

# DISPLAY PATTERNS OF TROPICAL AMERICAN "NINE-PRIMARYED" SONGBIRDS

## I. *CHLOROSPINGUS*

M. MOYNIHAN

THIS is the first in a series of papers on the behavior of tropical American finches, tanagers, and honeycreepers.

All or most of these birds are usually considered to be closely related to one another, and to the vireos, American warblers, and icterids (see, for instance, Mayr and Amadon, 1951; Beecher, 1953; Tordoff, 1954; Stallcup, 1954; and Wetmore, 1960). The group as a whole will be called "American nine-primaried songbirds" throughout this and the following papers of this series.

Most of the behavior patterns discussed in these papers are "ritualized" patterns, or "displays," *i.e.*, patterns that seem to have become specialized, in form and/or frequency, to subserve signal functions.

The principal objective of these papers is to present the material for a subsequent analysis of the evolution of display patterns. Special attention will be paid to those displays, and aspects of displays, that seem to be most significant from a comparative point of view.

The treatment of different species and groups of species will be very unequal in the following papers, as some species were observed at much greater length than others. The species will also be discussed in a somewhat arbitrary sequence, as some of them are still being studied at the present time.

### BUSH-TANAGERS OF THE GENUS *CHLOROSPINGUS*

Two species of *Chlorospingus*, the Brown-capped Bush-tanager (*C. ophthalmicus*) and the Sooty-capped Bush-tanager (*C. pileatus*), were observed during the present study. Both species are montane. They were studied in several areas near the town of Cerro Punta, on the Volcan de Chiriqui in western Panama. According to Hellmayr (1936), the Sooty-capped Bush-tanagers of this region belong to the nominate race, while the Brown-capped Bush-tanagers belong to the subspecies *novicius*.

Both Brown-capped Bush-tanagers and Sooty-capped Bush-tanagers are rather small, "chunky" tanagers. The sexes are similar in both species. The Brown-capped Bush-tanagers of the Volcan de Chiriqui have brown heads, with light-buffy throats and triangular white patches behind the eyes, and are largely olive above and yellowish below, with some white on the breast and abdomen. Sooty-capped Bush-tanagers are rather similar, but have black heads, with white stripes above and behind the eyes.

Both species occur in a wide variety of brush and forest habitats and are

very active and restless. Many of their feeding and locomotory patterns are very reminiscent of the corresponding patterns of many warblers of the genus *Basileuterus* and some finches of the genus *Atlapetes* (e.g., the South American species *A. rufinucha* and *leucoptera*).

Brown-capped Bush-tanagers are sometimes highly gregarious among themselves, especially during the nonbreeding season. Both Brown-capped Bush-tanagers and Sooty-capped Bush-tanagers often occur in mixed flocks with other species of birds.

Some of the habits of both Brown-capped Bush-tanagers and Sooty-capped Bush-tanagers, especially their gregarious reactions, have been described in more detail in an earlier publication (Moynihan, 1962).

Both species were studied during five different field trips to the Chiriqui area, during the following periods: 17–21 September 1958; 2–9 March 1959; 19–30 March 1960; 4–10 October 1960; 9–13 April 1961. Many individuals of both species performed many breeding behavior patterns during the periods of observation in March and April.

#### DISPLAYS AND RELATED PATTERNS OF THE BROWN-CAPPED BUSH-TANAGER

##### *Preflight Patterns*

Like many other passerine birds, Brown-capped Bush-tanagers sometimes perform one or more "Wing-flicking" and/or "Tail-flicking"<sup>1</sup> movements when they are preparing or "getting ready" to fly.

Wing-flicking is very simple. The wings are flipped upward and outward, and then down again, very rapidly. The two wings are moved more or less simultaneously. They are not spread, or only spread to a very slight extent, during most Flicking movements. The Wing-flicking movements of Brown-capped Bush-tanagers are comparatively extreme. They are more exaggerated in form (the wings going farther upward and outward), and more frequent, on the average, than the Wing-flicking movements of many other species of tanagers and finches.

The Tail-flicking of Brown-capped Bush-tanagers is somewhat more complex than their Wing-flicking. The tail is jerked suddenly to one side, and then brought back to its original position; or jerked first to one side, and then far to the other side, and then brought back to its original position. All these movements are always very rapid. Some Tail-flicking movements of Brown-capped Bush-tanagers seem to be purely lateral; but others include a vertical component as well. This vertical component is quite variable. Sometimes it is first up and then down (the tail going up as it is jerked to one side, and then down as it is brought back to its origi-

<sup>1</sup> The initial letters of the names of all probably or certainly ritualized behavior patterns will be capitalized throughout this and the following papers of this series.

nal position or jerked to the other side). At other times the sequence is first down and then up. In any case the vertical component is apparently always much less extreme and conspicuous than the lateral component. The lateral component is usually much more extreme in the Tail-flicking of Brown-capped Bush-tanagers than in the corresponding movements of many other species of tanagers and finches.

The tail is very seldom or never fanned during the Tail-flicking movements of Brown-capped Bush-tanagers.

The Tail-flicking and Wing-flicking movements of Brown-capped Bush-tanagers are usually synchronized with one another; *i.e.*, a bird usually performs one complete Wing-flicking pattern at the same time that it performs one complete Tail-flicking pattern.

The comparatively great exaggeration of these movements would suggest that they have become ritualized.

Brown-capped Bush-tanagers seem to perform Flicking movements in any and all situations, whenever they "want" to fly, but are hesitant to do so, either because they have to overcome some "inertia" before launching, and/or they are motivated by conflicting or incompatible "tendencies."

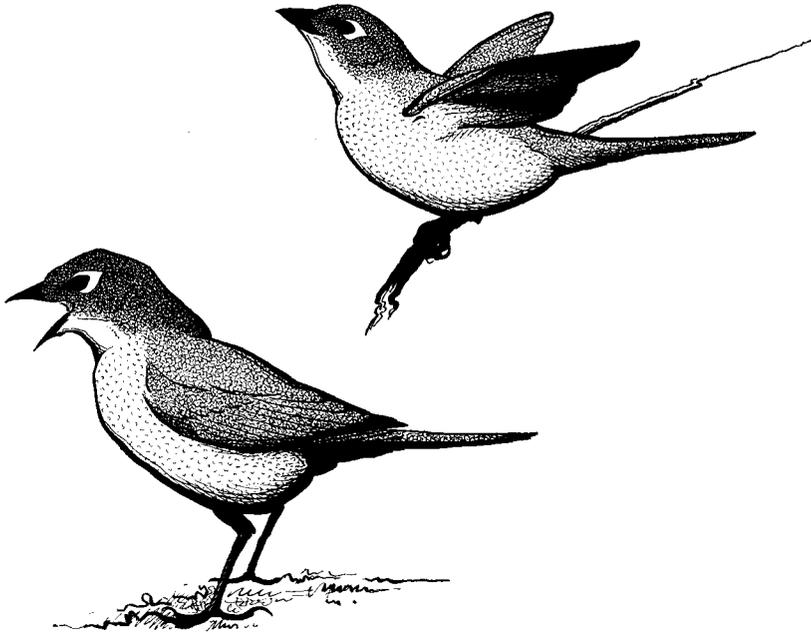
The term "tendency" will be used in a very broad and general sense throughout this paper to designate any "readiness to show a particular type of behavior" (Marler, 1956).

The great variety of situations in which Flicking movements are performed would suggest that they may be produced during almost any type of motivational conflict.

The Flicking movements of Brown-capped Bush-tanagers probably function as signals indicating a desire to fly. Other birds should be able to recognize that a bird performing Flicking movements is likely to fly within a few seconds. (This does not mean that Flicking movements are "purposeful" signals. Solitary birds usually or always seem to perform as many Flicking movements as birds with companions in otherwise similar circumstances.)

Brown-capped Bush-tanagers may also perform other patterns, in addition to Flicking movements, as preparation for flight. They may sleek or smooth down their head, neck, and body plumage; and/or stretch their necks forward; and/or point their heads and bills diagonally upward; and/or perform a variety of rather slight and irregular bowing and pivoting movements. These patterns are not exaggerated or stereotyped enough to be considered ritualized; but they are of some comparative interest because they are probably similar to the patterns from which elaborate displays of other American nine-primaried songbirds were originally derived. This is particularly true of the bowing and pivoting movements and the upward pointing of the head and bill.

All or most of these unritualized preflight patterns may occur in the same types of situations as Flicking movements; and they are frequently combined with Flicking (Figure 1A is a sketch of a bird performing Wing-flicking and pointing the head and bill upward).



**Figure 1. Display patterns of Brown-capped Bush-tanagers. A. Top. Wing-flicking, combined with unritualized upward pointing of the head and bill. The wings are seldom flicked higher than indicated in this drawing. B. Bottom. Gaping, superimposed upon an otherwise unritualized standing posture.**

All these preflight movements and postures, including both unritualized patterns and Flicking, are performed by both male and female Brown-capped Bush-tanagers. Males may tend to perform all or most of these patterns more frequently than do females, simply because they tend to become involved in situations (*e.g.*, on the boundaries of their territories) where motivational conflicts are almost inevitable rather more frequently than do females (see below).

#### *Tsit* Notes

The most common notes uttered by both male and female Brown-capped Bush-tanagers are moderately loud, hard, short notes. A single note of this type might be transcribed as *Tsit*. Such notes are uttered in a very wide variety of circumstances. They are almost always uttered by birds moving, in any way, near any other bird(s). They are often uttered in series. The number of notes in a single series is not fixed. The intervals between notes are sometimes extremely variable within a single series, and often very different in different series. Extremely accelerated series of

many *Tsit* notes are sometimes uttered by flying birds. Some of these series are so rapid that they are almost trills. *Tsit* notes may be uttered by birds performing any type of locomotory or prelocomotory movements, or sitting or standing in almost any type of unritualized posture. They are seldom or never accompanied by any special ritualized postures or movements except Flicking.

