DISPLAY PATTERNS OF TROPICAL AMERICAN "NINE-PRIMARIED" SONGBIRDS

II. SOME SPECIES OF *RAMPHOCELUS*

M. MOYNIHAN

THIS is the second in a series of papers describing the display behavior of some tropical American finches, tanagers, and honeycreepers. Throughout this paper, technical ethological terms will be used in the same sense as in the preceding paper of the series (Moynihan, 1962b), unless specifically stated otherwise.

THE CRIMSON-BACKED TANAGER (*RAMPHOCELUS DIMIDIATUS*)

Crimson-backed Tanagers are common in many areas of second-growth forest and scrub in central and eastern Panama. Some aspects of their behavior in some of these areas, including their general social and nesting habits, have been described in previous publications (*e.g.*, Skutch, 1954, and Moynihan, 1962a).

The following account of their display patterns is based upon observations of both wild and captive birds. Many individuals were observed in the wild, under more or less natural conditions, in the Canal Zone and adjacent parts of the Republic of Panama between January 1958, and January 1961. A few individuals were kept in captivity in large aviaries planted with natural vegetation on Barro Colorado Island during part of the same period. These captive birds had been trapped in various areas near Panama City. According to Hellmayr (1936), all of these birds are doubtless assignable to the subspecies *isthmicus*.

The observed display patterns of Crimson-backed Tanagers include locomotory, gregarious, hostile, and sexual reactions of adult and juvenile birds, and a few vocal patterns of nestlings.

Adult male and female Crimson-backed Tanagers are easily distinguished by differences in plumage and bill color. Juvenile birds of both sexes are similar to adult females, but can often be recognized by their duller plumage and other indications of immaturity (*e.g.*, shorter wings and tail, and a trace of yellow at the gape).

Preflight Patterns

Like all or most other American nine-primaried songbirds, Crimson-backed Tanagers frequently perform Tail-flicking and Wing-flicking movements when preparing to fly.

Their Tail-flicking movements are exaggerated in form. They are always or almost always primarily lateral. The tail is jerked far to one side, and

then returned (usually more slowly) to its original position; or jerked first to one side, then to the other side, and then returned to its original position. Most Tail-flicking movements also include a relatively slight vertical component. This may be simple, first down and then up, or first up and then down, or fairly complex, down-up-down or up-down-up. The simple up-down sequence seems to be most common.

Their Wing-flicking movements are usually less extreme. They are very similar in form to the corresponding movements of many other species, including the bush-tanagers of the genus *Chlorospingus*.[1] They are performed less frequently than Tail-flicking movements; but they are usually or always synchronized with Tail-flicking when they do occur.

In similar situations, adult male, adult female, and juvenile Crimson-backed Tanagers perform flicking movements with equal frequency. Such movements are performed in all social circumstances, by solitary birds as well as by birds in groups of their own and/or other species. Like the corresponding patterns of other species, they seem to be produced whenever any tendency to fly is partly inhibited or delayed, and probably function as signals indicating that the performing bird is likely to fly soon.

Hostile Behavior

Introduction. Crimson-backed Tanagers are moderately gregarious among themselves (Moynihan, 1961). Family groups of four to five birds sometimes stay together, more or less continuously, for periods of several months. Larger groups of two or three pairs or families are formed occasionally; but such associations tend to be relatively brief and loose.

This moderate degree of gregariousness is correlated with an appreciable development of hostile behavior. Even the members of a single family group tend to show considerable hostility to one another, and individual adult birds and pairs defend territories against other members of their own species.

Some of the stimuli releasing hostility by Crimson-backed Tanagers may have been revealed by the behavior of a captive young male observed in March 1958. This young male was kept in an aviary with many smaller birds of other species. He usually ignored all the smaller birds except a single adult male Yellow-bellied Seedeater (*Sporophila nigricollis*), which he attacked whenever the two birds happened to come within a few yards of one another. It was obvious that the seedeater was doing nothing to provoke these attacks. Adult male Yellow-bellied Seedeaters do not look (or sound) very much like Crimson-backed Tanagers, but they do have dark (brownish-black) heads and conspicuous silvery-white bills. It seems likely, therefore, that the attacks of this young Crimson-backed Tanager were simply responses to the sight of a white bill and dark head.

[1] All references to bush-tanagers of the genus *Chlorospingus* throughout this paper are based on Moynihan (1962b).

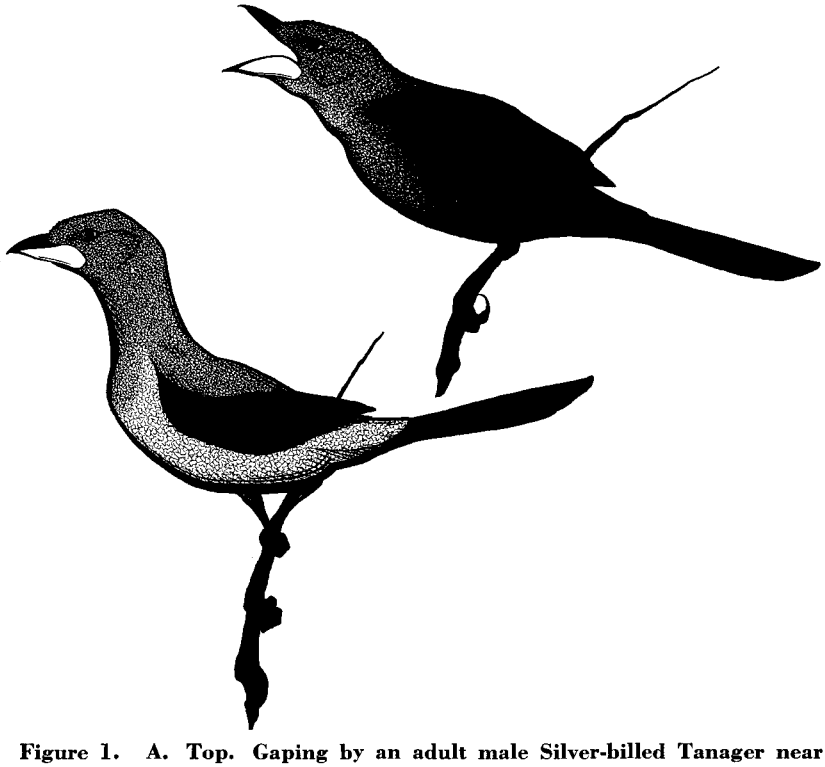

Figure 1. A. Top. Gaping by an adult male Silver-billed Tanager near Iquitos. This Gaping is superimposed upon an unritualized upward, aggressive, "jabbing" movement of the head and neck. B. Bottom. A typical extreme erect posture of the Crimson-backed Tanager.

Some certainly or probably unritualized hostile activities. Most of the obviously unritualized hostile activities of Crimson-backed Tanagers, including active escape, active attack, and fighting, are of little comparative interest, insofar as they are essentially identical with or very similar to the corresponding activities of many other species in form and (apparently) internal motivation.

Several other patterns frequently associated with overt attack, escape, and fighting are more interesting and more problematical. Among these patterns are erect postures, crouch postures, ruffling, and tail-fanning.

Crimson-backed Tanagers assume erect postures rather frequently during intraspecific disputes. A typical erect posture is shown in Figure 1B. The neck is stretched upward (while the head remains more or less horizontal), the legs are slightly flexed, and the whole plumage is smooth and very flat. Erect postures are usually assumed during fairly prolonged and vigorous disputes, and are usually accompanied by many Flicking move-

ments and frequently by Nasal Notes (see below) as well. They seem to be produced when a bird is "torn" by conflicting tendencies to advance and to retreat simultaneously, when it is impossible to resolve the conflict rapidly. Of all the birds I have watched, the ones that assumed erect postures most frequently, and assumed the most extreme erect postures, were wild birds engaged in disputes with captive birds in aviaries. These wild birds were unable to "get at" the captives and resolve their disputes by actual fighting. Erect postures are visually very conspicuous, but there is no definite evidence that they are ritualized. They are rather variable in form, and all or most of their components may be considered intention movements of flying (see Daanje, 1950). They are not exaggerated or stereotyped enough to suggest that they are anything more than combinations of intention movements.

I have observed erect postures only during disputes; but I should not be surprised if they also occurred, occasionally, in other situations that sometimes produce relatively prolonged conflicts between advance and retreat tendencies.

Crouch postures are even more variable than erect postures and are characterized only by flexing of the legs (sometimes much more extreme than in any erect posture) and some lowering of the head. In many cases the neck is also stretched forward to some extent when the head is lowered. The head is apparently always kept approximately horizontal. Some crouch postures are accompanied by pronounced ruffling of the plumage. The plumage is kept smooth in other crouch postures, but the body feathers are seldom or never smoothed as flat in crouch postures as in all or most erect postures. Some crouch postures are silent. Some silent crouch postures with ruffled plumage are also accompanied by Gaping (see below). Other crouch postures are accompanied by Harsh Notes, usually Muffled Harsh Notes (see below). Harsh Notes may be uttered by crouching birds with either smooth or ruffled plumage. (Two different types of crouch postures are shown in Figure 2.) Although some of the patterns frequently combined with crouch postures are obviously ritualized, this does not seem to be true of the basic crouch pattern itself. The crouch itself is similar to the erect posture in being comparatively little exaggerated or stereotyped and may be nothing more than another combination of unritualized intention movements. Crouch postures occur in an even wider variety of hostile and partly hostile situations than do the erect postures. As Gaping and ruffling appear to be at least moderately aggressive (see below), all or most crouch postures may be produced when the tendency to advance is relatively stronger than in all or most erect postures.

