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Animal art: Variation in bower decorating style among male bowerbirds *Amblyornis inornatus*

(cultural transmission/geographic variation/behavior)

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ABSTRACT **Courtship bowers of the bowerbird *Amblyornis inornatus*, the most elaborately decorated structures erected by an animal other than humans, vary geographically and individually. Bowers in the south Kumawa Mountains are tall towers of sticks glued together, resting on a circular mat of dead moss painted black, and decorated with dull objects such as snail shells, acorns, and stones. Bowers in the Wandamen Mountains are low woven towers covered by a stick hut with an entrance, resting on a green moss mat and decorated with colorful objects such as fruits, flowers, and butterfly wings. Young males build simpler bowers, and adult males differ among themselves. Experiments with poker chips of seven colors offered as decorations showed that individual birds prefer some colors over others, individuals and populations differ in these preferences, certain objects are placed in specific parts of the bower, and birds steal chips from neighbors. Bower style may be partly learned. Hence, geographically varying bower styles may be a culturally transmitted trait, like human art styles.**

Male bowerbirds of New Guinea and Australia build decorated structures termed bowers to woo females. The most complex bower—in fact, the most elaborately decorated structure built by an animal other than *Homo sapiens*—is that of the Vogelkop Gardener bowerbird *Amblyornis inornatus*. This species is confined to five remote mountains of Indonesian New Guinea that are hard to reach for political and logistical reasons: the Arfak, Tamrau, Wandamen, Kumawa, and Fakfak Mountains (1). Thus, only a few brief accounts of bowers in two of these mountains (Arfak and Tamrau) have been published (2–5).

This paper describes bowers of the Wandamen population and of the recently discovered Kumawa and Fakfak populations. Previous studies had shown that bower styles differ among the 14 bower-building species of bowerbirds (4, 6). It now turns out that styles also differ conspicuously between populations of *A. inornatus*. Within a population there are smaller differences between the styles of adults and immatures and of different adults. To confirm that these differences arise from intrinsic differences among birds rather than merely local differences in objects available for decorating bowers, I tested the decorating preferences of individual birds with standardized test objects: poker chips of seven different colors. Birds' choice and placement of chips agreed with many features of their use of natural decorations.

These bower style differences among populations beg the question as to how an individual bird acquires the style characteristic of its population. I suggest that bower style is not wholly innate but is partly learned, hence constitutes a culturally transmitted trait.

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BACKGROUND

Bowers are avenues, huts, or towers of sticks decorated with objects such as fruits, flowers, mushrooms, and stones. Males often hold a decoration in their bill while displaying to a female, and experiments confirm that bower structure and decorations influence females' choice of mate (7). Whereas males are polygynous and contribute nothing to the female after copulation, females perform the whole effort of building a nest and rearing the young. Species comparisons show that male bowerbirds with duller ornamental plumage build fancier bowers (4, 8). Thus, during bowerbird evolution the female's attention has been transferred from ornaments of the male's body to those of his bower. *A. inornatus* is the species with the dullest plumage (males and females identical, nearly uniformly brown) but with the largest and most elaborately decorated bower.

My studies in the Kumawa, Wandamen, and Fakfak Mountains were performed in February–March 1981 and August–October 1983. Bower sites in these uninhabited mountains lay at elevations of 1050–2075 m and were reached by cutting trails inland for 5–20 days from the coast.

NATURAL STRUCTURE OF BOWERS

Geographic Variation. *South Kumawa Mountains.* Bowers were spaced several hundred meters apart on ridge crests at sites well lit from the east, thus enhancing visibility during early-morning hours of peak display activity. Each bower incorporated one to five saplings ("maypoles"), about each of which was erected a tower 2–3 m high of interwoven sticks 20–90 cm long. Sticks were glued together at contact points with a white sticky substance (saliva?). Surrounding the sapling(s) was an almost perfectly circular mat of black dead moss up to 15 cm thick, with a diameter of 1.3–2.1 m and with the coefficient of variation of diameter in a given bower only 3%. (How a bird only 25 cm long lays out such a perfect circle is unknown.) At the base of each sapling was a cone of the same moss used for the mat.

All bowers of adult males had six types of decorations on or near the mat and segregated by type: pandanus leaves, each up to 2 m long and weighing up to 60 g (the bird weighs 120 g), dragged from a considerable distance and propped against a maypole at an angle of 30–45° or else laid on the ground; black elytrae of beetles; separate piles of hundreds of dark brown acorns, grey or brown snail shells, and dark brown stones; and a pile of black sticks from tree ferns and a substory tree. A whole bower and its decorations weighed several tens of kilograms. The piled sticks, elytrae, and moss mat and cone were naturally brown but in the bower were painted glossy black, apparently with an oily black substance in the bird's excrement. [Bower painting has been described previously for six species with avenue-style bowers (4, 6) but not for species with maypole-style bowers.]

