

THE BOWING DISPLAY OF PIGEONS IN REFERENCE TO PHYLOGENY

DEREK GOODWIN

IN his discussion of the relationships of the American ground doves Johnston (1961: 375) states that the "bow-coo" (bowing display) "is the only one of the series of acts [of courtship and pair formation] that is species-specific . . ." and that it "can be expected to become subject to intense selection to form an effective isolating mechanism." He quotes Lorenz to the effect that female Collared Doves (*Streptopelia decaocto*) and female Barbary Doves (*S. "risoria"*) do not respond to the bowing display of the male F₁ hybrids and concludes (p. 376) that "the bow-coo cannot be used as evidence for or against close relationship in doves, especially at generic level." I do not question Johnston's conclusions where they affect the generic position of *Columbina* (or *Columbigallina inca*) (formerly *Scardafella inca*). Nor do I suggest that generic status should stand or fall on the basis of the bowing display alone when this suggests conclusions opposite from those indicated by other characters. I do, however, think that the form of the bowing display is usually rather more conservative than otherwise, except in its finer details, and that it may often give a true indication of phylogenetic affinities.

OBSERVATIONS

I have seen the bowing display (or its homologue) in the following species: Turtle Dove (*Streptopelia turtur*), Collared Dove (*S. decaocto*), African Collared Dove (*S. roseogrisea*) [and its domestic descendent the Barbary Dove (*S. "risoria"*)], Mourning Collared Dove (*S. decipiens*), Red-eyed Dove (*S. semitorquata*), Red Collared Dove (*S. tranquebarica*), Spotted Dove (*S. chinensis*), Laughing Dove (*S. senegalensis*), Rock Pigeon (*Columba livia*), Speckled Pigeon (*C. guinea*), Wood Pigeon (*C. palumbus*), Trocaz Pigeon (*C. trocaz*), Stock Dove (*C. oenas*), Picazuro Pigeon (*C. picazuro*), Mourning Dove (*Zenaida [or Zenaidura] macroura*), Eared Dove (*Z. auriculata*), White-bellied Dove (*Leptotila jamaicensis*), Blue-headed Quail Dove (*Starnoenas cyanocephala*), Luzon Bleeding-heart (*Gallicolumba luzonica*), Blue-headed Wood Dove (*Turtur brehmeri*), Scaly Dove (*Columbina squammata*), Diamond Dove (*Geopelia cuneata*), Bar-shouldered Dove (*G. humeralis*), Zebra Dove (*G. striata*), Common Bronzewing (*Phaps chalcoptera*), Crested Pigeon (*Ocyphaps lophotes*), Plumed Pigeon (*Lophophaps plumifera*), Wonga Pigeon (*Leucosarcia melanoleuca*), and Green Imperial Pigeon (*Ducula aenea*). I have also seen what may have been the bowing display from the Pied Imperial

Pigeon (*Ducula bicolor*) and the Black-naped Fruit Dove (*Ptilinopus melanospila*) but in these cases I am not certain whether the movements were the true homologues of the bowing display, although I think it possible. My remarks will refer to the above-listed species, and my own observations on them, except when otherwise stated.

DISCUSSION

In *Streptopelia* the bowing display involves a downward movement of the head and foreparts with the coo given simultaneously. The tempo of the bow and its accompanying vocalization vary specifically (see Goodwin, 1956, for detailed description for most of the species listed) as do the precise degree of inflation of the neck and erection of its feathers and the position of the head at the culmination of each bow. The details of these last two features are closely dependent upon the position and type of display plumage exhibited. In spite of specific differences there is a strong over-all resemblance between the bowing displays of all the species of *Streptopelia*; this resemblance is especially evident when comparisons are made with other genera. It seems worth remarking on the fact that no *Streptopelia* erects or spreads its tail in its bowing display as do *Geopelia* and "*Scardafella*" with their very distinctively patterned and quite similar tails. Since the individuals of *Streptopelia* often throw their tails up when alighting and spread them very widely in their display flights, one might expect tail-raising or tail-fanning to have been incorporated in the bowing display of one or more species had there been intense selection for species-specific differences in the form of this display.

