

THE AUK

A QUARTERLY JOURNAL OF ORNITHOLOGY

VOL. 90

OCTOBER 1973

No. 4

NOTES ON THE BEHAVIOR OF THE WHITE BELLBIRD

BARBARA K. SNOW

LITTLE has been recorded of the White Bellbird (*Procnias alba*) in the field. In March 1960 I made brief observations on a single adult male in the Kanaku Mountains of southern Guyana, but my description of the displays was very incomplete (B. K. Snow 1961, *Auk* 78: 150). In 1970 I again had the opportunity to return to the Kanaku Mountains. This time my husband and I camped for nearly 3 months by Karusu Creek, a tributary of Moco Moco Creek, about 5 miles northwest of Nappi Creek where the earlier observations were made. Since my last visit I had completed a 3-year study of the closely related Bearded Bellbird (*Procnias averano*) in Trinidad (B. K. Snow 1970, *Ibis* 112: 299).

Adult males of the Bearded Bellbird are sedentary and advertise themselves by loud calls from the same perches in the forest throughout the year except for the molt period. The females, who alone tend the nest, visit the males on their display perches to mate, which is the only association between the sexes. This species is entirely frugivorous, even the nestling being fed only on fruit. In view of the apparently close relationship of all the four species of *Procnias*, the same kind of behavior and ecology is to be expected in the White Bellbird.

The male White Bellbird is one of the few land birds with an entirely white plumage. The wattle growing from the base of the upper mandible does not stick upwards, as shown in early illustrations of the species, but hangs down and is extensible. The female is olive-green above, whitish-yellow with darker streaks below, and lacks the wattle.

POPULATION AND MOVEMENT

From 16 January to 6 April I kept daily records of the number of White Bellbirds calling along the first forested mile of the Karusu Valley, and made weekly visits and records of the numbers calling between 1 and 2 miles up the valley. I estimated that there were approxi-

mately 14 different males, about half of them adults, heard or seen along the whole of the 2-mile stretch. It was not possible to make any assessment of females, who apparently are silent. The female Bearded Bellbird also is entirely silent. There was some calling throughout the time we were present, but individual males were by no means sedentary. When observations began we heard much calling from the tongues of hilly country on either side of the Karusu Creek where it emerges into the flat savanna country. But birds soon stopped calling there and slowly moved up the valley deeper and higher into the mountains, so that by the first week of April there was no calling along the first 2 miles of Karusu Creek, measured from its emergence into the flat country. By this time, from a point about $2\frac{1}{4}$ miles up the creek calling males were just audible higher up the mountain slopes.

Our visit coincided with the end of the dry season. Rain fell only on 12 and 13 February, 9 and 10 March, and from 23 March until we left. It seems probable that the movement of the Bellbirds was due to the effect of drought, which apparently reduced the abundance of fruit in the lower part of the valley. The fruits taken by another cotinga, the Capuchinbird (*Perissocephalus tricolor*), were studied in the same area of the Kanaku Mountains at the same time (B. K. Snow 1972, Ibis 114: 139), and there was evidence of a relative scarcity of fruit at the end of the dry season. Except for the molting recess, the only time the adult male Bearded Bellbirds studied in Trinidad deserted their calling territories was once towards the end of an unusually severe dry season.

In spite of this general movement, some adult White Bellbirds appeared to occupy fixed areas over a considerable period. A group of three to four adult males, one of whom was easily visible and could be regularly checked at the same calling perch, occupied the same patch of forest for 6 weeks after our arrival. It was interesting that after these adults moved up the valley, immature males then occupied the same forest, and in some cases the same actual perches that the adults had just vacated. They remained there for several days before moving in the wake of the adults up the valley. A comparable situation was found in the Bearded Bellbird: the immatures occupy forest on the fringes of that occupied by the adults, but the moment the latter desert their calling territories (in this case to molt) the immature males take them over.

THE CALLS AND THEIR VARIATIONS

The White Bellbird has two basic calls. One is a very musical two-syllabled "doing-doing" or "dor-ong" (Quelch 1892, Timehri N. S. 6: 164) uttered while the bird is stationary with a single opening of the beak. This call, referred to below as the the musical call, does not carry so

far as the other call, which is a sharp bell-like "ding-ding" or "kong-kay" (Quelch 1892, *ibid.*) referred to below as the bell call.