Central Kumawa Mountains. At a site 8 km by air north of the bowers just described, and within the same mountain range, Franz Sadsuitubun found 25 bowers similar to the

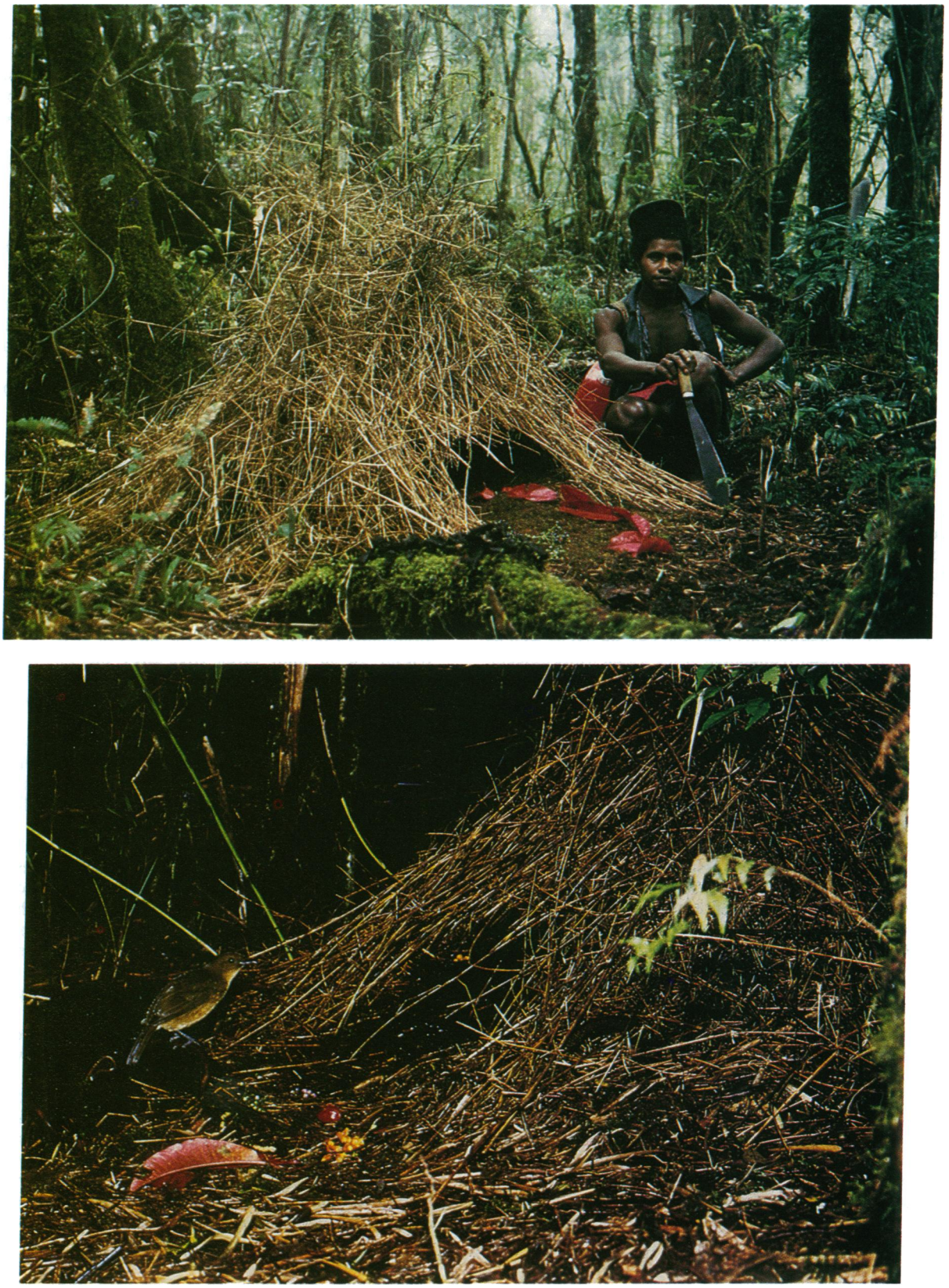

FIG. 1. (*Upper*) A Wandamen bower, showing hut, door, moss mat, red leaves and green fruit on the mat, and black bracket fungi on moss-covered root in foreground. (*Lower*) Bower owner on pile of black fungi facing door and hut, with red leaf, orange flowers, and red fruit outside hut, yellow fruits inside hut. (Photographs by J.D. and John Ratcliffe.)

south Kumawa bowers, except for being also decorated with colored fruits (red, yellow, green, blue, white, or black).

