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A Comparative Analysis of Courtship Movements in Closely Allied Bowerbirds of the Genus *Chlamydera*

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INTRODUCTION

Bowerbirds occur in Australia and New Guinea. Although they are closely related to birds of paradise, their ornamental plumage is largely limited to colorful crests, and, unexpectedly, the crests are lacking in certain species belonging to groups of closely allied species in which erectile, fiery orange or lilac-pink crests are characteristic.

Bowerbirds are unique in that they build ground structures of sticks in and around which they perform their courtship displays. These structures (the bowers) and their decorations are constructed and decorated in special ways depending on the species and its line of descent. At least four lines are involved: (1) the stage-building group, (2) the mat-building group, (3) the tower-building group, and (4) the avenue-building group. Groups 3 and 4 include species that build relatively simple towers or avenues composed of a moderate number of sticks and also species that build highly ornamented structures. Nevertheless, the latter remain clearly recognizable as to the group to which they belong. However, an important morphological difference occurs between the builders of the simple bowers and the builders of the elaborate ones: the builders of the elaborate bowers are the species in which the colorful crests are lacking!

Recently (1956) the writer called attention to the existence of this inverse ratio between the development of the bower and the develop-

ment of the sexual plumage. He postulated that it was due to the substitution of objects for bright plumage, presumably because objects are less of a liability than bright plumage to a ground-displaying bird. This hypothesis, which he called the "transferral effect," was based on an examination of study skins and of bowers.

NEW EVIDENCE FOR THE TRANSFERRAL EFFECT

In this paper a new line of evidence based on the comparative morphology of courtship movements is presented. Two closely allied species, one with and one without a crest, are compared as they display to their respective mates. Both are avenue builders. One, the Great Gray Bowerbird (*Chlamydera nuchalis*), was observed and photographed by John Warham in the Kimberley District of Western Australia in June of 1956. Males of this species have an iridescent, erectile, lilac, silver-tipped crest; females are generally crestless, except for a small percentage which have a reduced lilac-colored crest without silvery markings. The second species, which was watched by the writer, is the Fawn-breasted Bowerbird (*C. cerviniventris*). It was observed and filmed during a period of five days in the Finisterre Mountains of New Guinea, also in June of 1956. Both the male and the female of the Fawn-breasted Bowerbird are crestless and identical in appearance.

Because the essence of the transferral theory is that bright crests can be lost as a secondary result of the transfer of sexual signals from feathers to objects, it follows that the crestless species studied by the author may have evolved from stock which had crests such as are still worn by its nearest relatives. It also follows that if this should be the evolutionary history of the Fawn-breasted Bowerbird, some of its courtship movements may be such as to indicate the former presence of a crest.

In an attempt to unmask these movements, we referred to John Warham's (1957) observations of the crested species. Warham described the Great Gray Bowerbird as it displayed to a female at its bower as follows (1957, p. 75): "The male now stood just to one side watching the female round the side of the wall and apparently enticing her to enter the avenue. He began to display and suddenly opened the nuchal crest to reveal the lilac feathers which glowed like some exotic flower. His neck was bowed and the neck so bent that the color patch pointed in the female's direction [see fig. 1 of the present paper]; she must have been able to see it either through the tunnel of the bower or around the side of the wall. During the display the male held a piece of grass or the



FIG. 1. Stylized sketch showing male Great Gray Bowerbird (*Chlamydera nuchalis*) displaying his nuchal crest in the direction of the female. Based on a photograph (see fig. 2) and on a description, both by John Warham.

green bottle-top in his bill and, although he would remain motionless, occasionally with the head depressed, for most of the time this was jerked up and down rhythmically."

In the crestless species (the Fawn-breasted Bowerbird) I found that the male twisted its neck in a most unnatural way so that the back of



FIG. 2. Photograph of Great Gray Bowerbird. Male at bower. Female behind bower. See legend for figure 1.

its head was aimed towards the female (fig. 3). This action, although not of uncommon occurrence in the preliminary phases of courtship, became very uncommon as the display neared a climax. In making the awkward twisting motions, the male stood at one end of the bower