The adult male watched in 1960 always accompanied his bell call with a swinging display from the right to the left (Snow 1961, *ibid.*), and this was erroneously assumed to be the normal behavior. Studies of a number of different males at Karusu Creek showed that most males uttered two types of bell call, one accompanied by a swing of the head and body and one with the head and body kept still. In both types of call the two syllables are produced with a single opening and closing of the beak. The motionless bell call sounds less staccato and loud than the bell call with a swing, a difference that can be easily distinguished by ear when the calling bird is not visible. In the bell call with a swing the male leans well forward and to his right, then opens the beak wide to utter the first "ding" and, with beak still open, rotates his body rapidly through approximately 100° to utter the second "ding" facing to the left. While swinging from right to left, the wattle flies out almost horizontally. To prevent the wattle accidentally entering the wide-open gape as the bird swings round, it must be hanging on the right of the beak when the call starts. All the males seen clearly in the study area, a minimum of nine different birds, normally had the wattle hanging to the right of the beak and all, when uttering the bell call with a swing, invariably did the first "ding" to the right followed by one to the left. The same invariable right-to-left swing was noted in the Nappi Creek male in 1960, and in a captive adult male by Quelch (1892, *ibid.*).

The reason for the rigidity of this behavior is apparent from the sequence of events that take place when a calling male is visited by another male or by a female (see below).

The musical call and the bell call normally alternate in a regular way during a bout of calling. Typically one or occasionally two or more musical calls are followed by one, two, or three bell calls. These proportions varied from one bird to another, but remained relatively constant in individual adults and so were a useful aid to individual identification. There were other variations: one adult male uttered a single-syllabled musical call, a slightly longer "d-oi-ng," and delivered all his bell calls with the swinging display. Neither of these characteristics was found in the other calling males heard in the vicinity. This bird also had a high proportion of musical calls. The percentage of musical calls to total calls on the five different occasions when its calling pattern was recorded were 61, 61, 65, 67, and 74% (totals of 44, 54, 59, 146, and 29 calls recorded). Another adult male, seen over 6 weeks at the same calling perch, had a consistently low proportion of musical calls, between 29% and 40% (total 120 calls recorded), and on an average

TABLE 1
DIURNAL CALLING REGIME OF AN ADULT MALE THROUGHOUT ONE DAY¹

Time	Total calls	Percentage of bell calls	Percentage of bell calls with a swing out of total bell calls
07:00-08:00	39	64	20
08:00-09:00	70	60	28
09:00-10:00	101	58	22
10:00-11:00	147	59	11
11:00-12:00	51	60	0
13:00-14:00	27	57	0
14:00-15:00	53	58	0
15:00-16:00	48	56	7
16:00-17:00	53	59	32

¹All calls were recorded for 10-30 minutes of consecutive calling in each hour except the midday hour.

only 20% of his bell calls were delivered with the swinging display. The calling pattern of another adult male was noted for 10 to 30 minutes in every hour throughout a day (07:00 to 17:00) except for the midday hour. The results show an extremely consistent proportion of musical to bell calls (Table 1). This bird also showed a diurnal variation in the proportion of swinging bell calls, with the highest proportion in the morning and evening. This is an interesting point of comparison with the male Bearded Bellbird, whose loudest and most far reaching call, the "bock" call, is uttered most frequently at the beginning and the end of the day. From a study of the spectrograms D. W. Snow (pers. comm.) considers the Bearded Bellbird's "bock" and the White Bellbird's bell call to be homologous.

On several occasions when two or three males were audible to each other they timed their bell calls to follow each other and not overlap. Two other species of cotinga in which groups of males advertise themselves with loud calls, the Capuchinbird and the Screaming Piha (*Lipaugus vociferans*), also adjust their calls so that they do not coincide (Snow 1961, *ibid.*; 1972, *ibid.*).

Males were most often seen calling from perches at the level of or above the canopy, often from a dead branch or from a tree that was temporarily leafless so that the calling bird was visible from a distance. These exposed perches were used most frequently in the early morning and from midafternoon until calling stopped, usually around 17:20. Most adult males also called from perches beneath the canopy, particularly during the middle of the day. As they were much more difficult to watch under the canopy, few observations were made, but three different perches seen used were all horizontal perches free of the surrounding vegetation, some 60-70 feet above the ground.

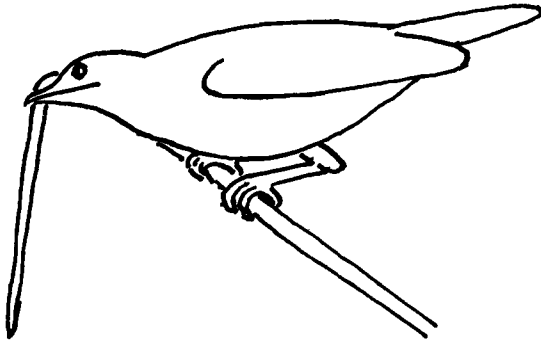


Figure 1. Adult male in the silent wattle-displaying posture.

