

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 149, NUMBER 5

DISPLAY PATTERNS OF TROPICAL
AMERICAN "NINE-PRIMARIED"
SONGBIRDS. IV. THE YELLOW-
RUMPED TANAGER

By

M. MOYNIHAN

Director, Canal Zone Biological Area, Smithsonian Institution



(PUBLICATION 4644)

LIBRARY
OF THE
AMERICAN MUSEUM
OF
NATURAL HISTORY

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 27, 1966

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 149, NUMBER 5

DISPLAY PATTERNS OF TROPICAL
AMERICAN "NINE-PRIMARIED"
SONGBIRDS. IV. THE YELLOW-
RUMPED TANAGER

By

M. MOYNIHAN

Director, Canal Zone Biological Area, Smithsonian Institution



(PUBLICATION 4644)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 27, 1966

PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A

DISPLAY PATTERNS OF TROPICAL
AMERICAN "NINE-PRIMARIED" SONGBIRDS.
IV. THE YELLOW-RUMPED TANAGER

By M. MOYNIHAN

*Director, Canal Zone Biological Area
Smithsonian Institution*

THIS is the fourth in a series of papers on the behavior of some neotropical finches, tanagers, and honeycreepers. It is largely concerned with the behavior of yellow-rumped tanagers observed under natural conditions in the Canal Zone, central Darien, and along the Atlantic coast of the Republic of Panama, between April 1958 and November 1962.

Earlier authors (e.g. Eisenmann, 1955) usually refer to these birds under the name *Ramphocelus icteronotus*. Recently, however, Sibley (1958) has shown that yellow-rumped tanagers interbreed with the birds usually called *R. flammigerus* on the western slopes of the western cordillera of Colombia. He suggests that the two forms are conspecific. If so, yellow-rumped tanagers should be known as *R. flammigerus icteronotus*.

The behavior patterns of yellow-rumped tanagers will be compared with the corresponding patterns of related species described in earlier papers of this series, especially the crimson-backed and silver-billed tanagers, *R. dimidiatus* and *R. carbo* (Moynihan, 1962c), and the brown-capped and sooty-capped bush-tanagers, *Chlorospingus ophthalmicus* and *C. pileatus* (Moynihan, 1962b). All behavioral terms will be used in the same sense as in these earlier papers unless specifically stated otherwise.

Yellow-rumped tanagers are common in many parts of central and eastern Panama. Some aspects of their ecology and general social behavior in this region have already been described in Moynihan, 1962a. Probably the most remarkable feature of their general social behavior is their high degree of intra-specific gregariousness. They are much more gregarious among themselves than are crimson-backed tanagers in the same region. During the nonbreeding season they

are usually found in groups, family parties of four or five individuals and larger flocks of up to ten or twelve individuals. These flocks are very active and mobile but tend to be long-sustained and well-integrated, the members staying close together or coming together repeatedly. Mobile flocks are smaller and less long-sustained on the average during the breeding season, but individuals still follow one another and feed together with some appreciable actual frequency. They also show a definite tendency to form breeding "colonies." Males defend individual territories during the breeding season, but their territories often are small and crowded together in clusters. Even when territories are large, the favorite perches or "stations" of neighboring males may be only a few feet apart. No attempt was made to discover or count nests during the present study, but it was obvious, from the general density of populations, that nests could not be very far apart in many areas (possibly they were less than 50 yards apart in some cases). It is also conceivable that some males are sometimes polygynous. At least several adult males were seen associating with two or more individuals in adult female or juvenal plumage during the first part of the breeding season.¹

The general social behavior of yellow-rumped tanagers in Panama probably is quite similar to that of the scarlet-rumped or "song" tanagers (*R. passerinii*) of Costa Rica described by Skutch, 1954.²

The preflight intention movements of yellow-rumped tanagers, including ritualized Wing-flicking and Tail-flicking, and all their observed unritualized hostile reactions, including both overt attack and escape, seem to be nearly or completely identical in form with the homologous patterns of crimson-backed tanagers (and, probably, all other species of *Ramphocelus*). Yellow-rumped tanagers also perform Gaping, which may be silent or accompanied by Hoarse Notes (see below) and is usually superimposed upon or combined with unritualized aggressive or advance ("pre-attack") movements or intention movements.

As would be expected, in view of their high degree of gregariousness, yellow-rumped tanagers are noisy. Their vocal repertory

¹ Adult females cannot be distinguished from juvenile birds of both sexes in the field by appearance alone. The individuals referred to as females, without qualification, in the following account were those which performed obviously sexual patterns with adult males.

² Yellow-rumped tanagers sometimes occur in mixed flocks with crimson-backed tanagers. This may help to explain certain features of the display behavior of the two species (see page 31).

includes many different kinds of sounds. It is difficult to describe adequately but its principal features may be summarized as follows.

To human ears, three patterns seem to be "extreme" types. These are Nasal Notes, "pure" Rattles, and melodious "Kioo" or "Klioo" Notes.

The ordinary Nasal Notes of yellow-rumped tanagers seem to be very similar to the typical Nasal Notes of crimson-backed tanagers in sound, motivation, and functions. A single Nasal Note might be transcribed by something like "Anh." Notes of this type are uttered by adults of both sexes and by juveniles. They seem to be purely hostile and produced when the tendency to escape is at least slightly stronger than the tendency to attack. They are usually or always alarm or warning signals, but may also serve as contact notes in many circumstances, helping to maintain cohesion among members of the same social group.

The pure Rattles, on the other hand, are very reminiscent of some of the Rattles of *Chlorospingus* species (crimson-backed and silver-billed tanagers seem to have little or nothing in the way of patterns of this type). They are series of very short notes, uttered very rapidly one right after the other. The length of the series is extremely variable. Typical pure Rattles are rather loud, moderately low in pitch, and mechanical or "wooden" sounding. They also are uttered by adults of both sexes and by juveniles and seem to be purely hostile. They are uttered with some appreciable frequency during disputes and fights between individuals of the same sex as well as during a variety of encounters between mates or potential mates. They are obviously aggressive and are usually uttered by attacking birds immediately before or during actual attack, or by birds which are at least advancing toward an opponent (or partner). They are relatively seldom uttered by retreating or escaping birds. They usually, perhaps always, function as threat, probably exclusively so during encounters between individuals of the same sex.

Like the adult males of many other species of tanagers and finches, adult male yellow-rumped tanagers perform "Dawn Calling" during the breeding season. Typical Dawn Calling is a series of notes uttered at approximately regular intervals. The individual notes are of moderate length, and the intervals between notes are usually at least as long as the notes themselves. In some cases all the notes of a series are essentially identical; in others a series will include several different kinds of notes which are not identical but are very similar to one another. Many Dawn Calling performances of some species

consist of two kinds of slightly different notes uttered in more or less regular alternation. In all types of Dawn Calling the length of the series of notes seems to be "indeterminate," i.e. not fixed, varying within very wide limits according to circumstances.

Melodious (and usually rather soft) "Kioo" or "Klioo" Notes are the most distinctive and easily recognized of the notes uttered by male yellow-rumped tanagers during typical Dawn Calling. In these circumstances they may be repeated by themselves alone or (more frequently) uttered in alternation with "Hoarse Flourishes" (see below). They are very similar in sound to, and presumably strictly homologous with, the typical Dawn Calling Notes of crimson-backed tanagers. They seem to be produced by thwarting of some sexual tendency, when overt expression of the tendency by sexual movements is frustrated by the absence of a suitable "object" or partner. They are apparently never closely associated with overt hostility. They are uttered only by males which have become temporarily separated from, or have lost, their mates. Series of such notes seem to be uttered only during the first few minutes of daylight, when almost all sexual activities are most vigorous, and seem to be confined to the height of the breeding season, i.e. the phase of the breeding cycle in which copulations are most frequent. This would suggest that they are very high intensity patterns. The sexual tendencies involved may be pairing and/or copulatory. (Notes of this type are not usually uttered *immediately* before copulation attempts (see below) but this does not necessarily preclude the possibility that birds uttering such notes have activated copulatory tendencies.) Very occasionally isolated adult males will utter the same or very similar notes singly during later periods of the day at the height of the breeding season. There is no reason to suppose that these single notes are not produced by the same type of motivation as the series during Dawn Calling. These single notes are very reminiscent of the "Plaintive Notes" of some other species of tanagers and finches. It is possible, therefore, that the "Kioo" or "Klioo" patterns of yellow-rumped tanagers are also largely or completely homologous with the Plaintive Notes of such species as the brown-capped bush-tanager and the green-backed sparrow, *Arremonops conirostris*.³ All or most of them probably function to attract females.

Yellow-rumped tanagers seem to utter Nasal Notes about as frequently as crimson-backed tanagers do in similar circumstances. They

³ All references to the green-backed sparrow throughout this paper are based upon Moynihan, 1963.

utter pure Rattles much less frequently than Nasal Notes. And their "Kioo" or "Klioo" Notes are relatively much less common than the most similar sounding notes of crimson-backed tanagers. All three extreme types of notes, as a group, are uttered much less frequently than a great variety of other notes which sound, to human ears, more or less intermediate between the extremes.

There does in fact seem to be almost complete morphological intergradation between the extremes. Almost every conceivable morphologically intermediate note is uttered at least occasionally, and some intermediates are very common indeed. The latter may be considered "nodal points" in the continuum connecting the extremes.

It will be convenient to give special names to some of the intermediates. Among these are Hoarse Notes, "Greeting" Notes, "Tzzheet" Notes, Hoarse Flourishes, and Thin Rattles.

The Hoarse Notes of yellow-rumped tanagers are harsh rasping sounds of more or less moderate length uttered singly or in short series of two or three notes one right after the other. Most notes of this type could be transcribed by something like "Zraa" or "Zraanh" or "Sraah." When uttered in series the successive notes usually are very similar to one another. They all sound very much like some of the Hoarse Notes of such related species as the crimson-backed tanager and the green-backed sparrow. In the latter species Hoarse Notes are easily recognized as qualitatively distinct from all other vocal patterns. This is not true of the Hoarse Notes of yellow-rumped tanagers. They usually or always have a slight trace of a rattling quality or "undertone." As a result they sound more or less perfectly intermediate between typical Nasal Notes and pure Rattles. They certainly intergrade with both.