Typical ruffling is characterized by a general raising of the feathers of

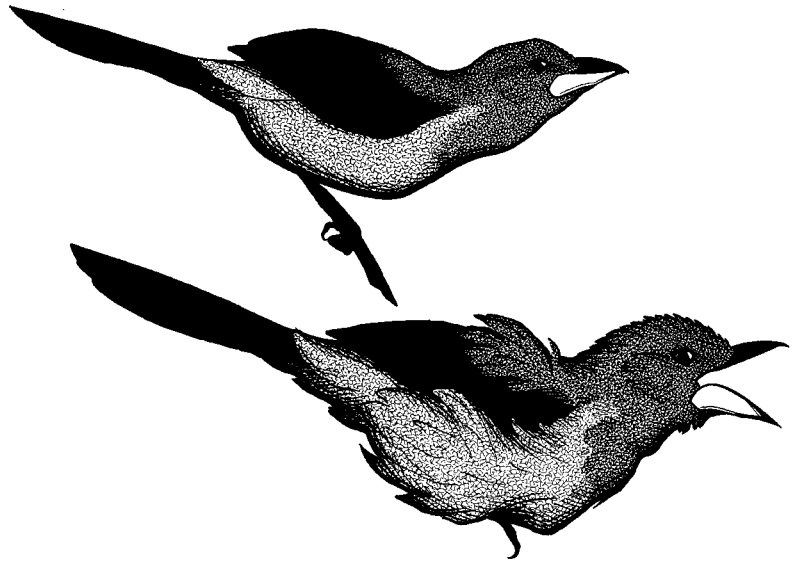

Figure 2. Crouch postures of the Crimson-backed Tanager. A. Top. A typical crouch posture without ruffling. This is frequently accompanied by Medium and/or Harsh Hoarse Notes. B. Bottom. An extreme crouch posture with ruffling and Gaping. This posture may also be accompanied by Medium and/or Harsh Hoarse Notes instead of Gaping.

the head, neck, breast, belly, and back (see Figure 2B). The rump feathers may also be raised in a few cases. Such ruffling may be combined with any sort of unritualized fighting or prelocomotory posture. It is also frequently accompanied by Flicking movements, Gaping, and/or Harsh Notes. All or most typical ruffling must be relatively aggressive, and is produced when the attack tendency is much stronger than the escape tendency. Ruffling is usually assumed by aggressive birds just before attacking, especially during violent fights, and may be either a ritualized display or an unritualized autonomic response to physiological changes accompanying violent activity (see Morris, 1956). The fact that typical ruffling is so general, involving most of the plumage, might support the latter hypothesis.

Crimson-backed Tanagers fan their tail feathers very frequently, in many different social situations. Such fanning may be combined with many different kinds of movements and postures, both ritualized and unritualized. The circumstances in which fanning occurs are so varied, in fact, that I found it impossible to determine the precise causation or function(s) of the pattern. All I can suggest is that it may be an indication of a strong escape tendency. Recently captured birds put into an aviary for the first time seem to do more fanning than relatively tame birds that have become used to living in aviaries.

One adult male also quivered his tail up and down very frequently after being

trapped and put in an aviary. These movements were very rapid but of very small amplitude. I did not notice similar movements in other circumstances; but I may have overlooked them because of their inconspicuousness.

With the possible exception of tail-quivering, all these problematical patterns are performed by adult males, adult females, and juvenile birds, although not necessarily with the same frequencies.

The comparative significance of these patterns is twofold. Even if they are not themselves ritualized, they may function as signals in much the same way as ritualized patterns, and they are certainly strictly homologous with ritualized patterns of some other species.

Gaping. Gaping is an unusually wide and prolonged opening of the bill. Gaping displays are performed by many different species of passerine (and other) birds; and the Gaping of Crimson-backed Tanagers is very similar to the corresponding displays of many other species of American nine-primaried songbirds. It seems to be an exaggerated and stereotyped derivative of the opening of the bill during biting. It is frequently combined with crouch postures, usually with ruffling (see Figure 2B), and with attack movements and/or intention movements (including diagonal upward "jabbing" patterns like the pattern of Silver-billed Tanagers shown in Figure 1A). It is obviously aggressive and functions as threat. It is always or almost always silent, and reveals the light-pink skin inside the mouth in a very conspicuous manner. It is another pattern performed by adult males, adult females, and juveniles.

When the Gaping of Crimson-backed Tanagers is combined with crouch postures (Figure 2B), the entire performance is reminiscent of the so-called "head forward threat" displays of many other passerines (see Andrew, 1961); but Crimson-backed Tanagers do not seem to have any distinct, integrated, head forward threat display (of the same type as other species) as such. Their Gaping is probably combined with other postures at least as frequently as with crouches; and their crouch postures seem to occur without more frequently than with Gaping.

Nasal Notes. Nasal Notes are probably the most common notes of Crimson-backed Tanagers, and the most distinctive in sound. A single note of this type might be transcribed as *Wah* or *Whanh* or *Anh.* Such notes are always monosyllabic, very nasal in tone, and slightly hoarse in quality. They are always essentially single, insofar as they are never integrated into distinct phrases of a particular number of notes; but they may be repeated almost endlessly, usually at more or less irregular intervals.

Nasal Notes are certainly uttered by adult males and females, and probably also by juvenile birds. They are not particularly closely associated with any special postures or movements. They may be uttered by flying birds, and by birds sitting or standing in any sort of unritualized

posture, with or without prelocomotory movements or intention movements (including Flicking movements).

They are also uttered in almost all social situations, whenever two or more (adult) birds, of the same or different pairs, are within sight and/or sound of one another; but they are uttered most frequently in certain particular types of obviously hostile situations. They are very common during intraspecific territorial disputes, but not, usually, when actual fighting occurs. During my own observations I heard Nasal Notes most frequently when wild birds noticed captive birds in aviaries, especially when the aviaries were near or within the territories of the wild birds. In such circumstances the wild birds uttered many Nasal Notes while flitting from perch to perch near the aviaries, both before and after trying unsuccessfully to attack the captive birds. Many Nasal Notes during territorial disputes are accompanied by slight and brief escape movements and/or intention movements; but such notes are seldom or never uttered during direct, sustained escape. Nasal Notes are also uttered very frequently by breeding birds, when their eggs or young are threatened by predators such as men or snakes (this has already been described by Skutch, *op. cit.*). Such notes are usually accompanied by frantic flying back and forth and vigorous intention movements of both attack and escape. (This combination of notes and movements may be considered a "mobbing" performance. Many other birds of other species may be attracted by such performances, and start to mob the predator themselves.) It has already been mentioned that Nasal Notes are sometimes uttered from erect postures. The plumage is often flatly smoothed even when Nasal Notes are accompanied by other postures. Nasal Notes are apparently never accompanied by ruffling.

All these facts would suggest that Nasal Notes are produced when the escape tendency is relatively strong, and when it is approximately equal to the attack tendency or (perhaps more probably) slightly stronger than the attack tendency. The actual strength of the hostile tendencies may be very different when Nasal Notes are uttered in different circumstances. Both the attack and escape tendencies may be quite strong during mobbing reactions. But Nasal Notes are also uttered by birds that do not seem to be very excited; and some of these latter notes may be produced when both the attack and escape tendencies are quite weak.

The signal function(s) of Nasal Notes are rather obscure, as the sound of such notes uttered by one bird seldom provokes simple unritualized reactions by other Crimson-backed Tanagers (except during certain mobbing reactions). It seems likely, however, that all or most Nasal Notes function as weak threat signals and/or alarm signals.

There is some evidence that Nasal Notes may also have some nonhostile function. The utterance of Nasal Notes by one bird of a mated pair sometimes seems to induce the utterance of similar notes, without any other indications of hostility, by its mate. I have also heard mated birds utter Nasal Notes immediately after their mates had uttered nonhostile Plaintive Notes (see below).

This might suggest that Nasal Notes may function as call notes or contact notes, at least occasionally, or that they are in process of acquiring such a function. It is not difficult to imagine how a very common but not very aggressive type of hostile note might be gradually changed into a nonhostile call or contact note in the course of evolution of a moderately gregarious species (and/or a species in which the pair bonds between mates are strong and long sustained).

Hoarse Notes. Several different vocal patterns of Crimson-backed Tanagers may be grouped together under the general name of "Hoarse Notes." The different types of Hoarse Notes are obviously closely related to one another, and probably somewhat more distantly related to Nasal Notes.

The two most common types of Hoarse Notes may be called "Muffled" Hoarse Notes and "Harsh" Hoarse Notes.

Both Muffled and Harsh Hoarse Notes may be uttered singly or in series of up to (at least) nine or 10 notes. They are both uttered most frequently in series of two, three, or four notes. They are similar to one another in sound, and must be transcribed in the same way. Typical series of these notes might be transcribed as *Whaah whaah whaah* or *wheeaah wheeah whah* or *Zhawhee whanh* or *Zhawee whanh whanh.* The notes of such series may be either brief and monosyllabic or moderately long and bisyllabic or quavering. If only one note of a series is bisyllabic or quavering, it is usually the first note, but it may be the last or the next-to-last note in an appreciable number of series.