Fakfak Mountains. Bowers were not seen by me, but, as described by local New Guineans familiar with them, they are similar in structure and decorations to the south Kumawa bowers and lack colored fruits.

Wandamen Mountains. Wandamen bowers (Fig. 1) differed drastically from south Kumawa bowers. There were only one or two towers only 0.4–0.8 m high, of sticks woven but not glued together. Covering the towers was a woven stick hut 0.9–2.2 m in diameter with an opening ("door") that faced downhill regardless of the compass direction. The mat and cones were of live green moss, not of dead moss painted black. The sole decoration shared with south Kumawa bowers was beetle elytrae. A large pile of black bracket fungi was placed downhill from the door. Decorations of many colors lay on the mat or inside the hut, but details differed among bowers (see below): orange or black fungi of several types; red leaves; orange bark; red, orange, yellow, green, blue, grey, brown, or black fruits; red, orange, yellow, or purple flowers; and red, yellow, green, or black butterfly wings.

Multiples of the same object (e.g., red flowers) were loosely grouped, as were objects of similar color (e.g., orange fruits with orange fungi, red flowers with red leaves). Certain decorations besides black bracket fungi tended to be at specific locations—e.g., red leaves, black fruits, and orange flowers solely outside the door; butterflies solely and blue fruits mainly inside the hut. When I shifted the position of a decoration, the bower owner either restored it to the original position or else discarded it in the forest. Decorations changed from day to day as birds replaced wilting flowers and rotting fruits with fresh ones.

Arfak and Tamrau Mountains. As described by previous authors (2, 5), bowers in these mountains agree with Wandamen rather than Kumawa bowers, except that Tamrau bowers use white decorations (sap and egg shells) as well as colored ones, whereas Wandamen bowers lack white objects.

Age-Related Variation. Compared to bowers at higher elevation, low-elevation bowers in the Kumawa and Wandamen Mountains were smaller and simpler in structure and had few and atypical or no decorations. For example, the lowest south Kumawa bower (SK1) had the smallest mat and cone, had the lowest tower, and was unique in lacking decorations, and its owner was sloppy about removing wind-blown leaves from the mat. The lowest Wandamen bower had no decorations, the second-lowest had only a few bracket fungi and no hut, and the third-lowest had a small hut and spartan and aberrant decorations (rotten fruit and two acorns). Among many New Guinea montane bird species (including two *Amblyornis* species) young males are known to occur at lower elevations than adults (8–10), and young male bowerbirds are known to build rudimentary bowers compared to adults (11, 12). Hence, low-elevation bowers of *A. inornatus* probably belong to immature males.

Individual Variation. Bowers of presumably adult males at higher elevation varied in mat and hut diameter, tower height, number of maypoles, and ornaments, as noted previously for Tamrau bowers (4, 5). In the south Kumawa Mountains male SK5 mixed grey and brown snail shells in the same pile, SK4 placed them in the same pile but with the brown shells toward the center of the bower, and SK2 and SK3 put the grey and brown shells in separate piles. Whereas almost all birds used beetle elytrae, Wandamen birds W9 and W10 made a separate pile of beetle heads, which other males discarded. W4 specialized in orange objects (fruit, flowers, seeds), W5 in butterfly wings, W6 in yellow flowers, W8 in purple flowers, and W10 in orange fungus.

Relation of Decorations Chosen to Those Locally Available. This geographic, age-related, and individual variation in bower decorations is not just due to variation in locally available objects. For instance, all birds had access to beetle heads along with elytrae, but most discarded the heads. Acorns and snails were commonly available in the Kumawa and Wandamen Mountains and were used regularly by the hundreds at south Kumawa bowers but never at Wandamen bowers, except for two acorns at one bower. Conversely, colored fruits, flowers, fungi, and leaves like those used in the Wandamen Mountains were available within a few meters of south Kumawa bowers but were ignored. White karst stones were widespread in the south Kumawa Mountains but were used at only one bower, whereas only two Wandamen birds used the widely available orange bracket fungi. Thus, decorations are not a random sample of available objects: different populations and individuals select on the basis of different rules.