The frequent correlation of *Tsit* notes with locomotory patterns might suggest that they are produced by much the same factors as Flicking movements, and subserve similar functions. There are other indications, however, that *Tsit* notes are at least partly independent of locomotion. *Tsit* notes are seldom or never uttered very frequently by solitary birds, no matter how active the solitary birds may be. This would also suggest that *Tsit* notes are produced by a narrower range of causal factors than Flicking movements (and all or most of the unritualized preflight patterns).

*Tsit* notes intergrade with both *Tuck* notes, which seem to be hostile,<sup>2</sup> and "Plaintive Notes," which seem to be produced when some sort of sexual motivation is activated (see below); but they do not seem to occur in significantly close association with either overt fighting or high-intensity sexual behavior. They are also uttered almost as frequently during the nonbreeding as during the breeding season. It seems likely, therefore, that all or most *Tsit* notes are uttered when both hostile tendencies and some sort of nonhostile, "friendly" motivation (perhaps any sort of "friendly" motivation) are activated simultaneously.

If so, it is not surprising that *Tsit* notes are so common. There is good evidence that Brown-capped Bush-tanagers are always or almost always both attracted to and repelled by other individuals of their own species. Brown-capped Bush-tanagers tend to be gregarious among themselves, and associate in flocks; but they also tend to dispute among themselves within the flocks. Almost any Brown-capped Bush-tanager is apt to alternate or combine advance and retreat movements and/or intention movements whenever it encounters any other bird of its own species.

*Tsit* notes may function as "call notes" or "contact notes." They are often very "contagious." The utterance of *Tsit* notes by one Brown-capped Bush-tanager frequently seems to provoke the utterance of *Tsits* by other Brown-capped Bush-tanagers in the same area. I have seen incidents that would suggest that Brown-capped Bush-tanagers are more attractive, both to other birds of their own species and to birds of other species, when they are uttering *Tsit* notes than when they are silent. Brown-capped Bush-tanagers in flocks tend to utter many *Tsits*, and the sound of these

<sup>2</sup> Throughout this paper the term "hostile" will be used to include all behavior produced by attack and/or escape tendencies.

notes may help to prevent members of a flock from leaving the flock, or getting left behind when the flock moves on.

Brown-capped Bush-tanagers utter *Tsit* notes much more frequently than individuals of many other species utter their corresponding call or contact notes. The comparatively great frequency of *Tsit* notes by Brown-capped Bush-tanagers may be an adaptation to promote gregariousness (see comments in Moynihan, *op. cit.*).

### *Some Purely Hostile Patterns*

Brown-capped Bush-tanagers perform a considerable variety of hostile behavior patterns.

Their hostile behavior includes both unritualized, overt, attack and escape movements, and several displays. Their unritualized attack and escape patterns are relatively simple, and very much like the corresponding patterns of most other small passerine birds in form; but their hostile displays are more complex and more interesting. Their hostile displays are usually associated with both overt attack and overt escape movements; but each distinctive type of hostile display is associated with overt attack and escape in a characteristically different way.

It is likely that the attack and escape tendencies of all or most American nine-primaried songbirds (like those of many other birds of other groups—see, for instance, Moynihan and Hall, 1954) are seldom or never activated independently of one another. Any stimulus that activates one of these tendencies probably activates the other, to some extent (although one of the tendencies may be stimulated so much more strongly than the other that it prevents or suppresses the overt expression of the other).

There is some evidence that Brown-capped Bush-tanagers perform relatively fewer unritualized hostile activities (especially aggressive movements), and relatively more ritualized hostile displays, than some other American nine-primaried songbirds (Moynihan, 1962). This may be another adaptation to promote gregariousness.

*Gaping.* Brown-capped Bush-tanagers sometimes open their bills unusually widely, and keep them open for a considerable length of time (perhaps up to a minute) during certain disputes. This Gaping is usually silent. I have seen Gaping only during disputes between captive birds; but it is probably also performed by wild birds under natural conditions (it is the sort of pattern that is easily overlooked at a distance). The Gaping I observed was frequently accompanied by aggressive-looking forward pecking or jabbing movements. It was superimposed upon a variety of unritualized prelocomotory standing and perching postures (*e.g.*, the posture shown in Figure 1B). Birds frequently Gaped immediately before pecking an opponent; but Gaping was not always followed by attack, and many attacks were not preceded by Gaping. Many or most of the disputes in which Gaping occurred were extremely vigorous and/or prolonged, and appeared to be high intensity.

These facts would suggest that all or most Gaping is produced when the attack tendency is strongly predominant. The actual strength of the escape tendency may be appreciable during Gaping; but the actual strength of the attack tendency must be very much greater.

The opening of the bill during Gaping is similar to the opening of the bill during biting, but more extreme or exaggerated. It is this exaggeration that suggests that Gaping is ritualized, probably a ritualized derivative of the biting used during fighting. Gaping is often intimidating. When one bird Gapes at an opponent, the opponent usually retreats or performs intention movements of retreating. Gaping may thus be classified as a threat display (Moynihan, 1955).

*Tuck notes.* Brown-capped Bush-tanagers frequently utter sharp *Tuck* notes in more or less mildly hostile circumstances.

Such notes may be uttered singly or in series. Series of *Tuck* notes are very irregular. The number of notes in series of *Tuck* notes seems to be completely "indeterminate," in much the same way as the number of notes in series of *Tsits*. A bird may continue to utter *Tucks* for a long period of time; but even the longest series of *Tucks* are not broken up into definite series of a regular, fixed number of notes. The pauses between successive *Tuck* notes may vary within a single series, and are often very different, on the average, in different series.

A nonterritorial Brown-capped Bush-tanager will often utter many *Tuck* notes when it comes close to another bird, of its own or another species, with which it is unfamiliar. A territorial Brown-capped Bush-tanager will often utter *Tuck* notes when it sees a territorial neighbor some distance away, or hears a vigorous dispute in a neighboring territory. Both territorial and nonterritorial Brown-capped Bush-tanagers tend to utter *Tuck* notes when they see a "potential predator," such as a human being, approaching rather slowly from a distance. *Tuck* notes are often accompanied by slight and brief advance and/or retreat movements; but they are not usually accompanied or immediately followed by extreme and vigorous attack or escape. When they do occur with extreme or vigorous hostile patterns, however, they are most often associated with aggression. They are, for instance, occasionally uttered by pursuing birds during hostile aerial chases. Rapid series of *Tucks* also intergrade with Rattle calls (see below), which seem to be definitely aggressive. Such facts would suggest that all or most *Tuck* notes are uttered when both the attack and escape tendencies are moderately weak, and the attack tendency is slightly (but only slightly) stronger than escape.

*Tuck* notes are combined with the same variety of locomotory and prelocomotory movements and intention movements as *Tsit* notes. They also seem to intergrade

with *Tsits*. I have heard birds utter notes that were more or less perfectly intermediate between typical *Tuck* notes and typical *Tsit* notes.

I have also heard Brown-capped Bush-tanagers utter notes that were distinctly more nasal than ordinary *Tuck* notes, but otherwise similar. Some of these notes were very reminiscent in sound of the common nasal hostile notes of some species of *Rhampocelus*. Unfortunately, I did not hear the nasal notes of the Brown-capped Bush-tanagers frequently enough to determine if they were anything more than variants of typical *Tuck* notes.

*Sreeee Notes*. Brown-capped Bush-tanagers utter several other hostile sounds in addition to *Tuck* notes and Rattles. Among these are some notes that might be transcribed as *Sreeee* and other notes that might be transcribed as *Zheeeeeeee*. These two types of notes are quite similar in sound, being characterized by thin, high *eeeeee* sounds; but they seem to occur in somewhat different circumstances, and are probably produced by different strengths of the hostile tendencies.

*Sreeee* notes are relatively soft, and very faintly rattling (it might be better to describe them as having a rattling "undertone"). They are seldom or never hoarse or husky in sound. They may be uttered singly, or in series of up to 20 notes. They tend to occur during moderately vigorous and prolonged disputes. I have heard them uttered during disputes among captive birds as well as by wild birds under natural conditions in the non-breeding season. The captive birds utter *Sreeee* notes while standing or perching in ordinary unritualized postures. Their *Sreeee* notes were frequently accompanied by Flicking movements and/or aggressive-looking forward pecking and jabbing movements. Sometimes a bird uttered one or more *Sreeee* notes just before actually attacking an opponent. Sometimes the *Sreeee* notes were uttered just before or just after silent Gaping. A few *Sreeee* notes may even have been combined with Gaping (they were uttered with the bill opened more widely than usual). The birds I heard uttering *Sreeee* notes in the wild were engaged in aerial chases. Most of the *Sreeee* notes during these chases appeared to be uttered by the pursuing birds rather than the pursued. Some of them were closely associated with Rattles.

Such facts would suggest that *Sreeee* notes may be produced by motivation that is more or less intermediate between the motivation producing typical silent Gaping and the motivation producing typical Rattle calls (see below).

*Zheeeeeeee Notes*. *Zheeeeeeee* notes are slightly hoarse in quality, and seem to lack the rattling undertone of typical *Sreeee* notes. Individual *Zheeeeeeee* notes are also longer and louder than *Sreeee* notes. *Zheeeeeeee* notes may be uttered singly or in short series of two, three, or four notes.

I have heard *Zheeeeeeee* notes only during prolonged and very active disputes between neighboring territorial birds during the breeding season.

During these disputes such notes are usually or always uttered by flying birds engaged in prolonged and rapid "pendulum" duels, chasing one another back and forth over the boundaries of their territories. This would suggest that the *Zheeeeeeee* notes are produced when both the attack and escape tendencies are strong and (possibly) rather evenly balanced.

*Harsh Notes.* Brown-capped Bush-tanagers sometimes become engaged in very prolonged and violent contact fights. Such fights may develop when one bird attacks another, and the latter refuses to retreat, or when two birds attack one another simultaneously. In either case, the two birds may grapple with one another, pecking and biting furiously, and also delivering blows with their feet and beating wings. Such fights may continue until the birds fall to the ground, tumbling over and over, still fighting, as they fall.