The bowing displays of *Columba palumbus* and *C. oenas* appear to be identical in form although the coos differ in sound and the movements used in the initial approach to the bird to be displayed to may also differ. In both species (except when the displaying bird is running or walking after another bird and displaying at the same time) it involves a deep bow and a raising of the tail. As the tail goes up it opens and then closes again and is nearly always closed by the time it reaches its highest elevation at the culmination of the bow. Many characters of *C. oenas* suggest that it is closely related to *C. palumbus* (Goodwin, 1959) although *oenas* differs from that species in ecology, in gait and proportions is rather nearer to *C. livia* and, like the latter and unlike *C. palumbus*, it does not throw up its tail a few seconds after alighting. The bowing display of *C. trocaz* is very similar to that of *palumbus* and *oenas*. In view of the obviously very close relationship of *trocaz* and *palumbus*, this might be expected although, in view of their apparent sympatry, the resemblance suggests that there has been little or no selection pressure for species-specific differences in the bowing display.

The bowing displays of *C. livia* and *C. guinea* are very similar to one another, although they differ in some details (Goodwin, 1956). Together with other behavioral and morphological characters they suggest a close relationship between these two species in spite of their considerable color differences (Goodwin, 1956a). Unlike *C. oenas* and *C. palumbus*, which are widely sympatric, often nest within sight of each other, and may even indulge in interspecific territorial fighting, *C. livia* and *C. guinea* are allopatric over by far the greater part of their ranges. Hence it must be admitted that, in their case, had similar ecologies and body proportions tended to result in convergence in the forms of their bowing displays there could have been little opportunity for selection against this because of any need for species-specific displays.

The bowing display of *C. picazuro* (Goodwin, in press) does not closely resemble that of any of the above species, nor those of two other Old World forms, the Snow Pigeon (*C. leuconota*) and the White-throated Pigeon (*C. vitiensis*), as described by Newman (1910, 1911). It does, however, closely resemble that of the Spotted Pigeon (*C. maculosa*) as described by the then Marquis of Tavistock (1914: 126-127), a species to which its plumage characters and geographical range suggest that it may be closely related. Thus, the bowing displays of these two species tend to confirm the opinions reached independently by Johnston and myself (Johnston, 1962; Goodwin, 1959) on the basis of morphological characters.

In *Phaps chalcoptera*, *Ocyphaps lophotes*, and *Lophophaps plumifera* the bowing display involves raising and spreading of the tail and a partial opening of the folded wings so that the iridescent wing markings are presented frontally. Seen from "pigeons-eye view," just in front of and on a level with the displaying bird, the sudden flash of color, even in *Lophophaps* (whose wings are less richly ornamented than the others), is striking. From the available descriptions it is evident that the bowing displays of *Geophaps* (Newman, 1908: 338; Tavistock, 1914: 131) and of the Brush Bronzewing, *Phaps elegans* (Seth-Smith, 1904: 266), are essentially similar. Their distribution and plumage characters suggest that the Australian bronzewings have all been derived from a common ancestor subsequent to the arrival of the latter in Australia. If this is so we have in these birds a group of species whose members, through adaptive radiation, vary greatly in size, shape, ecology, and general coloration, but which show no comparable differences in the forms of their bowing displays. Here, therefore, the latter are again a good indication of affinities. The alternative hypothesis, that is that the Australian bronzewings are polyphyletic and have all, in spite of differences of size, shape, and ecology,

developed fundamentally similar forms of display plumage and identical or nearly identical forms of bowing display, seems to me most unlikely.

In the species of *Geopelia* and *Leucosarcia melanoleuca*, the birds erect and spread the tail in their bowing displays but do not open and present the wings. I think, nevertheless, that their bowing displays, taken together with their distribution and some other aspects of their behavior (Goodwin, 1960), indicate a close affinity between them and the bronzewings. The loss of the wing-opening component of the bowing display could be an expected correlate of the loss of the iridescent wing markings if, as I think, *Geopelia* and *Leucosarcia* are offshoots from bronzewing stock. In this connection it might be mentioned that, although the tails of *Geopelia* are long and very conspicuously marked, this is not true of all the bronzewings or, indeed, of some other pigeons which also raise and spread the tail in the bowing display.

