

DISPLAY PATTERNS OF TROPICAL AMERICAN "NINE- PRIMARIED" SONGBIRDS

III. THE GREEN-BACKED SPARROW

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THIS is the third in a series of papers describing the display behavior of some tropical American finches, tanagers, and honeycreepers.

All the ethological terms in this paper will be used in the same sense as in the two preceding papers of the series (Moynihan, 1962b and 1962c). These earlier papers were concerned with some species of the genera *Chlorospingus* and *Ramphocelus*. All references to the behavior of either *Chlorospingus* or *Ramphocelus* will be based upon these earlier papers, unless it is specifically stated otherwise.

Green-backed Sparrows (*Arremonops conirostris*) are essentially "bush finches," and show a marked preference for scrubby habitats (see Skutch, 1954). They resemble many other species of similar habitat preference in shape and general tone of coloration. They are rather large-headed, with "chunky" bodies, rounded wings, a rather long tail, and long legs and large feet. Adults of both sexes are largely olive green above, with gray heads marked by black stripes through the eyes and along the sides of the crown, and are mostly gray below, with white throats. They also have conspicuous yellow patches along the edges of the wings. It is usually impossible, in the field, to tell the sex of a single bird by its appearance alone; but males usually appear to be slightly larger than their females when mated birds are seen together.

Green-backed Sparrows are much less gregarious than any of the species of *Chlorospingus* or *Ramphocelus* whose behavior has been studied. Mated Green-backed Sparrows usually remain associated with one another throughout the year; but neither mated nor single birds form flocks (larger than a single family group) of their own species alone, or associate frequently with mixed flocks of other species (see Moynihan, 1962a).

The following account of the displays of Green-backed Sparrows is based upon intermittent observations of both wild and captive birds between March, 1958, and June, 1961. The wild birds were studied in several areas of the Canal Zone, most intensively on Barro Colorado Island and near the town of Frijoles on the mainland shore of Gatun Lake. The captive birds were trapped near Frijoles or the town of Balboa, and then kept in large aviaries on Barro Colorado Island. All the birds studied were probably examples of the subspecies *A. c. striatipectus* (Hellmayr, 1938).

The observed displays and related patterns of Green-backed Sparrows include locomotory patterns, primarily or purely hostile patterns, and partly or primarily sexual patterns.

Locomotory Patterns

Green-backed Sparrows perform Wing-flicking and Tail-flicking movements, ritualized intention movements of flight, which are at least very similar to the Flicking movements of species of *Ramphocelus*. They also tend to fan their tails in a great variety of social situations. This Fanning is certainly not purely hostile (as the similar-looking fanning of Crimson-backed Tanagers, *Ramphocelus dimidiatus*, seems to be). It may be another ritualized intention movement of flight.

Much more peculiar are some tail-quivering movements. Individuals of many species, including Green-backed Sparrows, quiver their tails very rapidly when they "shake out" their plumage while preening. This quivering is usually vertical, straight up and down; and the amplitude of the movements is seldom large. Green-backed Sparrows also perform the same or similar movements, without any other preening or "comfort" components, in many other circumstances. Such tail-quivering is not associated with any (other) display particularly often; but it does tend to occur immediately after hops and short flights. Green-backed Sparrows are great hoppers (they never run); and often stand for a second or so after every hop. It is within such brief periods of standing that the tail-quivering is most apt to occur. This may be nothing more than a balancing reaction, but both male and female Green-backed Sparrows seem to perform relatively more tail-quivering in the course of certain obviously hostile encounters and certain pairing or partly sexual reactions (see below) than when they are feeding peacefully, even though they may hop as frequently while feeding as in pairing or hostile reactions. This would suggest that most of their tail-quivering may be an indication or expression of motivational conflict.

Tail-quivering is so conspicuous that it might be expected to function as a signal. The existence of such a function is also suggested by the fact that a mated bird hopping near its mate tends to perform tail-quivering more frequently when its tail is pointed directly toward its mate than when its tail is pointed away from the mate. It must be admitted, however, that the performance of tail-quivering by one bird seldom or never provokes any obvious response by any other bird(s) in the neighborhood. (Comparable tail movements by other birds of other groups, e.g., some thrushes and tyrannid flycatchers, are problematical in much the same way, being exaggerated in form, apparently in order to enhance their visual conspicuousness, but seldom or never inducing any obvious response.)

Primarily or Purely Hostile Patterns

Some Simple Movements and Postures. Most of the unritualized hostile patterns of Green-backed Sparrows seem to be essentially identical with the corresponding patterns of many related species. Green-backed Sparrows also assume hostile crouch postures and erect postures which are similar to the corresponding postures of Crimson-backed Tanagers. The crouch and erect postures of Green-backed Sparrows do not seem to be ritualized *per se*; but they are usually or always combined with ritualized patterns. The erect posture is probably most often accompanied by Short Hostile Notes, while the crouch posture is often combined with Ruffling patterns, especially Belly-ruffling (see below).

I have seen captive Green-backed Sparrows of both sexes open their bills, without uttering a sound, before and after attacking other birds of their own and other species. This "gaping" is extremely variable in form. Sometimes the bill is opened widely. More often it is opened only slightly. This would suggest that the gaping pattern may be almost or completely unritualized. Perhaps the Green-backed Sparrow is in process of losing a more exaggerated Gaping display, as exaggerated Gaping is widespread among many related species.

Short Hostile Notes. Green-backed Sparrows of both sexes frequently utter loud sharp notes in almost all sorts of hostile encounters. These notes vary considerably in tone. A single note of the most common type might be transcribed as *Chuck*. A less common type is nasal and metallic, and might be transcribed by *Chank*. The two types seem to intergrade; and intermediate notes are not rare. All these notes are essentially single. They may be repeated, but such repetitions are extremely variable, and obviously not ritualized, as such, in any way.