The Hoarse Notes of yellow-rumped tanagers are not only less distinct than those of crimson-backed tanagers and green-backed sparrows but also much less common. This seems to be due to the fact that yellow-rumped tanagers utter pure Rattles and Thin Rattles in many of the social situations in which the latter species utters one or more types of Hoarse Notes. Yellow-rumped tanagers seem to utter Hoarse Notes with appreciable frequency in only two situations. An individual caught by a predator (e.g. a human being) utters loud and long Hoarse Notes (often relatively high pitched and urgent sounding). These notes seem to be essentially similar to the patterns of crimson-backed tanagers which have been called "Hoarse Screams." Like the latter they seem to be purely hostile and high intensity, produced by strong activation of both attack and escape

tendencies. The two tendencies are probably more nearly equal in strength during Hoarse Screams than during either Nasal Notes or pure Rattles. Softer and shorter Hoarse Notes are uttered during intraspecific encounters. In the course of the present investigation they were heard most frequently during encounters between adult males and (known or presumed) females. They were uttered by males approaching or being approached by females, usually or always when the males were not very familiar with and/or obviously hostile toward the females. Some of these notes were combined with Gaping or actual attack movements. Similar notes certainly are uttered by both adult females and juveniles, although more rarely, in some hostile or partly hostile circumstances; but I cannot say very much about them, primarily because they are so soft that I may have missed many of them in the field. All these comparatively soft Hoarse Notes must be purely hostile or produced by simultaneous activation of both hostile and sexual tendencies. They probably are produced when the attack and escape tendencies are nearly equal to one another but weaker than when loud Hoarse Notes are uttered. If a sexual tendency is also involved, it is almost certainly relatively weak.

Adult males may utter slightly different "Greeting" Notes when joining or being joined by females with whom they are on fairly good terms. In their most typical form these notes are slightly hoarse in quality, but less so than the typical Hoarse Notes described above, and without any rattling undertone. They are very soft and apparently always uttered in series. Typical series might be transcribed as "Tsee-*whee-hee*" or "*Zhee-wee-tsee-tseewee*" or "*Zee-a-waa-zaa-waa.*" All these patterns sound intermediate between typical Hoarse Notes on the one hand and Hoarse Flourishes and/or "Tzzheet" Notes on the other hand. They certainly intergrade with the former and probably with the latter. The only birds heard to utter typical "Greeting" Notes were captive individuals kept in aviaries on Barro Colorado Island; but the notes are so soft that one would not expect a human observer to be able to hear them in the field. They probably are produced by the same hostile motivation as typical soft Hoarse Notes, with an added (or stronger) sexual component. The possession of a special "Greeting" pattern, obviously related to Hoarse Notes but apparently uttered only during encounters between males and females of the same species, may be another special resemblance between yellow-rumped tanagers and brown-capped bush-tanagers.

Among the most common vocal patterns of yellow-rumped tanagers are short, monosyllabic, rather high pitched and hard sounding notes

which might be transcribed as "Tzzheet." These notes are uttered by adults of both sexes and by juveniles, most frequently by adult males. With very few exceptions they are uttered only by individuals who are isolated or alone, i.e. who have become separated (by a distance of at least several meters) from their mates or other members of their own social group. Unlike the melodious "Kioo" or "Klioo" Notes they are uttered quite frequently at all times of the year and during all periods of the day.

There are many resemblances between these notes and the vocalizations of crimson-backed tanagers which were called "Plaintive Notes" in Moynihan, 1962c. The two patterns certainly are nearly identical in sound, especially when heard at a slight distance. In an earlier paper (Moynihan, 1962a), both were transcribed as "Tseet." Subsequent and closer observations, however, have revealed that the "Tzzheet" Notes of yellow-rumped tanagers are usually slightly harder and hoarser, with a more pronounced "buzzy" quality, than the corresponding notes of crimson-backed tanagers. They are, in other words, slightly more similar to typical Hoarse Notes in tone.⁴

It has been suggested that "Tseet" Notes are produced by thwarting of some gregarious motivation as well as several different types of "friendly" motivation, including pairing and parental tendencies. This may well be true of some or all "Tzzheet" Notes also, as they seem to occur in almost exactly the same range of circumstances. Both patterns may function as "summons," a means of calling in or attracting mates and other members of the family or social group. All these resemblances would indicate that the two patterns must be closely related phylogenetically.

"Tzzheet" Notes seem to be uttered more frequently on the average than the corresponding notes of crimson-backed tanagers in similar situations. They must have a comparatively low releasing threshold. They also are uttered in series more frequently than are "Tseet" Notes, and many series of "Tzzheets" are much longer than any series of "Tseets." Adult male yellow-rumped tanagers sometimes utter long series of "Tzzheet" Notes at very regular intervals of approximately the same length as the intervals separating "Kioo" and

⁴ The term "Plaintive" is not particularly suitable as a name for the crimson-backed tanager notes. It was applied to them only because they were thought to be strictly homologous with the Plaintive notes of other species. This may or may not be correct (see page 8). In order to avoid confusion these crimson-backed tanager patterns will be called simply "Tseet" Notes throughout the following discussion.

"Klioo" Notes during the Dawn Calling described above. They may utter such series at any time during the day, including the first half hour of daylight. Series of "Tzzheet" Notes at dawn are relatively most common early in the breeding season, before copulations have become frequent, and are relatively rare at the height of the breeding season, when "Kioo" or "Klioo" Dawn Calling is most common. If both performances are produced by thwarting of the same type of sexual motivation, it is probably weaker when the "Tzzheet" series are uttered than when the "Kioo" series are.

There are certain connections between "Tzzheet" Notes and unmistakably hostile patterns. Typical "Tzzheet" Notes intergrade with typical Hoarse Notes. They also are associated and intergrade with the partly hostile Thin Rattles relatively frequently (see page 9). Occasionally they are uttered immediately before or after actual fights and/or are accompanied by hostile Back-ruffling (see page 13). It is possible, therefore, that at least some "Tzzheet" Notes include a hostile component. If so the hostile component probably is relatively weaker than in the "Greeting" Notes.⁵

A variety of vocal patterns may be grouped together under the name of "Hoarse Flourishes." All are bisyllabic notes. They can be transcribed in many slightly different ways, e.g. "Tseeee-up," "Wheeeee-ah," "Tseeeee-yah," "Tseeyoo," "Eeyah," "Kheezaa," and "Kheezoo." All notes of this type sound like bisyllabic versions of typical "Tzzheet" Notes. The first syllable is always similar to a "Tzzheet" Note in pitch, and the second syllable is apparently always at least slightly lower in pitch. Both syllables are slightly hoarse in the same way as "Tzzheet" Notes. These Hoarse Flourishes

⁵ "Tzzheet" Notes are almost as similar to the typical Plaintive Notes of such species as the brown-capped bush-tanager and the green-backed sparrow as to the "Tseet" Notes of crimson-backed tanagers. They resemble those Plaintive Notes in some aspects of form, i.e. the fact that they include a fairly clear "eee" sound and are less harsh or rasping than many other vocal patterns of the species, as well as in their largely or completely nonhostile motivation and their function as "summons." If they do not include a hostile component they may be completely homologous with typical Plaintive Notes. If they are partly hostile they may be partly homologous, i.e. their basic form may be homologous with the Plaintive Notes of other species but their hoarse quality may have been derived from another source. In either case they are probably related to the "Kioo" or "Klioo" Notes (see also page 21).

The comparative position of the "Tseet" Notes of the crimson-backed tanager is somewhat obscure. They are less hoarse than "Tzzheet" Notes but hoarser than the Plaintive Notes of the brown-capped bush-tanager or the Green-backed sparrow. If the "Tzzheet" Notes are of compound origin it is possible that the "Tseet" Notes are also.

may be uttered by themselves alone or in a variety of obviously unritualized associations with many other vocal patterns, or in a close and apparently ritualized association with typical "Tzzheet" Notes and Thin Rattles. The latter performances seem to be something of a special case, and will be discussed separately below. The other Hoarse Flourishes are uttered almost exclusively by adult males and are particularly characteristic of the height of the breeding season. They are uttered in much the same way and in much the same circumstances as melodious "Kioo" or "Klioo" Notes. They are almost always uttered by isolated birds, singly, at any time of the day or in Dawn Calling series. They are, in fact, the most common of the Dawn Calling notes at the height of the breeding season, much more common than "Kioo" or "Klioo" Notes. Many Dawn Calling performances are composed of Hoarse Flourishes alone. Less frequently Hoarse Flourishes and "Kioo" or "Klioo" Notes are uttered in regular alternation. Typical Hoarse Flourishes intergrade with both typical "Tzzheet" Notes and typical "Kioo" or "Klioo" Notes. All this would suggest that Hoarse Flourishes are really intermediate between "Tzzheet" Notes and "Kioo" or "Klioo" Notes, produced by intermediate motivation. They certainly function as another summons to call in or attract mates.⁶

Thin Rattles are uttered by adult yellow-rumped tanagers of both sexes and by juveniles. A typical Thin Rattle sounds very much like a pure Rattle but is higher-pitched on the average and "thinner" in sound, less penetrating but not necessarily softer. Some Thin Rattles seem to remain at the same pitch throughout. In others the pitch declines gradually and continuously but only slightly. They all sound perfectly intermediate between typical pure Rattles and typical "Tzzheet" Notes, like more or less prolonged "Tzzheet" Notes which have broken up or like pure Rattles which have been transposed into a higher key. They also intergrade with both "Tzzheet" Notes and pure Rattles. They are frequently associated with both overt hostility, especially aggression, during disputes between individuals of the same as well as opposite sex, and with a variety of

⁶ The Hoarse Flourishes of yellow-rumped tanagers are somewhat similar to the Flourishes of *Chlorospingus* spp. in form, motivation, and function. They may be completely homologous with the latter. If, however, their hoarse quality is an indication that an hostile component is involved, then the homology probably is only partial. In any case, the relationship between the Hoarse Flourishes of yellow-rumped tanagers and the Flourishes of *Chlorospingus* spp. probably is exactly the same as the relationship between the "Tzzheet" Notes and the Plaintive Notes of the same species.

patterns containing obvious sexual elements during encounters between mates or potential mates. It seems likely, therefore, that they are produced by motivation which is intermediate between that of typical pure Rattles and that of typical "Tzzheet" Notes, i.e. when both hostile tendencies are activated, and the attack tendency is relatively much stronger than the escape tendency, but some non-hostile "friendly" tendency (or tendencies) is activated simultaneously. All or most Thin Rattles by themselves probably function as threat.