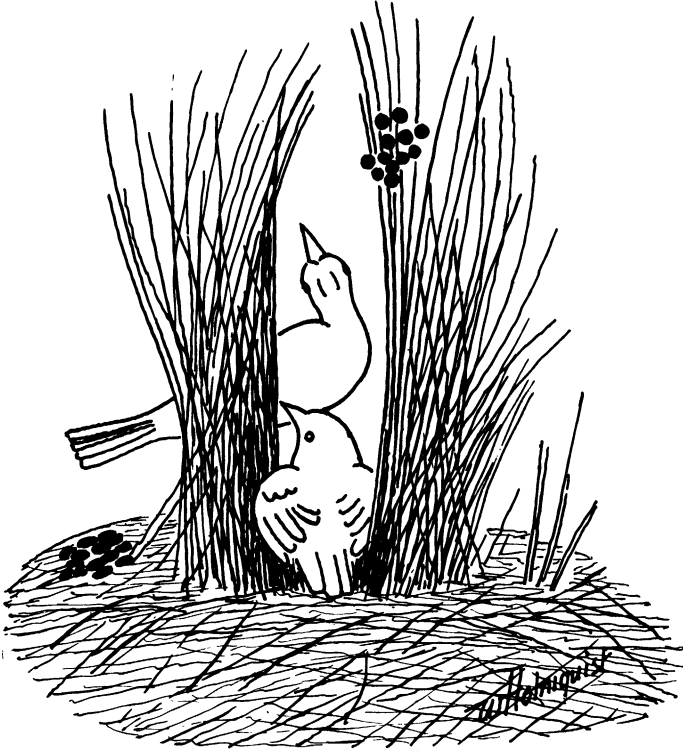


FIG. 3. Stylized sketch showing male Fawn-breasted Bowerbird (*C. cerviniventris*) turning crestless nape of head towards female. Based on studies of a 16-mm. film (see fig. 4 for one frame of this film).

and slightly to the side of the bower avenue. As the female approached, the male twisted the neck so that the top rear of its head faced in her direction. Even after she entered the bower and assumed a crouching position (fig. 3) the male occasionally showed the back of its head as though to display a nuchal crest. However, at this stage most of the male's movements were devoted to displaying with a large green berry or with a spray of small green berries. These he held in his bill and rapidly shook up and down, with his head pointed generally towards the female.

REMARKS

Warham's description of the head-twisting, crest-displaying movements of the Great Gray Bowerbird is an excellent example of the correlation between movement and bright feather structures which is a

not uncommon phenomenon in birds. Movement, which stems from motor patterns of the nervous system, is thought to be the more conservative. In other words, it is presumed to have a greater phyletic age than the organs (the feather structures) correlated with it. Therefore, in the case of the bowerbird's ornamental headdress, we must assume that movement preceded the acquisition of the crest and quite probably persisted after its loss. Because of this durability of movement



FIG. 4. One frame of a 16-mm. film of the courtship behavior of the Fawn-breasted Bowerbird (see fig. 3). The female (in bower) is able to see the male where he is standing. Owing to the "flattening" effect of telephoto-photography, an optical illusion is created which gives the appearance that the left wall of the bower screens the two birds.

over structure, one must ask if perhaps, instead of having been lost, the crest of the Fawn-breasted Bowerbird failed to develop, and why, if it did develop, it was discarded if movements correlated with crest display were retained.

In answer to the first question, judging from the morphology of closely allied species of bowerbirds and from the peculiar head-twisting movements of the courting males, it seems likely that the Fawn-breasted Bowerbird is descended from a stock in which the males wore crests. In

answer to the question as to the loss of the crest despite the retention of certain crest display movements, the movements correlated with display may (indeed should) have also undergone modifications, with the result that the movements correlated with the display of the crest have not persisted unaltered but are vestigial. Indeed it is probable that they were reduced through the redirection of crest-displaying movements to berry-exhibiting motions as a result of the transfer of sexual signaling from colorful feathers to colorful objects.

CONCLUSION

Both species display with objects in their bills, but only in the bird without a crest do the objects play a major part in the display. In both species head twisting appears to be for the purpose of displaying sexual plumage, but in the crestless species the head twisting is seen only as a vestigial movement. These facts support the theory of the transfer of sexual signals from plumage to objects, together with its hypothetical effects on the morphology of male bowerbirds.

SUMMARY

A comparative analysis of the courtship movements of two closely allied species of bowerbirds is presented. One male of a dimorphic species, the Great Gray Bowerbird (*Chlamydera nuchalis*), possesses a bright nuchal crest; the other, belonging to a monomorphic species, has no crest. Both were observed to display with the back of the head turned towards the female in an awkward manner, apparently intended to show the crest. The crested species displayed vigorously with the crest and to a minor degree with ornaments held in the bill; the crestless species displayed vestigially with the non-existent crest and then vigorously with ornaments held in the bill. The hypothesis is advanced that the vestigial head-twisting movements indicate that the crest has been secondarily lost as a result of the transfer of sexual signaling from sexual plumage to sexual objects. This hypothesis is presented as a second line of evidence for the transferral theory, a theory, based on an examination of study skins and of bowers, that presumes to account for the inverse ratio existing between the development of sexual plumage and the development of the bowers in certain species of the Ptilonorhynchidae.

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