Both Muffled and Harsh Hoarse Notes are usually very hoarse (much more so than typical Nasal Notes) and slightly nasal (less so than typical Nasal Notes). The principal difference, in sound, between typical Muffled Hoarse Notes and typical Harsh Hoarse Notes is loudness. Typical Harsh Hoarse Notes are moderately loud, while typical Muffled Hoarse Notes are very soft (sometimes inaudible at distances of more than one meter). Muffled Hoarse Notes might be described as "wheezing" or "whispering." Some or all Harsh Hoarse Notes are also much more rasping than Muffled Hoarse Notes.

Muffled and Harsh Hoarse Notes seem to intergrade. They are connected by a complete series of all possible intermediate notes; but such intermediate notes are probably not very much more common than either extreme Muffled or extreme Harsh Notes (*i.e.*, there is probably a real, if only partial, "barrier" of some sort between the two extreme types of notes).

Both Muffled and Harsh Hoarse Notes also intergrade with Nasal Notes, but much less frequently than with one another.

All these Hoarse Notes may be uttered from several different locomotory and prelocomotory postures, including crouches (see Figure 2A), and are sometimes accompanied by ruffling. They all occur in several different situations. These situations can be divided into two main categories: obviously purely hostile encounters between territorial neighbors and/or members of different pairs or family groups, and possible partly nonhostile encounters between mates.

During obviously purely hostile disputes, these Hoarse Notes are uttered most frequently when actual fighting is most common and most vigorous. They are often uttered by aggressive birds immediately before delivering an attack. These facts would suggest that all or most of these Hoarse Notes are produced when the attack tendency is much stronger than the escape tendency. The causal difference between Harsh Hoarse Notes and Muffled Hoarse Notes may be a matter of intensity. Birds that utter Harsh Hoarse Notes during vigorous disputes tend to switch to Muffled Hoarse Notes when the dispute starts to subside. This would indicate that both the attack and escape tendencies are sometimes or always weaker when Muffled Hoarse Notes are produced than when Harsh Hoarse Notes are produced. The causal difference between Hoarse Notes and silent Gaping may also be a matter of intensity. Birds uttering Muffled Hoarse Notes during a dispute tend to switch to Gaping as the dispute subsides. (This switch may be gradual, proceeding through a succession of intermediate stages, *i.e.*, softer and softer Muffled notes uttered as the bill is opened wider and wider.)

All of these Hoarse Notes seem to function as threat in obviously purely hostile situations.

Such notes are also uttered when one bird of a mated pair comes particularly close to the other, especially after the mates have been widely separated for some time. In such circumstances the notes may appear to be "greetings." "Greeting" patterns might be expected to be nonhostile or "friendly." Mated birds certainly do entertain "friendly" feelings toward one another. But there is good evidence that both the Muffled and Harsh Hoarse Notes themselves are purely hostile in all situations. They sound the same in all situations; and they are much less common during "greeting" encounters between mates than during obviously purely hostile encounters between territorial rivals and/or birds of different pairs or family groups. There are also other indications that mated birds are frequently hostile to one another (see below). It seems likely, therefore, that both the Muffled and Harsh Hoarse Notes during "greetings" between mates are

among the purely hostile components of an ambivalent, partly hostile and partly "friendly," situation.

The relative proportions of Muffled to Harsh Hoarse Notes are not necessarily the same in all situations. It is my impression, in fact, that Muffled notes tend to form a larger proportion of the total number of Hoarse Notes uttered during "greeting" encounters between mates than during obviously purely hostile encounters between other birds. This is only what would be expected if the Hoarse Notes are purely hostile and Muffled notes are produced by weaker hostile motivation than Harsh Notes (as mated birds must become habituated to one another).

The Hoarse Notes uttered during "greetings" are probably also threat. They frequently seem to induce slight escape intention movements, if not high-intensity sustained escape.

A third type of Hoarse Note may be called "Hoarse Screams." Hoarse Screams sound very much like Harsh Hoarse Notes but are much longer and louder (and possibly shriller and even harsher). They also intergrade with typical Harsh Hoarse Notes; but the intermediate notes do not seem to be very common. Hoarse Screams may be partly segregated from Harsh Hoarse Notes in much the same way as the latter are segregated from Muffled Hoarse Notes. I have heard typical Hoarse Screams only when trapped birds were being handled by a human being. These birds uttered Hoarse Screams while they struggled violently, biting and pecking and trying to escape at the same time. Such notes are probably of even higher intensity than Harsh Hoarse Notes, and are probably produced when both the attack and escape tendencies are even stronger than when all or most Harsh Hoarse Notes are produced.

Muffled Hoarse Notes, Harsh Hoarse Notes, and Hoarse Screams, and all notes intermediate between them, are uttered by adult males, adult females, and juvenile birds.

Many other species of American nine-primaried songbirds utter notes that seem to be more or less strictly homologous with some or all of the Hoarse Notes of Crimson-backed Tanagers.

In the case of some species, the notes that seem to be homologous with all or most of the Hoarse Notes (and, probably, the Nasal Notes) of Crimson-backed Tanagers are much less well differentiated, and are nothing more than slight variations of an essentially single, unitary pattern. It is possible that the different types of Hoarse Notes of Crimson-backed Tanagers have been derived from such a unitary pattern by a process of increasing division and segregation (the development of at least three different "typical intensities," to use the terminology of Morris, 1957). This possibility will be discussed in more detail in later papers.

As a group the Hoarse Note patterns of Crimson-backed Tanagers are

also reminiscent of and probably strictly homologous with a whole group of patterns, including *Zheeeeeeee* notes, Harsh Notes, and the "greeting" call, of Brown-capped Bush-tanagers (*Chlorospingus opthalmicus*). These latter patterns are much more distinct from one another, in sound and some other features, than are the corresponding patterns of Crimson-backed Tanagers. They may represent a further stage in the process of division and segregation.

Crimson-backed Tanagers may also utter Hoarse Notes that are slightly different from any of the patterns described above. Such notes might be called "Staccato" Hoarse Notes. They sound like Harsh Hoarse Notes but are briefer and more abrupt sounding. They are usually uttered in rapid series of more than three or four notes. A single series might be transcribed by something like *Ta ta ta ta ta ta. . . .* Staccato Hoarse Notes seem to be relatively rare. I heard them only during some partly or primarily sexual encounters between an adult male and an adult female (see below). I did not hear them frequently enough to analyze their causation or usual function(s). They may be nothing more than aberrant Harsh Hoarse Notes, without any special significance. It was my impression, however, that they might be more aggressive than other Hoarse Notes. Series of Staccato Hoarse Notes are sometimes so rapid as to be almost rattling; and all or most of the rattling calls of related species are certainly aggressive.

Plaintive Notes, Dawn Calling, and Related Patterns

Plaintive Notes. Crimson-backed Tanagers frequently utter notes that might be transcribed as *Tseeeet* or *Wheeeeet* or *Sseeeeeeeet.* (The latter may be the most common form.) Such notes are always at least moderately loud and sibilant. They are also usually slightly hoarse and buzzy, but much less so than most of the other notes of the species.

Such notes do not sound very plaintive; but they seem to be strictly homologous with the so-called "Plaintive Notes" of Brown-capped Bush-tanagers and other related species. They seem to occur in all or most of the same social situations, and subserve some or all of the same functions, as the Plaintive Notes of other species; and they resemble the latter in being relatively, if not actually, clear in tone. It will be convenient, therefore, to call them by the same name.

The Plaintive Notes of Crimson-backed Tanagers are essentially single notes, although they are sometimes repeated at more or less irregular intervals (in much the same way as Nasal Notes). They are uttered from all or most unritualized standing and sitting postures, and also (occasionally) from some of the same slightly ritualized postures as *Keeyoo* Dawn Calling notes (see Figures 3A and 3C). They are apparently never accompanied by ruffling. They are sometimes uttered by flying birds, but such cases seem to be relatively rare.