By themselves, however, they are relatively rare. They usually are uttered in very close temporal association with "Tzzheet" Notes and Hoarse Flourishes. This association is quite stereotyped in some ways and would appear to have become ritualized as a whole. A typical complete performance consists of one "Tzzheet" Note followed immediately by one Thin Rattle followed immediately by one Hoarse Flourish. The sequential relations appear to be almost invariable. Sometimes one of the three patterns may be omitted, but the remaining two apparently always occur in the same sequence as in typical complete performances. Thus, for instance, one may hear incomplete performances which consist of one "Tzzheet" Note followed by one Thin Rattle, or one "Tzzheet" Note followed by one Hoarse Flourish, or one Thin Rattle followed by one Hoarse Flourish, but not one Thin Rattle followed by one "Tzzheet" Note or one Hoarse Flourish followed by one "Tzzheet" Note. The nearest thing to a reversal of sequence occurs during some complex performances which consist of one "Tzzheet" Note, followed by one Thin Rattle, followed by one Hoarse Flourish, followed by a second Thin Rattle, followed by a second Hoarse Flourish; but these performances obviously are nothing more than two typical complete sequences uttered so rapidly that they are partly "telescoped" together. The length of the Thin Rattle in both complete and incomplete performances is extremely variable. Most of the terminal Hoarse Flourishes are short and rather "slurred," much shorter than many of the Hoarse Flourishes uttered singly or in Dawn Calling series. Almost all the Hoarse Flourishes associated with "Tzzheet" Notes and Thin Rattles are of the type which can be transcribed as "Eeyah."⁷

⁷ The complex "Tzzheet" Note—Thin Rattle—Hoarse Flourish performances, considered as a unit, seem to intergrade with both series of "Tzzheet" Notes and single Hoarse Flourishes. Intermediates may take such forms as a series of two or three "Tzzheet" Notes uttered more rapidly than usual and followed by a single brief note of slightly lower pitch (i.e. a trace of the second syllable of Hoarse Flourishes) or of an unusually prolonged Hoarse Flourish which includes a trace of rattle "undertone" toward the end of the first syllable. (These

If the individual patterns retain the same functions when they are uttered together as when they are uttered separately (and my observations would suggest that they do), then the "Tzzheet"—Thin Rattle—Hoarse Flourish performances probably function as "song," as the term is used in this series of papers. When uttered by a bird of one sex they may attract birds of the opposite sex and repel other birds of the same sex.

Adult male yellow-rumped tanagers frequently interrupt their Dawn Calling to utter purely or predominantly hostile notes. Such ambivalent performances may subserve the same functions as stereotyped "Tzzheet"—Thin Rattle—Hoarse Flourish patterns, but they are extremely variable in form and do not seem to be ritualized per se. Yellow-rumped tanagers apparently do not utter stereotyped series of Nasal Notes and "Tzzheet" Notes (or any other primarily sexual pattern) in regular alternation like the series of Nasal Notes and "Tseet" Notes uttered by adult male crimson-backed tanagers.

The "Tzzheet" Note—Thin Rattle—Hoarse Flourish complex, as a whole, is remarkably similar to the equally stereotyped Rattle—Flourish performances of brown-capped bush-tanagers. The rattling and Flourish parts of the sequences of the two species certainly are at least partly homologous. The Rattle—Flourishes of brown-capped bush-tanagers are often preceded by "Tsit" Notes. These "Tsit" Notes, when uttered by themselves alone, do not appear to be as strongly sexual as the "Tzzheet" Notes of yellow-rumped tanagers, but their association with Rattle—Flourishes would suggest that they may be phylogenetically related to "Tzzheet" Notes (and the Plaintive Notes of other species). This suggestion may be supported by the fact that sooty-capped bush-tanagers utter similar sounding "Tsit" Notes to call in or attract mates.

Yellow-rumped tanagers also utter rattling sounds which are very much softer than either typical pure Rattles or typical Thin Rattles. These may be called Muffled Rattles. They are rarer than the other kinds of Rattles, usually prolonged, and associated with vigorous reactions between individuals in close proximity to one another. They seem to be uttered most frequently by adult males approaching or being approached by adult females or juveniles at the height of the breeding season. Once I heard an adult male utter a Muffled Rattle immediately before an apparently successful copulation. Many similar or identical patterns were uttered during an unusually prolonged and

latter are also, of course, intermediate between simple Thin Rattles and Hoarse Flourishes.)

violent dispute (including many contact fights) between two adult males at the height of the breeding season. And once I heard a bird in female or juvenal plumage (probably an adult female) utter a single Muffled Rattle immediately before feeding another bird in similar plumage (presumably a juvenile). It is evident that Muffled Rattles are very high intensity patterns. They seem to intergrade with both typical pure Rattles and typical Thin Rattles. Possibly they are somewhat heterogeneous. Some Muffled Rattles may be nothing more than unusually soft pure Rattles, while others may be nothing more than unusually soft Thin Rattles. (All the extreme Muffled Rattles are so soft that I could never tell which of the louder Rattle patterns they most resembled in pitch). If the Muffled Rattles are heterogeneous in this way, then some may be purely hostile, produced when the attack tendency is strongly predominant over the escape tendency but both are stronger than during typical pure Rattles, while others may be partly hostile and partly sexual, produced when the relative strength of the hostile and sexual tendencies is the same as in typical thin Rattles but the actual strength of all the tendencies is greater.

Some or all of the Muffled Rattles of yellow-rumped tanagers may be strictly homologous with the Muffled Rattles which are uttered by male brown-capped bush-tanagers approaching females and immediately before copulations.⁸

⁸ Two other vocal patterns of yellow-rumped tanagers appear to be set somewhat apart from the mass of intergrading patterns described above.

One captive adult male was heard to utter many "Tsit" Notes. They were much softer and shorter than typical "Tzzheet" Notes. They were uttered singly or repeated at irregular intervals (i.e. they were never organized in regular series like Dawn Calling notes). The male uttered these notes after being in captivity, in the same cage, for over a year, whenever he saw a human being in the distance. If the human came closer he usually began to perform escape movements or intention movements and to utter typical Nasal Notes instead of the "Tsits." Thus it would appear that the "Tsit" Notes were low intensity alarm patterns. Presumably they were produced when the escape tendency alone was activated or (more probably) when both hostile tendencies were activated simultaneously and escape was much stronger than attack but both tendencies were weaker than when Nasal Notes are uttered. These "Tsit" Notes were much too weak to be heard in the field. Thus I do not know if they are really typical of the species or not. If so they may be strictly homologous with the soft "Tsip" or "Chik" alarm notes of green-backed sparrows. In any case it seems very unlikely that they are closely related to the louder but otherwise similar sounding "Tsit" notes of either *Chlorospingus* species or some other species of *Ramphocelus* (see pages 30 and 31).

One wild male in typical adult plumage was observed to perform something which looked like "silent song." He sat for several minutes opening and

Figure 1 is an attempt to show the relationships between the more common and easily recognizable vocal patterns of adult male yellow-rumped tanagers in diagrammatic form.

Of all the nonvocal display patterns of yellow-rumped tanagers, perhaps the most interesting and complex are the feather-raising patterns. Yellow-rumped tanagers apparently do not have any general ruffling pattern, involving all the head and body plumage simultaneously, like that of crimson-backed tanagers. Instead they have a variety of patterns of more limited extent. These include Head-ruffling, Head-fluffing, Back-ruffling, and Belly-fluffing. Tail-fanning may be associated with the same group of patterns. It will also be convenient to consider a special form of depression of the feathers, Crown-flattening, in connection with some of the feather-raising patterns.

All these patterns seem to be ritualized. With the exception of Tail-fanning, they seem to be performed only by adult males.

Back-ruffling is a more or less extreme raising of all the yellow feathers of the lower back and rump. The feathers are raised in such a way that their tips are conspicuously separated. The wings usually are drooped (but not spread to any appreciable extent) at the same time. Back-ruffling is a very common pattern. It occurs in a wide variety of social situations, but it seems to be much more closely linked to aggression than to any other kind of overt unritualized activity. It is frequently performed by attacking birds before and/or after delivering attacks. It may be silent or accompanied by vocalizations. By far the most common vocalizations associated with Back-ruffling are rattling patterns, all types of rattling patterns, including "Tzzheet"—Thin Rattle—Hoarse Flourish performances. All this would suggest that Back-ruffling is primarily an expression of the attack tendency. Various kinds of Back-ruffling performances are illustrated in figures 2 to 6 in conjunction with some notes on the circumstances in which they were observed.

Belly-fluffing is a raising of all the feathers of the lower breast and

closing his bill while his throat went in and out, just as if he were uttering many notes in rapid succession; but I could not hear any sound at all during the performance, even though I was less than five feet away from him at the time. His whole performance was very reminiscent of the initial stage in the development of "Juvenile Subsong" or "Whispering Warbles" in young male crimson-backed tanagers. Most of the other male yellow-rumped tanagers in the same area at this time were molting from juvenal plumage into adult plumage. It is possible that the male which performed "silent song" had just completed the molt into adult plumage and was still behaving as a young bird.

