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TERRITORIAL BEHAVIOR AND COURTSHIP OF THE MALE THREE-WATTLED BELLBIRD

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ABSTRACT.—The Three-wattled Bellbird (*Procnias tricarunculata*) was studied for 7½ weeks (April–June 1974) at Monteverde, Costa Rica. In the study area, measuring approximately 1,400 by 3,200 m, 13 adult males held territories from which they advertised themselves by loud calls for 83–93% of the daylight hours. The majority had a repertoire of three different calls. Evidence from a tape recording from Panama and descriptions from elsewhere in Costa Rica show that the Monteverde dialect is distinctive. Two individuals had part or all of their repertoire different from other Monteverde males but matching vocalizations from elsewhere. Males call from exposed perches above the canopy and from a special broken-off branch, the visiting perch, beneath the canopy. Calling males perform two displays involving flight, each preceded by a characteristic call. These displays and a silent wattle-shaking display are mainly performed when another bellbird visits a calling male. The visitors were usually females or immature males but occasionally adult males. At the climax of the visit, the territory-holding male leans over his visitor, perched at the broken-off end of the visiting perch, and utters some extremely loud calls into its ear. This usually makes the visitor leave. Both sexes receive the same treatment. During May and June, females were watched coming to the visiting perches of calling males on 20 different occasions, but none of these visits culminated in mating. The male's wattles are fully extended when he is calling in his territory, but are usually retracted when he leaves his territory to feed. During encounters between closely matched males, first one and then the other may extend the wattles and call. Bellbirds were seen feeding only on fruits, mainly drupes of the family Lauraceae but also other drupes, particularly a species of Rutaceae. An individual male feeding exclusively on the latter fruit took an average of 9.0 g of pericarp per hour. A comparison is made of the calls and displays of the four *Procnias* species, and it is suggested how these may be related to habitat.—*Old Forge, Wingrave, Aylesbury, Buckinghamshire, England.* Accepted 3 May 1976.

IN an attempt to discover more about the breeding behavior of the Three-wattled Bellbird (*Procnias tricarunculata*) for comparison with the Bearded Bellbird (*P. averano*) and the White Bellbird (*P. alba*) previously studied in Trinidad and Guyana (B. K. Snow 1970, 1973), I stayed at Monteverde in the Cordillera de Tilaran of Costa Rica from 25 April to 17 June 1974.

The Three-wattled Bellbird in adult male plumage is the most distinctive of the four bellbird species that make up the genus *Procnias*. Unlike the other three species in which the male is mainly white or very pale grey, the adult male is a bright rufous brown except for the head, neck, and upper breast which are white. One of its three pendant black wattles grows from the base of the upper mandible, the other two from either corner of the gape. The female and birds in juvenal plumage have no wattles and, as in the other species, are cryptically colored, olive-green above and yellow streaked with olive-green below. The size difference between the sexes is

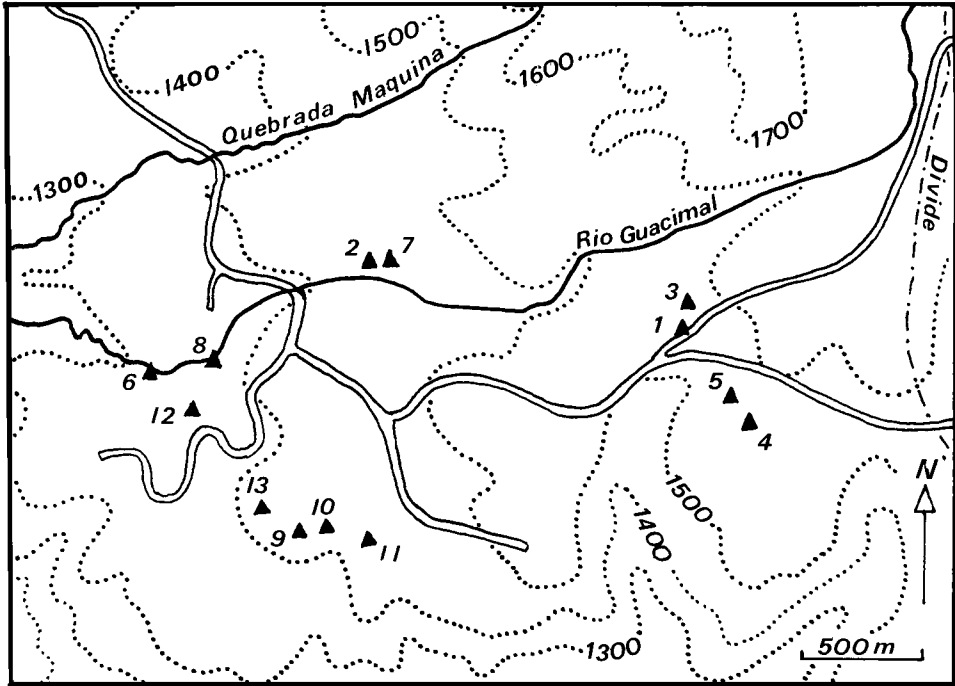


Fig. 1. Map of the Monteverde study area showing approximate positions of the advertising territories of the 13 adult males. The continental divide is at the right-hand edge of the map; contour heights in meters.

appreciable, the adult male having a mean wing length of 165.5 mm (39 specimens) compared to 145.1 mm (13 specimens) in the female (D. W. Snow 1973).

The Three-wattled Bellbird occurs only in Central America from western Panama to extreme southeastern Honduras. It makes extensive vertical migrations from sea level up to the highland forests (Skutch 1969). D. W. Snow (1973) has given reasons for supposing that it colonized Central America by a long-distance dispersal from some part of northern South America, perhaps in the comparatively recent past.

STUDY AREA AND METHODS

Monteverde is on the Pacific slope of the Cordillera at 1,400 m, 200 m below a pass through the continental divide. The study area (Fig. 1) lay between 1,300 and 1,560 m in the lower montane forest belt (Holdridge 1967). Within this 260 m of elevation span a marked moisture and temperature gradient causes many differences in the flora and avifauna. Most of the study area is in the Monteverde Quaker community farmland. This land was opened up to provide dairy pastures 24 years ago when approximately 70% of the forest was felled, leaving large tracts of untouched forest particularly near streams and on other steep slopes. Scattered mature trees were left in nearly all the pastures created. A small part of the upper elevations of the study area lies inside or adjacent to the Monteverde Cloud Forest Preserve, which straddles the divide and is almost entirely in its natural state.

The climate is dominated by moisture-laden air from the Pacific from approximately April/May until November/December and by strong and relatively dry winds from the Atlantic during the other months. The rainfall is high, the annual mean from 1962 to 1972 was 2,760 mm; monthly totals vary by as much as 500 mm in different years. The temperature varies between daily maxima of 80°F and minima of 55°F with the greatest fluctuations during the Atlantic-dominated weather periods.

I mapped the advertising or calling territories of 13 adult males, all of which I watched at their calling

territories for varying periods, totalling 134 hours, and also occasionally checked their presence during briefer visits. Observations were also made at some of the trees where bellbirds were taking fruit. The advertising song or call of five of these males was recorded on a Sony TC 800 B tape recorder at 7½ ips. Written records were made for all the males of the relative proportions of the three main types of calls and their variations. These variations made it possible to check the identity of six individuals. One male was watched for 31 hours from a blind, but all the other males were watched without a blind, either at a distance of several hundred meters or at ranges of 25–60 m. The adult males with territories within the farming community proved to be tame and easy to observe, those at the edge or inside the preserve were shy.

OCCUPATION OF TERRITORIES

Male Three-wattled Bellbirds call at Monteverde from March to July or August. In 1974 the first arrival was heard on 9 March (Powell pers. comm.). From 25 to 27 April only two males (nos. 1 and 2, Fig. 1) were holding advertising territories. The total of territory-holding males then increased to 3 by 28 April, 4 by 2 May, 5 by 4 May, 6 by 29 May, and 11 by 1 June. From 4 June onwards male 4, which had a distinctive call quite different from the others (see below), was absent, but two more adults took up territories on 15/16 June. Occasionally adult males took up temporary advertising territories (not shown in Fig. 1) near established males and held them for only 1 or 2 days. On visits to the watershed on 29 April and 14 May bellbirds were heard calling from the Atlantic slope, but on visits on 28 May, 7 June, and 14 June none were calling, which suggests a slow movement from the east up and over the watershed. No permanent advertising territories were found above approximately 1,560 m, although visits were made regularly up to nearly 1,700 m on the Chomogo trail, and this area is virgin forest. The lowest established territories were those of males 6 and 8 at 1,380 m. Below this elevation the altitude drops very rapidly, accompanied by an equally rapid change to a dryer semideciduous forest.

The number of the males from 3 to 13 corresponds to the order in which territories were taken up (Fig. 1). The first arrivals established themselves in the vicinity of male 1 at the upper altitudinal limits, and subsequent arrivals occupied territories near the lower altitudinal limits.