Some contact fights seem to be quite silent. Others are accompanied by irregular series of hoarse "Harsh Notes." Such notes might be transcribed by something like *Zhaaah zhaaah zhaaah. . .* or *Waaah waaah waaah. . .*

Unfortunately, I was never able to determine if the Harsh Notes were being uttered by only one or both of the birds involved in a contact fight. I think that they were usually uttered by both birds.

Harsh Notes seem to be related to *Zheeeeeeee* notes. The hoarseness of Harsh Notes appears to be an exaggeration of the hoarseness of *Zheeeeeeee* notes. I have also heard intermediate notes uttered during some territorial chases. Such intermediate notes might be transcribed by something like *Zheeeeaah zheeeeaah. . .*

The fact that Harsh Notes are only uttered by Brown-capped Bush-tanagers during the most violent fights would indicate that they are produced when hostile motivation is very strong, almost certainly stronger, on the average, than in any other purely hostile display of the species. The fact that birds engaged in contact fights with Harsh Notes do not usually retreat immediately would suggest that all or most Harsh Notes are produced when the attack tendency is slightly stronger than the escape tendency or when the two tendencies are nearly equal to one another. This last suggestion is supported by the frequency of intermediates between typical Harsh Notes and *Zheeeeeeee* notes.

The Harsh Notes of the Brown-capped Bush-tanager sound very much like the undoubtedly homologous notes uttered by many other species of American nine-primaried songbirds in similar circumstances. It may be significant, however, that Brown-capped Bush-tanagers do not utter Harsh Notes in all the situations in which some other species utter their corresponding notes. Individuals of many other species of American nine-primaried songbirds utter many Harsh Notes when caught and handled by a human being; but Brown-capped Bush-tanagers apparently always remain silent in such circumstances. This might suggest that Brown-capped Bush-tanagers do not utter Harsh Notes when their escape drive is as strong, relatively

and/or actually, as are the escape drives of some other species when they utter Harsh Notes.

### *Some "Song" Patterns*

The term "song" is unfortunately rather vague, as it has been applied to a great variety of different vocal patterns of different species, some of which are certainly neither homologous nor analogous.

In an earlier paper (Moynihan and Hall, *op. cit.*) it was suggested that the term "song" be restricted to the patterns that some authors (*e.g.*, Tinbergen, 1939; Nice, 1943; and Lack, 1943) have called "advertising song," *i.e.*, the vocal patterns of territory-owning males that simultaneously repel other males and attract females of the same species.

This restriction may be a little too narrow. It would be more logical to define song as "any vocal pattern which, when uttered by one bird, usually repels other birds of the same sex of the same species and attracts other birds of the opposite sex of the same species." This is the sense in which the term will be used throughout this and the following papers of this series.

Brown-capped Bush-tanagers do not have any single vocal pattern in their repertory that could be classified as song, in this sense, by itself alone; but they do utter two calls, "Rattles" and "Flourishes," which are reminiscent of some songs of some other species. Rattles and Flourishes may be uttered either separately or in very close association with one another. When they are uttered separately, it is obvious that they are produced by qualitatively different motivation and subserve different functions. When they are uttered together, however, they may produce the same effects as the true songs of other species.

Typical Rattles are very rapid series of very short, hard notes. A typical Rattle sounds like a greatly accelerated series of *Tuck* notes. The length of Rattles is extremely variable. Some of the longer Rattles seem to be ascending in a pitch, becoming gradually higher; but others may be steady in pitch, or even descending. Typical Rattles always begin abruptly.

Typical Flourishes are composed of two notes. These notes are not very long, but usually longer than *Tsit* or *Tuck* notes. The two notes of a Flourish are usually quite different in pitch. Sometimes the first note is higher than the second; sometimes the second is higher than the first. Most typical Flourishes could be transcribed as *Tseeeyooo* or *Heeehooo* or *Tsooweee*. They are sometimes abbreviated to a slurred *Eeyah*. The tone of Flourish notes is usually or always clear and whistle-like, and sometimes slightly plaintive.

Flourishes are usually preceded by one or more *Tsit* notes. The last *Tsit* note of a series immediately before a Flourish is often more closely

linked to the Flourish than to the other *Tsit* notes. Many *Tsit* note and Flourish patterns could be transcribed by something like *Tsit. . .tsit. . .tsit . . .tsitseeeyoo*. (In such cases the first *Tsit* notes and the first note of the Flourish are noticeably louder than the last *Tsit* note and the second note of the Flourish.) This would suggest that the *Tsit* note immediately before the typical Flourish notes is partly integrated into the Flourish pattern. There is other evidence that would suggest the same conclusion (see below).

Typical Rattles and Flourishes are not accompanied by any distinctive display movements or postures. They may be uttered by birds sitting or standing in any sort of prelocomotory posture, with or without Flicking movements, or hopping from perch to perch. Figure 6C is a sketch of a more or less typical posture accompanying many Rattles and Flourishes, uttered separately or together. Typical Rattles and combinations of Rattles and Flourishes may also be uttered by flying birds.

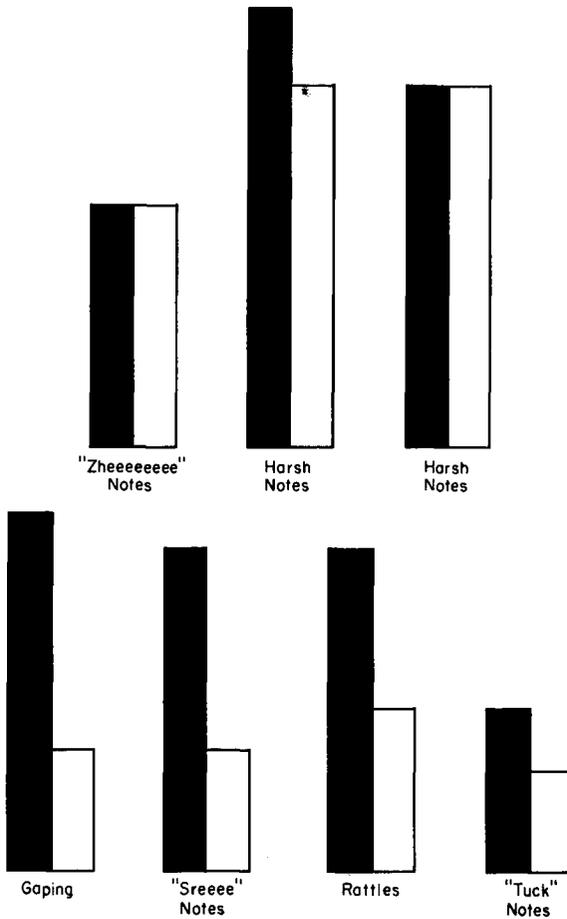
Typical Rattles uttered apart from Flourishes are significantly closely associated with overt aggression. Rattles are the most common calls uttered by aggressive birds immediately before attacking; although they are followed by attacks relatively less frequently than were the silent Gaping performances of the captive birds I observed. Rattles are perhaps most common during territorial disputes, when they are frequently uttered by territory-owning birds flying to repel intruders and chasing fleeing intruders. Rattles are seldom uttered by retreating or escaping birds in any circumstances.

These facts would suggest that all or most Rattles are uttered when the attack tendency is much stronger than the escape tendency, or when the attack tendency is relatively much stronger than when all or most *Zheeeeeeee* notes are uttered, but not, perhaps, as preponderant as during all or most silent Gaping performances. Rattles are probably uttered when both the attack and escape tendencies are stronger than when *Tuck* notes are uttered, but weaker, on the average, than when Harsh Notes are uttered.

The probable relative strengths of the attack and escape tendencies during typical performances of all the hostile display patterns of Brown-capped Bush-tanagers are summarized, in a rather crude form, in Figure 2.

Rattles seem to function as threat. Typical Rattles are uttered by both males and females. Males seem to utter Rattles much more frequently than do females; but brief typical Rattles by females are not actually rare.

Typical Flourishes uttered without accompanying Rattles are not usually closely associated with overt, unritualized activities of obvious significance; but they do not occur in as wide a variety of circumstances as do *Tsit* notes. They are usually or always uttered by territory-owning



**Figure 2.** The probable relative strengths of the attack and escape tendencies during typical performances of hostile displays by Brown-capped Bush-tanagers. The black bars represent the attack tendency, and the white bars the escape tendency. (Harsh Notes may be produced when the attack tendency is slightly stronger than the escape tendency and/or when the two tendencies are approximately equal.)

birds within their own territories. They seem to be uttered by males much more frequently than by females. They are uttered most frequently by unmated males and by mated males that have become separated from their mates. A territorial male without a female will usually utter many Flourishes until a female joins him. As soon as a female does join him, he usually stops uttering Flourishes (or, at least, stops uttering Flourishes by themselves alone, and begins to utter Flourishes and Rattles in combination).

This would suggest that males utter Flourishes when some sort of "sexual" motivation is thwarted.

Brown-capped Bush-tanagers (and many other American nine-primaried songbirds) seem to have at least two different types of "sexual" motivation. One, which may be called the "pairing" tendency, is expressed by attempts to join and/or attract a mate, and seems to be satisfied by the presence of a mate. Another, which may be called the "copulatory" tendency, is expressed by copulatory behavior, and seems to be satisfied by the performance of a successful copulation (males may be satisfied by the release of a seminal fluid, even when it is released in the wrong place). The overt activities of the pairing and copulatory tendencies are usually at least partly independent of one another.

The Flourishes of male Brown-capped Bush-tanagers seem to be produced by thwarting of the pairing tendency, not the copulatory tendency. Male Brown-capped Bush-tanagers utter Flourishes more or less frequently during all phases of the breeding cycle, and not only during the relatively brief period when copulations occur. Isolated males that show no indications of a desire to copulate when they are eventually joined by their mates may also utter Flourishes quite as frequently, or even more frequently, than isolated males that do attempt to copulate repeatedly when they are joined by their mates.

