin spire ⬚ fern court/vine curtain

⌣ cleared court only ⊥⊥ simple avenue bower ⬚ raised avenue ⬚ twin avenue

   c: crest   b: brilliant plumage   — no plumage dimorphism

Among spire bowers and avenue bowers complexity/size of bower increases with the number of lines present on the schematic.

possible reconstructions, but the common ancestor of avenue and maypole clades is unambiguously monomorphic.

Ambiguities in character evolution prevent us from determining whether characters are independently derived and therefore represent convergences, or whether they evolved once and were subsequently lost in other lineages. For example, the presence of the hut-type bower in *A. inornatus* (Arfak mountains) and in *A. subalaris* could be the result of two independent gains of this complex state. Alternatively, a large, complex hut bower may be the ancestral state in this clade. Ambiguities might be resolved by making assumptions about ancestral states independent of their (ambiguous) most parsimonious reconstruction. If (as seems likely) a simple maypole or single wall structure represents the ancestral condition of bowers, and hut bower evolution necessarily passed through a single spire stage, then the hut bowers of *A. inornatus* and *A.*

subalaris do represent convergence in a complex display trait (figure 2*b*). This occurs whether we envisage a single origin for bower-building (see Kusmierski *et al.* 1993) or two independent origins, one on the clade leading to avenue-builders and one to the maypole-builders. This unexpected result draws support from subsequent field observations (G. Borgia and M. Sejkora, personal observation) that *Am. inornatus* (Arfak) builds the bower from the top down whereas *Am. subalaris* builds bowers from the bottom up. Because our tests of phylogenetic constraint and directed, correlated evolution require an unambiguous resolution of trait history we examine both accelerated and delayed transformation optimizations of plumage and bower traits. In so doing we reduce the chance of incorrectly rejecting null hypotheses of no constraint and no correlated evolution while acknowledging that valid rejection of these hypotheses becomes more difficult when all reconstructions are considered equi-
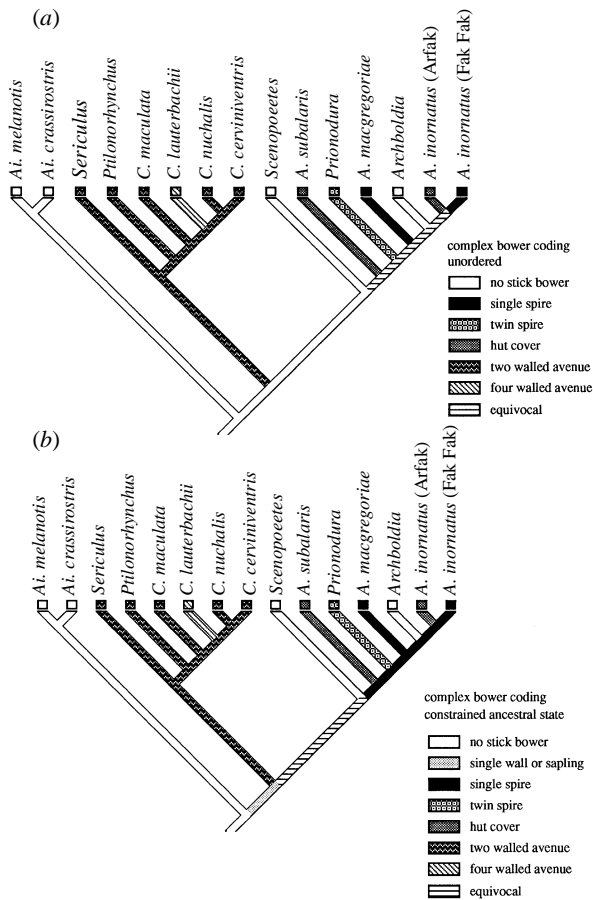
Figure 2. Evolution of bowers under a complex coding of character states. (*a*) Character types assumed to be unordered. Twelve equally parsimonious reconstructions of bowers exist for the maypole clade. (*b*) Character types are constrained such that a simple maypole or single wall bower existed prior to the divergence of avenue and maypole-builders, and that hut and twin spire bowers had first to pass through a single spire stage. Under this scheme hut bowers arose independently.

probable, particularly when combined with the reduced degrees of freedom associated with shared evolutionary history.