FLIGHT DISPLAY

When calling from their exposed perches, adult males may periodically fly to a nearby perch and back again. The bird lands from these short display flights with his tail fanned and keeps it spread for a second or two. Perches between which flight display was made were on the same level and approximately 7 to 8 feet apart. One was the bird's regular calling perch; only an occasional call was made at the other perch, and usually the flight there and back would be silent. Once an adult was stimulated to start the flight display by the arrival of two immatures into the same very large tree where he was calling. Neither visitor was very near him. An adult calling beneath the canopy was seen to make a similar flight display only once, probably because few observations were made at these perches.

The male Bearded Bellbird has a more ritualized display flight or leap between two branches about 4 feet apart. Typically the display is silent, performed beneath the canopy, and initiated by the arrival of a visitor. On landing from the display leap the tail is fanned and kept spread for 5 to 8 seconds.

VISITING BEHAVIOR

A calling male is often visited by other males, both adults and immatures. A total of seven such visits were seen. All took place at perches above the canopy and all lasted less than 6 minutes except for a 25-minute visit of a juvenile male to an adult male. Only once was a female seen visiting a male. The incident took place at a perch beneath the canopy and is described in detail below.

A calling adult male immediately falls silent when a visitor arrives in the same tree, but once an immature visited by a juvenile male con-

tinued to call. Visiting birds were never heard to call. Visitors usually first land at some distance from a calling male and after a minute or two move to the same branch with him. If the visitor is not on the left side of the occupying male, the latter turns on his perch to put the visitor on the left. He then leans well to the right with the wattle hanging down below the perch (Figure 1); some males spend several minutes in this position shaking the wattle. The occupying male finally utters a bell call with a swing from right to left and so directly toward the visitor. The visitor reacts by fluttering several feet away or flying right away. If he only flutters a few feet, he often returns and the performance is repeated a number of times.

On 2 March the calls of an adult male, who was easily audible but most of the time was not in view, were recorded throughout most of the day. A regular pattern of 20 to 30 minutes of calling, followed by 5 to 10 minutes of silence, persisted up until 14:22 when the calling stopped except for occasional bell calls with a swing. On going to investigate the change, I found a female-plumaged bird with the male. I believed it to be a female and not a juvenile male because only the one adult called in the vicinity all day. Juvenile males, like adults, are persistently vocal. The visit continued for 20 minutes and was entirely silent except for the male's occasional bell call with a swing. Both birds were beneath the canopy on a thin horizontal liana about 65 feet above the ground. The male was perched leaning to his right with his head below the level of his back and tail (Figure 1). To his left was an uncluttered section of horizontal liana. The female, already on the male's left, then approached with small side steps along the liana towards him. When she was 2 or 3 feet from him the male uttered a bell call with a swing towards her, which made her move a few feet away. After the call with a swing the male immediately resumed the silent wattle-displaying posture (Figure 1) and remained like this for 1 or 2 minutes while the female slowly edged along the liana towards him again. When the female was again within a few feet of the male a similar sequence was repeated and continued to be repeated for the 20 minutes I watched them. The only variation was that once as the male swung to the left he also jumped with a flutter about 2 feet to the left, at the same time turning to face in the opposite direction. It was significant that at her next approach the female came from the other end of the liana, which was now to the left of the male. In fact all her approaches were toward his left side. In the Bearded Bellbird the male's immediate prelude to mating is a silent display-preening followed by a leap with a loud "bock" onto the female's back. It is characteristic of the courtship of this species that at the male's mating leap the female frequently retires a

few yards, returning a minute or two later to the same position in front of the display-preening male, before finally remaining and accepting mounting.

The behavior sequence between the male and female White Bellbird was undoubtedly courtship. Almost certainly mating occurs when the male makes a bell call with a flutter and a turn to the left, and the female remains instead of retiring. Presumably the female must be perched facing in the opposite direction to the male just before mounting occurs. In the sequences observed she sometimes approached facing in the same direction as the male and sometimes in the opposite direction.

The only other evidence of breeding was obtained on 17 February, when a female was seen breaking off and dropping fine twigs from an understory tree (*Eugenia* sp.). Twigs from the same species of *Eugenia* were used in the nests of two other cotingas found in the area, the Capuchinbird and the Purple-throated Fruitcrow (*Querula purpurata*) (D. W. Snow 1971, Living Bird 10: 5). The nest of the Bearded Bellbird is a slight platform of resilient twigs, and presumably the White Bellbird builds a similar type of nest.