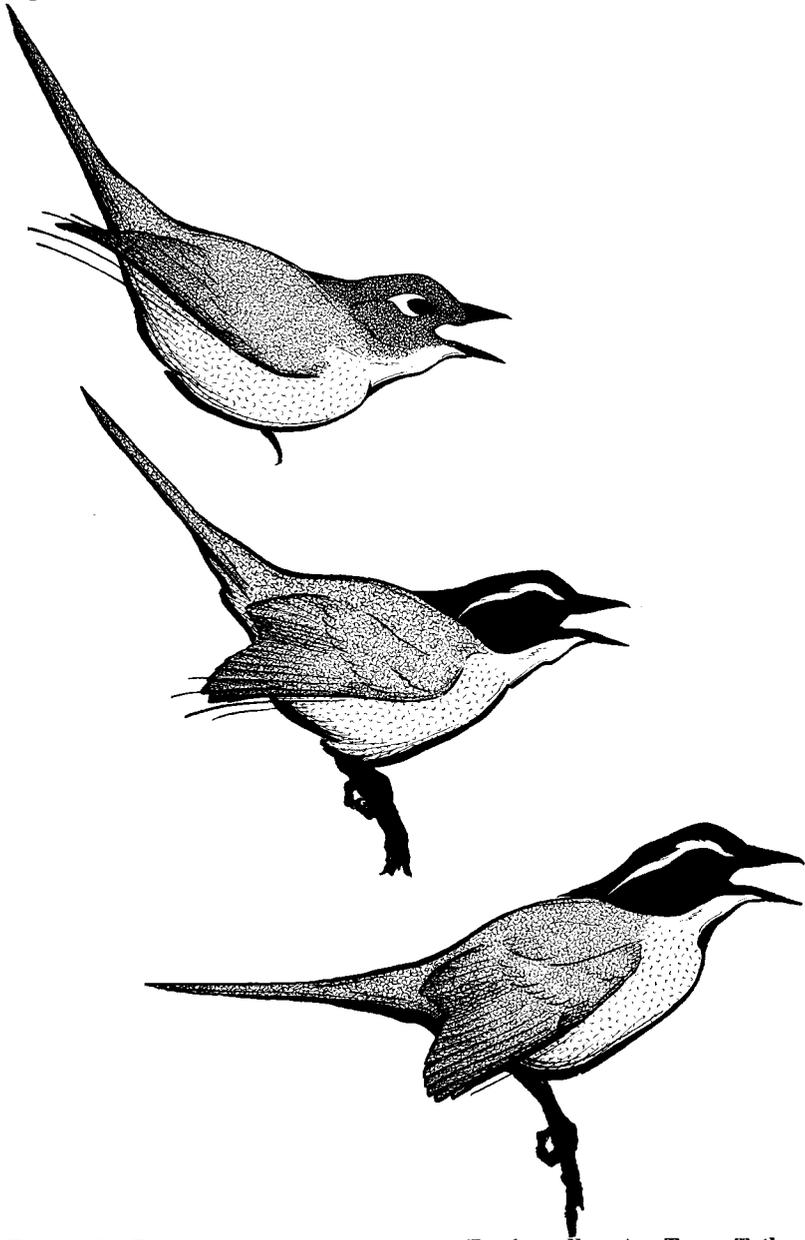
I think that territorial, mated, female Brown-capped Bush-tanagers may occasionally also utter Flourishes when they become separated from their mates. Such calls are probably also produced by thwarted pairing tendencies.

Flourishes of the *Tsooweee* type may be produced when the pairing tendency is stronger, and/or more strongly thwarted, than when Flourishes of the *Tseeeyooo* type are uttered. Birds that utter many Flourishes in a relatively short time tend to utter a relatively larger proportion of *Tsooweee* notes than do birds that utter fewer Flourishes in the same amount of time.

It seems very probable that the utterance of Flourishes by a male usually or always attracts his mate (and may also attract other females in search of a mate). At least, a solitary male uttering Flourishes is usually joined or visited by one or more females if he continues to utter Flourishes for any appreciable length of time. (This is really all that can be determined by observation of birds under natural conditions. Additional experimental work would be necessary in order to prove that the females that visit males uttering Flourishes are attracted by the Flourishes alone.)

It is possible that the utterance of Flourishes by a female may attract her own mate.

Very close associations or combinations of Rattles and Flourishes are usually uttered more frequently than either Rattles alone or Flourishes



**Figure 3.** Patterns accompanying some Rattle calls. **A.** Top. Tail-up Posture and Drooped Wing-quivering, accompanying High Rattles by a Brown-capped Bush-tanager. **B.** Center. Tail-up Posture and Drooped Wing-quivering, accompanying long Rattles by Sooty-capped Bush-tanagers. **C.** Bottom. Drooped Wing-quivering without Tail-up during long Rattles by Sooty-capped Bush-tanagers.

alone. In all such combinations the sequence is one Rattle, followed immediately, without the slightest interruption, by one Flourish. The length of the Rattles in such combinations is extremely variable; quite as variable as the length of the Rattles that are not associated with Flourishes.

All the Rattles combined with Flourishes are typical in pitch, loudness, and tonal quality (see also below).

Most combinations of Rattles and Flourishes are preceded by one or more *Tsit* notes. The note immediately before the Rattle-Flourish may be closely linked with the Rattle in the same way as some *Tsit* notes before Flourishes alone.

These preliminary *Tsits* are sometimes preceded by *Tuck* notes. A complex performance of this type might be transcribed as *Tuck tuck tuck tsit tsit tsit tsit-srrrrrrrrrrrrrrrrrrreeeyooo*.

Combinations of Rattles and Flourishes seem to be uttered in almost all the circumstances in which either Rattles and/or Flourishes are uttered apart from one another, and not in any other circumstances. They are uttered very frequently by solitary males on their own territories; especially when the solitary males are obviously acutely aware of the existence and presence of their neighbors, *e.g.*, when the neighbors are engaged in conspicuous hostile activities. (Combinations of Rattles and Flourishes seem to be particularly contagious. The sound of one bird uttering such a combination frequently induces the utterance of similar calls by all or almost all the other birds within earshot.) It is also common for a territorial male to utter one or more Rattle-Flourish combinations before uttering a Rattle alone and flying to attack an intruding neighbor. (In such circumstances, the Rattles of the Rattle-Flourish combinations tend to be relatively very long.) Mated birds frequently utter combinations of Rattles and Flourishes apparently as reactions to one another. This is particularly apt to occur when the mated birds do not seem to be on the best of terms with one another, *i.e.*, when they do not stay very close together and/or show obvious signs of hostility to one another (see below).

Combinations of Rattles and Flourishes are not infrequently uttered by female Brown-capped Bush-tanagers. Females seem to utter such combinations more often than they utter Flourishes without Rattles; but such combinations are probably uttered only by females that also utter Flourishes alone.

Combinations of Rattles and Flourishes are probably usually or always produced when there is a complex conflict of pairing and hostile tendencies. As far as I could tell, the signal effects of combinations of Rattles and Flourishes are usually or always a combination or summation of the effects usually produced by the two calls when they are uttered apart from one another.

*Other Partly or Purely Sexual Patterns*

A few Brown-capped Bush-tanagers observed in March and April appeared to be engaged in pair formation. Other Brown-capped Bush-tanagers observed at the same times were obviously already mated; but some of the mated birds did not seem to be very well adjusted to one another. Most of the Brown-capped Bush-tanagers observed in September and October were associated in large flocks; and there were few or no signs of the existence of pairs within such flocks.

These facts would suggest that the pairing bonds between mated Brown-capped Bush-tanagers are usually or always partly or completely dissolved or relaxed during the nonbreeding season; and that many new pairs need to be formed, or old pairs reformed, at the beginning of every breeding season.

I was unable to follow the complete development of breeding behavior, from the initial stage of pair formation (or reformation) until egg laying, in any single pair of Brown-capped Bush-tanagers. I did, however, see many pairs that seemed to have arrived at different stages of the breeding cycle; and it may be possible to "reconstruct" the usual sequence of events during the first part of the breeding season by comparing the observed behavior patterns of several of these pairs.

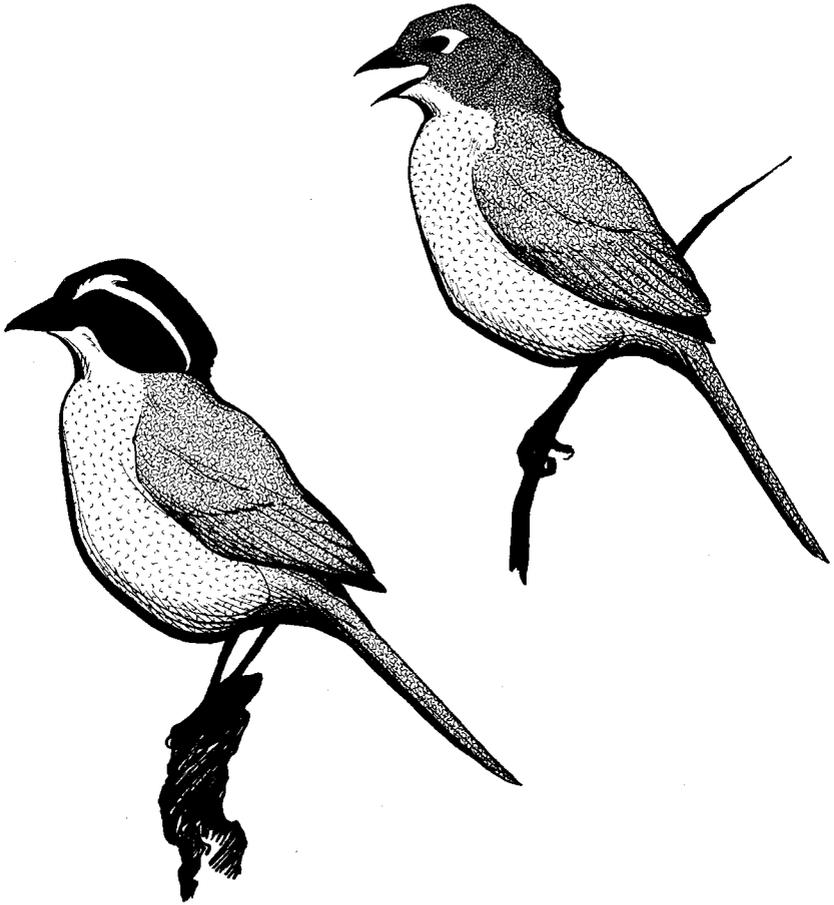
"*Dawn Calling.*" Six or seven different individuals were seen to perform a distinctive "Dawn Calling" pattern in March 1960 and April 1961.