CHARACTERISTICS OF INDIVIDUAL ADVERTISING TERRITORIES

All the advertising territories in the study area consisted mainly or entirely of forest. To be suitable, a territory must contain one or more emergent trees with an exposed, broken-off dead branch, from which the males spend some of their time calling. These high calling posts usually command an extensive view, often because they are on the edge of steep-sided valleys. In the partially cleared land of the Monteverde community the high calling posts are usually at the edge of the patches of forest commanding a view over the felled areas. Another essential feature of the advertising territory is a suitable 'visiting perch' beneath the canopy. This is the perch to which territory-owning males lead visiting females, immature males, and adult males. The requirements of this perch are fairly exact because of the stereotyped nature of the courtship movements and encounters between males that take place on it. The characteristic visiting perch is 10 to 22 m above the ground, under the canopy but in a partial light gap caused by the felling or falling of a tree or part of it. It is a broken-off branch with a diameter of 25–50 mm. Ideally the last 45–60 cm of the broken-off branch is uncluttered by side branches and grows upwards at an angle of 10° to 15° above the horizontal.

TABLE 1
CHARACTERISTICS OF VISITING PERCHES

Male	Height (m)	Length of bare terminal portion (cm)	Angle from horizontal	Light gap
1	15	46	15	yes
2	21	152	10	yes
3	12	46	30	slight
4	21	46	10	none
5	14	60	10	yes
6	12	46	10	none
	12	46	20	yes
	10	60	15	none
7	15	35	10	slight
9	15	38	10	yes
10	15	22	15	none
11	21	60	15	none

I assessed the characteristics of 12 visiting perches from below (Table 1). Only the visiting perches of males 1, 2, and 5 combined all the ideal characteristics and it is noteworthy that those of males 1 and 2 were occupied throughout the period of observation and that of male 5 from 4 May onwards. Male 3 occupied his less suitable perch from 28 April to 19 May and then left, apparently moving half a mile eastward (Fig. 1); and male 4, with a visiting perch that lacked a light gap, left his territory on 4 June. The remaining perches were occupied only from 29 May onwards and all had characteristics that probably made them less than ideal.

Territories varied in size. That of male 1, which occupied a level patch of forest on a spur overlooking a valley, measured 70 by 30 m. That of male 2, on the farmland edge of a tract of forest along the Rio Guacimal, measured 80 by 25 m. These early established males also called regularly but briefly in the territories of males 3 and 7 before the latter established themselves. Male 6 had a particularly large advertising territory of 450 by 50 m which included three visiting perches. It was on a tongue of

TABLE 2
FRUITS EATEN BY THREE-WATTLED BELLBIRD

	Fruit type	May 1-15	May 16-31	June 1-16
Lauraceae				
<i>Ocotea palmana</i> Mez	drupe	2	2	
<i>Ocotea endresiana</i> Mez	drupe	12	31	
<i>Nectandra salicina</i> Allen	drupe	4	16	132
<i>Nectandra</i> sp.	drupe		2	
Rutaceae				
<i>Stauranthus</i> sp.	drupe			33
Melastomaceae				
<i>Conostegia</i> sp.	berry			5
Flacourtiaceae				
<i>Hasseltia floribunda</i> HBK	berry	43	21	
Moraceae				
<i>Ficus</i> sp.	berry			4

Note: Fruits were also taken from four unidentified canopy-level trees that bore drupes ranging in size from 17 × 15 mm to 16 × 13 mm, and from an unidentified epiphyte and a vine. Data on *Nectandra* sp. from regurgitated seeds only; on *Conostegia* sp. and *Ficus* sp. from observed feeding only; on other species, from regurgitated seeds and individual feeding visits to trees combined. The following are the assessed average number of fruits taken per feeding visit: *H. floribunda* 10, *O. endresiana* 6, *Conostegia* sp. 5, *Ficus* sp. and *N. salicina* 4, *O. palmana* 2, *Stauranthus* sp. 1.

TABLE 3
MEASUREMENTS, WEIGHTS, AND PERICARP ANALYSIS OF TWO SPECIES OF FRUIT

	<i>Nectandra salicina</i>	<i>Stauranthus</i> sp.
Number	14	9
Mean length	37	30
Mean diameter	21	23
Mean weight of whole fruit	7.7	8.6
Mean weight of seed	4.6	5.4
Mean weight pericarp	3.1	3.2
Mean dried weight pericarp	1.0	1.0
Pericarp composition (percentage dry weight)		
Protein	7.7	8.0
Fat	44.1	8.7
Carbohydrate	41.7	69.0
Ash	2.5	6.4

land between two steep-sided valleys and included several small cultivated fields. Males 7 to 13, who established themselves from 29 May onwards, appeared to have smaller territories and some were only seen calling from one visiting perch and one high perch 30–45 m apart.

FOOD AND FEEDING BEHAVIOR

Like other bellbird species the Three-wattled Bellbird appears to eat only fruit. Data on the fruit taken were collected by direct observation of birds feeding and by collecting regurgitated seeds below visiting perches (Table 2).

Of the 16 different kinds of fruit eaten 11 were drupes, at least 4 being species of Lauraceae, a family known to be important in the diet of many specialized frugivorous birds (D. W. Snow 1971). The only fruit of another type that was taken in quantity was that of *Hasseltia floribunda*, a juicy berry containing 3–7 seeds; but as it is much smaller than most of the other main fruits that were taken (about 6 mm in diameter) it can have made only a minor contribution to the bellbirds' diet. An analysis of two of the drupes taken, *Nectandra salicina* (Lauraceae) and *Stauranthus* sp. (Rutaceae) shows a relatively high percentage of protein and fat in the pericarp (Table 3). Equally nutritious pericarps have been found in other species of Lauraceae (D. W. Snow 1962), but not previously in the Rutaceae. The fruit of *Stauranthus* is similar to a lauraceous fruit such as *Nectandra salicina* in size, relative weights of seed and pericarp, and the low pericarp water content; in both, the skin of the ripe fruit is black. The similarity strongly suggests convergent evolution of fruit characteristics related to dispersal by frugivorous birds.

I was able to record the exact quantity of fruit taken during 3 h 50 min while watching male 9 on the morning of 15 June. During the period of observation, from 0935 to 1325, male 9 was in view at all times, except for 6 min when he called just out of view. Except for this period he called entirely at his visiting perch and fed at two understory trees (*Stauranthus* sp.) 20 and 25 m from his perch. Altogether he made 11 visits to feed, each time eating one *Stauranthus* fruit and immediately returning to call at his visiting perch. The intervals between feeding were regular. Ignoring one long interval when the male flew to the *Stauranthus* tree but returned without feeding because of the arrival of a female, they varied from 11 to 23 min, averaging 17 min. Between 1 and 8 min (average 4.3 min) before going to feed, the bird

regurgitated the seed of a previously eaten fruit. After the observation period I collected these seeds from beneath the visiting perch; all proved to be *Stauranthus* sp. Allowing an average pericarp weight of 3.2 g (Table 3), this male's food intake was 9.0 g per h.

From measurements of gape widths of museum specimens D. W. Snow (1973) estimated 23 mm as the probable maximum fruit size which a male Three-wattled Bellbird could swallow. The largest regurgitated seed that I collected, a *Stauranthus*, had a width of 23 mm, corresponding to a fruit width of 25 mm when allowance is made for 2 mm of pericarp.

When feeding both the Bearded Bellbird and the White Bellbird pluck fruit on the wing, taking one at each flight, and very occasionally take an easily accessible fruit from a perched position. The Three-wattled Bellbird also takes fruit on the wing, but differs in regularly taking several sorts of fruits when perched. Those seen taken only from a perched position were *Ocotea endresiana*, *Conostegia* sp., *Ficus* sp., *Hasseltia floribunda*, and two other canopy-level trees that bore drupes. Usually taken on the wing were *Ocotea palmana*, *Nectandra salicina*, *Stauranthus* sp., a drupe-bearing tree, and a vine. To reach fruits growing near the ends of twigs without flying, the bellbirds edged out to the extremities so that they were clinging in a semivertical downward position, often having to maintain their balance by wing-flapping. When feeding at *Nectandra salicina* many bellbirds on first arrival attempted this method of feeding, and after unsuccessfully pulling at a number of fruits, resorted to plucking fruit on the wing, which was successful. Apparently fully ripe fruit could be plucked from a perched position; this was occasionally seen to succeed, but more force could be exerted on the wing to pull off less ripe, firmly attached fruit. Even so an adult bellbird could misjudge the ripeness of a fruit and I saw one hang momentarily by its beak from a fruit it was trying to pluck on the wing.

Whether a lauraceous fruit is taken perched or on the wing depends also on the way the tree presents the fruit to its avian disperser. Both size and presentation determine what birds exploit the different species. The bellbirds successfully exploited all the ripe lauraceous fruits noted at Monteverde; other largely frugivorous birds could exploit some but not other species.

In most species of Lauraceae the fruit grows in a cupule, much like an acorn cup, attached to a long pedicel that hangs down well below the twigs that bear them. The fruit of *Nectandra salicina* is presented in this way and was being extensively exploited by both bellbirds and Emerald Toucanets (*Aulacorhynchus prasinus*). Toucanets feed by leaning down and stretching out to pick fruit below the branch on which they are perched. They ate the fruit of *Nectandra salicina* from the end of April until I left, but I saw no bellbird feed at these fruits until 12 May, and they were not present in numbers until the end of May. This suggests that the toucanets may have an advantage over the bellbirds in being able to pluck fruit that is still very firmly attached. The Keel-billed Toucan (*Ramphastos sulfuratus*) also feeds on these fruits, and it is significant that when feeding they are able to pluck every fruit they reach out for and grasp in their mandibles, so they hardly move at all while feeding, whereas toucanets hop about all over the tree, look at and squeeze a number of fruits before pulling at one, and then sometimes fail to pluck it. Bellbirds, as well as doing much unsuccessful pulling at fruit while perched, sometimes make four or five flight sallies at fruit before successfully plucking one.