They are usually uttered by birds that have become separated from

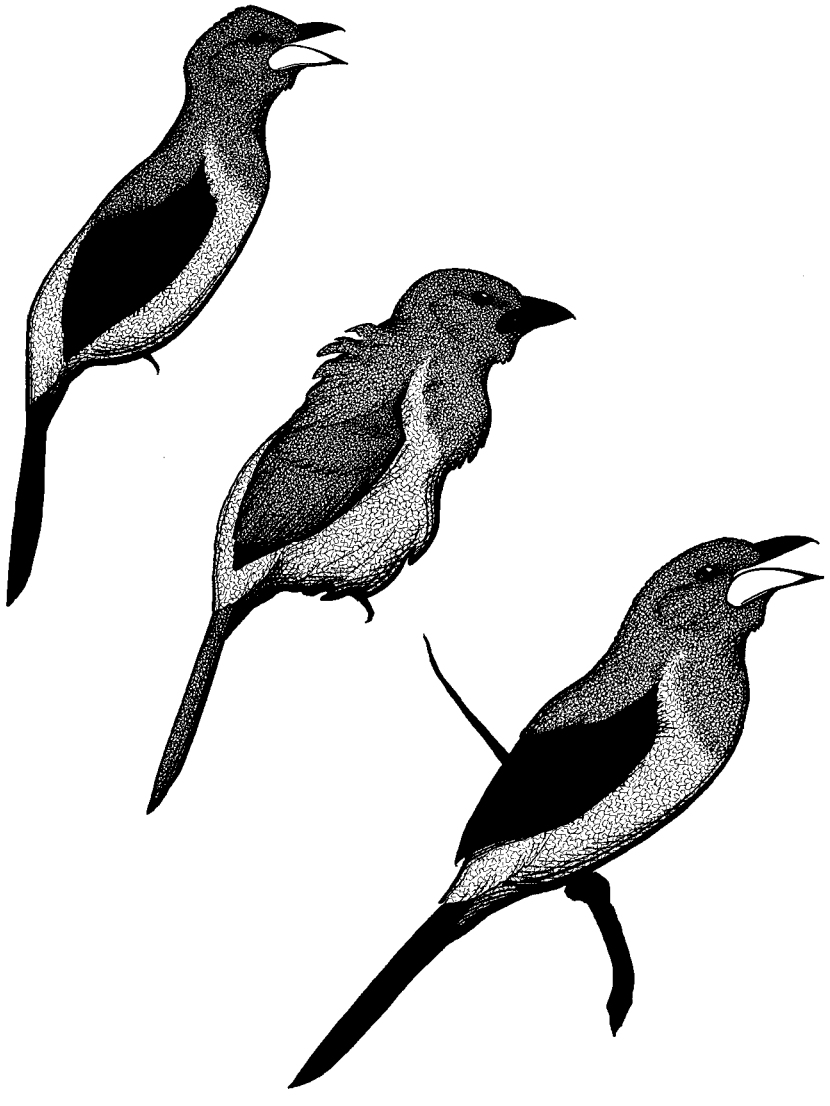

Figure 3. Postures accompanying some of the longer vocalizations of Crimson-backed Tanagers. A. Top. A posture occasionally accompanying Dawn Calling, series of Plaintive Notes, series of alternate Plaintive Notes and Nasal Notes, and "flourish"-like notes by adult males. B. Center. The posture usually accompanying Whispering Warbles or Subsongs by a juvenile male. C. Bottom. The most common posture accompanying Dawn Calling by adult males. This posture may also accompany series of Plaintive Notes, series of alternate Plaintive Notes and Nasal Notes, and the "flourish"-like patterns.

their usual companions. A solitary bird uttering Plaintive Notes usually or always stops uttering such notes as soon as it is joined by its mate or another member of its family group. Plaintive Notes seem to be uttered most frequently by adult males, but they are certainly also uttered by females and juveniles. They are uttered with some appreciable frequency throughout the year, and during all periods of the day.

This would suggest that they may be produced by thwarting of some gregarious motivation and/or several different types of "friendly" motivation, including pairing and parental tendencies. They may function as signals to "call in" or attract several different types of social companions.

Plaintive Notes sometimes intergrade with Muffled Hoarse Notes, but only in obviously ambivalent situations.

"Keeyoo" Dawn Calling. The most long-sustained and elaborate vocal patterns of adult Crimson-backed Tanagers are uttered by males in the early morning during the breeding season.

These vocal patterns are usually uttered from special perches. Males usually fly to these perches as soon as it starts to get light, well before sunrise. They usually select "exposed" perches, where they can be seen from all directions, and from which they can look in all directions. Under natural conditions such perches may be from three to approximately 12 meters above the ground. (A male kept in captivity usually chose a perch only one and one-half meters above the ground, in spite of the fact that there were higher perches available in his cage.)

A male may start to utter distinctive notes as soon as he reaches his perch. These notes can be divided into two slightly different types. A single note of the most common type might be transcribed as *Keeyoo*. A single note of the other type might be transcribed as *Kew*. Both types are usually or always clear in tone, and rather melodious. They are both uttered in series, together in the same series. Such series are "indeterminate," *i.e.*, they are continued for varying lengths of time, and are not usually divided into phrases of fixed, characteristic number of notes. The rhythm of these series is usually quite regular, each note being separated from the preceding and succeeding notes by approximately equal intervals of silence. The rhythms of different series may be slightly different; but the intervals between successive notes are seldom much longer than the notes themselves.

In some cases these series of notes consist of *Keeyoos* with only an occasional *Kew* interjected apparently at random. In other cases the *Kews* are more frequent and more regular in occurrence. Single *Keeyoos* and single *Kews* may be uttered alternately, or a single *Kew* may be inserted after every two *Keeyoos*. Such regular sequences are probably more common than irregular sequences including relatively fewer *Kew* notes.

Long series of *Keeyoo* and *Kew* notes seem to be almost or completely confined to the early mornings. They always or almost always stop an hour or so after sunrise, if not earlier (see below). They are generally similar to the vocal patterns of other species which have been called "song" or "dawn song"; but it may be preferable to refer to them as "Dawn Calling" (see below, and comments in Moynihan, 1962b).

A few other types of notes are sometimes interjected among the *Kew* and *Keeyoo* Dawn Calling notes. I have heard single Plaintive Notes interjected into otherwise typical Dawn Calling by a captive male. The same male also uttered occasional single *Kraaa* and *Kraanh* notes during some Dawn Calling. Both these latter types of notes were extremely "guttural," with a sort of rattling undertone. The *Kraanh* notes were also extremely nasal in tone.

Skutch (*op. cit.*) transcribes a "song" of Crimson-backed Tanagers as *Sweet, you do; sweet, you do, you do.* This is presumably a form of Dawn Calling including a relatively large proportion of what I have transcribed as *Kew* notes, or a combination of Plaintive Notes and *Keeyoo* notes (Plaintive Notes are higher pitched than *Keeyoo* notes), or a series of the "flourishlike" notes that are sometimes uttered during later periods of the day (see below).

Most of the postures accompanying typical Dawn Calling seem to be slightly ritualized. They tend to be slightly more rigid and stiff looking than ordinary sitting or standing postures. Probably the most common posture during Dawn Calling is the straight, diagonal posture shown in Figure 3C. The more upright posture shown in Figure 3A is sometimes assumed by males at the beginning of a Dawn Calling performance, but is seldom long sustained.

Some Dawn Calling performances are accompanied by the less stretched posture with fluffing of the breast and belly feathers shown in Figure 4B. The only male observed to assume this posture rather frequently was a captive male in a cage with a female who seemed to be dominant over him.

The postures accompanying Dawn Calling do not usually change when a switch is made from *Keeyoos* to *Kews* or vice versa, or when single Plaintive Notes, *Kraaa* notes, or *Kraanh* notes are interjected.

Dawn Calling is seldom accompanied by pronounced raising of other feathers in addition to the breast and belly feather. (I have seen males sitting with the forehead feathers erected, as shown in Figure 3A, during some Dawn Calling performances; but such cases seem to be relatively rare.) The Dawn Calling of Crimson-backed Tanagers is apparently never accompanied by special wing movements (aside from Flicking, which may occur, very occasionally, during the intervals between notes).

Male Crimson-backed Tanagers seldom sit in the same place throughout

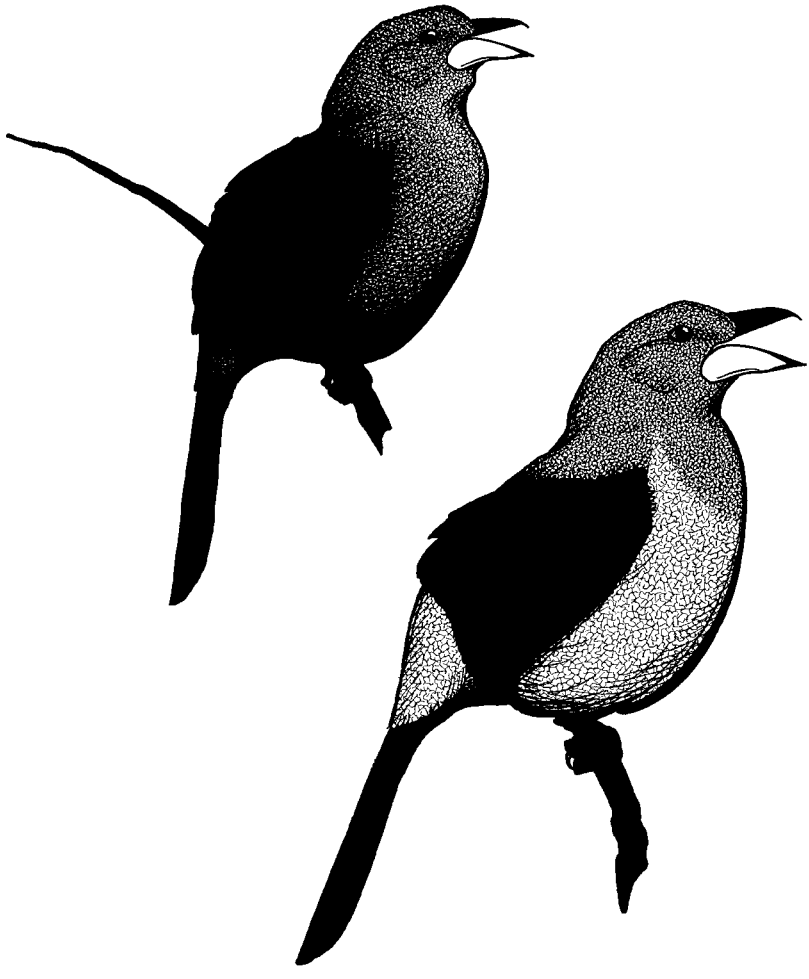

Figure 4. A. Top. A fluffed posture accompanying Dawn Calling by an adult male Silver-billed Tanager of the Trinidad race. B. Bottom. A fluffed posture sometimes accompanying Dawn Calling by an adult male Crimson-backed Tanager.

a long-continued Dawn Calling performance. They tend to fly back and forth between several perches, uttering a series of Dawn Calling notes at each perch. All the perches are usually essentially similar and fairly close together. The males do not continue Dawn Calling notes during the flights between perches.