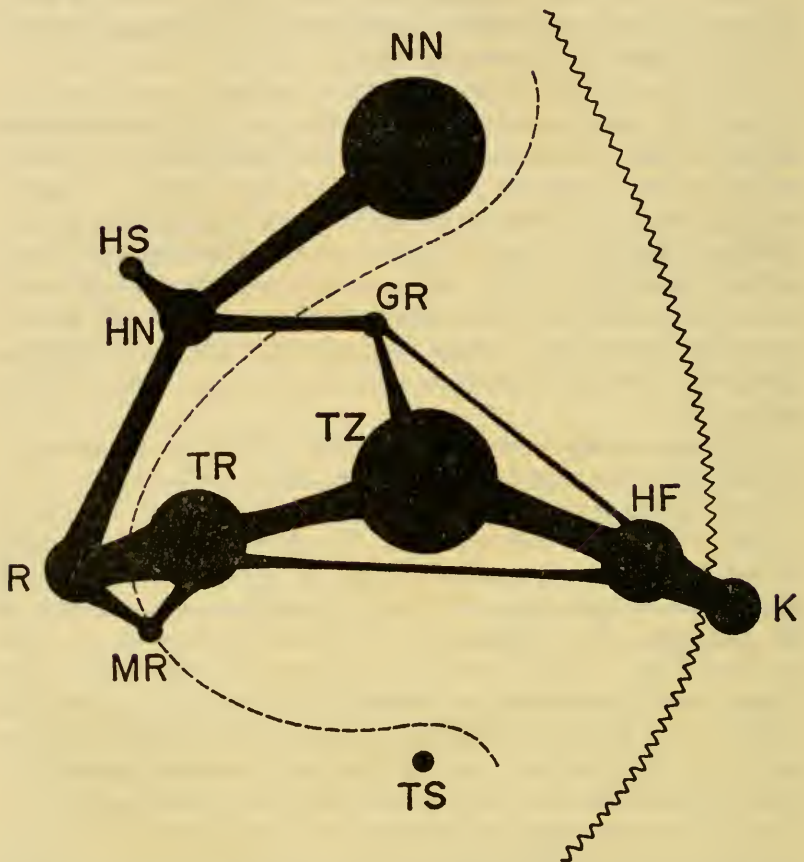


FIG. 1.—Apparent relationship between the most common and/or most easily recognized vocal patterns of adult male yellow-rumped tanagers. (NN=Nasal Notes. HN=relatively soft Hoarse Notes. HS=Hoarse "Screams." GR="Greeting" Notes. R=pure Rattles. TR=Thin Rattles. MR=Muffled Rattles. TZ="Tzzheet" Notes. HF=Hoarse Flourishes. K="Kioo" or "Klioo" Notes. TS=soft "Tsit" Notes.)

The size of the circles representing different types of notes is very roughly proportional to the frequency of the notes. The thickness of the lines connecting the different types of notes is very roughly proportional to the frequency of intermediates between the notes connected.

All the vocal patterns to the left of the zigzag line seem to contain hostile components (i.e. seem to be produced by hostile motivation, alone or in combination with other nonhostile tendencies). All the patterns to the right of the dotted line are frequently or always partly or wholly sexual.

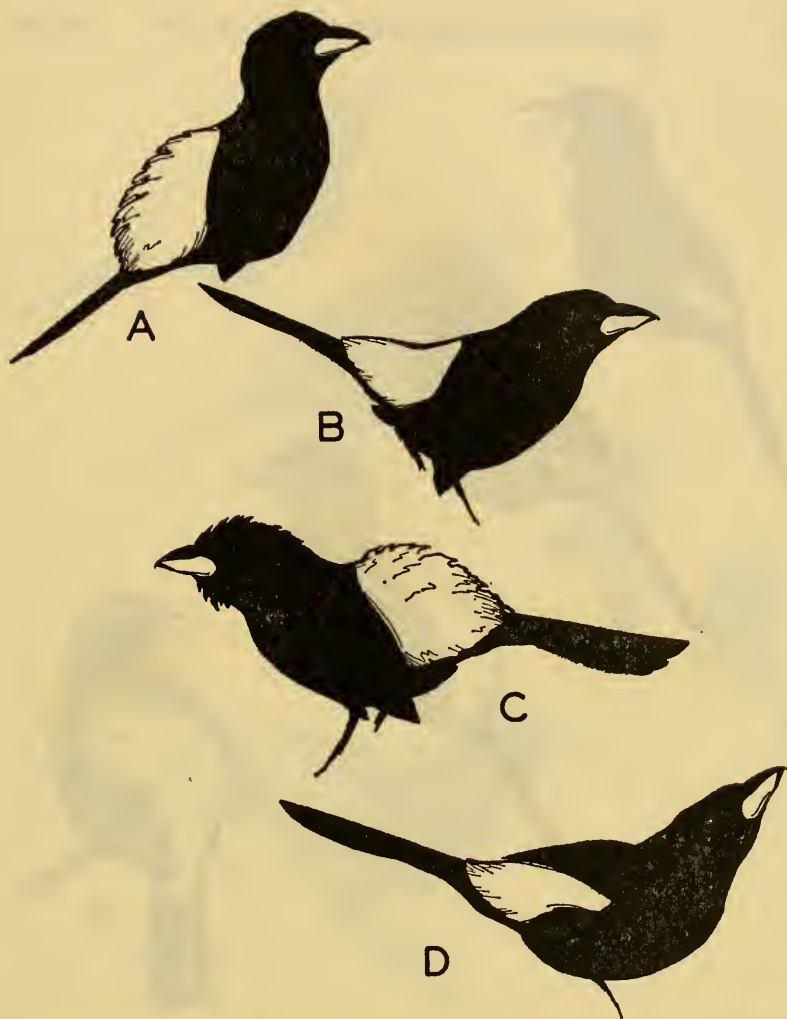


FIG. 2.—Display postures of adult male yellow-rumped tanagers.

From top to bottom:

a. Posture assumed by a male after a dispute with another male. With extreme Back-ruffling. At first the bird in this posture was silent; then it uttered Thin Rattles and/or pure Rattles.

b. Posture of a male immediately after Turning-away from a female at the height of the breeding season. The wings are drooped but there is no Back-ruffling. The bird was silent while it remained in this posture.

c. Posture of another male immediately after Turning-away from a female (with a second male perched near by). With Head-ruffling, Back-ruffling, and Tail-fanning. The Head-ruffling is somewhat anomalous, but closest to the "angular" type. The bird was silent while it remained in this posture.

d. Silent Bill-up Tail-up Posture, with Crown-flattening and asymmetrical positioning of the wings, assumed by a male immediately after an apparently successful copulation. (The tail may have been raised a little higher during part of the time that the male remained in the posture.)

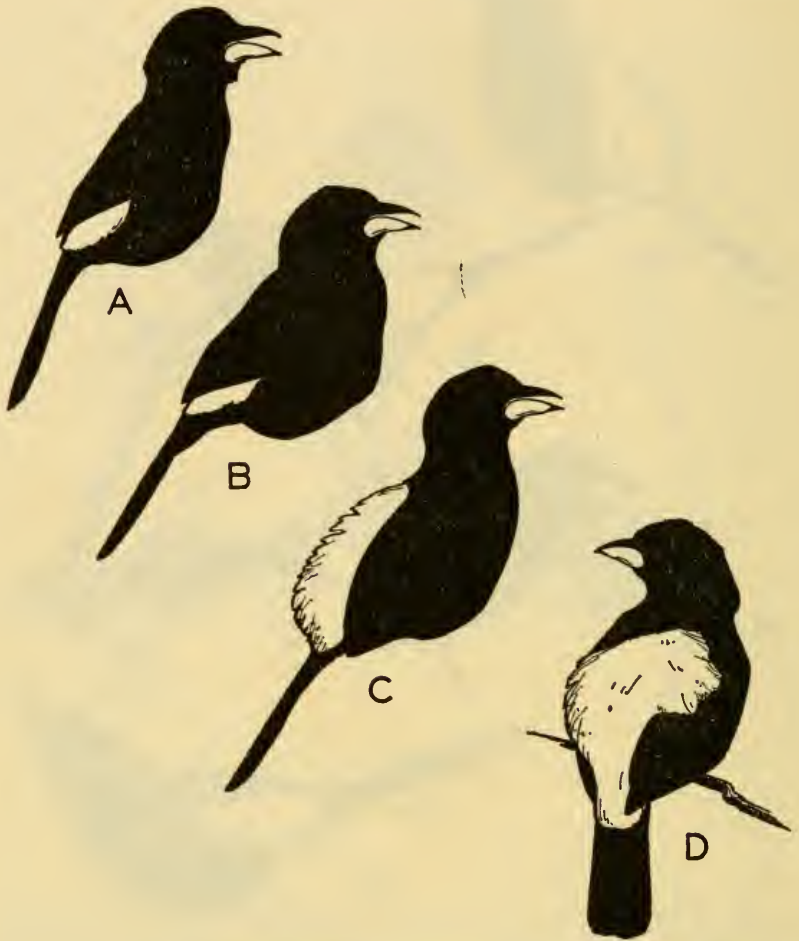


FIG. 3.—Postures accompanying vocal patterns of adult male yellow-rumped tanagers.

From top to bottom:

a. Typical posture accompanying Dawn Calling of Hoarse Flourishes and/or "Kioo" or "Klioo" Notes. With typical Head-fluffing.

b. Posture frequently or usually assumed when "Tzzheet" Notes are uttered in series. With some Head-fluffing and Belly-fluffing.

c. Most typical posture accompanying "Tzzheet"—Thin Rattle—Hoarse Flourish performances. With moderate Back-ruffling.

d. Posture assumed by a male uttering a series of "Tzzheet" Notes. This individual looked from side to side between and during the notes. It also performed Back-ruffling. The wings were held in such a way that the yellow area of the lower back and rump appeared to be irregular in shape (this is not uncommon).