EXPERIMENTAL STUDIES OF BOWER DECORATION

As tools to identify decorating rules, natural objects have the disadvantages of nonuniformity and hard-to-quantify availability. As standardized test objects of known availability, I used numbered, glossy, circular poker chips of hard plastic, 4 cm in diameter, 7 g in weight, and of seven colors: red, orange, yellow, blue, purple, lavender, and white. Bowerbirds' preferences may depend not just on hue but also on saturation, lightness, and surface characteristics. In addition, their perceptions of color will depend on the spectrum of illumination, the background, and details of their visual system, which may differ from that of humans. Thus, though I shall describe experimental results in terms of poker chip hue and though the resulting preferences correspond well to many features of natural bower decorating, the interpretation may actually be more complicated.

Weeding and Harvesting Tests. In the south Kumawa Mountains I placed chips on the mats of bowers SK1–SK5. Within 10–30 min, birds SK2–SK4 picked up all chips regardless of color and discarded them in the forest ("weeded" them), whereas SK1 and SK5 left all chips in place. I then placed three chips of each color near each bower, but no bird ever took chips to decorate the bower ("harvested" chips). These responses correlate with south Kumawa birds' failure to use natural colored objects as decorations, with SK1's and SK5's sloppiness at keeping the mat clean of fallen leaves, and with SK1's presumed immaturity.

In the Wandamen Mountains I first tested the three lowest-elevation bowers, which were also the smallest, simplest, and least decorated and were inferred to belong to immatures. These three birds all failed to weed chips placed on their mats, regardless of color. W1 failed to harvest any chips placed nearby, and W3 did not begin to harvest until the fifth day of testing.

The remaining Wandamen bowers were at higher elevation, had various colored natural decorations, and were inferred to belong to adults. Weeding tests at bowers W4 and W5 showed that both birds quickly expelled white chips placed inside the hut; W4 also expelled yellow, while red, orange, blue, and purple were left in place (lavender was not tested). In harvesting tests at bowers W4, W5, W8, and W9 with sets of three chips of each color placed outside the hut at a distance of 1–5 m, all four birds repeatedly harvested almost all available blue chips, no white, and some of other colors to decorate the bower mat. The preference ranking averaged over the four birds was blue > purple > orange > red > lavender > yellow > white, but preferences for colors other than blue and white varied among individuals (Table 1). The second preference was purple (W4, W9), purple nearly tied with red (W8), or orange tied for first with blue (W5). The percentage of available lavender chips harvested varied among individuals from 0% to 75%; yellow, 0–66%; red, 20–83%.

When I placed chips near bowers W8 and W9 and remained to watch, the owners promptly began to harvest colors in a temporal sequence matching approximately the final sequence of proportions found harvested after 0.5–1 day. For

FIG. 2. (*Left*) (Underexposed): bowerbird with blue poker chip in beak, selected from pile of chips of seven colors. (*Right*) Mat and door of bower decorated with red leaves, green and orange fruits (bottom left), blue fruits and red flowers (top), and poker chips. Note grouping of chips by color and position of blue chips inside hut.

instance, W9 first harvested blue chips (Fig. 2 *Left*), then purple, then orange, then lavender followed by red (or vice versa), but never yellow or white. This temporal sequence is virtually the same as W9's rank sequence of harvested proportions (Table 1).

Theft and Destruction. At almost every bower some chips that I set out during harvesting tests disappeared, suggesting the possibility of theft by another bower owner. Hence, I traced thefts by numbering chips. When I placed three chips of each color at bower W6, bird W5 stole within 3 hr all blue, orange, and purple chips, two red chips, and no yellow, lavender, or white; by the next morning, all yellow and two lavender; the remaining one lavender and three white were not subsequently stolen. This preference sequence (blue, orange, purple > red > yellow > lavender > white) matches that of the harvesting test for bird W5 (Table 1). Bower W6 was unusual in that its sole conspicuous natural decorations were yellow flowers. The poker chip thefts suggest that bird W5 may have been stealing the usual blue, orange, purple, and red fruits and flowers from W6's bower, leaving only the less preferred yellow flowers.

Table 1. Color preferences of individual Wandamen bowerbirds

	Bird				
Color	W1	W4	W5	W8	W9
Blue	0	100	100	100	93
Purple	0	45	79	87	63
Orange	0	27	100	75	40
Red	0	25	73	83	20
Lavender	0	0	32	75	28
Yellow	0	0	66	20	0
White	0	0	0	0	0

Twenty-one poker chips (three each of seven colors) were placed near a bower. Shown are the percentages of chips of each color "harvested" by each bird (= found on the bower's moss mat 4–21 hr later), based on 6–11 trials per bird.