Dawn Calling is primarily a pattern of isolated or solitary males. Under natural conditions males very seldom utter Dawn Calling if there is a

female within six to 10 meters of them, and never if there is a female close by. A male uttering Dawn Calling apparently always stops immediately when a female joins him.

This, and the fact that Dawn Calling is largely or completely confined to the breeding season, would suggest that all or most Dawn Calling is produced by thwarting of some sexual motivation. This is perhaps more probably a pairing than a copulatory tendency. Dawn Calling males are often ready to copulate when joined by a female (see below); but this does not seem to be true in all cases. I have seen males that made no attempt to copulate when they joined or were joined by their mates after a prolonged period of Dawn Calling. If both Plaintive Notes (see above) and Dawn Calling can be produced by thwarting of the same type of pairing motivation, then the fact that Dawn Calling is virtually restricted to the early mornings (when almost all other activities of birds are most intense) might suggest that it is produced when the pairing motivation is stronger than when Plaintive Notes are produced.

It is also conceivable that Dawn Calling is the result of some partly independent motivation of its own, a sort of "Dawn Calling tendency." This might help to explain why apparently frustrated males utter Dawn Calling instead of going to look for a female. It seems likely, however, that all or most Dawn Calling performances can be explained without assuming the existence of such a partly independent tendency.

I was not able to determine what, if any, are the causal differences between *Keeyoo* and *Kew* notes. The mere sound of the notes might suggest that the *Kews* are lower intensity than the *Keeyoos*.

The *Kraaa* notes are very enigmatic. They sound very much like abbreviated versions of the aggressive Rattles of some other species of *Ramphocelus* (*e.g.*, the Yellow-rumped Tanager, *R. icteronotus*) and many other species of other genera of American nine-primaried songbirds. They might conceivably be the remaining vestiges of a Rattle pattern which was more important and elaborate in the ancestor of the Crimson-backed Tanager.

Kraanh notes may be intermediate between typical *Kraaa* notes and typical Nasal Notes.

The fluffing of the breast and belly feathers during some Dawn Calling is probably an indication of an activated escape tendency, like the similar component of some other displays of other species (see, for instance, Hinde, 1955, and Morris, 1956).

If he continues the performance long enough, a male Crimson-backed Tanager uttering Dawn Calling is usually or often eventually joined by a female. The female may be attracted by the Dawn Calling itself. The Dawn Calling of Crimson-backed Tanagers may well play an important role in pair formation (similar patterns of related species seem to do so);

but unfortunately I never saw a clear-cut case of pair formation among the wild Crimson-backed Tanagers that I studied. All the males I saw and heard performing Dawn Calling under natural conditions were probably or certainly already mated. The Dawn Calling of such males may help to reinforce the pair bonds that they have already established.

Alternations and combinations of Plaintive Notes and Nasal Notes. If a male Crimson-backed Tanager is not joined by a female after he has uttered prolonged Dawn Calling, he will eventually stop, usually more or less abruptly, of his own accord.

He may then start to utter single Plaintive Notes and single Nasal Notes in regular alternation, and may continue to do so for a considerable length of time. Such series of alternate Plaintive Notes and Nasal Notes are usually indeterminate and very regular in rhythm, in much the same way as series of Dawn Calling notes. Sometimes all the notes are more or less evenly spaced. At other times they are organized into "doublets": Plaintive Note—Nasal Note—pause—Plaintive Note—Nasal Note—pause—Plaintive Note—Nasal Note—pause. . . . Both types of series are uttered from the same perches as Dawn Calling, and are usually accompanied by the same diagonal or upright postures, without fluffing. This might suggest that they are produced by the same causal factors as Dawn Calling, at a lower level of intensity (as the causal factors producing Dawn Calling presumably "run down" in the course of the morning); but there is little reason to believe that the individual Nasal Notes of such series are not produced by the same factors, and subserve the same functions, as individual Nasal Notes in other circumstances. Only the extreme regularity of the alternation of Plaintive Notes and Nasal Notes in such series might suggest that the series have begun to be ritualized as a whole.

A single captive adult male Crimson-backed Tanager sometimes uttered slightly different series of notes instead of alternate Plaintive Notes and Nasal Notes after Dawn Calling. These series were also indeterminate and regular in rhythm. Most of the notes of such series sounded like unusually thin and "wiry" Nasal Notes, *i.e.*, like typical Nasal Notes with a slight "tinge" of the quality of typical Plaintive Notes. They may well have been partly intermediate between typical Nasal Notes and typical Plaintive Notes. A few typical Nasal Notes were sometimes interjected (apparently at random) among the intermediate-sounding notes. Such series may have been produced by factors similar to those usually producing the series of alternate typical Plaintive Notes and typical Nasal Notes, with the addition of an extra hostile component. It was noticeable that the male tended to utter such series when another male Crimson-backed Tanager in a nearby aviary uttered many typical Nasal Notes.

Phrases uttered later in the day. If a male Crimson-backed Tanager

should find himself alone in midmorning or later in the day, he does not resume Dawn Calling or uttering alternate Plaintive Notes and Nasal Notes; but he may utter some vocal patterns that seem to be related to typical Dawn Calling. These are phrases of three or four notes that might be transcribed by something like *Whit Whew-hew* or *Tsee-hee tsuh-weeeee.* The individual notes of such phrases are very much like typical Dawn Calling notes in tonal quality. Such phrases are usually or always repeated; but they do not lose their identity as phrases and become indeterminate series of notes. The intervals between successive phrases are always much longer than the interval between notes within the phrases.

These phrases are uttered from exposed perches in much the same way as typical Dawn Calling and series of alternate Plaintive Notes and Nasal Notes, and are accompanied by the same range of postures as the latter. They also seem to be restricted to the breeding season; but they are relatively rare and are uttered much less frequently than either typical Dawn Calling or series of alternate Plaintive Notes and Nasal Notes.

In all cases that I observed, males that uttered these phrases silently flew away after having repeated the phrases for a few seconds or minutes.

It is difficult, therefore, to determine the significance of such behavior. All I can say is that the form and circumstances of these phrases might suggest that they are produced by factors similar to those producing typical Dawn Calling. They may be uttered when some pairing tendency is thwarted or when the pairing tendency is weaker than during Dawn Calling (but probably stronger than when some Plaintive Notes are uttered).

Comparison with Brown-capped Bush-tanagers. It may be useful to compare some of the patterns described above with certain displays of Brown-capped Bush-tanagers.

The Plaintive Notes and Dawn Calling of Crimson-backed Tanagers are so similar to the Plaintive Notes and Dawn Calling of Brown-capped Bush-tanagers, in almost all respects, that they must be strictly homologous with the latter; but the Plaintive Notes of Crimson-backed Tanagers are uttered much more frequently than the corresponding notes of Brown-capped Bush-tanagers.

The *Whit whew-whew* and *Tsee-hee tsuh-weeeee* phrases of Crimson-backed Tanagers are somewhat reminiscent of the "Flourishes" of Brown-capped Bush-tanagers. At least, they differ from the typical Dawn Calling of Crimson-backed Tanagers in some of the same ways that Flourishes differ from the typical Dawn Calling of Brown-capped Bush-tanagers. They may be homologous with the Flourishes, in spite of the fact that they are uttered much less frequently.

It seems likely that the comparatively high frequency of Plaintive Notes and the comparatively low frequency of Flourishlike notes by Crimson-

backed Tanagers are causally related to one another. Crimson-backed Tanagers seem to utter Plaintive Notes in most of the circumstances in which Brown-capped Bush-tanagers utter Flourishes.

Similarly, Crimson-backed Tanagers seem to utter Nasal Notes and/or Hoarse Notes in most of the circumstances in which Brown-capped Bush-tanagers utter Rattles.

These differences between the two species may be reflected in their "songs." The series of alternate Plaintive Notes and Nasal Notes uttered by Crimson-backed Tanagers, including both hostile notes and notes that seem to be attractive, may function as true song, according to the definition of song used here (*i.e.*, any vocal pattern that, 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). If so, the series of alternate Plaintive Notes and Nasal Notes are strictly analogous with the Rattle-Flourish combinations of Brown-capped Bush-tanagers. The arrangement of Plaintive Notes and Nasal Notes in such series is also similar to the arrangement of Rattles and Flourishes when Brown-capped Bush-tanagers utter many Rattle-Flourish combinations in succession (as they frequently do). This similarity is perhaps remarkable, as the analogous song patterns of the two species are (at best) only very partially and indirectly homologous with one another (and each species probably possesses patterns that are more strictly homologous with the song patterns of the other). There must have been strong selection pressure in favor of such arrangements.

Juvenile "Subsong." The only juvenile male Crimson-backed Tanager that I kept in captivity performed some patterns that might be called "Whispering Warbles." These patterns were first observed in the middle of March 1958, and were repeated from time to time until at least the middle of May of the same year.

I first became aware of these patterns when I saw the juvenile male sitting by himself on a high perch in his aviary, with his bill closed but with his throat moving in and out as if he were uttering long phrases of a dozen or more notes. I approached him within two meters while he continued this performance, but could not hear any sounds of any sort.