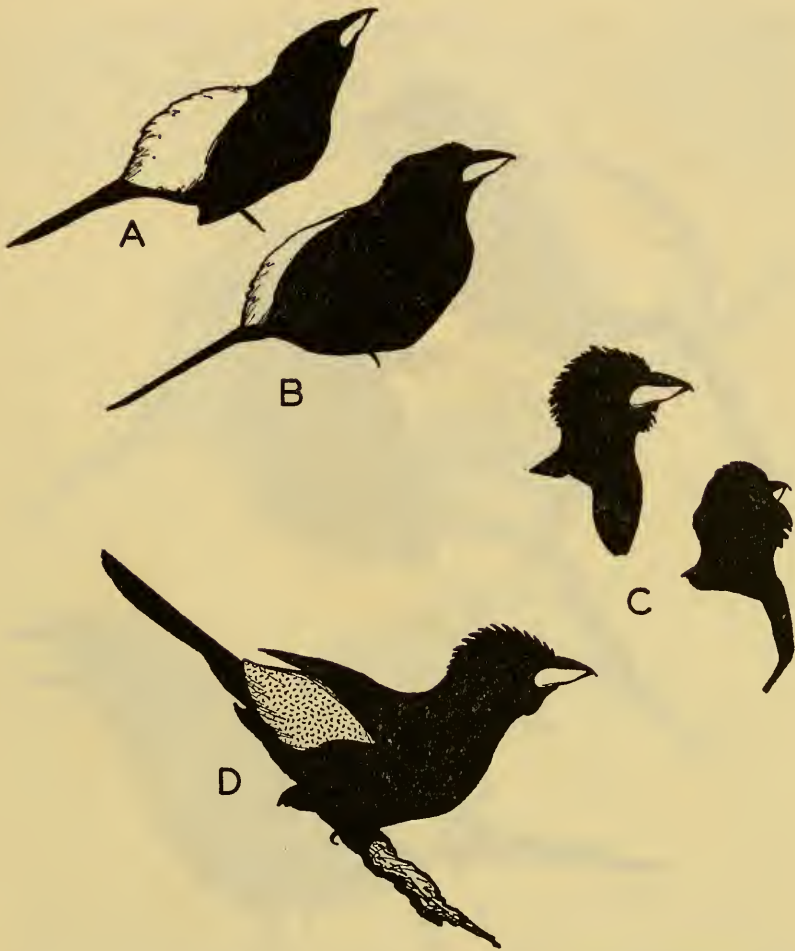


FIG. 4.—Postures of adult male yellow-rumped and orange-rumped tanagers.

From top to bottom:

a. Peculiar posture assumed by a captive male yellow-rumped tanager, kept in an aviary with a female of the same species, during a dispute with another male of the same species introduced into the same aviary. This appeared to be a preflight posture (the upward pointing of the head and bill being an intention movement of flying upward, not an indication of the ritualized Bill-up Tail-up). It was combined with Crown-flattening and extreme Back-ruffling, and accompanied by Thin Rattle—Hoarse Flourish calls.

b. "Fluffed Hunched" posture assumed by the introduced male during the same dispute. With a trace of Crown-flattening, slight Back-ruffling, and extreme Belly-fluffing. Silent.

c. Side and rear views of typical "angular" Head-ruffling by yellow-rumped tanagers.

d. Preflight, crouching, posture of a male orange-rumped tanager, with extreme "rounded" Head-ruffling.

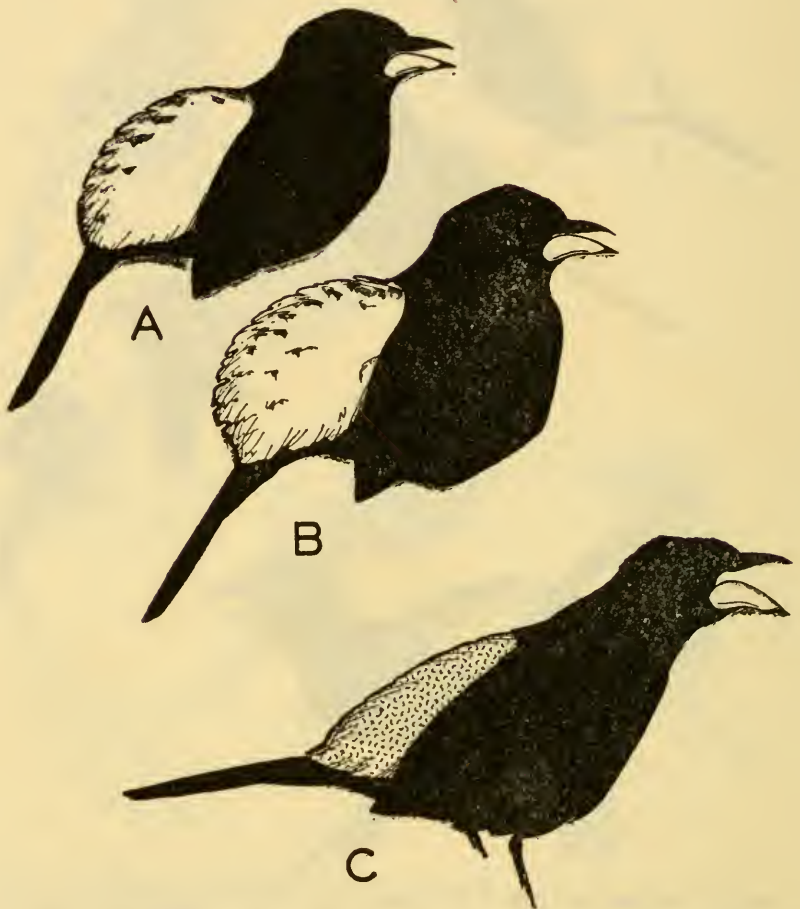


FIG. 5.—Postures of adult male yellow-rumped and orange-rumped tanagers. From top to bottom:

- a. Posture of a male yellow-rumped tanager uttering "Tzzheet"—Thin Rattle—Hoarse Flourish calls while alone. With extreme Back-ruffling, some Crown-flattening, and (perhaps) a trace of Belly-fluffing.
- b. Posture of the same individual uttering Thin Rattles, a few seconds later, after being joined by an adult female or a juvenile.
- c. Posture of a male orange-rumped tanager uttering Rattles while facing a female silver-billed tanager.

belly. This raising may be quite extreme, but the tips of the feathers are seldom or never separated from one another in a conspicuous manner. Belly-fluffing seems to be rarer than Back-ruffling. Birds uttering "Tzzheet" Notes may show a slight to moderate amount of Belly-fluffing (see figure 3b). This is particularly likely to occur when

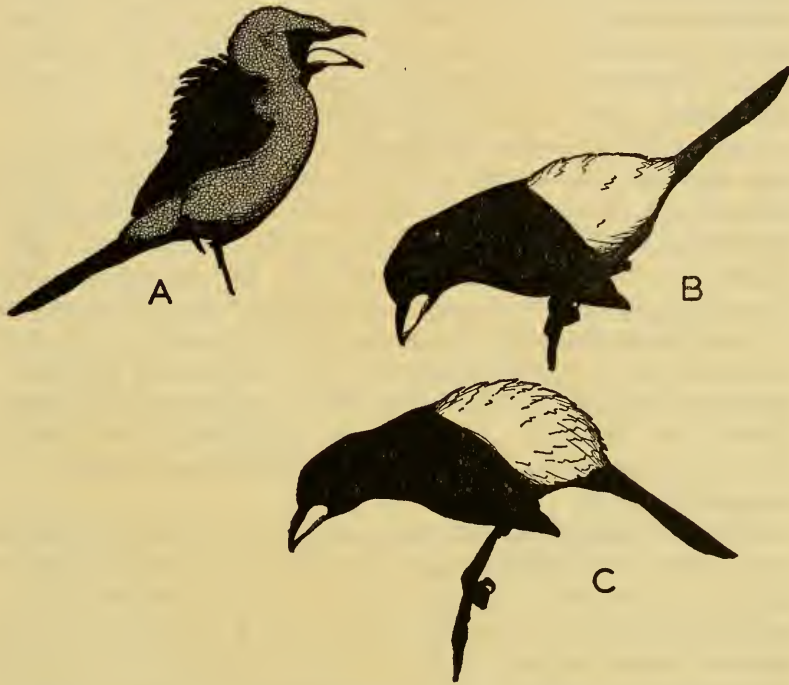


FIG. 6.—Postures of a black-throated tanager and a yellow-rumped tanager.

From top to bottom:

a. Back-ruffling and silent Gaping by the captive black-throated tanager in the New York Zoo.

b. and c. Head-down Postures of an adult male yellow-rumped tanager during a high intensity dispute in the wild.

they utter "Tzzheets" in series. I have seen really exaggerated Belly-fluffing only twice. In one case a wild adult male showed extreme Belly-fluffing in combination with Back-ruffling (see figure 5b) and uttered Thin Rattles after being approached by an adult female or a juvenile bird. In the other case a captive male assumed a rather low or "hunched" posture with Belly-fluffing, Crown-flattening, and slight Back-ruffling (see figure 4b), after being introduced into the cage of another pair of yellow-rumped tanagers and being

repeatedly threatened and supplanted by the male of the pair. The combination of a hunched posture with Belly-fluffing is very reminiscent of the "Fluffed Hunched Posture" of green-backed sparrows and the "fluffed postures" of many other passerines (Hinde, 1955). The latter seem to contain very strong escape components and function as appeasement. Perhaps the Belly-fluffing of yellow-rumped tanagers is also an expression of the escape tendency. (Female yellow-rumped tanagers may ruffle the feathers of the breast and belly in Bill-up Tail-up Postures in sexual situations [see page 24] but this probably is not strictly equivalent to the Belly-fluffing of males.)