They may be accompanied by ritualized postures or movements. They are often uttered by birds hopping or flying, more or less rapidly, in a perfectly normal manner (Green-backed Sparrows seem to have no ritualized flight patterns), as well as by birds standing in unritualized ordinary or erect postures. When they are associated with other ritualized hostile patterns, they are most often combined with Crest-raising (see below). In certain partly sexual situations, they may be accompanied by such patterns as Fluffed Hunched postures and/or Wing-trembling (see below). Notes uttered by hopping or standing birds are frequently accompanied by Flicking movements and/or Fanning.

Both the extreme types of notes and the intermediate notes are much commoner in obviously purely hostile encounters than in partly sexual encounters. In all types of encounters, they are uttered more often by obviously alarmed or escaping birds than by obviously aggressive ones.

This would indicate that they are probably purely hostile, and produced when the escape tendency is as strong or stronger than the attack tendency. The actual strength of the attack and escape tendencies producing typical *Chuck* notes may be very different at different times. Such notes may be uttered in both very prolonged and vigorous disputes and in brief, slight, disputes. I have heard extreme *Chank* notes only in very high intensity disputes. They may be produced when both the attack and escape tendencies are stronger than when all or most ordinary *Chuck* notes are uttered.

All these notes seem to function most often as not very aggressive threat patterns and/or alarm signals.

As a group, they are so similar, in almost all respects, to the Short Hostile Notes of some species of *Ramphocelus* that they must be strictly homologous with the latter. It will be convenient, therefore, to call them by the same name.

Like the homologous notes of Crimson-backed Tanagers, the Short Hostile Notes of Green-backed Sparrows sometimes seem to subserve a non-hostile function in addition to, or instead of, their usual hostile one. They may be used to maintain contact between mated birds which have become separated and lost sight of one another. They probably function as contact notes more frequently than the corresponding notes of Crimson-backed Tanagers, and seem to be more strongly "attractive." A mated Green-backed Sparrow which utters a Short Hostile Note is usually joined by its mate within a few seconds. The contact function of the Short Hostile Notes of Green-backed Sparrows may be comparatively highly developed as an adaptation to living in dense bush. Mated Green-backed Sparrows usually stay close to one another; but they probably tend to lose sight of one another more frequently than do mated Crimson-backed Tanagers which do not stay close together as consistently but usually move in higher and more open vegetation. They probably have a greater "need" for contact notes than do Crimson-back Tanagers. (It is interesting, in this connection, that Green-backed Sparrows have not evolved any special type of note whose principal or only function is to maintain contact between mates or other social companions. Such special contact notes seem to be largely confined to highly gregarious species, such as the Brown-capped Bush-tanager, *Chlorospingus ophthalmicus*.)

The notes which Skutch (*op. cit.*) describes as "deep nasal" in his account of the Green-backed Sparrow were probably Short Hostile Notes.

Once, when I flushed a pair of Green-backed Sparrows, apparently from a nest, both birds uttered a few single *Tsip* or *Chik* notes. These notes sounded rather like *Chuck* notes, but were very much softer. They were accompanied by many escape movements and intention movements, and may have been special alarm notes. They may have been closely related to, or modifications of, either ordinary *Chuck* notes and/or Soft Chatter notes (see below).

Hoarse Notes. Green-backed Sparrows utter a variety of notes which are obviously more or less strictly homologous with the Hoarse Notes of *Ramphocelus* species. These notes can be divided into Muffled Hoarse

Notes, Medium Hoarse Notes, Harsh Hoarse Notes, and Hoarse Screams.

The Muffled Hoarse Notes of Green-backed Sparrows, unlike the corresponding notes of Crimson-backed Tanagers, seem to be uttered only in partly hostile and partly sexual situations. They will be discussed below in connection with sexual behavior.

Medium Hoarse Notes are by far the most common vocal patterns of adult Green-backed Sparrows. They seem to be uttered almost equally often by males and by females. They are almost always uttered in series, usually of three to five notes. Typical series might be transcribed as *Wha-aa wha-aa wha-aa* or *Wha-anh wha-anh wha-anh*. The successive notes tend to become progressively softer and lower in pitch; but the whole series is moderately loud. Each individual note is usually slightly bisyllabic. All the notes are always hoarse, and sometimes slightly nasal as well. (Possibly the more nasal Short Hostile Notes are really partly intermediate between typical *Chuck* notes and typical Medium Hoarse Notes.) Medium Hoarse Notes are seldom accompanied by special ritualized postures or movements. They may be uttered by birds which are sitting, standing, hopping, or landing after a flight (possibly also by birds in full flight). They are uttered most frequently as "greetings." They are uttered by one or both birds almost every time a mated bird rejoins its mate, even when the two birds have been only a few feet apart. (The greeting "songs" described by Skutch, 1954, would seem to have been series of Medium Hoarse Notes. Skutch apparently did not hear such notes in other circumstances.)

Medium Hoarse Notes are also uttered, occasionally, as "landing calls" by birds landing some distance (at least 20 or 30 feet) away from their mates or any other birds of their own or other species. Some or all of these notes may be "mistakes." They may be uttered by birds which "expect" to find their mates closer to their landing sites than is actually the case.

These facts might suggest that all or most Medium Hoarse Notes are direct expressions of some "friendly" and/or purely locomotory tendency. There is other evidence, however, that they are usually or always purely hostile.

They frequently intergrade with Harsh Hoarse Notes, which are certainly purely hostile (see below). Every once in a while, a bird will attack its mate immediately after uttering "greeting" Medium Hoarse Notes. Such notes are also uttered by mated birds engaged in territorial disputes with their neighbors. Mated birds tend to utter such notes more frequently when they are hopping about together during territorial disputes than when they are equally active but not engaged in such obviously hostile reactions. They may utter Medium Hoarse Notes when

facing their opponents as well as when facing one another; and many or most of the notes uttered by birds facing their mates seem to be redirected upon, rather than provoked by, the latter. I have also seen solitary Green-backed Sparrows utter typical Medium Hoarse Notes when they were approached by birds of other species, e.g., Streaked Saltators (*Saltator albicollis*), Yellow-bellied Seedeaters (*Sporophila nigricollis*), and Clay-colored Thrushes (*Turdus grayi*), and engaged in disputes with variable Seedeaters (*Sporophila aurita*).