These individuals were territorial and did their Dawn Calling on their territories.

One of the individuals that performed Dawn Calling proved to be a male (this was shown by his behavior during copulations); and it seems very likely that all the birds that performed similar patterns but whose sex could not be definitely established were also males.

The main features of a Dawn Calling performance are as follows.

At the first sign of daybreak, well before sunrise, the performing bird flies to a high perch. This perch is usually or always "exposed," on a bare branch (in one area the birds selected perches on telephone wires, along the side of a road). The perch selected is usually 6–10 meters above the ground. As soon as it reaches the perch, the bird begins to utter a series of notes, each of which might be transcribed as *Tseet*. The number of notes in such series is indeterminate, in much the same way as in series of *Tsit* and *Tuck* notes. Unless interrupted, a bird usually continues to utter Dawn Calling notes for a considerable length of time. Some series of Dawn Calling notes include only two or three notes, but others may include 30 or 40 or more. Dawn Calling notes are usually uttered at fairly regular intervals. Each Dawn Calling note of a single series is usually separated from the preceding and succeeding notes by pauses of approximately equal



**Figure 4.** Some postures during early-morning displays. **A. Top.** A typical posture of Brown-capped Bush-tanagers during Dawn Calling without Upward Wing-quivering. **B. Bottom.** A typical posture of Sooty-capped Bush-tanagers during High Perching.

length. (One bird observed in 1960 occasionally interrupted the regular rhythm of its Dawn Calling by uttering two essentially similar notes one right after the other, with hardly any intervening pause; but such "doublets" were not uttered by any other birds during Dawn Calling.) The pauses between the notes of different Dawn Calling series are not always exactly the same; but they differ much less than the corresponding pauses in different series of *Tsit* and *Tuck* notes.

The actual Dawn Calling notes of different birds tend to be slightly different in length and/or tone. One bird persistently uttered compara-

tively short Dawn Calling notes. Several other birds uttered Dawn Calling notes that were very much longer, and more or less hoarse in tone. Such differences may facilitate individual recognition.

The postures accompanying Dawn Calling are usually ordinary sitting or perching, accompanied, in many cases, by some slight fluffing of the lower breast and belly feathers (see Figure 4A).

A bird may utter a long series of Dawn Calling notes without performing any special movements; but this is not usual.

Most Dawn Calling is accompanied by at least a slight trace of "Upward Wing-quivering." The wings are lifted out, away from the body, and usually raised to some extent and partly spread. At the same time they are quivered very rapidly. These quivering movements are usually quite extreme, *i.e.*, the tips of the wings usually move through rather wide arcs during the quivering.

Sometimes a bird will continue Upward Wing-quivering almost steadily for several minutes during Dawn Calling. More often, the Upward Wing-quivering comes in "bursts," periods of Upward Wing-quivering alternating with periods when the wings are folded back in their normal resting position. There appears to be complete intergradation between performances in which the wings are quivered almost steadily and performances in which the wings are quivered very briefly at relatively very long intervals. The pauses between bursts of Upward Wing-quivering are often extremely variable in length, even during a single series of Dawn Calling notes. When the Upward Wing-quivering occurs in distinct bursts, it is not usually correlated precisely with the actual utterance of the Dawn Calling notes. Sometimes the Upward Wing-quivering occurs just as the notes are uttered; sometimes in the intervals between notes.

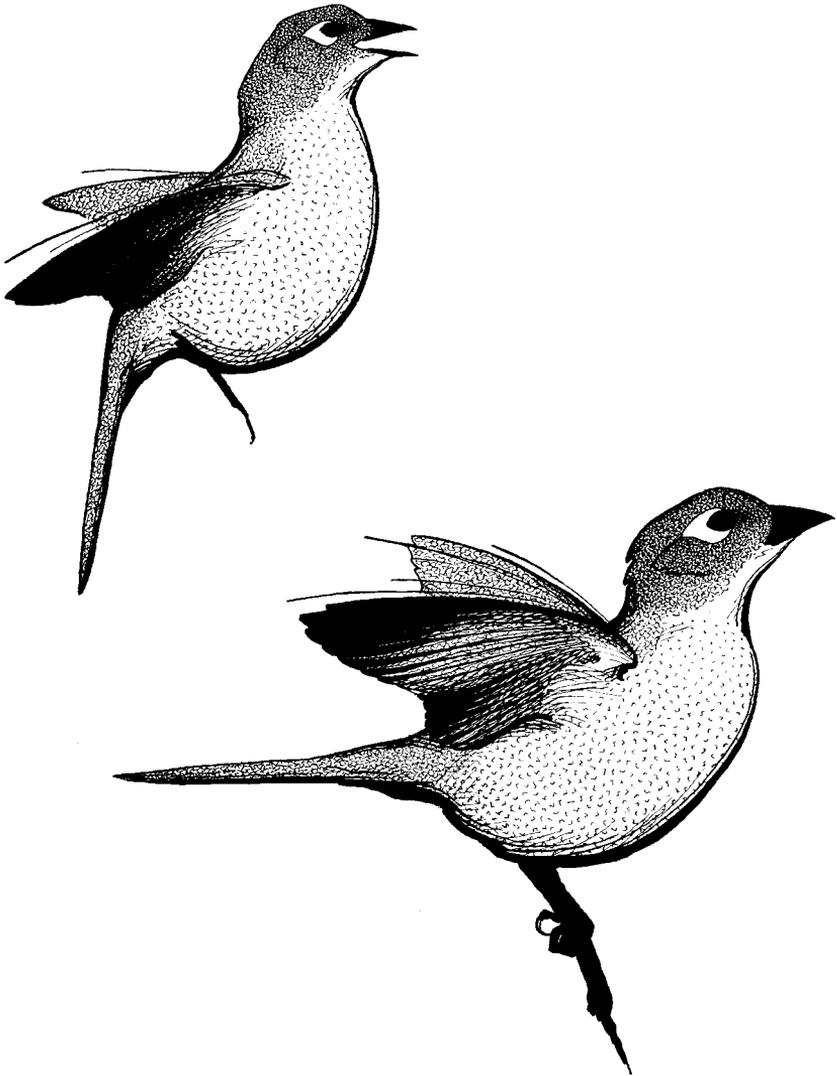
Figures 5A and 5B show typical Dawn Calling postures with Upward Wing-quivering.

Some birds tend to look from side to side quite regularly during Dawn Calling.

A bird uttering Dawn Calling notes may change perches during the performance. It may even frequently fly back and forth between several perches, pausing to utter Dawn Calling notes in the usual postures with Upward Wing-quivering at each perch. It may also continue to utter Dawn Calling notes in flight between perches. The form of the flights accompanied by Dawn Calling notes is perfectly normal and unritualized.

When a bird utters Dawn Calling notes at several different perches, it usually selects perches that are quite close together. Usually all the perches are almost equally high and exposed.

Dawn Calling birds tend to do more frequent and more vigorous Upward Wing-quivering during performances that include frequent changes



**Figure 5.** Postures of Brown-capped Bush-tanagers during Dawn Calling with Upward Wing-quivering. These are the two extreme types of postures frequently assumed by Brown-capped Bush-tanagers during Dawn Calling. Intermediate postures may be more common than either of the extremes.

of perches than during performances that are confined to a single perch. They also tend to do particularly vigorous Upward Wing-quivering just after landing on a perch, and when territorial neighbors come particularly close.

Most long-sustained Dawn Calling performances are occasionally interrupted by brief periods during which the performing birds go to feed. Dawn Calling birds may also become involved in territorial hostilities with their neighbors; but they usually break off such hostilities as soon as possible to return to Dawn Calling.

In certain circumstances (see below) Dawn Calling may be continued for as much as an hour after sunrise. In such cases it usually stops gradually. Pauses for feeding become increasingly frequent, and other calls begin to be uttered between bursts of Dawn Calling. The first calls to be interspersed between bursts of Dawn Calling are usually Flourishes, followed very shortly by Rattle-Flourish combinations. Finally, the Dawn Calling stops completely, while the Rattle and Flourish patterns may continue.

I have never heard Dawn Calling except in the early morning. This is the sort of vocalization that some authors (*e.g.*, Skutch, 1954, and Willis, 1960) have called "dawn song" (in contrast with "day song"—which would include Rattles and Flourishes in the case of the Brown-capped Bush-tanager).

Dawn Calling is only performed by birds that are alone on their territories, but it is definitely performed by both mated and unmated birds.

Mated birds perform Dawn Calling when temporarily separated from their mates. The Dawn Calling performances of the mated birds I observed were always very brief, because these birds were never separated for very long from their mates. A mated Dawn Calling bird always stops Dawn Calling immediately as soon as it is joined or rejoined by its mate.

The longest Dawn Calling performances I observed were given by unmated birds. Unmated birds may remain alone on their territories throughout the whole of the early morning, or are visited rarely by other birds, presumably potential mates, at relatively very long intervals. If an unmated Dawn Calling bird should be visited by another bird, it always stops Dawn Calling immediately, and then, if the morning is not too far advanced, resumes Dawn Calling immediately when the visitor leaves.

One known male that did vigorous Dawn Calling during the period of my observations in April of 1961 usually attempted to copulate with his mate almost immediately after she joined him in the early mornings and he had stopped Dawn Calling (see below); but other mated birds that also did vigorous Dawn Calling did not perform copulatory or precopulatory patterns when joined by their mates.

It is probable, therefore, that Dawn Calling is uttered by males when their pairing tendencies are thwarted by the absence of their mates. The complexity of most Dawn Calling performances, and their restriction to the early morning (when almost all activities are most vigorous), would suggest that the pairing tendencies of all or most males performing

Dawn Calling are stronger, on the average, than those of birds uttering Flourishes.