Crown-flattening is less conspicuous than the feather-raising patterns and easily overlooked in the field, but it is certainly combined with a variety of other displays, including Thin Rattles, Bill-up Tail-up patterns, and "Turning-away" (see page 23), in addition to Belly-fluffing and Back-ruffling (see figures 2b, 2d, 4a, 4b, and 5a). There is no very obvious "common denominator" to all the situations in which Crown-flattening occurs. In almost all cases, however, it is shown by males in close association with (known or presumed) females at the height of the breeding season, and it can occur immediately after copulation. It may be an expression of some sexual tendency or tendencies (or a particular combination of sexual and escape tendencies).

All yellow-rumped tanagers seem to perform Tail-fanning that is very similar to the Tail-fanning of crimson-backed tanagers. Like the latter it is performed in such a very wide variety of situations that it is particularly difficult to interpret. Perhaps it is an indication of an activated escape tendency. If so it probably is performed when the escape tendency is weaker and/or in less conflict with other tendencies than when all or most Belly-fluffing is produced. It is frequently performed by individuals who are not performing any other ritualized displays (except Flicking movements) at the same time.

The patterns involving raising of the head feathers are much more conspicuous than either Crown-flattening or Tail-fanning but perhaps equally problematical.

There may be two slightly different types of Head-ruffling. In one type all the feathers of the crown are raised to a more or less extreme degree. The tips of all the crown feathers are well separated from one another. When viewed from the side the general effect is exactly the same as in the Head-ruffling of orange-rumped tanagers, illustrated by figure 4d. The top of the head appears rounded with the highest point near the center of the crown. This is usually, perhaps always,

accompanied by some raising of the feathers of the chin, throat, and cheeks. "Rounded" Head-ruffling of this type seems to be performed most frequently by birds disturbed by the presence of a potential predator. It is frequently associated with Nasal Notes and may be produced by similar motivation, i.e. when the escape tendency is stronger than the attack tendency but the latter is by no means negligible. Part of this pattern, i.e. the raising of the crown feathers, may be strictly homologous with the "Crest-raising" of green-backed sparrows and some other "emberizine" finches (see Andrew, 1961). The other type of Head-ruffling is illustrated by figure 4c. In this pattern the head does not appear to be rounded. When viewed from the side there are more or less distinct peaks at the forehead and nape as well as in the center of the crown. The feathers of the chin, throat, and cheeks also are raised, perhaps more so on the average than in the "rounded" Head-ruffling. This type of Head-ruffling may be called "angular." It occurs during many encounters between males and females but usually not in close association with successful copulations. It seems to be characteristic of situations in which both hostile and sexual tendencies are activated simultaneously and are in strong conflict with one another. It may be intermediate between "rounded" Head-ruffling and Head-fluffing.

The most typical form of Head-fluffing is illustrated by figure 3a. The feathers of the crown are raised to a very considerable extent, but their tips are not well separated from one another. When viewed from the side the head appears to be roughly square or trapezoidal, with one angle at the front of the crown and another at the back of the crown. There is no peak in the center of the crown. The cheek and throat feathers may be raised but seldom or never as much as in extreme Head-ruffling. Typical Head-fluffing usually or always accompanies Dawn Calling, especially Dawn Calling of Hoarse Flourishes or "Kioo" or "Klioo" Notes, and is rare or absent in other circumstances. A less extreme form of Head-fluffing sometimes accompanies series of "Tzzheet" Notes later in the day (see figure 3b). It seems likely that Head-fluffing is primarily or exclusively an expression of sexual motivation, but not the same sexual tendency (or combination of tendencies) as Crown-flattening. It may have been derived by exaggeration and (increased) ritualization from the more or less square but less "swollen" head-shapes frequently assumed by such species as the silver-billed tanager and the *Chlorospingus* bush-tanagers during Dawn Calling.

Yellow-rumped tanagers may have one other purely or primarily

hostile display. This was seen only during one prolonged territorial dispute between two adult males. One of the males repeatedly supplanted the other. Between supplanting attacks the aggressive male adopted a distinctive and presumably ritualized Head-down Posture. The usual form of this pattern is shown in figure 6c. The head was lowered and the neck stretched forward while the bill was pointed diagonally downward. This was accompanied by a moderate amount of Back-ruffling, with the usual drooping of the wings. The tail was lowered but apparently not fanned. The feathers of the head may have been raised, at least occasionally, but apparently never to an extreme degree. Every once in a while the tail was suddenly raised to the position shown in figure 6b, but this may have been nothing more than a balancing reaction. Both the Head-down Postures and the supplanting attacks were accompanied by many rattling patterns, usually or always Thin Rattles. This Head-down Posture is one of the more peculiar patterns of the species. It is rather different from anything observed in other species of *Ramphocelus* or other genera of supposedly closely related tanagers. It may resemble certain patterns of "emberizine" finches (Andrew, 1961), but the evidence is insufficient to determine if it is partly or wholly homologous with the latter or if it has evolved (as a social signal) independently.

The copulatory patterns and associated or related reactions of yellow-rumped tanagers were observed in only one area, near the mouth of the Rio Piedras on the Atlantic coast, in February and March of 1962. They were not studied at length simply because they were relatively rare and performed less frequently than hostile or other sexual reactions. (This seems to be characteristic of almost all the tropical members of the American "nine-primaryed" songbird group).

Among the most conspicuous reactions of the species is Pouncing. It was observed five times. In each case an adult male which had been sitting on a high perch or flying high above the ground suddenly swooped down at a bird in adult female or juvenal plumage. (The males involved were different in each case. I am almost certain that all the birds that were swooped at were adult females. As far as I could tell there were no birds in the area at the time which performed typical juvenile behavior patterns.) In four out of the five cases the bird that was swooped at was flying, in an apparently unritualized manner. In the other case it was perched quietly in low scrub. In all cases the swooping male uttered rattling noises during the descent. All males uttered Thin Rattles; several uttered pure

Rattles and/or Muffled Rattles. The swoops of the males brought them very close to the females but not, I think, into actual contact. In four out of the five cases the female reacted to the swoop by flying away very rapidly. In two of these cases the male followed and a long twisting chase ensued. In the other two cases the male turned away, landed on a perch, and relaxed. After one swoop both birds landed in a tree about ten feet apart from one another. The male uttered pure Rattles and/or Thin Rattles, facing the female, while the female did silent Gaping in the direction of the male. Then the female flew away and the male did not follow. This swooping behavior of male yellow-rumped tanagers is very reminiscent of the Pouncing of male song sparrows (*Melospiza melodia*) described by Nice, 1943, but seems to be performed much less frequently. Although the accompanying Rattles indicate that some hostility is involved, the pattern may be primarily an attempt at forced copulation or rape.

Turning-away is another apparently ritualized pattern which seems to be performed only by adult males in the presence of females at the height of the breeding season. It is most common immediately after a male joins or is joined by a female. The two birds usually face one another when they first come together. But then the male may deliberately turn away and stand for at least a few seconds rigid and motionless with his tail pointing directly toward the female. In this position the male usually performs typical Back-ruffling (the ruffling may appear even before he turns) and holds his head fairly low (in any case, his head and foreparts must be more or less hidden from the female). His tail may be approximately horizontal or slightly raised. Sometimes it is fanned. Figure 2c shows a posture of this type. The male usually falls silent as soon as he turns away from the female. Only once did I hear a male utter a single note, a Hoarse Flourish, while he stood motionless.⁹

Two apparently successful copulations were observed. Both occurred early in the morning, approximately one half hour after dawn. The birds involved were not the same in the two performances. One performance began when the male flew into a tree where the female was already perched. He perched on a branch about ten

⁹ Once a male was seen to stand in a slightly more distinctive posture after Turning-away. The wings were drooped as during typical Back-ruffling, but the yellow feathers of the lower back and rump were not erected to any appreciable extent (see figure 2b). As this was the only time that a male was ever seen to perform conspicuous wing-drooping without ruffling of the yellow feathers, in any circumstance, the performance may have been nothing more than an individual aberration.

feet above her, then flew straight down on to her back. She went into a Bill-up Tail-up Posture just before he landed. Her wings were stretched out horizontally at the same time but they were not Quivered. The male began copulatory movements as soon as he landed. These seemed to be essentially identical with those of related species. The copulation itself was brief. As soon as he finished the male flew away and disappeared from view. The female remained in the Bill-up Tail-up Posture for some seconds afterwards. She also kept her wings out horizontally and performed two or three "spasmodic" bursts of very rapid Wing-quivering (definitely separated by brief periods in which the wings were held quite motionless). Then she gradually relaxed and assumed an unritualized posture. As far as I could tell both birds were absolutely silent throughout the whole performance. The other copulation began when the male flew straight on to the female's back without any preliminary perching near her. He uttered one Muffled Rattle in flight. The female went into a Bill-up Tail-up Posture as he approached. Her head and bill were pointed nearly vertically upward while her tail was raised diagonally. The feathers of her breast and belly were ruffled, but much less so than in the homologous postures of many related species. She spread her wings out horizontally but did not Quiver them. The male began copulatory movements as soon as he landed, and the copulation itself was almost as brief as the one described above. After dismounting the male perched right beside the female with his body parallel to hers and facing in the same direction. She remained in a Bill-up Tail-up Posture with her wings held out motionless. He also assumed a Bill-up Tail-up Posture (with Crown-flattening). His posture is illustrated in figure 2d. His wings were not stretched out horizontally. They were folded on his back, but one was held much higher than the other. As a result his yellow rump was revealed quite conspicuously on the side on which the wing was high. This was the side nearest the female. After a few seconds the male flew away. The female immediately came out of her Bill-up Tail-up Posture, but she kept her wings out horizontally. Then she performed three spasmodic bursts of Wing-quivering as she gradually lowered her wings (without folding them). Then she flew to another perch a few feet away. There she performed several more bursts of Wing-quivering while her wings were still drooped. Then she relaxed.