When he repeated this performance a few days later, a few sounds had begun to be audible. It was now possible to distinguish very faint whispering or twittering phrases while his throat went in and out as before. These phrases gradually became slightly louder, and more melodious or warbling, during subsequent repetitions during the next few weeks; but they always remained very much fainter than any other vocal patterns of the species.

They were always so faint that their structure was difficult or impossible to recognize. As far as I could tell, they were usually or always rather

formless jumbles, largely composed of short and not very distinctive notes uttered very rapidly one right after the other.

Some of the later Whispering Warbles also included one or more *Keeyoo* notes, like the *Keeyoo* notes of typical adult Dawn Calling, but much fainter. Similar faint *Keeyoo* notes, Muffled Hoarse Notes, and/or typical Nasal Notes were sometimes uttered immediately before, immediately after, and/or between Whispering Warble phrases.

The juvenile male always sat alone while he uttered these phrases, usually in the posture shown in Figure 3B, with the upper back feathers ruffled or fluffed. Sometimes he also turned his head sharply from side to side, as if looking for something; but this behavior was seldom followed by attempts to join other birds in the same aviary or any other significant social reactions. (There were many other birds of other species, and one adult male Crimson-backed Tanager, in the same aviary at the time.) The juvenile male usually uttered Whispering Warbles during the middle of the day as well as during the early mornings. He apparently stopped uttering such phases when he became attached, presumably mated, to a female Yellow-rumped Tanager.

This might suggest that his Whispering Warbles were produced by thwarting of a pairing tendency. They may also have contained a hostile component, as they were associated with Nasal Notes and Muffled Hoarse Notes (and fluffing or ruffling of the upper back feathers occurs during various hostile displays of other species of tanagers).

These Whispering Warbles would seem to be basically similar, in form and some other features, to the patterns of many other species of passerine birds that have been called "subsong" (see Lanyon, 1960). The adult Dawn Calling patterns may develop from, or out of, Whispering Warbles during ontogeny. Unfortunately, I never heard Whispering Warbles uttered by wild birds under natural conditions, and so could not trace their normal course of development.

Copulations and Associated Patterns The only Crimson-backed Tanagers that I observed attempting to copulate were a pair of captive adults; and these birds performed apparently successful copulations only after I had kept the male separated from the female for a couple of weeks.

When I finally released the male in the aviary where the female had remained throughout the period of separation, the general sequence of events was as follows:

The birds were first together at 06:00 (just as it was beginning to get light). Initially, they merely flew about the aviary in an excited manner, and kept rather far apart from one another most of the time. When one bird did happen to land close beside the other, one or both uttered Hoarse Notes, usually or always Muffled Hoarse Notes. The male sometimes

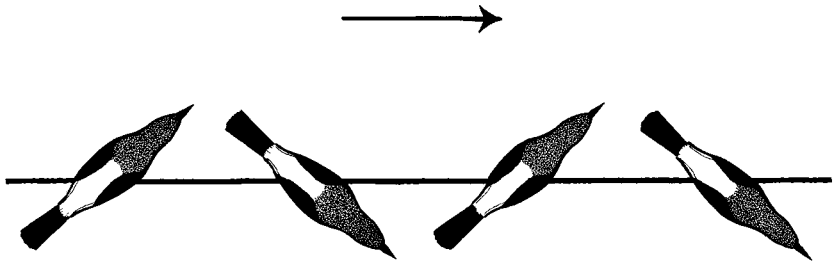

Figure 5. Pivoting by an adult male Crimson-backed Tanager. This is a diagrammatic sketch, showing the positions of a male at the end of four successive hops along a branch toward a female. The positions are drawn as seen from above. The arrow points in the direction of the female. The hops during Pivoting are not always as long as indicated in this diagram.

assumed a crouch posture (as in Figure 2A) or a low-intensity indication of a Bill-up Tail-up posture (see below) when he perched, momentarily, between periods of flying about.

After approximately half an hour, the male suddenly began to try to mount the female. His initial approaches to her were very characteristic. He would land on the branch on which she was sitting, but some considerable distance away from her, and then advance toward her by "Pivoting" hops. This Pivoting seemed to be essentially identical in form with that of some estrildine finches, *e.g.*, the Zebra Finch, *Poephila guttata* (see Morris, 1954). Facing diagonally toward the female, the male would swing first to one side, then to the other, then back to the first side, then back to the other side, etc., changing position at each hop (see Figure 5). This was not accompanied by special postures. As soon as the male reached the side of the female, he would lean forward and "peer" into her face, usually (I think) touching her bill with his. This appeared to be an intention movement of feeding the female (in one case, at least, the male may actually have passed food to the female). Then he would try to mount immediately.

When he did this the first time, the female did not display before he mounted. As soon as he got on her back, however, one or both birds uttered soft, rapid Muffled Hoarse Notes. The male then flew away, without attempting to lower his tail and to bring his cloaca into contact with that of the female.

A few minutes later, the female suddenly began to display while the male was some distance away. She suddenly pointed her head and bill diagonally upward, raised her tail, stretched her wings out horizontally, erected all her breast and belly feathers, and fanned her tail feathers. This posture may be called the Bill-up Tail-up posture, and it is shown in Figure 6B.

Figure 6. Copulatory postures of Crimson-backed Tanagers. A. Top. a low-intensity Bill-up Tail-up posture of a male. B. Center. A Bill-up Tail-up posture of a female, with wings spread out horizontally. C. Bottom. An extreme Bill-up Tail-up posture of a male, with one wing raised much higher than the other.

The female was quite silent in this posture; and she did not quiver her wings.

The male responded by flying to the branch on which the female was perched, and then approaching her with Pivoting and "peering" as before. He mounted her again, but she uttered Hoarse Notes and he slipped off. She remained in the Bill-up Tail-up posture, with spread wings and ruffled breast and belly feathers. He tried to mount her a third time a few seconds later, but she uttered Hoarse Notes again, and he flew away.

This whole procedure, in almost exactly the same form, was repeated several times within the next few minutes. Finally, the male mounted the female and remained on her back until he had completed an apparently successful copulation; he then flew straight from her back to a branch about a meter away. As soon as he landed, he went into a Bill-up Tail-up posture. This was very much like the corresponding pattern of the female, but the wings were slightly drooped instead of being extended horizontally (see Figure 6A). The male was also silent in this posture.

The two birds continued to perform high-intensity sexual behavior during the next half hour; but the form of the male's approaches to the female changed completely. Every once in a while, he would assume a very exaggerated Bill-up Tail-up posture, with extreme ruffling of the breast and belly feathers and tail fanning, and extreme raising or extension of the wings. In most cases one wing was raised much higher than the other. Sometimes one wing was raised almost vertically while the other was extended almost horizontally (see Figure 6C). I think that the raised wing was usually the wing nearest the female; but there were certainly some exceptions to this general rule. The male assumed these extreme Bill-up Tail-up postures when perched far away from the female as well as when perched right beside her. His wings were usually held more asymmetrically when he was close to her than when he was far away.

The female usually assumed a Bill-up Tail-up posture (as before) at approximately the same time as the male.

The male would then try to mount, usually after the two birds had remained in their Bill-up Tail-up postures for several seconds. He always stretched his neck upward, keeping his head horizontal or even pointing his bill slightly downward, just before mounting, but he never performed any Pivoting or "peering."

These copulation attempts were always very brief and rapid; but some of them seemed to be successful. Most of them were quite silent.

As far as I could tell, all the actual copulatory movements of both the male and female were essentially the same during all copulation attempts, irrespective of differences in the preceding patterns, and similar to the corresponding movements of other passerines.

The later copulation attempts were not followed by much displaying. The female usually remained in her Bill-up Tail-up posture during the copulations, and sometimes maintained the posture for a few seconds afterwards. The male sometimes briefly assumed a Bill-up Tail-up posture after dismounting. Both birds usually performed several bill-wiping movements after both apparently successful and obviously unsuccessful copulation attempts.

After several apparently successful attempts, the frequency and vigor of the sexual relations gradually declined. The male continued to mount the female occasionally; but his preliminary Bill-up Tail-up patterns became less and less extreme. First he stopped raising his wings, and then he lifted his bill and tail less. Eventually, he was attempting to mount the female after only the faintest and briefest indication of Bill-up Tail-up posture, hardly more than an intention movement of assuming the posture, or without any preliminary display at all. The female assumed Bill-up Tail-up postures less and less frequently, and her Bill-up Tail-up postures also became less extreme. None of the copulation attempts at this stage were successful. The male seemed to be unable to complete the attempts. He usually flew away from the female almost immediately after mounting, without attempting to lower his tail. These unsuccessful attempts were also accompainied by Muffled and/or Staccato Hoarse Notes by one or both birds.

All or almost all sexual behavior had stopped by 08:30.

The same birds performed a few more copulatory patterns early the next morning, but almost always less vigorously than at the same time on the preceding day. One or two copulation attempts shortly after dawn may have been successful; but all the later attempts were obviously unsuccessful. The intervals between attempts were also relatively long—longer on the average than on the preceding day. All displays before copulation attempts were Bill-up Tail-up patterns. The male never approached the female with Pivoting and "peering." All or almost all the copulation attempts were accompanied by Muffled Hoarse Notes, usually by the female (the male may have uttered a few Muffled Hoarse Notes with some of his Bill-up Tail-up patterns). The female also attempted to peck the male once or twice when he came close to her. He seemed to be rather afraid of her after the first few copulation attempts. He sometimes flinched when she flew toward him; and he spent considerable time sitting more or less motionless in a rather hunched posture with almost all his plumage fluffed.