The fruits of *Stauranthus* sp. were occasionally fed on by the Emerald Toucanet, but they were evidently at the upper size limit, for most that were picked were

dropped, and only about one in five was eaten after much maneuvering in the beak. This fruit is presented on a short stout pedicel, so is easily available to perched birds. Although the bellbirds sometimes took it while perched, much more often (80% of observations) they took it on the wing. As with *Nectandra salicina*, there was some evidence that they resorted to feeding on the wing when perched feeding had failed.

The bellbird competes with the Mountain Thrush (*Turdus plebejus*) and to a lesser extent the White-throated Thrush (*Turdus assimilis*) for the relatively smaller fruit (17 × 13 mm) of *Ocotea endresiana*. These fruits grow upwards, well embedded in a cupule, and presented in the center of a whorl of ovate rigidly coriaceous leaves with stout petioles. The leaves surrounding the fruit form the external surface of the crown of the tree, and both the thrushes and the bellbirds perch on the leaf whorls and pluck the fruit without going below the tree's canopy. Emerald Toucanets were plentiful in the places where *O. endresiana* was fruiting, but in 3½ h watching were not seen to take the fruit. It was probably the presentation of the fruit that was unsuitable for them rather than the smaller size, as toucanets took many smaller fruits of other families.

Adult male bellbirds holding advertising territories spent only brief periods of a few minutes feeding, and I never saw them behaving as though searching for fruit trees. Instead they flew directly to a fruiting tree, sometimes inside their territories, but often several hundred meters or as much as a kilometer away. Longer flights were above the canopy in long undulating sweeps with occasional rests on tree tops, particularly when returning up the mountainside. During June at least six adult males from surrounding calling territories came to feed at the three fruiting *Nectandra salicina* trees on the edge of male 8's territory. A large emergent tree in fruit on the borders of the calling territories of males 4 and 5 was visited by these two birds and also by males 1 and 3. This area is approximately 70% forest and backed by the Preserve. Even in undisturbed habitat it is probably usual for males to range some distance from their calling territories to feed.

Female bellbirds were seen feeding at *O. endresiana* in the same manner as the males, and they also took the fruits of *N. salicina* on the wing, swallowing them after landing. The fruit of *N. salicina* has a conspicuous orange spot at its point of attachment to the cupule, the widest end, and a number of times I saw a female, on landing, maneuver the fruit in her beak to swallow it orange spot first. The Emerald Toucanet also swallowed this fruit the same way round. A fruit near the upper size limit for a species is often maneuvered in the beak before being swallowed, probably to assess the suitability of its size. D. W. Snow (1973) concluded that 19 mm was the maximum diameter of fruit exploitable by female Three-wattled Bellbirds, so many of the fruits of *N. salicina* (diameter 19–24.5 mm) may well be too large.

VOICE

The Three-wattled Bellbird in Monteverde has three basic advertising songs or calls: a very loud monosyllable (Fig. 2A) lasting half a second, and two much longer multiple calls of which some of the notes are muted. The single-syllable call, which I transcribed as "bock," is not associated with display movements; the two multiple calls are frequently, but not always, followed by particular display movements.

The multiple call that precedes changing place on the visiting perch (see below) begins with a high amplitude "bock" (Fig. 2E), similar to the monosyllabic call,

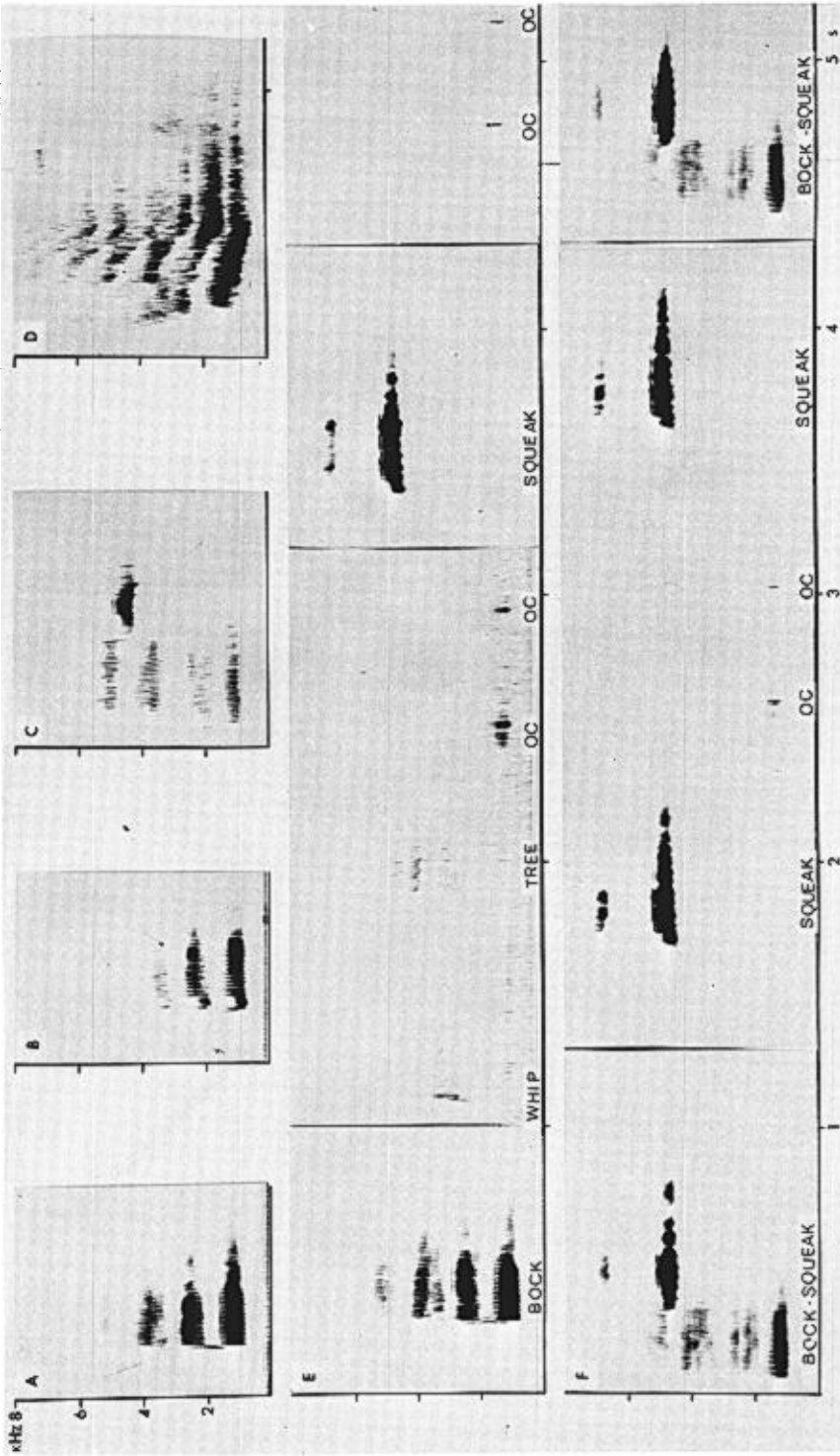


Fig. 2. Sonograms of the advertising calls of the Three-wattled Bellbird. (A) adult "bock," (B) immature "bock," (C) immature "bock-squeak" from the flight-display call, (D) the squawklike "bock" of an immature *P. nudicollis*, (E) adult changing-place call, (F) adult flight-display call.

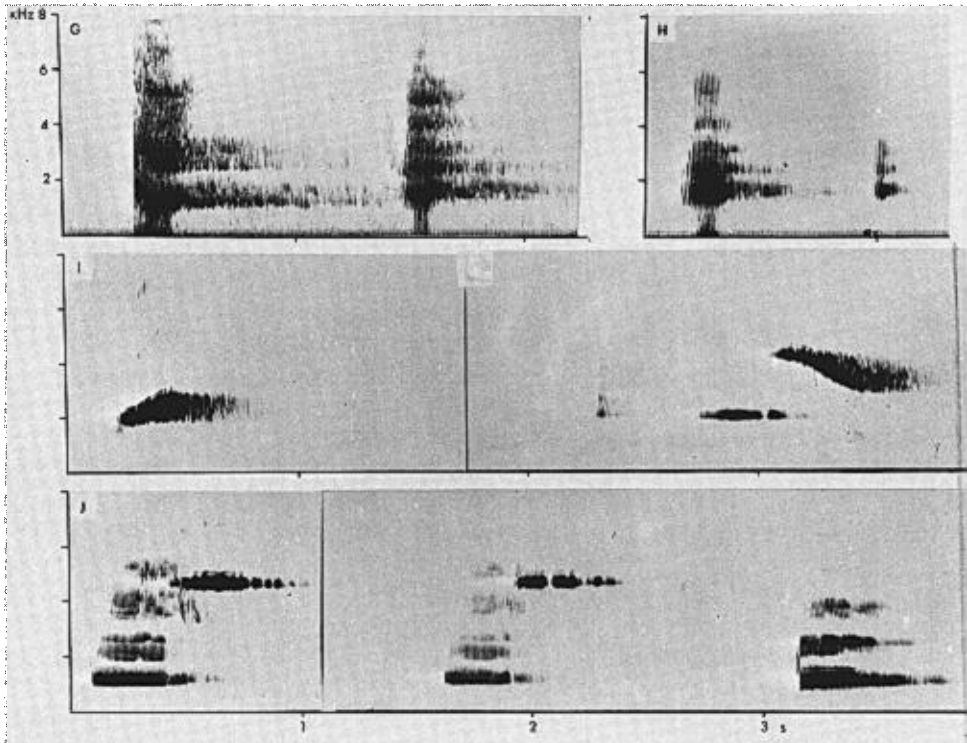


Fig. 3. Sonograms of the advertising calls of some individual bellbirds in the study area. (G) "yock-ack," the flight-display call of male 4; (H) "ack-ick," the changing-place call of male 4 (the muted notes that follow the "ack-ick" not illustrated); (I) the whistle uttered by male 5; (J) innovations of male 6.