In *Gallicolumba luzonica* the bowing display consists of throwing the head upward and backward and presenting the upthrust breast with its "bleeding heart" fully exposed to view. The display of *G. crinigera* is, apparently, identical (Newman, 1909: 225). It would be interesting to learn the bowing displays of *G. rufigula* and *G. tristigma*, which are obviously closely related to the bleeding-hearts but do not possess similar ornamental breast plumage.

The bowing display of "*Scardafella squammata*" is like that of *inca* as described by Johnston (1960). Johnston implies that other *Columbina* [or *Columbigallina*] species do not raise the tail in this display so here we evidently have a case where the form of bowing display does not appear to indicate phylogenetic affinities. It is possible, however, that certain affinities of these ground doves (and of other pigeons elsewhere) may be obscured by size differences. Tail raising in the bowing display occurs in some other American pigeons that may not be so far from "*Scardafella*" as their appearance suggests. The bowing display of the White-winged Dove (*Zenaida asiatica*) involves raising and spreading of the tail, although the latter is only open for a moment and then closed again (Wetmore, 1920). The bowing display of *Starnoenas* I have only seen once, so I am not sure if what I saw was typical. The bird bowed its head and raised and fanned its tail in a manner very similar to that described by Jones (1948) for the Ruddy Quail Dove (*Geotrygon montana*). This might well indicate affinity between these two American genera but more information on the bowing displays of other species of *Geotrygon* is needed.

The bowing display, or rather its homologue, in *Zenaida macroura* and *Z. auriculata* is identical and consists of standing and cooing with considerable inflation of the neck. That of *Leptotila jamaicensis* is similar to

this, except that the bird stands in a more horizontal posture with its head more lowered. The affinities of *Leptotila* are rather obscure but are almost certainly with other American genera and the form of bowing display of *jamaicensis* may be one indication of this. The bowing display of *Turtur brehmeri* also consists of standing still and cooing, but after having first made several movements in which the head is deeply lowered so that the underside of the bill touches, or nearly touches, the belly. Whether the similarities of their bowing displays indicate any fairly close relationship between *Turtur* and *Zenaida* or is merely due to convergence must at present be an open question.

The bowing display of *Ducula aena* consists of a movement in which the head is lowered quickly onto the breast so that the crown and nuchal region (which in some forms of the species has a contrasting patch of color) is frontally presented. The head movements that I saw from *Ducula bicolor* and *Ptilinopus melanospila* were very similar to the above, and in the latter species served to exhibit its black nuchal patch. I am, however, doubtful as to whether these posturings of the two latter were homologous with the bowing display of other species.

I have here used such terms as "form of bowing display" to mean the movements and postures involved. This meaning seems implicit in many of Johnston's observations in reference to "*Scardafella*." The cooing that accompanies the bowing display must also be considered. This may function as an isolating mechanism, but I doubt if it is one of major importance because in many species the differences between their display coos are, at least to human ears, much less marked than the differences between their advertising coos (perch coo, song). Often the display coo sounds blurred or muffled (e.g., *Streptopelia semitorquata*), is extremely faint (e.g., *Columba oenas*), or is subject to considerable individual variation (e.g., *Columba palumbus*). Females of *C. livia*, *C. oenas*, *Streptopelia risoria*, and *Streptopelia senegalensis* that have seemingly considered themselves paired to me did not respond more intensely to my imitations of their species' display coos than they did to human words spoken in rather similar tones. Lorenz's findings that females of *S. decaocto* and *S. risoria* did not respond to the bowing display of the F₁ hybrids is surprising in view of the frequency with which these forms form mixed pairs when they come into contact. Their bowing displays and other posturings seem identical, but their display coos and all their other vocalizations except the distress call sound very different. At the moment of writing (March, 1964) there is in the London Zoo a male *decaocto* paired to a female *roseogrisea* (wild form) and I am told that this pairing took place even though a male *roseogrisea* was present in the aviary. Also *C. oenas* and *C. palumbus* form mixed pairs rather readily in captivity and if one

factor facilitating this is the seemingly identical (or very similar) form of their bowing displays this suggests that other factors function to prevent such interspecific pairing in the wild.