Little evidence for phylogenetic inertia as defined by Maddison (1990) was found in bowerbird display characters. Perhaps suprisingly we found more evidence for inertia in behavioural than morphological display characters. No morphological trait exhibited inertia. Among bower characters we found constraints operating on the use of avenue walls in bowers ($p = 0.008$), but not so the use of maypoles (although we found near significant constraint ($p = 0.066$) if we assumed that *Scenopoeetes*' court clearing around saplings constituted use of a maypole in bower design. Whether general bower form was constrained depended on our coding of bower design. When a simple three-state coding was used, consisting of no bower, use of maypole, use of avenue, we found significant inertia ($p = 0.010$) if bowers evolved twice. If we accept the reconstruction in which bowers evolved once, inertia becomes non-significant ($p = 0.063$). When more complex codings were invoked no constraint was observed. It seems therefore that bowers,

crests and brilliant body plumage are labile characters. Some constraint acts at the more fundamental level of bower design, but beyond this the characters seem to evolve free from the effects of their evolutionary history.

This freedom from phylogenetic constraint has a number of implications. It shows that display traits in bowerbirds do not make good characters for tree reconstruction beyond the clustering together of the avenue-builders and of the catbirds. The single maypole surrounded by a circular court is not sufficient to define a coherent group of related species: *Archboldia* (with no bower) and *Prionodura* (with two spires and a raised display perch) fall within the group of currently recognized *Amblyornis* species. We have demonstrated that previously presumed synapomorphies, such as hut-building in maypole-builders and crests in avenue-builders and sympleisiomorphies in display architecture (e.g. lack of stick bower), are in fact the result of convergence or reversals. This contrasts with Winkler & Sheldon's (1993) finding of concordance between molecular and behavioural phylogenies based on nest architecture in swallows, and suggests that when morphological or behavioural characters are subject to the strong and fluctuating pressures of sexual selection they can make poor phylogenetic markers. The lack of concordance between behavioural and molecular phylogenies in swiftlets (Lee *et al.* 1996), however, indicates that characters other than those that are sexually selected may also fail to accurately reflect phylogeny.

There is a second consequence of little observed phylogenetic constraint. Our findings lead us to propose that judiciously constructed comparative studies of courtship display in bowerbirds can be used effectively to test models of display evolution and sexual selection without the confounding factors of non-independence caused by shared evolutionary history. This is consistent with Borgia's (1995*a*) evidence for functional design in bowers and associated display traits in bowerbirds. For example, avenue and maypole bowers act as a barrier between males and females during courtship, allowing the female to leave if she is not prepared to mate. Although limiting the opportunity for forced copulations, the protection probably enhances female visitation at male courts resulting in a net increase in male mating success. In bowerless *Archboldia*, compensatory behaviours that produce functionally equivalent results have evolved. Male courtship involves males staying close to the ground, from where they are not able to force copulation with females; the vine curtains partitioning the court contribute by making males stay low in courtship chases. The sister group relationship between *Archboldia* and *Am. inornatus* indicates that such shifts between functional states may be quite rapid. In another case, bowers of *C. maculata* are divergent from those of close relatives in having an especially wide avenue separating thin, straw (instead of stick), see-through walls that are oriented so that the male displays into the bower wall instead of the bower entrance (Borgia 1995*b*). Males are highly aggressive in courtship display and the wide avenue allows the

female to look through the see-through wall to see the displaying male from a position that is safe from attack. The numerous changes that distinguish *C. maculata* from its close relatives are functional and coordinated in allowing males to present aggressive displays while maintaining reduced threat (costs) to visiting females. In both *Archboldia* and *Chlamydera* therefore, display differs dramatically from bower-building relatives. However, among species, display trait function is consistent in affording assessing females protection from forced copulations by courting males (Borgia 1995 *a*, *b*).

In bowerbirds it has been posited that there has occurred directional transfer of signal from plumage to bower. Ancestral species were assumed to build simple bowers and be dimorphic and that plumage dimorphism decreased as bowers became more complex (Gilliard 1969). Maddison's test of correlated character evolution revealed significant support ($p = 0.04$) for this transferral hypothesis in avenue-building species, with complex/large bowers being gained in branches leading to *C. cerviniventris* and *C. lauterbachii*, both of whom are drably plumed and crestless. No such association was seen between loss of plumage dimorphism and bower complexity in maypole-builders or all bowerbirds together (figure 3). These associations were also tested on the alternative, weighted maximum likelihood tree; results were unchanged. In *Prionodura*, there has been an increase in bower size in conjunction with an increase in plumage brightness. *A. inornatus* (Arfak) may be the only example of a maypole-builder in which bower size has increased and plumage brightness decreased, but the absence of huts with no increase in male plumage colour in Fak Fak populations of *A. inornatus* does not support this. Finally, *Archboldia* may represent a transferral of focus from bower to plumage. Significant correlation existed between the gain of body dimorphism and loss of display courts if courts were considered ancestral and plumage dimorphism evolved twice and was lost once ($p = 0.0294$), or the dimorphism was gained independently three times ($p = 0.0147$), providing further evidence for rejecting the idea that the shift of focus from morphology to behaviour is universal in bowerbirds.