It seems likely, therefore, that the Medium Hoarse Notes themselves are direct expressions of the attack and escape tendencies alone. Any sexual tendencies that may be activated in birds uttering such notes may affect the orientation of the birds without being directly concerned in the production of the strictly vocal part of the behavior. Green-backed Sparrows seem to direct or redirect Medium Hoarse Notes toward their mates more frequently than is usual in the case of most comparable hostile patterns of most related species; but there is reason to believe that this habit is adaptive (see below).

The Medium Hoarse Notes of Green-backed Sparrows are relatively seldom accompanied by retreat movements, even in territorial hostilities. This would suggest that they are produced when the attack tendency is relatively stronger than when all or most Short Hostile Notes are produced.

The Medium Hoarse Notes in territorial disputes seem to intimidate opponents. Some or all of the "greeting" notes may also function as threat; but this is probably not always their most important function. The extreme frequency of Medium Hoarse Notes as "greetings" would indicate that the hostile tendencies of any Green-backed Sparrow are almost always stimulated by any approach by or to its mate; but the fact that overt fighting is relatively rare after such "greetings" indicates that this hostility is rigidly controlled. The Medium Hoarse Notes may contribute to this control in several ways. They may serve as "safety valves," allowing mates to express their hostility towards one another in a relatively harmless manner. Their frequent repetition without subsequent attack may also tend to facilitate and accelerate the habituation of mates to one another, especially during pair-formation (see below).

It is probably an indication of how strong the pair-bonds between mated Green-backed Sparrows usually are, and need to be, that several of their most common hostile reactions to one another may have the direct or indirect effect of reinforcing the pair-bonds between them.

Harsh Hoarse Notes sound much like Medium Hoarse Notes, but are more rasping, usually louder, sometimes longer, and usually uttered in more irregular series. I have heard such notes only in violent territorial

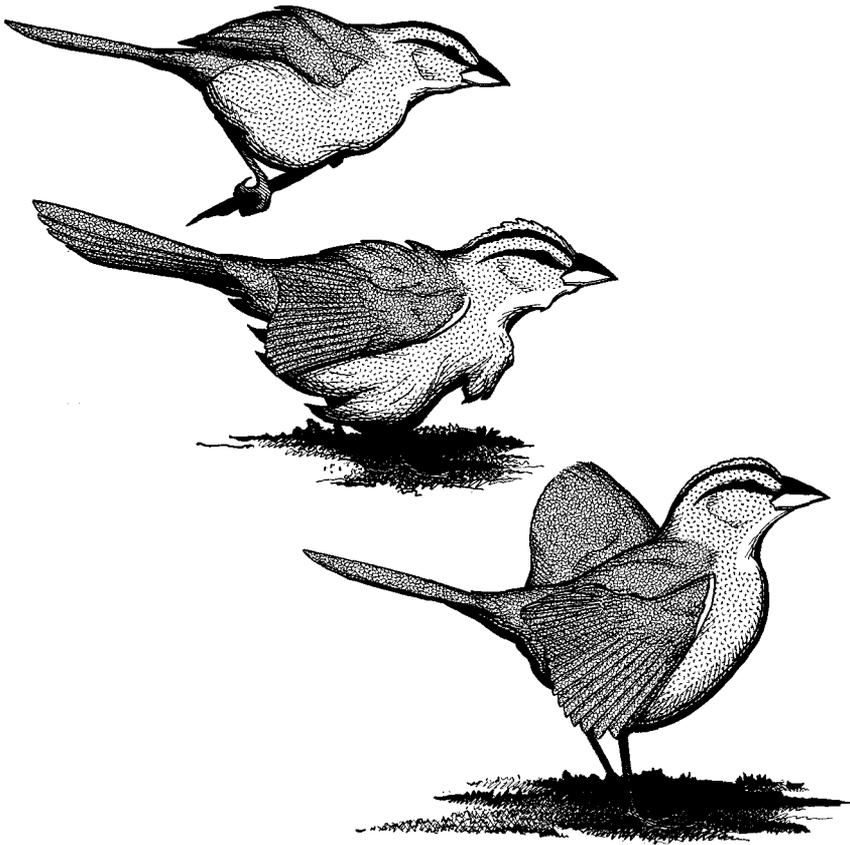


Figure 1. a. Top. A crouch posture with fluffing of the breast and belly feathers. b. Center. A crouch posture with Crest-raising, Belly-ruffling, and Wing-spreading. c. Bottom. A Fluffed Hunched posture with Single Wing-raising (and a very slight trace of Crest-raising, of rather unusual form).

disputes, when they are almost always directed by opponents at one another. They may be accompanied by unritualized attack or chasing movements and/or high intensity displays such as Crest-raising, Belly-fluffing, and Wing-spreading (see below). They are obviously threat; and presumably produced when both the attack and escape tendencies are stronger than when Medium Hoarse Notes are produced. They are certainly uttered by males, and probably also (although less frequently) by females.

Hoarse Screams are even louder, longer, slightly higher-pitched, and more urgent-sounding. They are frequently uttered by trapped birds (both males and females) when being handled; but I have not heard

them in other circumstances. Trapped birds make vigorous attempts to escape; but they also bite and peck when handled. This would suggest that Hoarse Screams may be produced when both the attack and escape tendencies are even stronger than when all or most Harsh Hoarse Notes are produced.

It is my impression that the various types of Hoarse Notes uttered by Green-backed Sparrows are more similar to one another in sound than are the various types of Hoarse Notes uttered by Crimson-backed Tanagers.

Ruffling Patterns. Both male and female Green-backed Sparrows may erect several different tracts of feathers in purely hostile encounters. This feather erection can be divided into Crest-raising and Belly-ruffling.