followed by a muted series transcribed as "whip-tree-oc-oc-squeak-whip-oc-oc" (the second "whip" faint and not visible on sonogram) with the "squeak" considerably louder than the rest. The other multiple call precedes the flight display (Fig. 2F); it begins and ends with a lower amplitude "bock" with a "squeak" at 5 kHz incorporated into its end. These two "bock-squeaks" enclose a more muted sequence of "squeak-oc-oc-squeak."

These three calls formed the basic repertoire of all the territory-holding adult males except 4 and 5. Male 5, besides uttering the three calls described above, occasionally emitted a loud melodious double whistle (Fig. 3I). Only this bird was heard to make the whistle, and G. Powell during 4 years residence had heard it only from male 5's advertising territory, but so different is it from the other calls that he had not attributed it to a bellbird. These whistles are uttered at irregular intervals; for instance during a period of 4 h 50 min when male 5 was calling in his territory, he uttered nine whistles, the intervals between whistles ranging from 2 to 58 min with an average of 26 min. I saw him whistle only once; he was at his visiting perch and no special behavior accompanied the call.

Equally surprising were the calls of male 4, which were unlike the calls of other Monteverde birds. I failed to get a tape recording of male 4, but a recording from Cornell University Library of Natural Sounds made at Volcan de Chiriquí in Panama sounds very similar, and sonograms from these recordings (Figs. 3G and H)

are used to illustrate the differences. Male 4 uttered three calls. The first, a "yock-ack" (Fig. 3G), preceded the flight-display and was therefore functionally equivalent to Figure 2F. The second call, a monosyllabic "yock" similar to the "yock" shown in Figure 3G, has a harsh throaty element compared to the equivalent monosyllabic "bock" (Fig. 2A) of the other Monteverde bellbirds. The third call consists of a disyllabic "ack-ick" (Fig. 3H), followed by an extremely muted series of notes like an echo that is not audible beyond about 15 to 30 m and proved impossible to illustrate on the sonogram. The whole call lasted 3 sec and preceded the changing-place display, so it is functionally similar to the call illustrated in Fig. 2E.

While male 4 was the only territory-holding male in the study area with these calls, on 2 June an adult male uttered a mixture of calls for half an hour from a dead tree in a pasture about 300 m from male 8's territory. His calls consisted of a monosyllabic "bock" entirely similar to those of the normal Monteverde birds (Fig. 2A), a "yock-ack" that preceded the flight display and sounded similar to male 4's call, and an "ack" followed by an extremely muted series of calls, the whole preceding the changing-place display.

The "bock," whether a single call or incorporated into a multiple call, is the loudest sound produced and can be heard at a distance of at least a kilometer. The quieter portions of the multiple calls cannot be heard beyond approximately 200 m, and when there is any wind are inaudible at a lesser range. During both multiple calls the beak is kept wide open and air is expelled throughout the call; before these calls the bird can be seen inhaling air by a swallowing action. During encounters on the visiting perch and occasionally at other times an extremely loud "bock" is added to the end of the changing-place call, so that the whole sequence lasts for 8 sec with the gape continuously wide open. I have called this the challenge call. With a close view of a calling bird it is possible to predict this call by the more extensive air-swallowing motions that precede it, which make the perch branch shudder.

While there is much individual variation, such as the curtailment of multiple calls, the three basic calls are uttered in roughly equal proportions. These three different calls are repeated one after another, over and over again, and it is rare for the same call to be repeated twice running. This pattern changes when a calling male receives a visit from another bellbird; then monosyllabic calls normally cease and the two multiple calls are uttered alternately. If the visitor comes to the visiting perch then usually only the challenge call or changing-place call are uttered.

While this was the general pattern of calling for all adult male territory holders, individuals differed consistently in the rate of calling, the proportions of the three basic calls used, and whether or not multiple calls were curtailed (Table 4). For instance male 1 never uttered incomplete multiple calls and had a low calling rate and a consistently high proportion of flight display calls. Male 3, whose calls were recorded when it occupied a territory close to male 1, showed the same calling rate, probably because neighboring males counter-call and make a low percentage of complete flight display calls, but a relatively high proportion of curtailed ones. Male 2 had a high calling rate and the highest percentage of monosyllabic calls. The high calling rate is reflected in that of its closest neighbor, male 7, with whom it counter-called. Males 6, 7, and 9 all showed much variety in their calling, and each produced different innovations by recombining components of other calls. The most striking innovator was male 6 with a call (Fig. 3J) which consisted of one or two "bock-squeaks" similar to those in the flight display call, followed by the monosyllabic "bock," the whole delivered without intervening muted calls with a single opening of

TABLE 4
 PERCENTAGES OF DIFFERENT CALLS AND CALLING RATES OF EIGHT MALE TERRITORY-HOLDERS¹

	Male							
	1	2	3	4	5	6	7	9
Total calls documented	935	521	277	110	77	58	117	918
Average calls per minute	2.3	3.6	2.3	3.0	3.9	3.9	4.0	3.5
Monosyllabic "bock"	28	46	28	11	39	5	31	34
Flight display call	33	18	19	47	16	7	17	27
Changing-place call	28	26	40	37	34	36	26	24
Challenge call	10	3	2	0	4	2	6	3
Incomplete flight display call	0	7	10	5	6	2	10	1
Incomplete changing-place call	0	0	1	0	0	7	6	8
Mixed innovation	0	0	0	0	0	40	2	3
Premating call	0.1	0.2	0	0	2	0	2	0

¹ Periods when a visiting bellbird was within a male's calling territory are excluded from the figures.

the beak. It is noteworthy that he uttered the two basic calls from which the innovation is derived proportionately less. The characteristic innovation of male 9 started with a monosyllabic "bock" immediately followed by a single "bock-squeak" and thus was similar to male 6's innovation but in reversed order. The mixed call of male 7 consisted of the first 3 seconds of the changing-place call immediately followed by the beginning of the flight display call, the whole lasting 6¼ sec.

A combination of calls, always accompanied by behavior that probably precedes mating and shown as the "pre-mating call" in Table 4, was rare but exactly the same in the four individuals in whom it was recorded, suggesting it may be common to all adult males. It consisted of the flight display call without the terminal "bock-squeak," followed by various movements described below and ending with a loud monosyllabic "bock."

DAILY RHYTHM

Established adult males spend the greater part of the day calling in their territories. On 20 May a continuous watch was maintained on male 2 from 0500 until 1520, when cloud and heavy rain, starting at 1523 and continuing until nightfall, stopped all further activity. During this period of 10 h 20 min male 2 called for 87% of the time, 27% from the visiting perch and the remainder from high posts. He mainly called from two different high posts but occasionally from others, including some just outside the advertising territory where he stopped briefly when flying to and from feeding. He frequently changed his calling position, 23 min being the longest consecutive period of calling from any one high post.

There were 17 silent periods, 1-17 min in duration, with an average of 5 min. As far as could be ascertained, these silent periods were all devoted to feeding, mostly outside his territory, either at *Nectandra salicina* trees ¾ km away or in a patch of forest 300 m away across some pasture land. Between 0700 and 1200 male 2 was visited 9 times by female-plumaged bellbirds and once by an adult male; during these 5 h he was present and calling 95% of the time. No neighboring bellbirds were audible throughout the day's observation.

Observations on other males with established territories showed that they spent comparable proportions of time calling. A watch on 2 May from 0605 until 1630 showed male 1 calling 83% of the time, with only 9 silent periods averaging 12 min each. Probably the longer silent periods were taken up with visits to male 3, who 5

days previously had established a calling territory 250 m from male 1. A total of 73 h spent watching male 1 on 20 different days showed him calling between 73 to 95% of the time (average 84%). Male 9, with several *Stauranthus* trees with ripe fruit close to his visiting perch, spent 93% of his time calling out of 9 h 25 min observation on 5 different days; the average length of his silent feeding periods was 1.9 min.

More observations were made in the morning than the afternoon, partly because it usually rained in the afternoon and also because several long watches early in my study indicated that female-plumaged birds usually came to the visiting perches in the mornings. Out of 20 such visits 19 were in the morning, two thirds of them between 0700 and 0900.