What use might our independently derived phylogeny and character state reconstructions be in testing alternative models of sexual selection given that the inference of process from pattern is a challenging task? In the runaway model, drift along lines of equilibria that result from the opposing forces of natural and sexual selection on the male trait and female preference can produce bouts of rapid evolution. This has been cited as a potential cause of large-scale shifts in the degree of elaboration of male display traits (Lande 1981; Prum 1997) and an often accepted view is that runaway produces irregular patterns of evolution of male display traits (Arnold 1983; Kirkpatrick 1987). At first sight this appears to be reflected in our phylogeny. That covariance between male trait and female choice can exist in the evolution of sexually selected characters is not disputed, but whether a Fisherian process alone can be used to predict the type
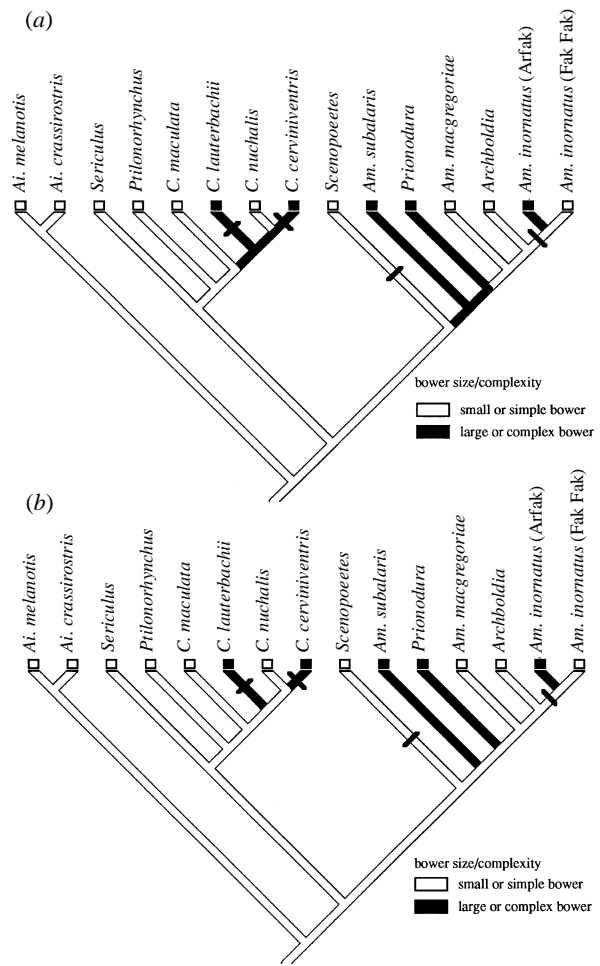

Figure 3. Evolution of large/complex bowers and the loss of plumage dimorphism. *Am. inornatus* (Arfak), *Am. subalaris*, *Prionodura*, *C.lauterbachii* and *C. cerviniventris* are considered to have large/complex bowers. By virtue of its similarity to the bower of *A. macgregoriae*, the maypole bower of *Am. inornatus* (Fak Fak) was deemed to be a non-complex bower. (*a*) Acctran resolution of bowers, deltran resolution of plumage dimorphism. Bold lines indicate loss of plumage dimorphism, considered ancestral according to Gilliard's transferral hypothesis. There are four losses of plumage dimorphism according to the reconstruction, two occurring on branches where complex bowers have arisen. (*b*) Deltran resolution of bowers, deltran resolution of plumage dimorphism. Four losses of plumage dimorphism occur, two on traced branches.

of changes that occur in display trait evolution is far less certain. More recently studies of sexual selection have shifted from the dichotomy of good genes versus runaway models, both of which represent indirect benefits, to begin testing the alternative dichotomy of direct versus indirect benefits (Kirkpatrick & Ryan 1991). Direct benefits can be of the form of material contributions of males to females, but may also be what Borgia (1979, 1995*a*) terms proximal benefits (for example, a bower operating to provide females with protection from forced copulations by males as they assess aspects of display). Recent demonstrations of proximate benefits processes occurring in bowerbirds (Borgia 1995*a*,*b*) are also consistent with the lack of morphological and behavioural constraints in bowerbirds demonstrated here.

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