In Crest-raising, all the feathers of the central part of the forehead and crown are erected (see Figures 1b, 5, and 6). These feathers are not lengthened or otherwise modified in structure; but they are rather conspicuous when erected because their light gray color contrasts with the black stripes on either side of the crown.

In Belly-ruffling, all the feathers of the breast and belly are erected so that the tips of all or most are distinctly separated (see Figures 1b and 5b).

These two patterns may occur either separately or (more often) together. They are not always equally well developed when they occur together. Birds which perform Crest-raising without Belly-ruffling, or extreme Crest-raising with only slight Belly-ruffling, tend to perform many escape movements or intention movements, while birds which perform Belly-ruffling without Crest-raising, or extreme Belly-ruffling with only slight Crest-raising, tend to perform many attack movements or intention movements. This seems to indicate that Crest-raising is primarily an expression of the escape tendency, while Belly-ruffling is primarily an expression of the attack tendency.

Both Ruffling patterns are more common in prolonged and vigorous territorial disputes than in brief and slight disputes. They are also more common in high intensity pairing and other sexual reactions than in ordinary "greeting" encounters between well-adjusted mates. This would seem to indicate that they are both produced by relatively strong motivation.

In purely hostile encounters, Crest-raising may be associated with Short Hostile Notes, Belly-ruffling may be associated with Harsh Hoarse Notes, and the two together may be associated with Short Hostile Notes, Medium and/or Harsh Hoarse Notes, and/or Wing-spreading. Notes with Ruffling patterns are probably produced by motivation which is similar to, but slightly stronger than, the motivation producing the same notes without Ruffling.

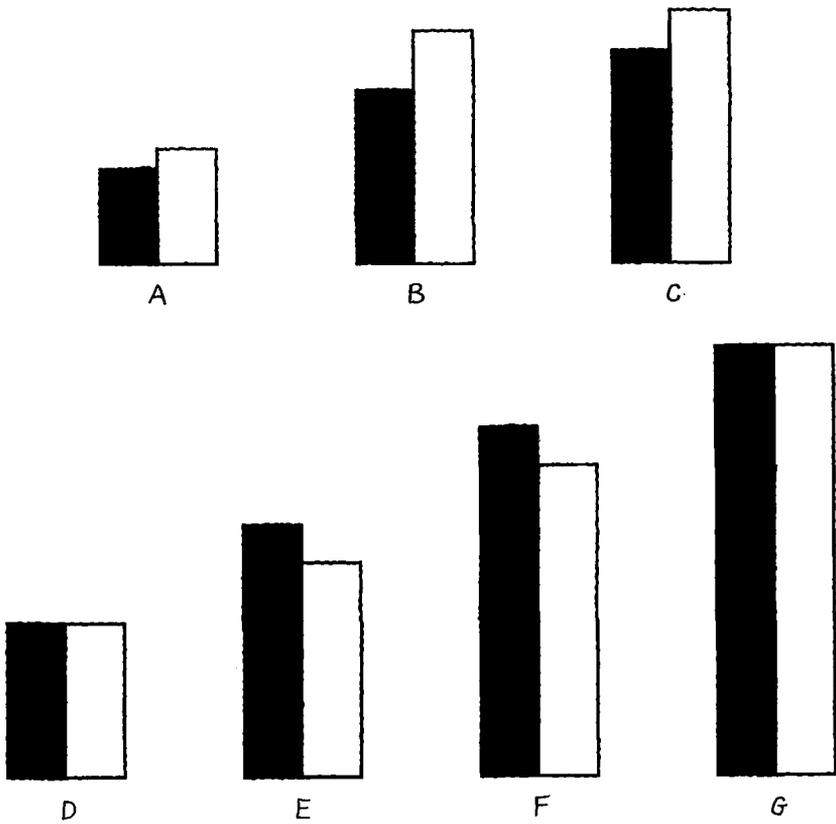


Figure 2. The probable relative strength of the attack and escape tendencies during typical performances of some hostile displays of Green-backed Sparrows. The black bars represent the attack tendency, and the white bars the escape tendency. A. *Chuck* Short Hostile Notes. B. *Chuck* Short Hostile Notes with Crest-raising. C. *Chank* Short Hostile Notes with Crest-raising (and possibly slight Belly-ruffling). D. Medium Hoarse Notes. E. Harsh Hoarse Notes with Belly-ruffling. F. Harsh Hoarse Notes with Belly-ruffling, Wing-spreading, and slight Crest-raising. G. Hoarse Screams.

Wing-spreading. In this pattern, both wings are lifted or stretched out simultaneously, and then held out, more or less motionless, for several seconds or even minutes. The two wings are always lifted or spread more or less symmetrically, but the level at which they are held is extremely variable. They may be raised nearly vertically, kept approximately horizontal, or lowered so that their tips are well below the level of the back. (Even when lowered, the tips are always well away from the body.) All forms of Wing-spreading may be silent or accompanied by Harsh Hoarse

Notes. They are apparently always accompanied by Belly-ruffling and at least a slight trace of Crest-raising, and are sometimes combined with crouch postures (Figure 1b).

I have seen Wing-spreading only in very high intensity disputes, territorial disputes between neighboring Green-backed Sparrows at the height of the breeding season and, once, in a furious dispute between a pair of Green-backed Sparrows and a single White-throated Crake (*Laterallus albigularis*). In such disputes, the Wing-spreading is usually associated with both vigorous attack and vigorous escape movements; but it is probably performed most often by birds advancing toward an opponent and/or just before attacking an opponent.

These facts suggest that Wing-spreading is performed when both attack and escape tendencies are strong, probably stronger, on the average, than in any other purely or predominantly hostile display of the species (except Hoarse Screams), and when the two tendencies are approximately equal to one another or the attack tendency is just slightly preponderant (less preponderant than when all or most Harsh Hoarse Notes are uttered apart from Wing-spreading).

Wing-spreading is almost certainly threat. It is particularly conspicuous because it reveals and emphasizes the yellow patches on the wings.