Dawn Calling may function as a signal to attract females. Mated males seem to use it to summon their mates; and unmated males may use it to attract potential mates.

*Plaintive Notes.* Brown-capped Bush-tanagers sometimes utter notes that are quite similar in sound to the notes of Dawn Calling, but somewhat longer and often slightly plaintive in tone. A single "Plaintive Note" of this type might be transcribed as *Tseeet* or *Tseeee*.

Plaintive Notes may be uttered singly or in series. Series seldom include more than three or four notes. Plaintive Notes are also frequently uttered as doublets, two notes uttered one right after the other with hardly any intervening pause: *Tseeee-tseeee*. In such doublets the second note is usually louder and more urgent sounding than the first.

Plaintive Notes are not accompanied by special ritualized postures or movements.

I have heard Plaintive Notes only during the breeding season. This is another type of vocal pattern that seems to be uttered only by unmated birds and/or mated birds separated from their mates. Plaintive Notes are certainly uttered by males; and I think that they are also uttered by females. Unlike the Dawn Calling notes, they are not restricted to the early mornings.

Plaintive Notes are sometimes combined with Flourishes. Many combinations of this type might be transcribed as *Tsee-tseeee tseeyooo* or *Ta-tseeee tiseeeyooo* (the latter pattern probably includes a single *Tsit* note in addition to the other two components).

Plaintive Notes are obviously produced when some sort of sexual motivation is thwarted; but I have not heard them frequently enough to determine how their causation differs from that of simple Flourishes and Dawn Calling. It is possible that Plaintive Notes are produced when both pairing and copulatory tendencies are activated and thwarted simultaneously and/or when a pairing tendency intermediate in strength between the pairing tendencies of Flourishes and Dawn Calling is activated and thwarted.

It should be mentioned that Plaintive Notes, Dawn Calling notes, and the *eee* notes in Flourishes are all very similar in sound (without the rattling undertone of *Sreeee* notes or, usually, the hoarse quality of *Zheeeeee* notes). This would suggest that the causal differences between the three patterns are not actually very great.

*Hostility between mates or potential mates.* Some reactions observed in March 1960 may have been examples of the behavior of potential mates when they first encounter one another.

One bird, presumably a male, uttered relatively prolonged Dawn Calling in the morning for several days in a row. On two successive days this bird

was visited by another bird while it was still Dawn Calling. I could not tell if the visitor was the same on both days. In any case, it seems likely that the visitor or visitors were female(s).

On the first day the visitor flew straight into the territory of the Dawn Calling bird, but perched about five–six meters away from the latter. The owner of the territory stopped Dawn Calling immediately, turned to face the newcomer, and began to utter *Tsit* notes. These *Tsit* notes were repeated again and again, at a gradually but rapidly accelerating rate, until they developed into a thin, high-pitched, rattle sound (definitely higher pitched than ordinary Rattles in other circumstances). This rattle sound was continued for several seconds, becoming even higher pitched as it continued. At approximately the same time that the *Tsits* became rattling, the bird dropped its wings slightly, and began to quiver them. As soon as the quivering started, the bird leaned forward a little, breast lowered, and then gradually lifted its tail higher and higher. At the climax of this movement the bird reached the posture shown in Figure 3A. Then the performance stopped abruptly; the bird relaxed; and I saw that the visitor had gone.

The extreme posture reached at the climax of this performance may be called the "Tail-up Posture." The accompanying wing-quivering may be called "Drooped Wing-quivering"; and the accompanying sound may be distinguished from ordinary Rattles as the "High Rattle."

On the second day the Dawn Calling bird was approached by a visitor in the same way and at approximately the same time. This approach provoked a whole series of High Rattles, one right after the other; but, unfortunately, I could not see the accompanying postures and movements because of intervening vegetation. The High Rattles were followed by a variety of hostile and partly hostile reactions, including ordinary Rattles, Rattle-Flourishes, *Tuck* notes, and aerial chases, until the visitor disappeared again (about 15 minutes later).

On both days the territory-owning bird that did the Dawn Calling early in the morning was occasionally associated with another bird near the border of its territory (or, at least, the area that it defended early in the morning) during later periods of the day. These associations were apparently always brief. They were not accompanied by High Rattles; but both birds uttered many *Tuck* notes, and one or both uttered ordinary Rattles and Rattle-Flourish combinations while they were together. I could not tell if the bird associated with the owner of the territory during these later periods of the day was always the same bird or not. It is possible that this associated bird was a female, and/or the same bird that visited the owner of the territory early in the morning; but this is by no means certain. Brown-capped Bush-tanagers retain gregarious tendencies during the breeding season, and may even form flocks at the height of the breeding season, especially during the middle of the day

(see Moynihan, 1962). It is possible, therefore, that these brief associations between the territory-owning bird and other bird(s) during the later periods of the day were expressions of gregariousness quite apart from pairing.

On subsequent days it was obvious that this territorial bird had acquired a mate that remained, almost steadily, associated with it throughout the whole day. There was (still) a considerable amount of hostility between the mates on these days; but neither of them uttered High Rattles at any time, or performed Drooped Wing-quivering, or assumed any trace of a Tail-up Posture.

The hostility between "well-mated" birds was observed in more detail and under better observational conditions in several other pairs.

In some pairs one of the birds of the pair, presumably the male in all or most cases, performed many more hostile, especially aggressive, displays than the other bird of the pair. In such cases the two birds of the pair usually alternated long periods of hopping and flying rapidly through and around their territory with brief periods of perching. Their movements were usually more or less synchronized. When one bird of the pair stopped moving, the other bird usually stopped too; and when one bird resumed its movement, the other bird usually started to move again within a few seconds. It was usually obvious that one of the birds of the pair consistently followed the other. In some pairs the bird that appeared to be male was the consistent follower; but in at least one other pair the consistent follower was the bird that appeared to be female. When the presumed male was the follower, he usually uttered many *Tuck* notes, Rattles and Rattle-Flourishes, both when moving and when perched. The presumed female usually remained silent, or uttered only a few *Tuck* and/or *Tsit* notes. The presumed male sometimes uttered as many aggressive calls during such performances as during territorial disputes with neighbors; but he seldom or never actually attacked the presumed female. When the presumed female perched, the presumed male usually perched a short distance (0.5 to 3 meters) away from her, without making any attempt to get closer. While perched, the presumed male usually faced directly toward the presumed female and uttered many Rattles and/or Rattle-Flourish combinations, one right after the other. While the male did this, the female usually sat quietly, in a more or less "relaxed" looking posture, frequently or usually facing directly away from the presumed male. When the presumed female persistently followed the presumed male, she was equally silent; but the presumed male uttered many Rattles and a few Flourishes facing directly away from her!

During such incidents one or both birds of the pair occasionally flew away to engage in territorial disputes with neighboring birds. Some of these reactions looked very much like redirection activities (see Bastock,

Morris, and Moynihan, 1953), as if the mated birds were venting upon their neighbors the hostility aroused by their mates.

It seems likely that such couples, in which one of the birds was so much more aggressive than the other, were relatively recently formed pairs. I saw no traces of copulatory or precopulatory behavior in such pairs.

In other pairs there is much less hostility between the mates, but what hostility there is tends to be more evenly balanced. Both birds of such a pair may utter a variety of ordinary hostile calls, apparently provoked by and directed toward the mate; but such calls are seldom or never very common (except, sometimes, when there is a good deal of loud disputing going on in adjacent territories, and the mated birds seem to be infected by the general contagiousness of so many hostile calls).

It seems likely that such pairs are usually or always well-established pairs of not very recent formation. The only pair of birds observed to perform successful copulations (see below) was a pair of this type.

*General comment on pair formation.* The different behavior of the different pairs described above would suggest that pair formation among Brown-capped Bush-tanagers is usually more or less as follows:

1. An unmated male attracts a female by Dawn Calling (and, possibly, Flourishes and Rattle-Flourish combinations).

2. The first few times an unmated male is visited by a female, he usually reacts by performing an elaborate High Rattle plus Drooped Wing-quivering plus Tail-up display, sometimes followed by more ordinary hostile or partly hostile displays, *i.e.*, Rattles, Rattle-Flourish combinations, and/or *Tuck* notes. The female does not display very much, and usually leaves very soon; but she may return.

3. If the female returns repeatedly, the male stops performing High Rattle plus Drooped Wing-quivering plus Tail-up displays, while continuing to perform many ordinary hostile, aggressive patterns. The female still does not display to the male very frequently; but she tends to remain with him for longer and longer periods of time.

4. If the female sticks with the male, he may gradually perform fewer and fewer aggressive, hostile displays. By this time, pair formation may be completed.

5. The male continues to perform Dawn Calling (in the early morning) and utter Flourishes and Rattle-Flourish combinations (during the rest of the day) throughout the whole period of pair formation, and later, whenever he becomes separated from the female. Thus, his attractive signals remain frequent while his repellent signals become rare.

The whole process of pair formation among Brown-capped Bush-tanagers would appear to be explicable in terms of the interaction of attack, escape, and pairing tendencies. If so, it is basically similar to the pair-formation process of most other species of birds.

Most of the calls uttered during pair formation also occur in other situations, apart from pairing. They sound more or less the same in all situations. There is no reason to suppose that they are not produced by

the same motivation in pair formation as in other situations. The orientation of the birds uttering some of these calls during pair formation may be slightly different, on the average, from the orientation of birds uttering the same calls in other circumstances; but this does not necessarily mean that the motivation actually producing the calls themselves during pair formation is in any way distinctive.

The most problematical of the pair-formation displays are the High Rattle, Drooped Wing-quivering, and Tail-up patterns. The very elaboration of these patterns would suggest that they must be produced by some very strong motivation. The general resemblance between High Rattles and ordinary Rattles (and the fact that High Rattles do not seem to occur in any other circumstances) would suggest that the High Rattle contains a hostile component. It is possible that the High Rattle plus Drooped Wing-quivering plus Tail-up performance is produced when both sexual and hostile tendencies are very strong (stronger, together, than in any other displays of the species).