I think it highly likely that in some species the colors and color pattern exhibited in the bowing displays may function as a "last-ditch" hindrance to interspecific pairing. There are several closely related sympatric species that show striking differences in head or neck color, or both, although they are similarly colored elsewhere. In the case of *C. oenas* and *C. palumbus* a very great difference in the appearance of the displaying bird, seen "pigeon's-eye view," is dependent mainly on the white neck patches of *palumbus* and the very different irises, which are blackish-brown in *oenas* and yellow in *palumbus*. On the other hand, in some related and sympatric pigeons, such as the ring-necked African species of *Streptopelia*, the color differences, even of the head and neck, are very slight. Judging by the readiness with which these forms often interbreed in captivity it seems probable that their color differences are also negligible to avian eyes and that, in a wild state, other factors prevent interspecific pairing, for one thing, probably a wider and freer opportunity for the selection of mates. Probably their very different-sounding advertising coos play a large part here.

CONCLUSION AND SUMMARY

In many pigeons the form of the bowing display is very similar or seemingly identical in related species, even when these show considerable morphological divergence. Selection for species-specific recognition marks appears often to have influenced the display plumage, and perhaps also the iris color, to a much greater extent than it has the movements involved in display. The form of the bowing display cannot be dismissed as of little or no account *per se* but must be considered at least as likely to indicate phylogenetic affinities as any other character.

LITERATURE CITED

- GOODWIN, D. 1956. Observations on the voice and displays of certain pigeons. *Avicult. Mag.*, **62**: 17-33, 62-70.
- GOODWIN, D. 1956a. Remarks on the Rock and Speckled pigeons. *Bull. B.O.C.*, **76**: 6-9.
- GOODWIN, D. 1959. Taxonomy of the genus *Columba*. *Bull. Brit. Mus. (Nat. Hist.) Zool.*, **6**: 1-23.
- GOODWIN, D. 1960. Some observations on the Diamond Dove. *Avicult. Mag.*, **66**: 97-105.
- GOODWIN, D. 1964. Some calls and displays of the Picazuro Pigeon. *Condor*, **66**: 418-422.
- JOHNSTON, R. F. 1960. Behavior of the Inca Dove. *Condor*, **62**: 7-24.
- JOHNSTON, R. F. 1961. The genera of American ground doves. *Auk*, **78**: 372-378.

- JOHNSTON, R. F. 1962. The taxonomy of pigeons. *Condor*, **64**: 69-74.
- JONES, T. 1948. The Red Mountain Dove. *Avicult. Mag.*, **54**: 48-50.
- NEWMAN, T. H. 1908. Nesting of the Partridge Bronzewing Pigeon. *Avicult. Mag.*, New Ser., **6**: 337-343.
- NEWMAN, T. H. 1909. Bartlett's Bleeding-heart Pigeon. *Ibid.*, **7**: 225-234.
- NEWMAN, T. H. 1910. Nesting of the White-throated Pigeon. *Avicult. Mag.*, 3rd Ser., **1**: 158-164, 193-195.
- NEWMAN, T. H. 1911. The Snow Pigeon. *Ibid.*, **2**: 173-178.
- SETH-SMITH, D. 1904. Notes on the habits in captivity of the Brush Bronzewing Pigeon. *Avicult. Mag.*, New Ser., **2**: 211-214, 263-266.
- TAVISTOCK, MARQUIS OF. 1914. Foreign doves at liberty. *Avicult. Mag.*, 3rd Ser., **5**: 123-132.

British Museum (Natural History), Cromwell Road, London, SW 7, England.