These yellow patches are usually hidden by body feathers in non-hostile situations. They are sometimes partly visible in a variety of hostile encounters in which Wing-spreading, as such, does not occur. They are presumably visible in such circumstances because the carpal joints have been lifted very slightly. Such slight lifting may be an intention movement of Wing-spreading.

I think that complete Wing-spreading may be performed only by males.

Partial Summary. The probable relative strength of the attack and escape tendencies producing typical performances of some of the hostile displays of Green-backed Sparrows is shown, in diagrammatic form, in Figure 2.

Partly or Primarily Sexual Reactions

Plaintive Notes. Both male and female Green-backed Sparrows utter more or less prolonged, essentially single notes, which are rather high pitched and clear in tone, apparently produced by thwarting of some sexual (probably pairing) tendency, and seem to be used by mated birds to summon or attract their mates. These notes are very similar to, and undoubtedly homologous with, the Plaintive Notes of *Ramphocelus* species, and may be called by the same name.

They are somewhat variable in a few respects. Some are much longer than others. Most are slightly bisyllabic, and the relative length and

pitch of the two syllables may differ. Different types of Plaintive Notes might be transcribed as *Whecoo*, *Wheeeoooot*, *Tseeeeeeeewut*, and *Tseweeeeeeeet*.

Plaintive Notes are uttered most often by birds which have become separated from their mates; but they are also uttered by birds near their mates just before flying away. They seem to be very effective as signals. When a bird utters a Plaintive Note, it is almost always joined or followed by its mate almost immediately.

The high, sharp, whistles described by Skutch (1954) were probably typical Plaintive Notes.

Song or Song-like Patterns. The song or song-like patterns of Green-backed Sparrows are probably the most distinctive of their displays.

They include two different types of notes. Both are short, but usually or always quite different in pitch. Typical notes of the first type might be transcribed as *Whit* or *Wheet* or *Whooeet*. Such notes are similar to some Plaintive Notes, but less whistle-like. Typical notes of the second type might be rendered *Chu* or *Chewa*. It will save space to call all of the first type "W Notes," and all of the second type "CH Notes."

These notes are usually uttered in phrases; and a typical "complete" song or song-like performance is composed of two phrases. The first phrase includes both W Notes and CH Notes, while the second, following immediately, is composed of CH Notes alone.

The W Notes and CH Notes of the first phrase are usually uttered alternately. The first note of the phrase is usually a W Note. The CH Notes may be either *Chu*'s and/or *Chewa*'s. The number of notes per phrase is highly variable. I have heard phrases which consisted of no more than one W Note and one CH Note; but most include at least two or three notes of each type.

Some first phrases include "extra" notes, which may be either W Notes and/or CH Notes, inserted among the regularly alternating notes. They may be inserted apparently at random or at regular intervals. A particularly common variation is a phrase which is largely or completely composed of "triplets," two W Notes followed by one CH Note. The first W Note of each triplet is usually a *Whit*, while the second is usually a *Wheet*, noticeably higher in pitch than the first note.

The second phrase is always an accelerating series of *Chu* notes. The number of notes per phrase is also variable; but uninterrupted phrases seldom or never include less than 10 or 12 notes.

Typical "complete" song or song-like performances might be transcribed by something like *Whit chu whit chu whit chu whit chu chu chu chu chu chu chu-chu-chuchuchuchu* or *Wheet chu wheet chu wheet wheet wheet wheet wheet wheet wheet wheet chu chu chu chu-*

chu-chu-chuchuchu or *Wheet chu whit chu chewa chewa chewa chewa chewa chu chu chu chu-chu-chu-chuchuchuchuchu*.

Skutch (1954) transcribes the first phrase of one of these performances as "tock tock chuck, tock tock chuck," while Eisenmann (1952) transcribes CH Notes as "Cho."

Green-backed Sparrows utter their songs or song-like patterns most often in the early morning, often beginning well before sunrise. The frequency of these patterns usually declines, gradually but irregularly, as the morning wears on. They are not, however, as strictly confined to the early mornings as the Dawn Calling patterns of Brown-capped Bush-tanagers or Crimson-backed Tanagers.

They are uttered only by males, usually sitting or standing on moderately high and exposed perches within their territories. They are seldom accompanied by special movements or postures. During the first part of the morning, they are usually uttered from sitting postures with the neck stretched diagonally upward (see Figures 3a, 3b, and 3e). Later, they are usually uttered from more relaxed postures, with less stretching of the neck. They may also be accompanied by conspicuous ruffling of the back and, usually to a lesser extent, the belly feathers during the later part of the morning (see Figures 3c and 3d). This ruffling is probably an intention movement of preening. Similar ruffling accompanies preening in all circumstances, and the birds which utter songs or song-like patterns with ruffling usually start to preen as soon as they stop uttering these patterns.

All the songs or song-like patterns are usually uttered by unmated males or males which have become separated from their mates. Mated males almost always stop uttering these patterns when they join or are joined by their mates. This suggests that such patterns are produced when some sexual tendency is thwarted. This sexual tendency is probably a pairing tendency, not a copulatory tendency, as songs or song-like patterns are uttered throughout the breeding season, long before and long after the relatively brief phase in which copulations occur (see below), and are uttered at least as frequently by males which do not attempt to copulate with their mates after joining or being joined by them as by males who do make vigorous attempts to do so.

This would indicate that some or all of the factors producing songs or song-like patterns are similar to (or even identical with) the factors producing Plaintive Notes. There is other evidence that these patterns are related to Plaintive Notes. Not only do W Notes sound much like Plaintive Notes, but typical Plaintive Notes sometimes take the place of W Notes in some otherwise typical song or song-like performances.