COMPARISON WITH THE BEARDED BELLBIRD

The advertising and courtship behavior of the male White and Bearded Bellbird are strikingly similar. Both call from high exposed perches above the canopy and also from beneath the canopy. Having attracted a female the Bearded Bellbird courts and mates with her at his perch beneath the canopy. The evidence points to the White Bellbird doing likewise. The adults of both species immediately stop calling at the arrival of a visitor of either sex. The male Bearded Bellbird then invariably does a silent flight display. There is some evidence that the White Bellbird is also stimulated into the flight display by the arrival of a visitor. Both species land from the flight display with fanned tails. If the visitor comes to the same branch as the occupying male, the male Bearded Bellbird does a leap with a loud "bock" towards the visitor, and the White Bellbird does a bell call with a swing, and at times also a jump with a flutter, toward the visitor. In both species this is almost certainly also the mounting movement. In both species males regularly visit each other and the response to a visitor of the same sex is initially similar to the response to a visitor of the opposite sex.

The males of both species, particularly the immatures, prefer to call within hearing of another calling male. When no other males are audible the Bearded Bellbird calls from beneath the canopy for most of the day, but if other males are audible he spends a much larger proportion of time calling from the high perches. The same tendency is found in the

White Bellbird: most calling was from high perches at Karusu Creek where several males were calling whereas the solitary adult male at Nappi Creek called from below the canopy throughout the day.

CALLS AND PLUMAGES OF IMMATURE MALES

An estimated minimum of eight different immature males were heard calling at different times in the study area. Two were subadults with entirely white plumage except for one or two green feathers. Four were immatures with varying mixtures of white and green feathers, all with wattles obviously shorter than an adult's. Two were juvenile males in the green female plumage, one of which had the very small beginnings of a wattle.

In the Bearded Bellbird the young male spends many months learning to call and, judging from the plumages and calls, this is probably also the case in the White Bellbird. The juvenile male without a wattle was watched calling on 2 February about 40 yards from an adult. He leaned slightly forward, opened his beak, and emitted some parrotlike squawks and squeaks, almost identical, except slightly higher in pitch, to the earliest attempts at calling by the juvenile Bearded Bellbird. On 24 February, about a mile from the previous incident, the juvenile with the bud of a wattle visited a subadult male and then started calling 30 yards away. His call was an extremely squeaky attempt at a bell call, recognizable as such by the rhythm. As the young Bearded Bellbird first learns the "bock" call, this is another indication that the bell and "bock" calls are homologous.

The immature with the least developed calls had a wattle half the length of an adult's, the wings were largely green, the tail mostly white, and the back mottled green and white. He could make the musical and the bell call, but neither had the ringing quality of the adult. He frequently uttered a single-syllabled bell call, either at the beginning or the end of a rather short swing. When the bell call was two-syllabled it often had an element of the musical call in it.

All the other immature males observed frequently uttered single-syllabled bell calls and all their calls were slightly shorter than the equivalent adult's calls. The calling of the subadults sounded slightly less ringing and full than the adult's calls but the difference was very slight. A study of skins of all four bellbirds (D. W. Snow, pers. comm.) suggests that the fully adult plumage is not acquired until the third year of life at the earliest.

ACKNOWLEDGMENTS

I acknowledge with thanks financial assistance from the Frank M. Chapman Memorial Fund of the American Museum of Natural History. I should also like to thank my husband for help in the field and in the preparation of this paper.

SUMMARY

White Bellbirds were studied for nearly 3 months in the Kanaku Mountains in southern Guyana, at the end of the dry season, from January to April 1970. Males were found to occupy fixed calling perches for limited periods, but they moved gradually to higher altitudes in the course of the observation period, apparently as fruit became scarce at lower levels in the mountains.

They have two main calls, a drawn-out musical call and a staccato double bell call. The latter call is of two audibly distinct types, one uttered with the head and body motionless and the other with a violent swing of the head and body from right to left. Typically these calls alternate regularly during a bout of calling, but males show individual differences in their calling patterns.

Males were visited on their display perches by other males, and once a female was seen to visit a male. A courtship sequence is described which, taken in conjunction with the behavior shown during visits by males, indicated that the female normally approaches the male on his left-hand side, and that the males mount after a right to left swing. This explains the invariable right-to-left direction of the swing that accompanies the bell call.

The calls of immature males in different plumage stages indicated that male White Bellbirds, like the Bearded Bellbird, take many months to perfect their calls.

Old Forge, Wingrave, Aylesbury, Buckinghamshire, England. Accepted 17 January 1973.