The bellbird's daily calling ends well before sunset which was at approximately 1730. Male 1 finished calling at 1610 on 2 May, 1628 on 6 May, and 1631 on 22 May; male 2 finished at 1637 on 19 May, male 9 at 1654 on 2 June, and male 8 at 1712 on 15 June. The progressively later times are probably attributable to increasing competition as additional adult males took up advertising territories. No evidence showed that this final period of the day was used for feeding; the males apparently went to roost at this relatively early hour.

During 11½ hours of daily activity an adult male bellbird spends on average 1¾ hours feeding. Assuming a rate of 3 calls per min (Table 4) it will utter in a day over 2,000 calls of extremely high amplitude, the production of which must be a considerable item in its energy budget.

The proportion of time spent calling at visiting perches compared to calling at high posts varied. In 14 periods of observation on male 1 totalling 39 h of calling, the proportion delivered from the visiting perch fluctuated between 3 and 22%, averaging 13%. Male 2 spent 15% of a total calling time of 13 h 20 min at his visiting perch. These observations were on six different days and do not include the whole day's observation on this bird when 27% of his calling was from the visiting perch. The percentage was higher on this day because of the persistent visits of other bellbirds (see next section). Males 1 and 2 were both early established at calling territories and therefore presumably dominant over later arrivals, who differed in calling for a far higher proportion of time at their visiting perches. Ten days after establishing himself near male 2, male 7 spent the whole of a 2½-h observation period at his visiting perch except for 4 min spent feeding. Male 9, a late arrival to a small patch of woodland where 3 adult males held territories, spent 90% of a total of 5¾ h calling at his visiting perch.

DISPLAY

Adult male bellbirds performed three different displays at their visiting perches and high calling posts. One of these displays, wattle-shaking, is silent. The other two, the flight and changing-place displays, are always preceded by specific calls.

While calling and displaying the adult male bellbird extends his three wattles to their greatest length and raises his contour feathers, particularly the white feathers of the forepart of the body (Fig. 4). When a male leaves his territory to feed and when he is visiting another adult male, the wattles are retracted to about a third of their former length (Fig. 5A). This extension and retraction of the wattles was first noted by Crandall (1948) in a captive immature male. Sometimes the upper wattle when retracted lies curled on the crown of the head (Fig. 5B). The extension and retraction of the wattles is accomplished in approximately 5 to 10 sec. In agonistic encounters

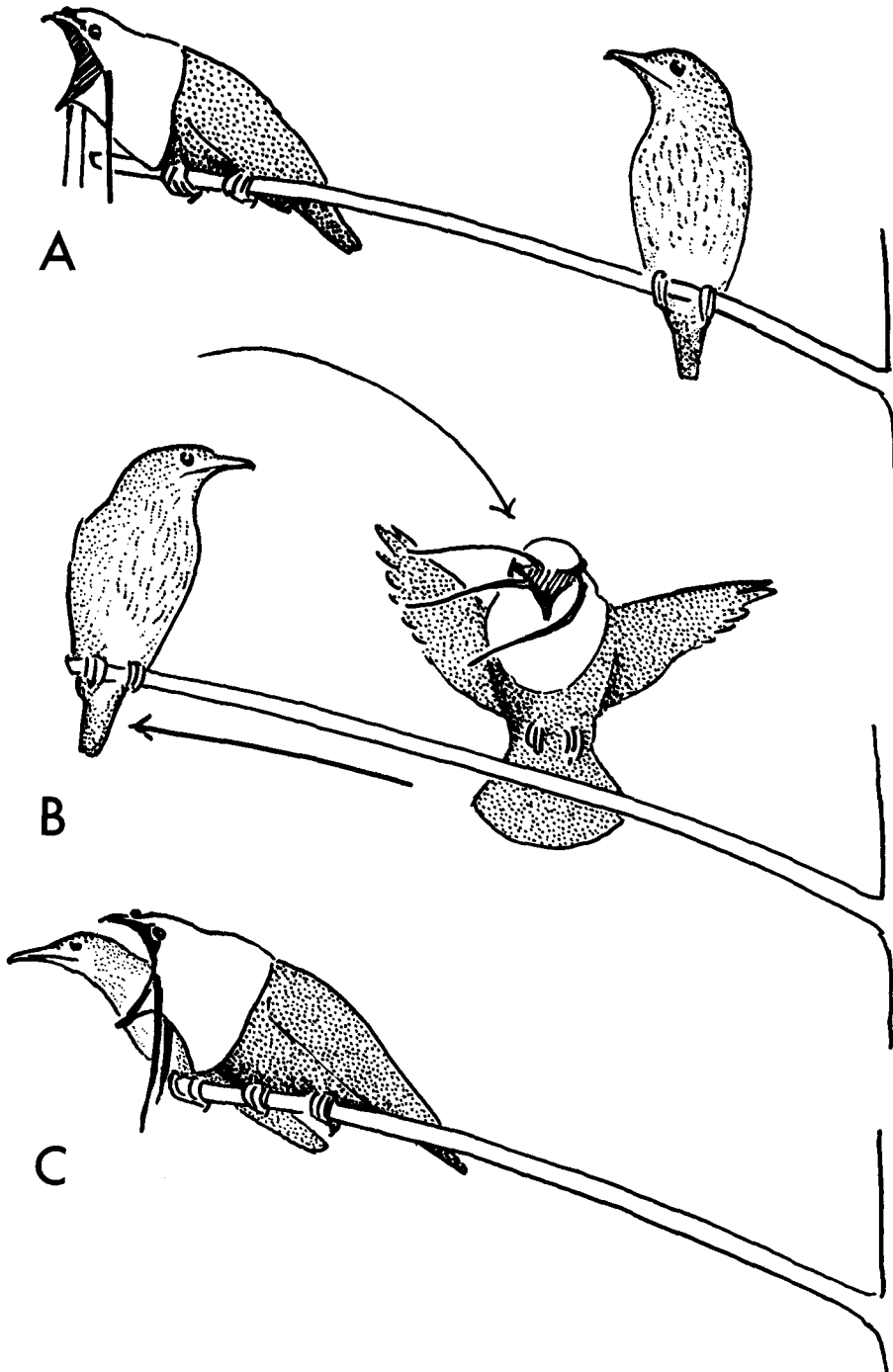


Fig. 4. (A) male uttering the changing-place call at the outer position on his visiting perch, visiting female at inner position; (B) male changing place with female by flying over her as she moves to outer position; (C) male uttering a close-up call into the female's ear.

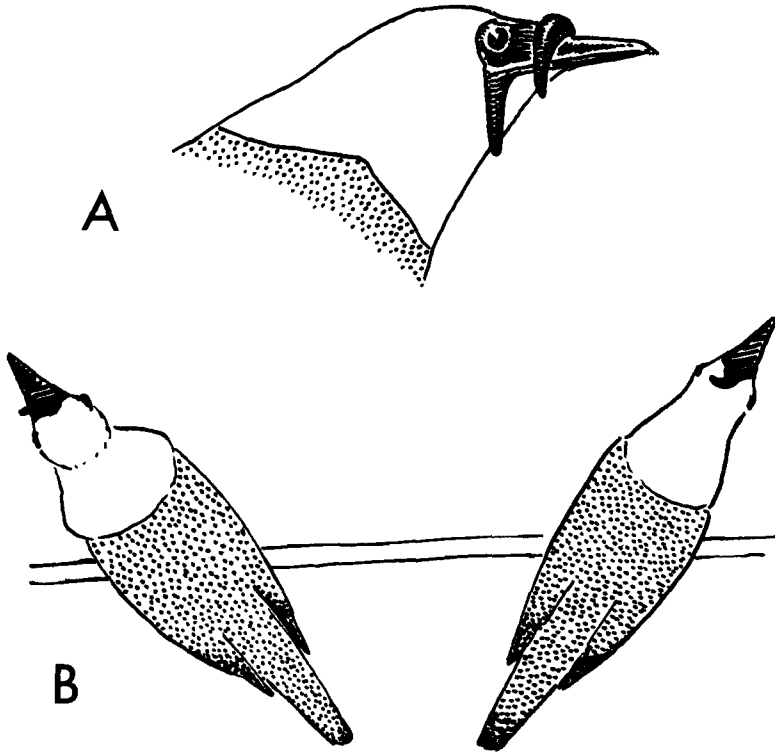


Fig. 5. (A) adult male with wattles retracted; (B) view from above of two adult males in the facing half away position (subordinate male on right with wattles retracted).

between closely matched males first one and then the other may extend and display their wattles; while the calling bird's wattles are extended the other's are retracted.

Wattle-shaking display.—While adult males extend their wattles whenever they are calling in their territories, it is only when another bellbird visits them that they display their wattles by silently shaking them. During this display the body of the displaying bird is in a crouched horizontal position with head, back, and tail in line and the folded wings held slightly away from the body. Every few seconds the bird looks down, at the same time shaking his head and wattles. Between each downward head-shake he looks up at the visiting bird above him, so that the movement looks like a bow, or, if the visitor is in a lateral position, he tilts his head sideways to eye the visitor. Periodically during the silent wattle-shaking display, which may continue for several minutes, the displaying bird—while keeping his body in the same crouched position—moves laterally about 25–30 cm along the perch and then a few seconds later moves back again. The lateral movement is accomplished by a number of small quick sideways hops.