The CH Notes, however, are quite similar to typical Short Hostile

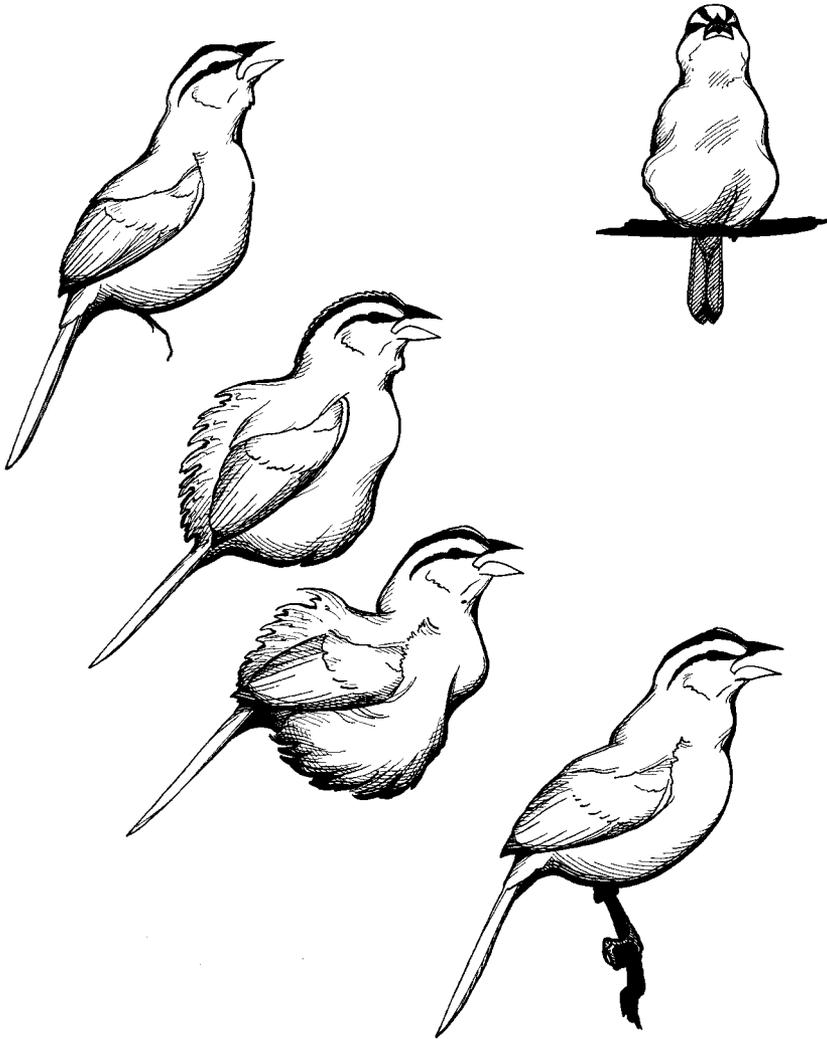


Figure 3. Postures accompanying W and CH Notes. a. Top right. Front view of a posture with neck stretched diagonally upward. b. Top left. Side view of a posture with neck stretched diagonally upward. c and d. Center. Two postures with ruffling and relatively little stretching of the neck. e. Bottom. Side view of a posture with neck stretched diagonally upward. This is probably the most common posture accompanying W and CH Notes early in the morning.

Notes in tonal quality. This suggests that some or all of the song or song-like performances may include a hostile component. They are certainly not uttered in most obviously hostile disputes; but I have seen a

few incidents which would suggest that they may be at least related to hostility in certain circumstances. The most interesting of these incidents occurred after a prolonged and vigorous territorial dispute between a mated pair and a single intruder. As soon as the pair had chased away the intruder, the male of the pair uttered a full series of song or song-like patterns, including typical first and second phrases, while he sat right beside the female. This was reminiscent of the "triumph ceremonies" of other species, and many "triumph ceremonies" seem to include a hostile component (see, for instance, Moynihan, 1958).

Even if the CH Notes of Green-backed Sparrows are not partly hostile, it seems likely that they have been derived from Short Hostile Notes, widespread among many different species of tanagers and finches, in the course of evolution.

The frequent alternation of W and CH Notes is very similar to the series of alternate Plaintive Notes and Short Hostile Notes uttered by some species of *Ramphocelus*. It is possible that the song or song-like patterns of the Green-backed Sparrow have been derived from such alternations of Plaintive Notes and Short Hostile Notes. At the same time, they seem to have replaced the Dawn Calling patterns which are widespread among related species but seem to be completely lacking in the repertory of the Green-backed Sparrow.

The accelerated CH Notes of the second phrase may represent an early stage in the evolution of the rattling or buzzy notes which are characteristic of the "songs" of many other species of "emberizine" finches (see Mayr, Andrew, and Hinde, 1956).

It is difficult to determine what, if any, are the causal differences between the typical first and second phrases of the song or song-like patterns of Green-backed Sparrows. "First" phrases without any subsequent accelerated series of CH Notes are not uncommon; but accelerated series of CH Notes without at least a trace of a preceding first phrase are rare or absent. I have heard birds utter phrases of W and CH Notes without accelerated series of CH Notes both very early in the morning, when they sang such phrases almost continuously for minutes on end, and appeared to be generally excited or highly motivated, and later in the morning, when they were much less continuously vocal and their tendency to utter song or song-like patterns was obviously "running down." It is possible that patterns composed of W and CH Notes without the subsequent accelerated series of CH Notes are nothing more than incomplete versions of the whole performance (all of which may result from the same causes); and that they are uttered in more or less the same form irrespective of why the performance is incomplete.

The most problematic aspect of the W and CH Note patterns of Green-backed Sparrows is their function(s). If they are really produced by pairing and hostile tendencies, they may, together, constitute a real "song," as the term is used in these papers, i.e., they may simultaneously attract birds of the opposite sex and repel birds of the same sex; but I have not been able to prove that this is actually the case. A male uttering these patterns is usually joined by his mate (or another female, if he

is unmated) and seldom visited by other males; but it is extremely difficult to establish that these effects are the direct results of the W and CH Notes alone.

Some W and CH Notes have a definite "rattling" undertone, while others seem to be perfectly "clear." Different males seem to utter notes with rattling undertones with different frequencies. This may facilitate individual recognition.