Two of the display patterns associated with copulations are of some comparative interest. The holding of the wings in an asymmetrical position after copulation may be related to the asymmetrical raising

of the wings by male crimson-backed tanagers before copulation. Wing-quivering seems to be obsolescent in yellow-rumped tanagers. It is performed less frequently than in some species of related genera. Perhaps it is on the way to complete disappearance, as it seems to have done already in crimson-backed tanagers.¹⁰

In addition to the possible cases of attempted rape described above, four reactions which may have been unsuccessful copulation attempts were observed. In all four cases an adult male flew to a presumed female uttering Thin Rattles and/or Muffled Rattles as he did so. Once the male hovered over the female's back, apparently attempting to land there. The other times the male landed beside the female. Twice the female responded by assuming a Bill-up Tail-up Posture. When this happened the male retreated at once. (Bill-up Tail-up Postures seem to be part of "soliciting" in many passerines, but they may not encourage copulatory behavior by male yellow-rumped tanagers.)

When precopulatory behavior is stopped short or cut off abruptly, without leading to actual copulation, male yellow-rumped tanagers tend to perform one or more rapid bill-wiping movements. Similar movements are performed by males of many related species in similar circumstances. This is the sort of reaction which looks, at least superficially, like "displacement."

DISCUSSION

Three aspects of the display repertory of yellow-rumped tanagers seem to be particularly significant:

1. The remarkable resemblance of some of the vocal patterns, especially the Rattle—Hoarse Flourish "complex," to some of the vocalizations of *Chlorospingus* species.

¹⁰ There are indications that the yellow color of the rump is essentially a non-hostile (perhaps positively sexual) sign stimulus. The contrasting black, or the combination of black with a light bill, may be a hostile sign stimulus. I have seen a wild male yellow-rumped tanager attack an adult male blue-black grassquit (*Volatinia jacarina*). Adult male blue-black grassquits have almost entirely black plumage and silvery bills. As the individual that was attacked did not seem to be doing anything to provoke hostility, it may have been attacked simply because of its appearance. If so the stimuli releasing attack may be essentially the same in both yellow-rumped tanagers and crimson-backed tanagers. If black is a hostile stimulus in both species, they differ significantly from species of certain other groups of American "nine-primaried" songbirds, e.g. honeycreepers of the tribe Dacnini. (This will be discussed in more detail in a later paper.)

The similarities are extensive and detailed enough to suggest that *Ramphocelus* and *Chlorospingus* are closely related to one another.

The two genera are kept far apart from one another in current classifications and checklists, e.g. Hellmayr, 1936; but the differences between them, e.g. in bill shape, body proportions, and the absence of bright plumage in males of *Chlorospingus*, may be nothing more than superficial adaptations to particular habitat preferences and feeding methods.

2. The large number of different types of display.

Two general features seem to be characteristic of the display behavior of many highly gregarious species of the American "nine-primaried" songbird group, and probably many other groups as well (see Moynihan, 1960 and 1963). Highly gregarious species seem to express a larger proportion of their hostility by means of display, and a smaller proportion by overt unritualized activity, than do less gregarious species. They also, in many cases, have fewer recognizably distinct types of partly or purely hostile displays or partly independent components of displays than less gregarious species. (As the great majority of displays in all species are at least partly hostile, this latter statement means, in fact, that highly gregarious species tend to have a lesser total number of types of display than less gregarious species.)

The highly gregarious yellow-rumped tanagers seem to conform to the first of these general rules but not to the second. They do express a very large proportion of their hostility by display. (It is noticeable, for instance, that they relatively seldom perform overt attack and escape movements without also performing some display, usually vocal, at the same time.) They do not, however, have a relatively small number of different types of display. They certainly have many more different types of display than such extremely gregarious species as the plain-colored tanager, *Tangara inornata* (personal observation). They even have more different types of display than the moderately gregarious and closely related crimson-backed tanagers. They seem, in fact, to have at least as many different types of display and partly independent components of displays as the very slightly gregarious green-backed sparrow (which seems to be as nearly completely nongregarious as any species of neotropical tanager or finch).¹¹

¹¹ The variety of different signals in the repertory of yellow-rumped tanagers is even greater than would be suggested by the number of different components alone. This is because the different components can be combined in a rather

The differences in numbers of displays between yellow-rumped tanagers and other highly gregarious tanagers may be correlated with, i.e. causally related to, differences in breeding behavior. All the other highly gregarious tanagers whose behavior has been studied in detail tend to feed and move about in groups, but they do not show the tendency to breed close together which is so conspicuous in yellow-rumped tanagers. Behavioral interactions between birds breeding in colonies or semi-colonial groups may be particularly complex (simply because the constant presence of other individuals will stimulate many incompatible tendencies, such as sex and hostility, that are stronger on the average during the breeding season than at other times of the year). A great variety of signal patterns may be necessary in order to regulate or control such complex interactions with maximum efficiency. (Another factor of slightly different order may be involved. Colonial or semi-colonial breeders such as yellow-rumped tanagers may have developed, or retained, comparatively strong aggressive tendencies in order to prevent their strong gregarious tendencies from leading to overcrowding or general promiscuity. There is evidence that a high degree of aggressiveness in itself favors the development or retention of a great variety of displays, irrespective of the social structure in which the aggressiveness is expressed. See Moynihan, 1963.)

3. The intergrading of the vocal patterns.

The major vocal patterns of yellow-rumped tanagers intergrade with one another more frequently and more conspicuously than the corresponding patterns of any other American "nine-primaried" songbird whose behavior has been studied. This seems to be a highly specialized character and must be adaptive. The only other groups of animals in which a similar contrast between species with intergrading vocal patterns and species with distinct, nonintergrading patterns has been recognized is the mammalian order of primates. Among primates there is evidence to suggest that the species with intergrading vocal patterns are those which are least dependent upon vocal signals *alone* for the regulation of their social behavior. Intermediate (and ambivalent) notes, produced by intergrading, have certain advantages as signals. They may convey complex messages (i.e. the precise combination of tendencies in the animal producing the notes) in very

surprisingly large number of different ways, e.g. the combinations of one vocalization with several different types of feather-raising and of one type of feather-raising with several different types of vocalization. Different combinations of display components seem to be more common in the repertory of yellow-rumped tanagers than in those of many or most related species.

abbreviated form (i.e. coded with maximum efficiency). But they also have certain disadvantages. They may be difficult to read or decipher because of their complexity or easily confused with other (related) vocal patterns, simply because they are not always very distinctive in sound (they must resemble the other notes between which they are intermediate). These disadvantages may be avoided if the intermediate vocal patterns are usually or always accompanied by other information which will make their meaning clear. Thus among primates the species or classes of individuals that utter many intermediate or intergrading vocal patterns are diurnal and/or highly gregarious and/or tend to remain in very close contact with the other members of their own family group. Any individual of these species or classes hearing calls or notes from another individual of the same species will usually perceive visual, olfactory, or tactile signals or other stimuli from its companions and/or receive visual or olfactory clues from the physical environment at the same time. These visual, olfactory, or tactile aids should enable the receiving individual to grasp the meaning or significance of any vocal pattern, even when the latter is difficult to decipher or ambiguous in itself. (This aspect of vocalization in primates is discussed in more detail in Moynihan, 1964.) It is possible that the different types of vocal repertory in different species of tanagers are adaptive in much the same way as the corresponding types of repertory in primates. Perhaps yellow-rumped tanagers can "afford" to utter many intermediate notes simply because they are usually within sight, as well as sound, of their most important social companions, competitors, and rivals *throughout the year*. They must receive visual clues and stimuli with a larger proportion of the vocalizations to which they should respond than do individuals of other species which are more isolated during the breeding season.

SOME PATTERNS OF ORANGE-RUMPED TANAGERS

Two adult male orange-rumped tanagers in the New York Zoo were observed briefly during a few days of October 1958. They were labeled "*flammigerus*," and probably were hybrids between *f. flammigerus* and *f. icteronotus*. They were kept in separate aviaries. There were many other birds of different species in both aviaries, including other species of *Ramphocelus*. Both orange-rumped tanagers performed an appreciable number of displays and related or associated patterns. They became engaged in disputes with a variety of other species. They even performed a few partly sexual patterns.

One of them was particularly interested in a female silver-billed tanager, while the other seemed to have formed pair-bonds with a juvenile black-throated tanager (*R. nigrogularis*).

The orange-rumped tanagers were observed to perform Flicking movements, Gaping, Head-ruffling (see figure 4d), Back-ruffling, Belly-fluffing, and "silent song," and heard to utter Nasal Notes and Rattles. Some of these patterns, e.g. the Nasal Notes, were apparently identical with the corresponding displays of Panamanian yellow-rumped tanagers. Others differed to some (usually slight) extent. Some of the differences are listed below.

Both orange-rumped tanagers performed silent Gaping rather more frequently than the yellow-rumped tanagers kept in captivity on Barro Colorado Island. Much of this Gaping was done with the head lowered and the neck stretched forward. A Gaping bird usually faced straight toward the other bird releasing the performance. The combination of Gaping with lowering of the head and stretching of the neck may have been ritualized per se to form a "head forward threat" display like that of many other passerines (see Andrew, 1961). Once a bird in this posture looked downward. This was reminiscent of the Head-down display posture of yellow-rumped tanagers (except that the Gaping was maintained throughout).

Once a bird was seen to perform Back-ruffling that involved the black feathers of the center of the back as well as the orange feathers of the rump and lower back.

The most extreme Belly-fluffing observed is shown in figure 5c. This is considerably less extreme than the most exaggerated Belly-fluffing of yellow-rumped tanagers or crimson-backed tanagers, but it may well have been low intensity.

All the Rattles sounded like the pure Rattles of yellow-rumped tanagers.