Perhaps the most interesting feature of the behavior of the birds on this second day was the fact that the male did considerable Dawn Calling in the intervals between copulation attempts (usually when he was at least a meter or more away from the female). This may have been an

indication that the mating of the two birds was not satisfactory (*i.e.*, under natural conditions, the male might have started attempts to secure another female at this stage).

When the same birds were observed again in the early morning three days later, the male still uttered Dawn Calling from time to time, and the only remaining indications of copulatory tendencies were a few brief and slight Bill-up Tail-up patterns by the male when he happened to find himself close to the female.

The general motivation of these precopulatory patterns is fairly obvious. The Bill-up Tail-up patterns must be produced when some copulatory tendency is strong. The fact that the male sometimes remains in an extreme Bill-up Tail-up posture for some seconds before attempting to approach the female might suggest that all or most of his Bill-up Tail-up patterns are produced when both a copulatory tendency and some other, incompatible type(s) of motivation are activated simultaneously. The other tendency most likely to be activated in such situations is escape. Some attack tendency may also be activated at the same time; but it is presumably relatively weak. Most of the components of the Bill-up Tail-up patterns are difficult to analyze separately. The only exception is the asymmetrical wing raising, which is obviously an intention movement of mounting. The Pivoting approaches of the male are presumably produced when his copulatory tendency is relatively and/or actually stronger than when all or most of his Bill-up Tail-up patterns are produced; but the side-to-side component of Pivoting may be another indication of an activated escape tendency.

It is quite likely that well-mated Crimson-backed Tanagers in the wild usually perform less elaborate and prolonged precopulatory displays than did the captive birds whose behavior is described above. Most tanagers of other genera usually perform very few or no special precopulatory displays under natural conditions.

Mr. Edwin Willis (pers. comm.) observed one copulation by wild Crimson-backed Tanagers that is of interest in this connection. It occurred when a female approached a Dawn Calling male. The male stopped Dawn Calling, flew straight to the female, and copulated with her, apparently successfully, without any other precopulatory (or postcopulatory) display. The whole performance would seem to have been quite similar to some copulatory reactions of Brown-capped Bush-tanagers.

This would seem to confirm the suggestion that the behavior of the captive birds described above was more or less "abnormal." Their reactions were not, however, peculiar to themselves alone. Several other captive males were seen to approach other females, assume Bill-up Tail-up postures (without wing raising), and attempt to mount the females. None of these attempts was successful, perhaps because there was too much hostility between the males and females. All or most of these attempts were accompanied by many Muffled Hoarse Notes by either one or both of the birds involved.

Perhaps the behavior of the captive pair described above was "typical" of the

species when the female is not "properly" responsive to the copulatory advances of the male.

General Comment

From a comparative aspect, the most interesting features of the display behavior of Crimson-backed Tanagers are the variety of hostile Hoarse Notes, including "greeting" notes and harsh notes during fighting; the warbling "Subsong" of juvenile birds; the relatively great frequency of Plaintive Notes, and their use to "call in" a variety of social companions; the frequent utterance of Plaintive Notes and Nasal Notes in regular alternation; the rarity of rattling and flourishlike notes; and Dawn Calling in the form of indeterminate repetition of essentially identical notes, without the accompaniment of special wing movements.

All or most of the displays of Crimson-backed Tanagers are partly or completely homologous with displays or related patterns of Brown-capped Bush-tanagers; but some homologous displays or components of displays are rather different in form and/or frequency in the two species. The extensive and fundamental similarities between the display repertories of the two species are not always obvious on first observation.

Some Calls of Nestling Crimson-backed Tanagers

In March 1961, I made some very brief and intermittent observations of two nestling Crimson-backed Tanagers during the last three days before they left the nest. These young birds begged from their parents by uttering hoarse *Zhee zhee zhee zhee* . . . or *Whee whee whee whee* . . . notes. When I picked them up in my hands, they struggled briefly and uttered hoarse notes that were intermediate between their typical begging notes and adult Hcarse Notes in tone, and similar to the begging notes in rhythm. Such notes were probably at least partly hostile. The nestlings sometimes stopped struggling, and lifted their heads as in begging, while they continued to utter the presumably hostile notes. This behavior would suggest that begging notes and Hoarse Notes may be closely related in the ontogeny of the species.

SOME PATTERNS OF SILVER-BILLED TANAGERS (*R. CARBO*)

Only a few Silver-billed Tanagers were observed during the present investigation. Some wild birds, presumably typical *carbo carbo,* were observed near Iquitos, Peru, in December 1958; and other wild birds of the race *magnirostris* were observed in Trinidad in July 1961. (These subspecies are assigned on the basis of the ranges cited by Hellmayr, *op. cit.*) Two captive birds in the Bronx Zoo were watched for a few days in October 1958 and September 1959. The provenance of these captive birds was unknown; but they looked very much like birds of the nominate race.

All these Silver-billed Tanagers performed Wing-flicking and Tail-flicking movements that seemed to be identical with the corresponding movements of Crimson-backed Tanagers. The Iquitos birds were also seen

to assume erect and crouch postures, and perform silent Gaping (Figure 1A) like Crimson-backed Tanagers.

The birds at the Bronx Zoo frequently uttered loud, single notes that might be transcribed as *Tsit*. The birds at Iquitos uttered notes that were similar but quite metallic and slightly nasal in tone. The Trinidad birds uttered similar notes that were even more nasal than those of the Iquitos birds (but still not as nasal as the typical Nasal Notes of Crimson-backed Tanagers). The notes of the Trinidad birds might be transcribed as *Ckunk* or *Chak*, rather than *Tsit*. All these notes were uttered in social situations like those in which Crimson-backed Tanagers utter Nasal Notes, and may well have been strictly homologous with the latter.

All of these notes (and especially those of the Trinidad birds) were also intermediate in sound between the typical Nasal Notes of Crimson-backed Tanagers and the *Tuck* notes of Brown-capped Bush-tanagers. As *Tuck* notes are also hostile, this would suggest that *Tuck* notes and Nasal Notes may be strictly homologous with one another. It may be convenient, therefore, to refer to *Tuck* notes, Nasal Notes, and all the intermediate-sounding notes of Silver-billed Tanagers by the generic term of "Short Hostile Notes."

The Silver-billed Tanagers at the Bronx Zoo uttered Muffled Hoarse Notes as "greetings" when one bird landed beside the other. The Iquitos birds uttered Muffled Hoarse Notes both as "greetings" and during obviously purely hostile encounters, and Harsh Hoarse Notes during fighting. All these Hoarse Notes sounded exactly like the corresponding notes of Crimson-backed Tanagers.

The Iquitos and Trinidad birds uttered Plaintive Notes. I did not notice any difference between the Plaintive Notes of the Trinidad birds and those of Crimson-backed Tanagers. The Plaintive Notes of the Iquitos birds seemed to be uttered in the same circumstances as those of Crimson-backed Tanagers, and many of them could be transcribed as *Wheeeeet*, but others were uttered in bursts of two or three syllables or notes, *Tsuh-wheeeeet* or *Tuh-wheeeeet wheeeeet*.

Silver-billed Tanagers seem to have a variety of Dawn Calling and/or similar and closely related patterns.

One of the birds at the Bronx Zoo, an adult male, was observed uttering long, indeterminate series of *Wheeeeet* or *Tseeeeet* notes early in the morning in September 1959. Most of the notes of these series were monosyllabic, although a few were definitely slightly bisyllabic. The bisyllabic notes were scattered apparently at random throughout the series. The male sat by himself, in a rather hunched, diagonal posture, while he uttered these series. He always stopped uttering them immediately whenever he was joined by the other Silver-billed Tanager, an adult female, in the same cage.

(Adult males and females of this species are also easily distinguishable by their morphological characters, especially the colors of their bills.)

An adult male at Iquitos was observed uttering slightly different notes in indeterminate series one morning just before sunrise. These notes were trisyllabic *Duh-uh-wheeeeeeeets*. The male was alone while he uttered these series, and was sitting in a rather erect posture on a low perch in a bush.

All of the notes of the early morning calling of the Bronx Zoo bird, and the third syllables of the notes uttered by the Iquitos bird, were very similar to or even indistinguishable from typical Plaintive Notes. Plaintive Notes and Dawn Calling patterns may be even more closely linked to one another in the repertories of these Silver-billed Tanagers than in the repertory of Crimson-backed Tanagers. The complete trisyllabic notes of the Iquitos bird may also have been most nearly strictly homologous with some of the combinations of Plaintive Notes and *Kew* or *Keeyoo* notes and/or some of the flourishlike phrases uttered by Crimson-backed Tanagers.