Pair-formation and Associated Patterns. Mated birds of most species of tropical tanagers and finches usually remain associated with one another throughout the year, for several consecutive years. Except (probably) in the case of some highly gregarious species, they also tend to maintain their pair-bonds at full strength throughout the period of association. Green-backed Sparrows are typical in this respect. Pair-formation seems to be a relatively rare phenomenon among them. It may occur only once in the lifetime of many individuals, when they first become independent of their parents (if they have not already formed bonds with a nest-mate at an even earlier stage). It probably occurs in later stages of the life cycle only when a bird of a well-established pair dies or leaves as the result of some very unusual event.

I observed only one clear-cut case of pair-formation among Green-backed Sparrows in the wild; but several encounters between my captive birds resulted in the formation of pairs, and may throw some light upon some of the behavior patterns occurring during normal pair-formation. One of these encounters between captive birds will be described first, as it was observed under particularly favorable conditions, at very close range.

I had kept a single female Green-backed Sparrow alone in a large outside aviary for several months when, in April of 1960, it was discovered that she had built a nest and laid an egg in it. A male was then introduced into her aviary.

The female immediately began to utter a rapid series of rather short, very soft, plaintive-sounding Whisper Notes, which might be transcribed as *Wheoo wheoo wheoo wheoo* At the same time, she assumed a Bill-up Tail-up posture, with all her breast and belly feathers very ruffled, and raised and Quivered her wings (see Figures 4a and 4c). This Wing-quivering was very similar to the "Upward Wing-quivering" of Brown-capped Bush-tanagers. The actual quivering movements were of considerable amplitude. The male responded to this display by flying straight toward the female, in an aggressive-looking way, and supplanting her. She flew away a few feet, landed on another branch, and immediately assumed a Bill-up Tail-up posture with Wing-quivering and Whisper Notes again; the male supplanted her again; etc. etc. They continued in this way, with undiminished vigor, for almost an hour. Then they started to "relax" a little. The first sign of this was that the male some-

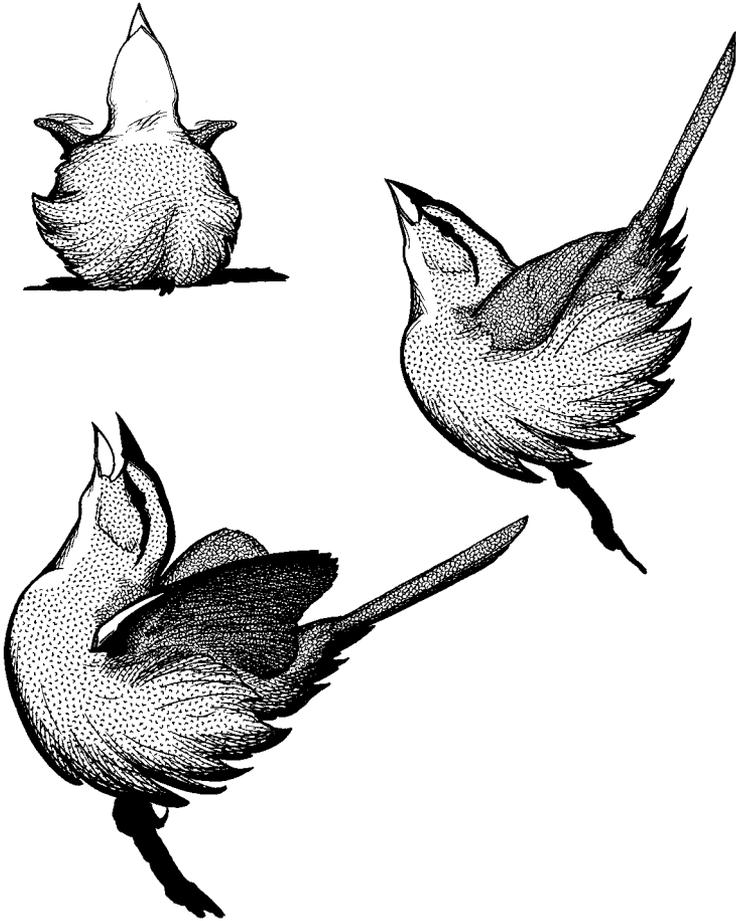


Figure 4. Bill-up Tail-up postures. a. Top left. Front view of a typical posture with Wing-quivering and Whisper Notes. b. Right. A typical posture without Wing-quivering or Whisper Notes. c. Bottom left. Side view of an extreme posture with Wing-quivering and Whisper Notes.

times did not supplant the female as soon as she began to display. Then the female began to stop displaying, for brief periods at first, even when the male did not supplant her, and resumed displaying less rapidly after flying away when he did supplant her. After a couple of hours, they stopped displaying and supplanting almost completely.

At one stage of this process, when the male did not always actually supplant the female but still came very close to her occasionally, she sometimes reacted to his approach in an interesting way. If she was displaying in a Bill-up Tail-up posture with Wing-quivering and Whisper

Notes before the male approached, she would stop Wing-quivering and uttering Whisper Notes, and raise her tail even higher than before, usually lowering her head at the same time (see Figure 4b), as soon as he came within approximately a foot of her. After holding this posture for a few seconds, she usually flew away.

When the female stopped the Bill-up Tail-up display with Wing-quivering and Whisper Notes of her own accord, she almost always performed a few hurried bill-wiping movements within a second or so after stopping.