Interbower warfare was not confined to theft: when I trapped the adult male owner of a south Kumawa bower in a net, immature males repeatedly raided the bower, pulled sticks from the tower, stole decorations, and messed up the mat. Since male mating success in bowerbirds depends on the bower, the surest way for a male to impair a rival's sex appeal is to wreck his bower, as also observed for other bowerbird species (11, 12).

Wandamen birds also tried to steal other man-made objects to decorate bowers, such as my yellow Kodak film cartons (placed next to yellow fruits), blue matchbox (placed next to blue fruits), and black camera. Bird W9 hopped onto one of my field associate's shoes and tried to pull off his blue sock and brown shoelace.

Positioning. Wandamen birds often grouped chips of the same color with each other and with natural decorations of a similar color (Fig. 2 *Right*). In a few cases chips of different colors were stacked, and the color preferred in harvesting tests was generally placed on top. Among harvested chips, colors that were preferred (as judged by the harvested proportions in Table 1) tended to be placed inside the hut, with less preferred colors on the mat outside the door. For instance, the percentages of harvested chips placed inside the huts of birds W5, W8, and W9 were blue, 96% (Fig. 2 *Right*); orange, 79%; purple, 77%; red, 68%; yellow, 48%; lavender, 21%. The corresponding numbers for the proportions of available chips harvested by these three birds are very similar: 98%, 83%, 76%, 56%, 35%, and 33%, respectively.

Observations of birds showed that decorating decisions are not automatic but involve trials and "changes of mind." For instance, bird W9 initially brought red and lavender chips inside his hut and then eventually placed the red chip next to a red fruit in front of his door but discarded the lavender chip in the forest. W5 ignored available purple chips during his

first two tests, brought them inside the hut on tests 3 and 4, placed them outside the door on tests 5 and 6, and resumed bringing them inside on tests 7–10.

Comparison with Natural Decorations. These tests with poker chips show that *A. inornatus* males do select among potential decorations (possibly, but not provenly, by hue) and that different individuals and populations differ in their selection criteria. Poker chips elicit decisions similar to those elicited by potential natural decorations, as shown by numerous parallels: the undiscriminating behavior of low-elevation (presumed immature) Wandamen and Kumawa birds; use of colored poker chips and natural objects by Wandamen but not Kumawa birds; selective positioning (e.g., grouping by color or placing blue chips or fruits preferentially inside the hut); and selective theft. Since man-made objects can be standardized and have experimentally determined availabilities, they may offer advantages for analyzing bowerbirds' decorating decisions.

IS BOWER STYLE A CULTURALLY TRANSMITTED TRAIT?

How is geographic and individual variation in *A. inornatus* bowers maintained? There are two linked but separate questions: how males learn in what style to build and how females learn what style to prefer in choosing a male. Against a strictly genetic hypothesis (i.e., that bower style is wholly instinctive) stand the facts that populations of various mountains are almost identical morphologically despite their very different decorating styles (1) and that birds only 8 km apart in the Kumawa Mountains differ significantly in style (using vs. not using colored fruits).

I suggest that learning plays at least some role in bower style. Young male Satin and Macgregor's bowerbirds build bowers ineptly and with colors atypical of adults, spend much time watching old males at bowers, and take 4–7 years to develop the typical adult bower style (11, 12). A role of learning for *A. inornatus* males is tentatively suggested by the spartan, atypical bowers at low elevations, attributed to young males, and by the repeated testing of colored chips before settling on a final use. Young males may learn by watching older males or by discovering through trial-and-error what attracts females, or by both means. Females sometimes go about in groups to visit bowers, so that younger females might learn taste in bowers from older females (11, 12).

By this argument, geographically varying bower styles might be a culturally transmitted trait, like human art styles and bird song dialects (13). For instance, young Kumawa males would learn to gather snail shells and acorns, glue together stick towers, and paint the mat black, whereas young Wandamen males would learn to gather fruits and flowers, weave stick huts, and make a mat of live green moss. Individual style differences within a population may also be partly learned: a young male that often watches at the bower of an older male specializing in green butterflies may thereby learn to prefer green butterflies. These speculations can be tested by studies of cage-reared birds (what sort of bowers do they build if they cannot learn by observation?) or by study of a wild population for many years (do new fads arise and spread, as true for songs of birds and whales?).

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