Flight display and changing-place display.—The flight display and the changing-place display are also performed mainly in response to the approach of a visiting bellbird; they were also occasionally seen when there was no evidence of an approaching visitor. The flight display immediately follows the call named after this display (Fig. 2F). From his calling perch the bird flies to another 3–5 m away and at the same level. As he lands he briefly fans his tail and assumes a crouched horizontal

position similar to the posture assumed during the head-shaking display. He then returns to the calling perch, landing in the same crouched position with tail fanned. Individuals repeatedly use the same nearby perch as the terminus of the flight display, which, like the principal calling perches, becomes worn and conspicuously free of the festooning mosses found on all the other branches.

The changing-place display immediately follows the other multiple call (Fig. 2E). It was so called because during the display the male may change places with a visitor on the calling perch. In this display the male flutters up 30 to 50 cm above the calling perch and lands back on the same perch in the crouched position with tail fanned. He often lands facing in the opposite direction, the position at which he relands depending on the presence or absence of a visiting bellbird on the perch and on the latter's position.

The frequency with which the changing-place and flight displays were performed varied greatly. All adult males periodically called for as much as 10 to 15 min without displays. This calling was usually from a high post that lacked an emergent dead branch. An example of the typical frequency of displays over a long period was obtained from continuous observations on male 9 calling at his visiting perch for 3 h 12 min. During this period 9% of 157 flight-display calls and 15% of 178 changing-place calls were followed by the appropriate displays. During this time a female-plumaged bird spent two periods of 6 and 5 min at the visiting perch. A higher proportion of display, 46% of flight-display calls and 76% of changing-place calls, was shown by male 1 during 17 min of calling immediately prior to the arrival of a female at his high-post tree. The female was probably visible to him throughout the 17 min, probably feeding at a nearby *Ocotea endresiana* tree in fruit. For brief periods of 2 or 3 min when a visitor is only a few feet away from a male at his visiting perch, all multiple calls are followed by display. Changing-place displays are consistently more frequent than flight displays, largely because they continue after a visitor lands at the visiting perch whereas flight displays rarely continue.

Visiting sequence.—Both female and male bellbirds visit calling adult males in their territory. Visiting males may be fully adult or immature. During my observations immatures were usually in female-type plumage with the three wattles beginning to grow. Bellbirds flying any distance do so above the canopy and this is the route taken by a visitor to a calling male. Males calling at high posts have an extensive view and invariably spotted approaching visitors before I was aware of them.

As described in the previous section, the first response of the calling male is an increase in the number of flight and changing-place displays; then if the visitor comes to the high-post tree, the owning male starts the wattle-shaking display and decreases the proportion of monosyllabic calls. Usually at this stage, particularly if the visitor is a female or immature male, the owning male flies down to the visiting perch. If the visitor follows, it first perches a few feet above the visiting perch and watches the owning male, who now stops the monosyllabic call, follows each multiple call with a display, and spends an increasing proportion of time in the silent wattle-shaking display. For several minutes before the visitor flies down to the visiting perch the owning male stops all display except the silent wattle-shaking. Once a female landed on the visiting perch when the male was uttering a flight-display call, whereupon he terminated it in the middle and started the wattle-shaking display. If the visitor lands on his inner side, the displaying male turns slightly away from the visitor and utters the changing-place call (Fig. 4A), followed by the display,

and relands at the inner position and facing in the same direction as the visitor. While the displaying male is airborne the visitor moves along the perch to the outermost end of the broken-off branch (Fig. 4B). After relanding the owning male moves to a position close beside the visitor and prepares, by inhalations of air through his nostrils, to utter a close-up call. A close-up call is usually the challenge-call but sometimes the changing-place call; when used below, the term denotes either of these calls uttered by the male in the ear of his visitor. As the male opens his beak wide to utter the call he leans right over the visitor. The latter leans as far away as possible, clinging precariously to the very end of the branch (Fig. 4C). The delivery of the call, with the visitor flinching at the tremendous noise, is an amazing sight and can only be described as an ordeal by sound which few visitors withstand. Only once out of the 51 times I watched a male leaning over a female to deliver a close-up call in her ear did she remain for the complete call. Most visitors left, often appearing to fall off the end of the perch, before the second loud "bock." Some left at the first "bock" or even before it was uttered. At whatever stage the visitor leaves, the male at once cuts short the call. If the visitor leaves before the first "bock" the male, although he has visibly inhaled air and opened his beak wide, stops and utters no sound. Frequently when the visitor leaves it flutters up and lands again at the inner position on the visiting perch and the whole sequence is reenacted, occasionally four or five times running. The whole series then has a dance-like quality reminiscent of some manakin (Pipridae) displays except for the slow speed of performance. Sometimes when the visitor retires at the close-up call it flies to a nearby branch and shortly after returns to the visiting branch. Often a visitor lands in the outer position, initially or at a return; then no changing-place occurs, instead the owning male after some wattle-shaking display hops close beside the visitor and utters the close-up call in its ear.

Although visiting sequences involving the changing-place display and a close-up call most often occur at visiting perches, they also regularly occur at high calling posts, but only if these are dead branches with broken-off ends. Most encounters between adult males were at such high posts. Only three encounters between adult males were seen at visiting perches, except for those between males 6 and 8 (see below).

Most of the high-post encounters I watched were between male 8 and the many bellbirds that came to feed at the fruiting *Nectandra salicina* trees just beside his territory. Many of these appeared to be perfunctory routine visits and not a serious challenge to his territorial rights. Both adult and immature males sometimes came in twos to male 8's high-post tree and came in turn to the calling perch and went through the visiting sequence.

Although the visiting sequence is undoubtedly part of courtship none of the sequences observed between males and apparent females culminated in copulation. On the only occasion when the female did not fly off at the challenge call, the male, still close beside her, uttered a flight-display call without the final "bock-squeak" (Fig. 2F), immediately followed by a flutter along the perch about a foot away from her. Turning as he landed he crouched and with a loud "bock" fluttered back towards her, but at this point she left. Almost certainly this flutter back with the "bock" is the mounting movement; it is very similar to the mating-leap of the Bearded Bellbird. The whole movement, first away from and then back towards the female has been therefore termed the pre-mating movement and call. Although it was seen only once in the presence of another bellbird, some adult males practiced the pre-mating se-

quence at infrequent intervals (Table 4). In these practice movements a male always flutters away from the outermost position on the branch, then turns to utter the "bock" facing back toward the outer end. Sometimes he flutters back with the "bock" but often remains stationary and makes a wing-flicking flight intention movement.

Encounters between adult males.—Many encounters between adult males do not develop into the ritualized visiting sequence. These encounters occur when an adult has to leave its territory to feed and to do so passes through or near another adult's territory. As already mentioned, when flying to feed, bellbirds land and rest approximately every 500 m, usually on some tree top. I never saw one make a long sustained flight. The usual sequence of events is as follows. If the territory owner is calling from a high post, he immediately spots an intruder and will fly at once to perch near him. Then for about a minute the two silent adults perch in a crouched position about a foot apart and facing half away from one another (Fig. 5B). The intruder is recognizable by his contracted and the territory owner by his elongated wattles. After a brief period the intruder flies on, followed by the territory owner; sometimes both land again for another brief silent spell or the intruder flies right on to feed and the territory owner calls briefly at the point where he stops his pursuit, which may be as much as a quarter of a mile from his territory.

Much more prolonged encounters occur when an adult male first attempts to establish himself at a calling territory. The sequences detailed below show the significance of extended wattles in the degree of dominance a male is commanding, and for the evidence it provides that a male attempting to establish himself, initially defends the lowest perch, the visiting perch. This probably accounts for the far higher proportion of time spent at visiting perches by more recently established males than by the longer established males.

The most complete observations were made on the interactions between males 6 and 8, the former identifiable by his distinctive calls (Fig. 3J). Male 6 had established himself by the beginning of June in a rather large calling territory (Fig. 1) that included a high calling post at the edge of a ravine, with a direct view along it to the territory male 8 was trying to establish during the second week of June. This latter territory, which initially straddled the ravine, was probably not ideal as recent tree-felling left no visiting perch beneath the canopy; instead a fully exposed broken-off branch of a nearly dead and leafless tree was used as a visiting perch. This tree grew halfway down the ravine and the upper part of it, about 5 m above the visiting perch, was used as a high calling post. All these factors produced unusually good conditions for observation.

I watched male 8 here for 2½ h on 12 June. During this time six encounters took place between him and male 6. Between these encounters, which lasted from 3 to 5 min each, male 8 called at the high post or the visiting perch in this tree. During the first two encounters male 6 silently chased male 8 round and round the tree displacing him approximately every 4 sec; occasionally both males remained stationary and silent doing the wattle-shaking display, or facing half away from each other (Fig. 5B). When he arrived on these first two visits male 6 had his wattles retracted, but he soon elongated them and by the end of the first encounter they were more elongated than those of male 8.