Both orange-rumped tanagers also uttered moderately loud (but not metallic) notes that might be transcribed as "Whit" or "Tsit." They were uttered singly and in series when the birds were more or less isolated (as much as possible within the aviaries), and were not accompanied by overt indications of alarm. This would suggest that such notes are largely or completely homologous with the "Tzzheet" Notes of yellow-rumped tanagers, *not* the softer "Tsit" Notes uttered by one yellow-rumped tanager in captivity. Sometimes single moderately loud "Whit" or "Tsit" Notes were uttered immediately before and/or immediately after Rattles. Such compound calls presumably are related to the "Tzzheet"—Thin Rattle—Hoarse Flourish per-

formances of yellow-rumped tanagers. Both orange-rumped tanagers usually sat without moving while they uttered "Tsit" or "Whit" Notes, with or without Rattles.

The "silent song" patterns were performed by only one of the orange-rumped tanagers. I was told that this individual had assumed adult plumage only a few months earlier. Its "silent songs" were largely inaudible at a distance of three feet. Occasionally, one or more soft but clear "Whit" or "Tsit" notes were interjected, apparently at random, in otherwise silent "phrases."

SOME PATTERNS OF BLACK-THROATED TANAGERS

In addition to the single individual in the New York Zoo, a few black-throated tanagers were observed in the wild near Iquitos, Peru, in December 1958. The general social behavior of these Peruvian birds is described in Moynihan, 1962a. They were keeping together in what looked like a family group, including both adults and young, and also were associating with a family group of silver-billed tanagers. They performed a few displays, including Flicking movements of the usual *Ramphocelus* type and silent Gaping from a variety of unritualized postures. During one violent intra-specific dispute, one bird performed Gaping while its opponent kept its bill almost or completely closed, and one or both birds uttered rapid "twittering" phrases of short notes which sounded like some type of Hoarse Notes. During another intra-specific dispute, one or more birds uttered similar "twittering" series of Hoarse Notes without any sign of Gaping. Several times an adult was heard to utter series of three to eight "Whi-it" or "Wheeeet" Notes when it flew ahead of its companions. These appeared to be a type of "summons," presumably related to the Plaintive Notes of many other species, the "Tzzheet" Notes of yellow-rumped tanagers, and the "Tseeet" Notes of crimson-backed tanagers.

The individual at the New York Zoo was observed to perform similar Flicking and silent Gaping and assume "head forward threat" postures like orange-rumped tanagers. Once, when it was attacked by a barbet in the same aviary, it responded by Gaping in an upright posture and ruffling the black feathers of the upper back (see figure 6a).

All the black-throated tanagers near Iquitos uttered many loud, metallic sounding "Tsit" Notes. These were *very* similar to the "Tsit" Notes uttered by silver-billed tanagers in the same region (although perhaps slightly softer) and were uttered in similar social circum-

stances. There is some evidence that the "Tsit" Notes of these silver-billed tanagers are "Short Hostile Notes" and homologous with the Nasal Notes of crimson-backed tanagers. This may also be true of the "Tsit" Notes of Peruvian black-throated tanagers. If so, such notes are not strictly homologous with either the "Tsit" Notes of the captive yellow-rumped tanager on Barro Colorado Island or the "Tsit" Notes of the captive orange-rumped tanagers in the New York Zoo. (I might add that none of the black-throated tanagers observed near Iquitos or in the New York Zoo uttered any notes which sounded more like the Nasal Notes of other species.)

In any case it is possible that the resemblance between the "Tsit" Notes of the black-throated tanagers and silver-billed tanagers near Iquitos is an example of some kind of mimicry. This resemblance may facilitate associations between the two species, and such associations may be advantageous (to one or both species) in some circumstances. (It may be significant that the Short Hostile Notes of silver-billed tanagers in Trinidad, where black-throated tanagers are absent, are rather different in sound.) It is equally possible that the similarities between the Nasal Notes of yellow-rumped tanagers and crimson-backed tanagers facilitate associations between these two species.

The vocalizations of the captive black-throated tanager in the New York Zoo were rather puzzling. It uttered Rattles quite like those of the orange-rumped tanagers. It also uttered "Tsit" Notes, softer and less metallic than those of the Iquitos birds, by themselves alone and immediately before and/or after Rattles. These "Tsit" Notes may have been strictly homologous with those of the orange-rumped tanagers. (This particular black-throated tanager may also have been imitating, or have learned part of its repertory from, the orange-rumped tanager in the same aviary.)

GENERAL COMMENT

It may be useful to emphasize certain aspects of the display behavior of the genus *Ramphocelus* as a whole.

1. There is no display or combination of displays that can be considered diagnostic of the genus, i.e. that is performed by all the species of the genus and not by species of other genera.

2. All or most of the displays performed by some but not all of the species of *Ramphocelus* are also found in some species of other genera. In most cases the homologous patterns of species of other

genera are very similar to the corresponding displays of *Ramphocelus* species in form, function, and causation.

3. In view of these similarities between *Ramphocelus* species and species of other genera, it is perhaps remarkable that there are so many differences between the yellow-rumped tanager and the crimson-backed tanager. The display behavior of the yellow-rumped tanager, as a whole, seems to be as much like that of the brown-capped bush-tanager as like that of the crimson-backed tanager, while the display behavior of the crimson-backed tanager seems to be as much like that of *Tachyphonus rufus* as like that of the yellow-rumped tanager. (The behavior of *Tachyphonus* species will be discussed in a later paper.)

Comparable contrasts are found within other genera, e.g. *Saltator*, *Cyanerpes*, and *Diglossa*. It does, in fact, seem to be characteristic of many groups of American "nine-primaried" songbirds that the differences between the display repertoires of different species of the same genus are at least as great as the differences between their repertoires and those of some species of other genera.

4. The differences between the purely or predominantly sexual displays of yellow-rumped tanagers and crimson-backed tanagers are not greater than the differences between some of their other displays. Some of the patterns apparently used by males to attract mates, e.g. some Dawn Calling notes, are actually quite similar in the two species. This would suggest that much of the divergence between the display repertoires of these two sympatric species is not primarily, or not only, an adaptation to maintain reproductive isolation between them.

ACKNOWLEDGMENTS

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

I am grateful to Mr. William G. Conway for facilitating observations of captive birds in the New York Zoo, and to Dr. Philip Humphrey and Mr. Eugene Eisenmann for checking specimens in the United States National Museum and the American Museum of Natural History.

SUMMARY

This is primarily a study of the behavior of yellow-rumped tanagers (*Ramphocelus flammigerus icteronotus*) observed under natural conditions in Panama.

Yellow-rumped tanagers are highly gregarious. They even associate in semicolonial groups during the breeding season.

They are highly vocal. They utter Nasal Notes, Rattles, and melodious "Kioo" or "Klloo" Notes, plus a great number of intermediate notes and calls, all or most of which intergrade with one another.

The comparatively great frequency of intermediate and intergrading vocal patterns may be a result of the extreme gregariousness of the species. Any individual hearing a call or note will usually receive visual information from its companion(s) at the same time. This will facilitate the interpretation of any vocal message, even when the latter is ambiguous or would be difficult to decipher by itself alone.

Yellow-rumped tanagers seem to have more different types of display and partly independent components of display than all or most related species. This may be correlated with their semicolonial breeding habits.

Many of the vocal patterns of yellow-rumped tanagers are very similar to patterns of brown-capped bush-tanagers (*Chlorospingus ophthalmicus*). The similarities are extensive and detailed enough to suggest that the genera *Ramphocelus* and *Chlorospingus* are closely related to one another.

There is no display or combination of displays diagnostic of the genus *Ramphocelus* as a whole. The display repertoires of some species of other genera are not more different from those of some species of *Ramphocelus* than the latter are from one another. There is some evidence that many of the differences between the repertoire of the yellow-rumped tanager and that of the sympatric crimson-backed tanager (*R. dimidiatus*) subserve other functions instead of, or in addition to, the maintenance of reproductive isolation between the two species.

BIBLIOGRAPHY

ANDREW, R. J.

1961. The displays given by passerines in courtship and reproductive fighting. *Ibis*, vol. 103a, pp. 315-348.

EISENMANN, E.

1955. The species of Middle American birds. *Trans. Linn. Soc. New York*, vol. 7, pp. 1-128.

HELLMAYR, C. E.

1936. Catalogue of birds of the Americas. Part IX, Tersinidae-Thraupidae. *Field Mus. Nat. Hist. Publ. 365, Zool. Ser.*, vol. 13, pp. 1-458.

HINDE, R. A.

1955. A comparative study of the courtship of certain finches (Fringillidae). *Ibis*, vol. 97, pp. 706-745.

MOYNIHAN, M.

1960. Some adaptations which help to promote gregariousness. Proc. 12th Internat. Ornithol. Congr., pp. 523-541.
- 1962a. The organization and probable evolution of some mixed species flocks of neotropical birds. Smiths. Misc. Coll., vol. 143, no. 7, pp. 1-140.
- 1962b. Display patterns of tropical American "nine-primaried" songbirds. I. *Chlorospingus*. Auk, vol. 79, pp. 310-344.
- 1962c. Display patterns of tropical American "nine-primaried" songbirds. II. Some species of *Ramphocelus*. Auk, vol. 79, pp. 655-686.
1963. Display patterns of tropical American "nine-primaried" songbirds. III. The green-backed sparrow. Auk, vol. 80, pp. 116-144.
1964. Some behavior patterns of platyrrhine monkeys. I. The night monkey (*Aotus trivirgatus*). Smiths. Misc. Coll., vol. 146, no. 5, pp. 1-84.

NICE, M. M.

1943. Studies in the life history of the song sparrow and other passerines. Trans. Linn. Soc. New York, vol. 6, pp. 1-328.

SIBLEY, C. G.

1958. Hybridization in some Colombian tanagers, avian genus *Ramphocelus*. Proc. Amer. Phil. Soc., vol. 102, no. 5, pp. 448-453.

SKUTCH, A. F.

1954. Life histories of Central American birds, families Fringillidae to Coerebidae. Pacific Coast Avifauna, vol. 31.