Two adult male Silver-billed Tanagers of the Trinidad race were observed to utter Dawn Calling that was obviously strictly homologous with the typical Dawn Calling of Crimson-backed Tanagers. Both birds began their Dawn Calling before sunrise, when they were sitting alone on high perches. The Dawn Calling of one male might be transcribed as *Chewaa chewaa chewaa-a chewaa chewaa chewaa-a.* . . . The Dawn Calling of the other male might be transcribed as *Chew chewaa chewaa chewa*-a *chewaa chewaa chew chewa*-a. . . . (The syllables in Roman type in this latter transcription were much higher in pitch than the other syllables and notes of the series.) The Dawn Calling notes of the first male were quite hoarse, but those of the second male were much less so. The first male also interjected occasional *Chak* or *Chunk* notes in some of his Dawn Calling. The first male sat in a rather erect posture, looking from side to side, throughout his Dawn Calling. The second male sat in an erect posture when he began the performance, but gradually relaxed, and fluffed his plumage (see Figure 4A), as the performance continued. This fluffing seemed to be an intention movement of preening (the male began to preen vigorously as soon as he stopped Dawn Calling), rather than an indication of escape like the similar-looking fluffing of Crimson-backed Tanagers described above. The first male stopped Dawn Calling when he was joined by his mate and two juvenile birds. The second male was never joined, but stopped of his own accord approximately an hour after dawn.

The Dawn Calling of Trinidad Silver-billed Tanagers is also closely associated with Plaintive Notes. Dr. David Snow (pers. comm.) has heard Trinidad birds utter Dawn

Calling that was composed of *Chip chewee* doublets and Plaintive Notes, usually one Plaintive Note after every three or four doublets.

I also heard one Trinidad Silver-billed Tanager utter a very rapid series of much more distinctive phrases one morning about an hour after dawn. Each of these phrases consisted of one (probably typical) Plaintive Note, followed by three to six short and rather staccato notes. Unfortunately, I could not get a good view of the bird uttering these phrases. It was definitely not one of the birds that uttered the Dawn Calling described above; but it was probably an adult male. As a whole, this series of phrases did not seem to be strictly homologous with any common call of Crimson-backed Tanagers; but it may have been related to certain calls of Scarlet-rumped Tanagers, *R. passerinii* (see below), and Yellow-rumped Tanagers (to be described in a later paper).

The captive male Silver-billed Tanager at the Bronx Zoo was once seen to feed the female in his cage. He uttered a few Muffled Hoarse Notes when he first approached the female with food in his bill; but neither bird performed any other display before or after the feeding.

Two juvenile Silver-billed Tanagers that I observed very briefly in Trinidad performed energetic food begging whenever they happened to come close to an adult female, presumably their mother. They sat in semi-hunched postures, quivered their wings vigorously, and uttered loud and rapid *Zhaaa-tseetsee zhaaa-tsee-tsee...* calls during this begging. The adult female responded by feeding the young birds at least twice.

De Carvalho (1957) lists a number of vocal patterns that he heard uttered by Silver-billed Tanagers, of the race *carbo,* near Belem in Brazil. His descriptions of these patterns are not lengthy or detailed, and his transcriptions of some of the calls are rather difficult to equate with my own transcriptions; but he seems to have heard all or most of the calls and notes cited above, and possibly some others. His account would suggest that Silver-billed Tanagers may utter a greater variety of vocal patterns than Crimson-backed Tanagers.

SOME PATTERNS OF THE SADDLE TANAGER (*R. BRESILIUS*)

A single adult male Saddle Tanager was observed very briefly at the London Zoo in September 1959. I do not know what part of Brazil he came from, or the subspecies to which he belonged. He was kept in a small cage by himself at the zoo; but he uttered a number of vocal patterns while I watched him.

Among these were single *Wheeeee* notes that may have been Plaintive Notes, and single *Chuck* or *Chup* notes that may have been short Hostile Notes.

Late one afternoon this Saddle Tanager began to utter many phrases of three notes each. A single phrase of this type could be transcribed as *Chup chuh-wheeee,* and appeared to be nothing more than a combination of an ordinary *Chup* note and a prolonged Plaintive Note. Then the bird began to utter very long, "flowing" phrases. On first hearing, these

phrases seemed to be rather formless, melodious warbles. Closer analysis revealed that they were jumbles of typical single *Chup* notes, typical single Plaintive Notes, *Chup chuh-wheeee* phrases, and many other three-note phrases of a different type that could be transcribed as *Whee whee-wheeee*. The sequence of different notes and phrases appeared to be perfectly random. The bird continued to utter these long, flowing jumbles of notes and phrases for at least 10 minutes, with only occasional and very brief interruptions. He sat more or less motionless on a perch throughout most of this period.

The whole performance was very reminiscent of the Whispering Warble performances of the juvenile Crimson-backed Tanagers described above, although the phrases uttered by the Saddle Tanager were louder than all or most of the phrases uttered by the juvenile Crimson-backed Tanager. This Saddle Tanager was certainly adult, as he had been in the zoo since 1951; but he may have retained an essentially juvenile subsong pattern much longer than usual as a result of being kept in the abnormal conditions of captivity.

The next morning at dawn, he uttered long indeterminate series of *Wheeeeee* and *Wheee-eeee* notes. This appeared to be a form of Dawn Calling, or something very closely related to Dawn Calling. It was most similar to the early morning vocalizations of the captive male Silver-billed Tanager at the Bronx Zoo.

NOTES ON THE SCARLET-RUMPED TANAGER (*R. DIMIDIATUS*)

Skutch (*op. cit.*) has described several display patterns of the Scarlet-rumped Tanagers of the Pacific coast of Costa Rica (*R. passerinii costaricensis*). It may be useful to list these patterns and compare them, very briefly, with displays of Crimson-backed Tanagers. The nonvocal display patterns mentioned by Skutch include silent Gaping (with or without Crouching) and a couple of movements associated with copulations (tail raising by the female and the raising of one wing by the male). The vocal displays include *ac* or *wac* notes, which are probably Nasal Notes according to the terminology used in this paper; *pzzt* and *pzzt weet* notes, which may be Plaintive Notes; *whip* notes that seem to function as alarm signals; Dawn Calling, which Skutch calls "song" and transcribes as *viree-viree-vireo-viree-vireo* . . .; and a rather elaborate *zzt not churry not churry* pattern, which is certainly not homologous with any regular call of Crimson-backed Tanagers (although it may, conceivably, be related to certain patterns of Silver-billed Tanagers).

ACKNOWLEDGMENTS

This report is part of a study supported by the National Science Foundation (NSF G 5523).

I should like to thank Dr. William Beebe, Dr. Jocelyn Crane, and Dr. David Snow for their kindness and assistance during field work in Trinidad, Dr. Desmond Morris for facilitating observations in the London Zoo,

and Mr. William G. Conway for facilitating observations in the Bronx Zoo.

I am also grateful to Dr. Snow and Mr. Edwin Willis for allowing me to cite certain of their unpublished observations.

SUMMARY

This is primarily a study of the display behavior of Crimson-backed Tanagers (*Ramphocelus dimidiatus*), based upon observation of both wild and captive birds.

Most of the observed displays of Crimson-backed Tanagers can be divided into purely hostile displays and partly or primarily sexual displays. The purely hostile displays include Gaping, Nasal Notes, and a variety of Hoarse Notes. The partly or primarily sexual displays include Plaintive Notes, Dawn Calling, "Flourishes," regular alternations of Plaintive Notes and Nasal Notes, and elaborate Bill-up Tail-up patterns (with raising and/or extension of the wings, but no quivering).

Brief observations of a few Silver-billed Tanagers (*R. carbo*) and a single captive Saddle Tanager (*R. bresilius*) would suggest that at least some of their displays are very similar to those of Crimson-backed Tanagers.

All or most of the displays of Crimson-backed Tanagers are probably homologous with previously described displays or related patterns of Brown-capped Bush-tanagers (*Chlorospingus opthalmicus*), but a considerable number of them are rather different from the corresponding patterns of the latter species in either form and/or frequency.

LITERATURE CITED

ANDREW, R. J. 1961. The displays given by passerines in courtship and reproductive fighting. Ibis, **103a**: 315–348.

CARVALHO, C. T. DE. 1957. Notas sobre a biologia do *Ramphocelus carbo*. Bol. Mus. Para. Emilio Goeldi, Zoologia, **5**: 1–20.

DAANJE, A. 1950. On locomotory movements in birds and the intention movements derived from them. Behaviour, **3**: 48–98.

HELLMAYR, C. E. 1936. Catalogue of the birds of the Americas. Part IX, Tersinidae-Thraupidae. Zoological Series Field Mus. Nat. Hist., **13**: 1–458.

HINDE, R. A. 1955. A comparative study of the courtship of certain finches (Fringillidae). Ibis, **97**: 706–745.

LANYON, W. E. 1960. The ontogeny of vocalizations in birds. *In* Animal sounds and communication. Ed. W. E. Lanyon and W. N. Tavolga. American Institute of Biological Sciences, Washington, D. C. Pp. 321–347.

MORRIS, D. 1954. The reproductive behaviour of the Zebra Finch (*Poephila guttata*) with special reference to pseudofemale behaviour and displacement activities. Behaviour, **6**: 271–322.

MORRIS, D. 1956. The feather postures of birds and the problem of the origin of social signals. Behaviour, **9**: 75–113.

MORRIS, D. 1957. "Typical intensity" and its relationship to the problem of ritualization. Behaviour, **11**: 1–12.

MOYNIHAN, M. 1962a. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithson. Misc. Coll. 143, **7**: 1–140.

MOYNIHAN, M. 1962b. Display patterns of tropical American "nine-primaried" songbirds. I. *Chlorospingus*. Auk, **79**: 310–344.

SKUTCH, A. F. 1954. Life histories of Central American birds. Pac. Coast Avif., **31**: 1–448.

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