At the end of the first two encounters male 6 called briefly at the visiting perch. At the third encounter, after some chasing male 8 went to the visiting perch and performed the wattle-shaking display and then started to call, but male 6 displaced him in the middle of the first call. During the fourth encounter male 6 arrived, as previously, with retracted wattles and only partially elongated them. For the first half of the encounter he occasionally displaced male 8, but far less frequently than in the earlier encounters; during the second half, male 8 remained on the visiting perch doing the silent wattle-shaking display and was not displaced.

During the last two encounters male 6 had retracted wattles throughout the visit. As he flew in, male 8, who had been calling at the high post, flew down to the visiting perch and did the wattle-shaking display there. At the fifth encounter, when male 6 tried to displace him from the visiting perch he flew away for half a minute and then back again. At the last encounter, when male 6 tried to displace him, he flew slightly up in the air and immediately relanded. During the remainder of these two encounters male 8

performed the silent wattle-shaking display, and male 6, also on the visiting perch, had his back half turned towards male 8. After all the encounters, when male 6 flew off male 8 immediately started to call again.

Observations at the same tree early in the morning of 17 June showed a development in the agonistic relationships of males 6 and 8. Male 8 was calling at the visiting perch when male 6 flew up the ravine and landed at the inner position of the perch. The visiting sequence including changing place then occurred with male 8 in the role of the dominant territory owner, but male 6 did not move when male 8 uttered the changing-place call in his ear. At this male 8 slowly edged away about 30 cm and then half a minute later again went very close and uttered the challenge call, which again failed to move male 6.

The same sequence was repeated a third time without male 6 moving. While the challenge call was uttered male 6 perched at the very end of the visiting perch and leaned as far away as possible from the sound. He flinched at each "bock," especially at the second "bock," which is particularly loud. Throughout these incidents male 8's wattles had been fully elongated and those of male 6 retracted, but after the last challenge call, as male 8 edged about 30 cm away from male 6, the latter slowly elongated his wattles while male 8's were becoming retracted.

Then the visiting sequence was reenacted with male 6 in the dominant role of the calling bird. At the first "bock" of the challenge call male 8 flew to another perch but returned half a minute later and again the visiting sequence was reenacted. This time male 8 withstood the first "bock" of the challenge-call but retired at the second very loud "bock" and flew over to the other side of the ravine and called there. Meanwhile male 6 called briefly at the visiting perch from which he had just ousted male 8.

Evidently between 12 and 17 June male 8 progressed from a situation where male 6 could chase him at will within his territory to a situation where male 6 approached him through the ritualized visiting sequence. Although this also led to male 8 being ousted from his visiting perch, it probably represented a greater degree of equality. While male 8 was submitting to the dominance of male 6 he was himself maintaining the position of dominant territory owner over at least four other adult males who came from farther away to feed at the fruiting *Nectandra salicina*. After feeding, these adults usually visited male 8 at a high post on the south side of the ravine and always retired at the first "bock" of his close-up call.

Apart from the encounters between males 6 and 8, the only other encounter at which a visitor failed to be driven off by close-up calling was between male 7 and an immature male. When his first close-up call (a changing-place call) failed to dislodge the visitor, male 7 spent half a minute with his back half turned to the visitor. He then again crouched over him and uttered the challenge-call, and at the second "bock" the visitor left.

IMMATURE MALES

No immature males were seen or heard for the first 3 weeks of observation. During the second half of May and the first week of June immatures were twice seen visiting adult males. Between 8 and 16 June at least six immature and one subadult male were frequently seen in the study area. Thus the adult males apparently migrate up the mountain in advance of the immatures. The six immatures were probably in or approaching their second year of life (D. W. Snow 1973); three were in the green juvenile plumage with all three wattles growing, two were in the same plumage except that a few adult body feathers were beginning to replace the juvenile ones, and one was in juvenile plumage without wattles. This last bird was presumed to be a male because it was trying to call. Young Bearded and White Bellbirds also make their first attempts to call just before the wattles start growing early in their second year.

According to the timing of plumage changes worked out from the study of museum specimens by D. W. Snow (1973), males are halfway through the change from juvenile to adult plumage early in their third year of life. This should be a conspicuous and easy plumage to identify; but no males in this plumage were seen, so possibly at this age the complete vertical migration is not undertaken.

Only one probable fourth-year bird was seen; it was in adult male plumage except for a few green feathers on the lower breast and belly. On 8 June it was visiting males 2 and 7 and was probably the male that called irregularly for the next few days up the valley from these two territories.

Migration to the breeding grounds serves an important function for second-year males, as this is the age at which they probably learn the calls and so need to be near calling adults. There is no such obvious reason for third-year males to visit the breeding grounds, as it is unlikely that they would have the chance to breed or effectively defend an adequate calling territory.

The first calling from a young male was heard on 20 May, from a bird in juvenile plumage without wattles. The call was a squawk very similar to the earliest calling attempts of the Bearded and White Bellbirds. A young male in similar plumage watched calling for 15 min on 9 June was uttering a throttled "bock" (Fig. 2B). This was sometimes followed by gurgling and squeaks; at other times the beak remained open and no noise was emitted.

Two young males (in juvenile plumage, with wattles) watched calling on 8 June were following a throttled "bock" with a squeak, a pause, and then another squeak, which from the timing rather than the faint noises emitted was evidently an attempt at the changing-place call. The calls of a slightly older second-year bird, with scattered adult feathers over the head and body, were more mature. The "bock" sounded nearly adult, both as a monosyllable and at the beginning of the changing-place call. This bird was also uttering the flight-display call in which the "bock-squeak" (Fig. 2C) differed from that of the adult (Fig. 2F) by the incompleteness of the note at 5 kHz. This appears to be a note from a second sound source (Greenewalt 1968), so is probably difficult to perfect.

The second-year males moved about together in small parties of two or three and occasionally four individuals. They came to the fruiting *Nectandra salicina* together and then together visited the calling adult males nearby. Periodically on the fringes of the adults' territories one or two practiced calling, sometimes in the same tree. Perhaps these social bonds between young males continue into adulthood. If this is so, it might account for the fact that the two adult males in the study area with calls that had evidently not been learned at Monteverde occupied adjacent calling territories (males 4 and 5, Fig. 1).

FEMALE BEHAVIOR AND BREEDING

No evidence of breeding was obtained during my visit¹ beyond the fact that adult males and apparently females were present in some numbers and the preliminaries of courtship were taking place. Although the size difference between the sexes is considerable, it is a difficult criterion to use for identification in the field. Birds in female plumage were presumed to be females and not immature males if they were silent and solitary. Apparent females were seen on 25 of the 39 observation days in May and June. Watches at the *Nectandra salicina* trees in June showed that at least six individual females were converging there to feed. They came in singly from the surrounding forest and left again alone.

¹ In August 1975 the guard of the Monteverde preserve found a Three-wattled Bellbird's nest which he showed to Ron Tomlinson, a resident of Monteverde. Tomlinson briefly watched the female building the nest, a structure of loosely woven twigs ca. 20 cm long and ½ cm thick. It was sited 6½ m up in the crotch of an understory tree just inside the forest canopy on the edge of a pasture. The nest never had any contents on later visits.

Judging from my observations of 20 visits by females to visiting perches, none of which culminated in mating, preliminary courtship must be protracted. The length of a female's visit varied greatly. Some lasted only 2 min, the female coming down once to the visiting perch and leaving when the male uttered a close-up call; the longest lasted 19 min, during which the male uttered the close-up call nine times and each time the female retired either to the inner position or to a perch a few feet away.

DISCUSSION

Local dialects.—Verbal descriptions of bird songs are notoriously difficult to compare. Even so it is fairly certain that the usual calls of the Monteverde bellbirds are not the same as those described in previously published accounts of this species. The whistle uttered only by male 5 (Fig. 3I) closely fits the description by Wetmore (1972) of "a high-pitched whistled double note, 'whit see,' given rather slowly." Ridgway's (1905) description is also apt: "a wonderfully loud clear and prolonged whistle," although he makes no mention of two syllables. These two authors were respectively describing the species from Panama and the Atlantic slope of Turrialba (130 km ESE of Monteverde). Both authors mention another call always associated with the whistle. Ridgway describes it as immediately preceding it and sounding like an "explosive whack as from a mallet on a hollow log of hard wood." Wetmore says that the second call immediately follows the whistle and is a "harsher, loud metallic call." No such call was associated with the whistle of male 5. Possibly the whistle is not part of the vocal repertoire throughout the species' range in Panama, as a 2-min recording in the Cornell Library of Natural Sounds from Volcan de Chiriquí does not include a whistle.

Skutch (1969), describing the species at Vara Blanca (78 km ESE of Monteverde) during the breeding period and at El General (160 km SE of Monteverde) during its nonbreeding period, emphasizes the difference in character between the two notes he heard, one that he describes as a dull throaty "buck," probably comparable to the "whack" of Ridgway, and the other as a sharper higher pitched "wheat," which must be the equivalent of a single syllable whistle. So different were the two notes that, before observation proved otherwise, Skutch surmised that they were uttered by different individuals, possibly the "buck" by the male and the "wheat" by the female. The usual calls of the Monteverde bellbirds show no comparable differences, except that the whistle of male 5 was entirely different from the other calls.