*A possible "greeting" display.* In April of 1961, I twice heard a very soft, somewhat hoarse *Tazazazaza* call uttered by one bird of a pair of Brown-capped Bush-tanagers feeding in a tree only a few feet above my head.

These calls were not accompanied by any special postures or movements, and the circumstances in which they occurred were not such as to reveal their causation or function(s) very clearly; but they sounded very much like the "greeting" calls uttered by mated birds of many other species of tanagers and finches.

It is conceivable that Brown-capped Bush-tanagers utter such calls more or less frequently. I may not have noticed such calls before simply because they are too soft to carry any appreciable distance.

*Copulatory behavior.* Copulation attempts by Brown-capped Bush-tanagers seem to be restricted to a very brief phase of the breeding cycle.

I saw copulation attempts only in April 1961. During this period I saw 12 apparently successful copulations. They were all performed during the early mornings of two successive days by the birds of a single pair.

The two birds of the pair apparently roosted separately. At least the male began Dawn Calling before daybreak, and was certainly alone on his territory by the time it became light enough to see clearly. The female appeared in the territory, some distance away from the male, 10 to 20 minutes after dawn.

The male stopped Dawn Calling as soon as the female appeared, flew straight toward her, landed on a perch right beside her, mounted her immediately, and immediately copulated with her. The copulations were very brief. After the first copulations, the male flew straight off the back of the female, perched briefly on an adjacent branch, and then flew back and copulated with her again. On the first morning the male copulated with the female three times in rapid succession after she first appeared in

the territory. On the second morning he copulated with her four times in rapid succession after she first appeared. He flew straight off the back of the female after each copulation, and perched briefly on an adjacent branch before copulating again. After the last copulation of each of these series, he flew farther away, and the female eventually followed him.

After these initial series of copulations, the two birds did considerable feeding. The female apparently left the territory from time to time, but never stayed away very long. The male resumed Dawn Calling and/or uttered Rattle-Flourish combinations whenever he became separated from the female. Additional copulations took place at more or less irregular intervals during the hour or hour and a half after the first burst of copulations. These were essentially similar to the earlier copulations in form, except that the male sometimes flew straight on to the back of the female, without perching beside her beforehand. These later copulations did not usually occur in rapid series. Only once did two copulations occur one right after the other after the initial encounters between the two birds.

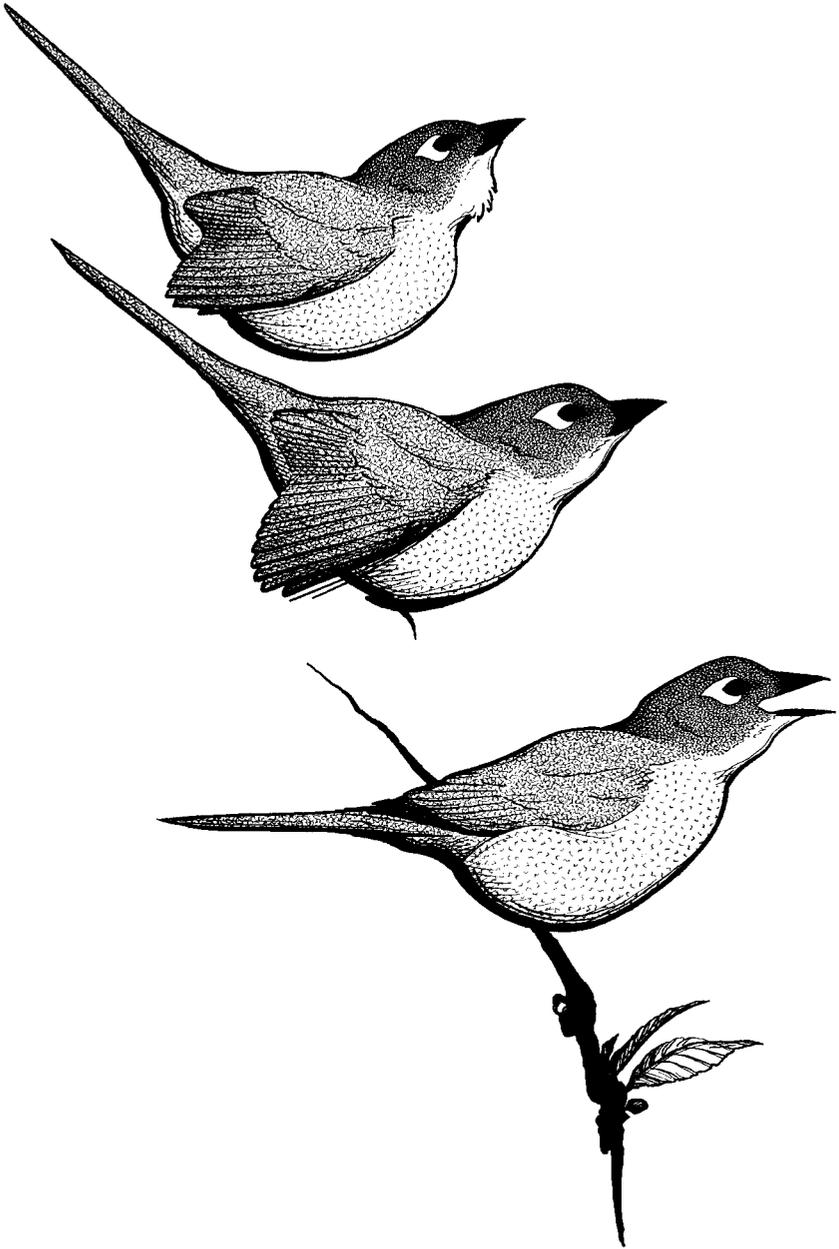
These copulations were not associated with very prolonged or conspicuous displays.

On the first day the male uttered a Rattle-Flourish combination as he flew to the female, and landed beside her for the first time. On the second day he uttered a plain Rattle, without Flourish, when he flew to her for the first time. During the first burst of copulations on the first day, he did not display between copulation attempts. During the first burst of copulations on the second day, he uttered prolonged but otherwise ordinary Rattles between the copulations, while he was perched on adjacent branches.

The male's displays before the later copulation attempts were slightly more varied. Once he uttered a Rattle-Flourish combination. Once he uttered a plain Rattle. Once he uttered an ordinary Rattle, followed immediately by a distinctive "Muffled Rattle" (see below). Once he uttered a few *Tsit* notes. The remaining time he did no displaying at all.

The male also uttered Muffled Rattles, immediately after ordinary Rattles, on several other occasions, when he flew toward the female without subsequently trying to mount her. These Muffled Rattles sounded exactly like ordinary Rattles, but very much softer. They were not extremely high pitched and "thin" sounding like High Rattles. It seems likely that they were produced by some combination of hostile and copulatory tendencies.

The female never began to display until the male had come very close or actually mounted. Then she always assumed a Wings-drooped Tail-up Posture. This posture was slightly variable. Two typical variations are shown in Figures 6A and 6B. It will be seen that these postures are similar



**Figure 6.** Display patterns of Brown-capped Bush-tanagers. **A.** Top. An extreme Wings-drooped Tail-up Posture, with ruffling of the throat feathers, sometimes assumed by a female during and/or after copulation attempts. **B.** Center. A less extreme Wings-drooped Tail-up Posture frequently accompanied by Wing-quivering. **C.** Bottom. A typical posture frequently accompanying Rattles, Flourishes, and Rattle-Flourish combinations.

to the posture accompanying the High Rattle performance described above. The copulatory postures seem to differ from the High Rattle posture in only two significant features. The copulatory postures were always accompanied by fluffing of the breast and belly feathers and some diagonal upward pointing of the head and bill. In some cases the throat feathers were also fluffed or ruffled.

The female always maintained a Wings-drooped Tail-up Posture after the male mounted and throughout the period he remained on her back.

As far as I could tell, the actual copulatory movements of both male and female were essentially the same as the copulatory movements of males and females of most other species of passerine birds.

Most of the actual copulations of these Brown-capped Bush-tanagers were quite silent (although I was never close enough to the copulating birds to be sure that they did not utter very soft notes). Once the male uttered several Rattle-Flourish combinations after mounting the female; but I think that he uttered these calls before he was able to bring his cloaca into contact with the cloaca of the female.

The female sometimes remained in the Wings-drooped Tail-up Posture after the male dismounted. During the initial series of copulations in the early mornings, she usually remained in the Wings-drooped Tail-up Posture and also quivered her wings (see Figure 6B) between copulations. This quivering seemed to be almost identical in form with the Drooped Wing-quivering accompanying the High Rattle described above.

The significance of these resemblances between the display postures and movements of the female during copulation performances and the postures and movements of the presumed male during the High Rattle performance is difficult to assess—primarily because the latter was seen only once. It should be mentioned, however, that some other American nine-primaried songbirds perform similar patterns in both copulatory situations and purely hostile and/or ambivalent hostile-pairing situations.

Neither the male nor the female performed any special postcopulatory displays.

I saw a few reactions among birds of other pairs of Brown-capped Bush-tanagers in April 1961 that may have been unsuccessful copulation attempts. Males were seen to fly toward their females, uttering Rattles and/or Rattle-Flourish combinations, and apparently attempting to mount; but the females always flew away immediately.

#### *Comparative Comment*

Some display patterns, or components of displays, of Brown-capped Bush-tanagers seem to be particularly significant from a comparative point of view. Among these are the following:

1. Rattling aggressive notes.
2. Hoarse notes during fighting.

3. Pairing calls containing clear (and sometimes plaintive) *eeee* sounds.
4. The simple "day song," including distinct hostile and pairing components.
5. Dawn Calling, a high-intensity pairing display in the form of indeterminate repetition of essentially identical notes.

It is also interesting that the purely hostile display repertory of Brown-capped Bush-tanagers does not seem to include as many special postures and movements as the corresponding repertoires of many other species of American nine-primaried songbirds.

#### SOME DISPLAYS OF THE SOOTY-CAPPED BUSH-TANAGER

The following account of display patterns performed by Sooty-capped Bush-tanagers is incomplete.

I did not observe as many Sooty-capped Bush-tanagers as Brown-capped Bush-tanagers; furthermore, my observations of Sooty-capped Bush-tanagers were briefer than my observations of Brown-capped Bush-tanagers. The Sooty-capped Bush-tanagers that were studied performed fewer displays than did most Brown-capped Bush-tanagers during similar periods of time. This comparative rarity of displays seems to have been largely or completely due to two factors. Sooty-capped Bush-tanagers are less gregarious than Brown-capped Bush-tanagers, and members of different family groups of Sooty-capped Bush-tanagers encounter one another less frequently than do members of different family groups of Brown-capped Bush-tanagers. All the Sooty-capped Bush-tanagers observed during the breeding season were already mated, and the mated birds seemed to be so well conditioned to one another that they seldom reacted to one another in any very complex way.

It is obvious, therefore, that the displays that seem to be performed by Sooty-capped Bush-tanagers were only part of the full display repertory of the species.

*Flicking movements.* Sooty-capped Bush-tanagers seem to have the same range of preflight patterns as Brown-capped Bush-tanagers. All the preflight postures and movements of Sooty-capped Bush-tanagers, including both unritualized patterns and flicking movements, seem to be essentially similar to, or even identical with, the corresponding patterns of Brown-capped Bush-tanagers in all respects.

*Vocal patterns—general comments.* Sooty-capped Bush-tanagers are usually quieter than Brown-capped Bush-tanagers. They tend to utter fewer calls and notes than Brown-capped Bush-tanagers in many situations. This may be correlated with the lesser degree of gregariousness shown by Sooty-capped Bush-tanagers (Moynihan, 1962).

Some of the vocal patterns of Sooty-capped Bush-tanagers are obviously homologous with the vocal patterns of Brown-capped Bush-tanagers, and



These series seem to be *Tsit*-Rattle-Flourish combinations, strictly homologous with the *Tsit*-Rattle-Flourish combinations of Brown-capped Bush-tanagers. They are essentially identical with the homologous patterns of Brown-capped Bush-tanagers in form, but they are relatively much less common. Sooty-capped Bush-tanagers apparently never utter such series as frequently as do Brown-capped Bush-tanagers (in many circumstances), and seldom or never utter such series as frequently as they utter Rattles without Flourishes or Rattles associated with Flourishlike calls in another way.

The most conspicuous Flourishlike calls of Sooty-capped Bush-tanagers are composed of three notes, and are most characteristic of particularly vigorous territorial disputes. A single call of this type might be transcribed by something like *Tsee-wee-yoo*. Such calls sound very much like slightly modified or more elaborate versions of the usual Flourishes of Brown-capped Bush-tanagers or the Flourishes sometimes uttered by Sooty-capped Bush-tanagers immediately after Rattles. They might, conceivably, be nothing more than the usual "complete" Flourish pattern of Sooty-capped Bush-tanagers; but their associations with other patterns are slightly distinctive. They sometimes appear to be interspersed among Rattles and *Tsit* notes in a purely random manner. More often, they occur immediately after series of *Tsit* notes, either immediately before Rattles or quite apart from any immediate conjunction with Rattles.

The motivation and functions of these Flourishes and Flourishlike calls are difficult to assess. They may be produced when pairing motivation is thwarted; but this is not the only possibility. Such calls are very seldom or never uttered apart from territorial disputes. Even more significantly, a mated Sooty-capped Bush-tanager temporarily separated from its mate does not usually utter such calls (see below). It is possible, therefore, that all or most of the Flourishes and Flourishlike calls of Sooty-capped Bush-tanagers are essentially or purely hostile.

The fact that the Rattles and Flourishlike calls of Sooty-capped Bush-tanagers are frequently uttered in different sequences might suggest that the internal factors controlling these patterns are less closely linked than are the corresponding factors controlling the Rattle and Flourish patterns of Brown-capped Bush-tanagers.

One other call is sometimes uttered by Sooty-capped Bush-tanagers during territorial boundary disputes. This is a series of three or four *Tseweet* or *Tseweet* notes. Such series are often preceded by series of *Tsit* notes. Some, at least, of the *Tseweet* notes are faintly buzzy, or have a slight rattling undertone. They may be homologous with the *Sreeee* or *Zheeeeeee* notes of Brown-capped Bush-tanagers.

The Flourishes and Flourishlike calls, *Tseweet* notes, and shortest

Rattles of Sooty-capped Bush-tanagers are delivered from ordinary, un-ritualized, sitting or perching postures.

Longer Rattles are usually or always accompanied by Drooped Wing-quivering (see Figure 3C). Some Rattles with Drooped Wing-quivering are also accompanied by raising of the tail. This may develop into a rather extreme Tail-up pattern (see Figure 3B). The Drooped Wing-quivering and Tail-up patterns of Sooty-capped Bush-tanagers are very similar to the corresponding patterns of Brown-capped Bush-tanagers in form; but Sooty-capped Bush-tanagers certainly perform these patterns in noncopulatory situations much more frequently than do Brown-capped Bush-tanagers. Both the Drooped Wing-quivering and Tail-up patterns of Sooty-capped Bush-tanagers may be purely hostile.

*Harsh Notes.* Sooty-capped Bush-tanagers utter Harsh Notes. These notes sound like the homologous notes of many other species; and are uttered in the same circumstances as the Harsh Notes of Brown-capped Bush-tanagers.

*Possible pairing reactions.* Sooty-capped Bush-tanagers perform several patterns that are more or less reminiscent of the Dawn Calling performances of Brown-capped Bush-tanagers.

In March 1960 at least three different birds were seen to perform a conspicuous "High Perching" pattern on several successive days. These birds were territorial; and each of them was proved to be mated at the time it performed the High Perching. All three birds were probably males.

A typical High Perching performance began at dawn, before sunrise, when a bird flew to a high, exposed perch on a tree within its territory. The height of the perches selected was somewhat variable, ranging from approximately 6 to 20 meters above the ground. The highest perches selected were far above the level at which the Sooty-capped Bush-tanagers of the area usually moved and fed and performed all their other activities.

After reaching a perch, the bird usually sat quietly for some minutes. Sometimes a bird sat continuously on the same perch for a half hour or more. More often, it flew back and forth between several high and exposed perches, sitting on each perch for several minutes.

A bird usually assumed a rather distinctive posture while sitting on high perches. The feathers of the lower breast and belly were usually fluffed, while the feathers of the crown were arranged in such a way that the head looked very "angular" (see Figure 4B). This posture appeared to be essentially identical with the posture usually assumed by Brown-capped Bush-tanagers during Dawn Calling. The Sooty-capped Bush-tanagers performing High Perching also tended to look from side to side in the same way as some Brown-capped Bush-tanagers during Dawn Calling.

It is perhaps surprising, therefore, that the Sooty-capped Bush-tanagers were always absolutely silent while they sat on their high perches, and never performed any quivering movements.

The Sooty-capped Bush-tanagers I watched sometimes continued High Perching for approximately an hour after dawn (with occasional interruptions for feeding); but they never performed anything similar during later periods of the day.

The mates of the birds performing High Perching did not seem to react to such performances. They fed and moved about their territories in the usual way of Sooty-capped Bush-tanagers in the early morning, without appearing to pay any attention to their High Perching mates.

In one case I know that a bird performing High Perching belonged to a pair that was fairly well advanced in the breeding cycle. The birds of this pair were seen nest building only a few hours after one of them had performed High Perching.

These facts would suggest that High Perching may be a reduced remnant or "vestige" of a more elaborate performance like the Dawn Calling of Brown-capped Bush-tanagers. It is conceivable, of course, that unmated male Sooty-capped Bush-tanagers perform real Dawn Calling when trying to attract a potential mate; but mated Sooty-capped Bush-tanagers certainly do not perform Dawn Calling in the same circumstances as mated Brown-capped Bush-tanagers.

I also saw a few solitary Sooty-capped Bush-tanagers occasionally during later periods of the day in March 1960. Some of these birds could not be identified individually; but they were probably all mated birds, only temporarily separated from their mates. They sometimes sat on low perches in the shrubbery and uttered a series of *Tsit* notes, without assuming any distinctive postures or performing any special movements. Some of these series of *Tsit* notes were unusually slow and regular in rhythm. It is conceivable that the birds uttering such series were trying to "call in" their mates.

Unfortunately, I never saw copulatory or precopulatory patterns performed by Sooty-capped Bush-tanagers.

*Comparative comment.* The distinctive features of the known display behavior of Sooty-capped Bush-tanagers that seem to be most significant from a comparative point of view include the following:

1. The relatively frequent performance of Drooped Wing-quivering and Tail-up patterns in noncopulatory (possibly purely hostile) situations.
2. The variability of the associations between Rattles and Flourishes or Flourish-like notes.
3. The absence of vocal components in some or all High Perching performances.

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## SUMMARY

Many displays of Brown-capped Bush-tanagers (*Chlorospingus ophthalmicus*) and a few displays of Sooty-capped Bush-tanagers (*C. pileatus*) were studied during several periods of field observations in Chiriqui, in western Panama, between September 1958 and April 1961.

The purely hostile displays of Brown-capped Bush-tanagers include Gaping, *Tuck* notes, *Sreeeee* notes, *Zheeeeeeee* notes, Harsh Notes, and Rattles.

The partly or purely sexual displays of male Brown-capped Bush-tanagers include "Flourishes," Dawn Calling performances, Plaintive Notes, and Muffled Rattles.

One male Brown-capped Bush-tanager was observed to perform an elaborate complex of displays, including a High Rattle call, Drooped Wing-quivering, and a Tail-up Posture, in circumstances that appeared to be partly hostile and partly sexual.

Female Brown-capped Bush-tanagers may assume Tail-up Postures and perform Drooped Wing-quivering in copulatory situations.

All the observed displays of Sooty-capped Bush-tanagers seem to be homologous with displays, or components of displays, of Brown-capped Bush-tanagers.

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*Canal Zone Biological Area, Smithsonian Institution, Drawer C, Balboa, Canal Zone.*