Without tape recordings further comparisons are too speculative to be profitable, but obviously the species' calls differ greatly in different parts of its range. Such differences suggest a high degree of physical separation between populations. In the Three-wattled Bellbird only during the presumed breeding period, March to July, is the species divided into isolated populations. At this time they are concentrated in montane forests between 1,300 and 1,600 m; during the rest of year they range widely over forested and semiforested country down to sea level and even to the islands off the Panama coast (Slud 1964, Wetmore 1972). This suggests that the formation of dialects may depend on the return of young males to their natal areas during a critical learning period. Judging from the plumage of the young males that I watched, this period is when they are 12 to 15 months old. The maintenance of separate dialects by traditional migration patterns may now be partially breaking down under the rapid destruction of forests for dairy farming at the breeding altitudes. Judging from the frequency of innovation and variation in the calls of the Monteverde population,

coupled with the evidence that vocalizations are largely learned, possibly even a local population has no fixed pattern of vocalizations but one that is constantly changing and evolving.

Function of multiple calls.—A possible function of the very different volumes of the different parts of the multiple calls is apparent when one tries to locate a calling individual. The loud explosive “bock,” while effective in advertising the bird and its approximate direction at a long distance, when heard at close quarters is so all-pervasive as to be nondirectional, whereas the quieter squeaky “bock” of the flight-display call and the quiet sections of the changing-place call are an immediate aid to locating a bird. In the challenge call the same quiet portions appear to serve a different purpose. When an owning male is uttering this call in the ear of a visitor the quiet section evidently produces a build-up of tension in the visitor so that many leave just before the final “bock.” While this is advantageous when the visitor is a male challenging the owning male’s rights, it has no obvious advantage in the courtship of the female; in fact it must tend to make courtship more prolonged by repeatedly driving the female away.

Where contact between the sexes exists only for mating, the female undergoes no gradual conditioning to the close presence of the prospective mate. In this situation a preceding call indicating that a display movement is imminent may be advantageous. As described above, the two displays of the Three-wattled Bellbird involving flight are consistently preceded by special calls.

Comparison of the four bellbird species’s calls.—In this and the following section I have drawn on my own field observations, and other published accounts, of three of the four bellbirds. I have not seen the fourth species, *P. nudicollis*, in the field, and no account of its display has been published, but I have made limited use of observations and recordings of two males in the London Zoo, and D. W. Snow (1973) has published sonograms of two of its calls.

Recordings and descriptions at present available suggest that the Three-wattled Bellbird has the most varied repertoire of the four species, and that it may show the most marked local differences between populations. (The suggestion by D. W. Snow (1973) that the calls of the Three-wattled Bellbird are reminiscent of the unformed calls of young males of the other species appears to be valid for the population in Panama where the recording he used was made, but is not true of the Monteverde population.) The calls of the Monteverde birds show some resemblances to those of the other bellbird species. The monosyllabic “bock” of the Monteverde birds is very close to the “bock” of *P. averano* and *P. nudicollis*, and the squeaky “bock” that begins and ends the flight-display call (Fig. 2F) is very similar to the repeat call of *P. nudicollis*, both consisting of a less loud “bock” immediately followed by a high-pitched note apparently from a different sound source.

Available information indicates that each of the four species has a repertoire of at least three different calls. I described the three different calls of the Three-wattled Bellbird earlier. *Procnias averano* has a single loud “bock,” a less loud repeated “tock,” and a double-syllable “kay-kong” also repeated in a series. The population in Trinidad has lost the last of these calls, apparently between 1895 and 1958. *Procnias nudicollis* has a single loud “bock,” a softer repeated call, and a quiet call, which is the repeated call uttered at greatly reduced volume with the beak almost closed. *Procnias alba* has only two calls, but the loudest one, the bell-call, may be uttered in two ways that are audibly quite distinct, either in a motionless position or with a violent swinging movement of the body from right to left. In all four species young

males first learn the loudest call, the "bock" in *P. averano*, *P. nudicollis* and *P. tricarunculata*, and the bell-call in *P. alba*. The earliest attempts at these calls consist of very similar squawks in all four species. The squawk of *P. nudicollis* (Fig. 2D) was recorded from a young male at London Zoo. When recorded he had been practicing for about 5 months and most "bocks" were relatively mature, but he occasionally reverted to squawks.

Comparison of the displays of the four species.—As the observations on *P. nudicollis* were made on two males in captivity only tentative conclusions can be drawn on the functions of its calls and behavior movements. In the other three species the advertising and courtship behavior of males have the following similarities: all call from above the canopy on high exposed branches and also have a special perch beneath the canopy to which the owning male leads visiting bellbirds. Here the same display movements are performed whatever the sex or plumage of the visitor. One of these display movements is a flight-display in which the male lands in a crouched position with tail fanned. The display to visitors at close quarters is largely silent and includes gazing intently at the visitor interspersed with head movements that shake or move the wattles. Although *P. nudicollis* has no wattles, it also does a silent headshaking interspersed with looking up as though at an imaginary visitor. The loudest call of each species is incorporated into the climax of the display at the visiting perch. This climax is either the mounting of the female or the final ousting of a visiting male. In each species it is a sudden call and movement towards the visitor from a position 30 to 60 cm away on the visiting perch: in *P. averano* a leap with a "bock," in *P. alba* a bell-call with a swinging movement or a flutter, and in *P. tricarunculata* the final flutter with a "bock" of the premating movement (p. 640). *Procnias nudicollis* after a period of silent head-shaking also suddenly leaps with a "bock" along the perch, probably an analogous movement.

The differences in the epigamic displays of the three species that have been studied in the field are related to differences in the visiting perch. Thus in the drier tropical forests of southern Guyana where I studied *P. alba*, woody lianas are abundant, and an uncluttered horizontal section of woody liana was the usual visiting perch of this species. The significance of this type of visiting perch lies in the fact that the visitor does not have to occupy an exact position on the perch, as do the visitors of *P. averano* and *P. tricarunculata*, but a position to the left of the calling male. From whichever side of the horizontal liana the visitor approaches, the calling male can if necessary convert it to a left flank approach by turning on the perch. The male needs to be approached from the left side because his single wattle normally hangs to the right of the beak and as the visitor approaches he utters the first note of the disyllabic bell-call while facing to the right and then swings his body through approximately 100° to utter the second note directly at the visitor on his left. While swinging from right to left the wattle flies out horizontally and would undoubtedly be in danger of entering the wide open beak if the direction of swing were reversed. Lianas growing horizontally between trees were not seen in the extremely wet epiphyte-laden forest of Monteverde nor were they a common feature of the forest where *P. averano* was studied in Trinidad.

The visiting perch of *P. averano* is the lowest side branch of a small understory tree or sapling. Ideally it is an uncluttered horizontal branch with a downward curve at its outer or distal end. These characteristics are important because throughout encounters the advertising male maintains a position below his visitor and finally, before the mating leap, perches at the lower or distal end of the visiting perch while

the visitor perches at the slightly higher inner position. The evidence also points to the lower position being the dominant one in *P. tricarunculata*, and this probably underlies its choice of a visiting perch growing upwards at an angle of 10 to 15° above the horizontal. Thus if a visitor lands at the slightly lower inner position on the visiting perch, the owning male immediately changes place with the visitor (Fig. 4B) so that he is in the lower position for the ultimate challenge of the close-up call.

The broken-off branch used as a visiting perch by *P. tricarunculata* can only be common in forests where tree and branch falls are frequent. Three ecological features of Monteverde are possibly effective in causing the abundant falls: the frequent electrical storms, the high winds associated with the change from the Atlantic- to the Pacific-dominated weather, and the great burden of epiphytes the trees support.

The agonistic displays of *P. tricarunculata* are more elaborate and ritualized than those of *P. averano* and *P. alba*. The two latter species are sedentary or largely so; hence confrontations between males determining their position in a dominance hierarchy are likely to occur less often than in males of *P. tricarunculata*, which migrate annually to the breeding grounds and have to reestablish an advertising territory in competition with other adult males.

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LITERATURE CITED

- CRANDALL, L. S. 1948. Notes on the display of the Three-wattled Bellbird (*Procnias tricarunculata*). Zool. N.Y. 33:113-114.
- GREENEWALT, C. H. 1968. Bird song: Acoustic and physiology. Washington, Smithsonian Institution Press.
- HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.
- RIDGWAY, R. 1905. A winter with the birds in Costa Rica. Condor 7: 151-160.
- SKUTCH, A. F. 1969. Life histories of Central American birds III. Pacific Coast Avifauna, No. 35. Berkeley, California.
- SLUD, P. 1964. The birds of Costa Rica. Bull. Amer. Mus. Nat. Hist. 128:1-430.
- SNOW, B. K. 1970. A field study of the Bearded Bellbird in Trinidad. Ibis 112: 299-329.
- . 1973. Notes on the behavior of the White Bellbird. Auk 90: 743-751.
- SNOW, D. W. 1962. The natural history of the Oilbird, *Steatornis caripensis*, in Trinidad, W. I., part 2. Population, breeding ecology and food. Zoologica 47: 199-221.
- . 1971. Evolutionary aspects of fruit-eating by birds. Ibis 113: 194-202.
- . 1973. Distribution, ecology and evolution of the Bellbirds (*Procnias*, Cotingidae). Bull. Brit. Mus. Nat. Hist. 25: 369-391.
- WETMORE, A. 1972. The birds of the republic of Panama, part 3. Smithsonian Misc. Coll. 150: 1-631.