This encounter was accompanied by a variety of other notes and calls in addition to the Whisper Notes by the female. Both birds uttered many Medium Hoarse Notes, often in long series, throughout the encounter, both when they were close together and when they were rather far apart from one another. The female uttered many Short Hostile Notes (of the *Chuck* type) in the first part of the encounter, usually when she was flying away from the male. Both birds uttered Plaintive Notes. These were uttered most often by the female when she was far away from the male. One bird, almost certainly the male, uttered several bursts of a distinctive Soft Chatter immediately before series of Medium Hoarse Notes. Each burst of Soft Chatter was a series of (usually four to six) soft but hard and short notes, and might be transcribed by something like *Tuk tuk tuk tuk*

Two days later, when the birds were observed again, they were quite calm. The male had stopped supplanting the female, and she had stopped performing the Bill-up Tail-up display with Wing-quivering and Whisper Notes, although the male made no attempt to copulate with her. Both birds still uttered a considerable number of Medium Hoarse Notes and Plaintive Notes, but the female had stopped uttering Short Hostile Notes. The male uttered a few bursts of Soft Chatter while moving near the female. This Soft Chatter was not particularly closely associated with Medium Hoarse Notes, and sometimes included more notes than the Soft Chatter heard previously. The male also uttered Muffled Hoarse Notes occasionally when he landed near the female. These notes sounded like ordinary Medium Hoarse Notes, but were usually much softer and shorter, and seldom or never bisyllabic. Sometimes they seemed to intergrade with ordinary Medium Hoarse Notes. At least twice, when the male was hopping near both the female and the nest, he uttered some soft short notes which were rather warbling in effect. I could not tell whether these were slightly modified Muffled Hoarse Notes or a definitely different type of call. In any case, they were not followed by anything distinctive in the way of overt unritualized behavior by either bird.

The clear-cut case of pair-formation in the wild occurred in June, 1961, when the female of a pair I had been watching for some time disappeared, in the late afternoon or night of the second day after I had collected the eggs that she had just laid.

The first morning after she disappeared, her mate uttered a lot of song or song-like patterns, without, apparently, inducing any response by other birds in the neighborhood. I did not watch during the afternoon that day. At dawn the next morning, there was already a new female in his territory. (This was definitely not his old mate. She lacked some wing feathers which the old female had when last seen, and she behaved in a very different way from the old female.)

When I first noticed the new female, she was hopping and feeding on the ground, while the male uttered W and CH Notes in a tree some distance away. She uttered many bursts of soft Hoarse Notes (see below) and Short Hostile Notes, and some single Plaintive Notes, while she was on the ground by herself. She also assumed a Bill-up Tail-up posture and raised and Quivered her wings (in exactly the same way as the captive female described above) from time to time in the intervals between periods of feeding. (This display was probably accompanied by Whisper Notes; but I was too far away to be able to hear them.) She made no attempt to approach the male immediately before, during, or after these Bill-up Tail-up performances. The male continued to utter his songs or song-like patterns almost all the time the female was displaying on the ground. He only stopped, momentarily, when she happened to come very close to the base of the tree in which he was perched (she did this in the course of feeding). The two birds continued to behave in this way for quite a long time. Occasionally one or both of the birds disappeared from my sight for a few seconds or minutes (they may have gone to feed some distance away), but they always resumed behaving as before as soon as they returned.

Then, about one-half to three-quarters of an hour after sunrise, the female began to try to approach the male a little more closely. She would hop or fly up into nearby shrubbery or trees, and try to approach the male by a circuitous route. Sometimes she performed Bill-up Tail-up and Wing-quivering patterns as she approached, sometimes not. In any case, the male never let her get very close. He always flew away, sometimes uttering Short Hostile Notes, before the female came within 20 feet of him.

When this happened, the female usually went down to the ground again, to resume hopping, feeding, and displaying as before. Only once did she remain in a tree after the male flew. Then she sat quietly in Fluffed Hunched posture (see Figure 5a). This posture was character-

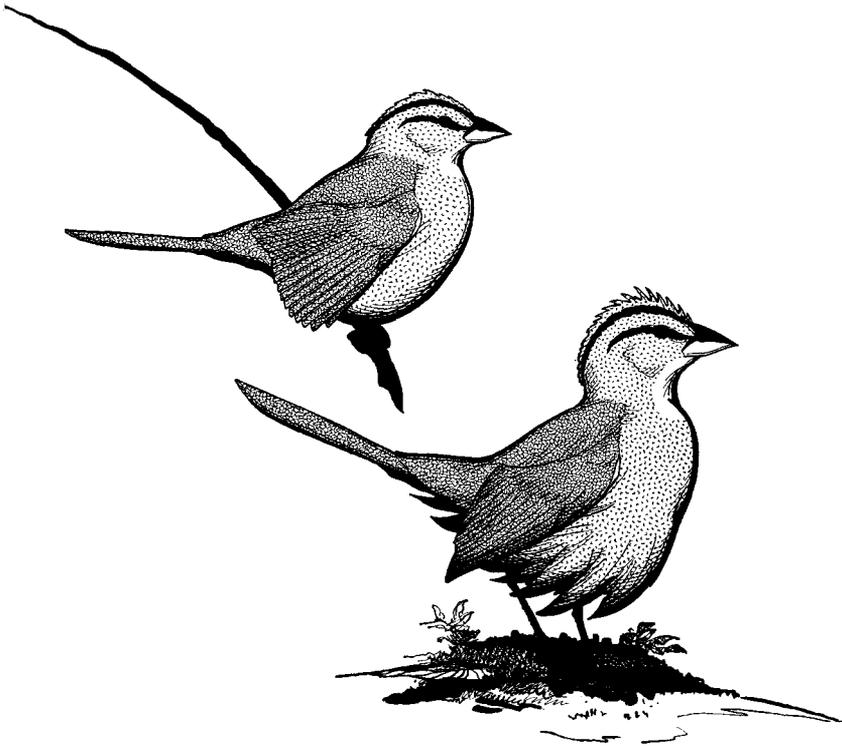


Figure 5. a. Top. A typical Fluffed Hunched posture with drooped wings and slight Crest-raising. b. Bottom. An erect posture with Crest-raising, Belly-ruffling, and raised tail.

ized by retraction of the head and neck (so that the head appeared to rest on the shoulders), slight Crest-raising, extreme fluffing of the breast and belly feathers (quite different from Belly-ruffling, insofar as the tips of the belly feathers were not distinctly separated), and slight drooping of the wings. The primaries were also spread to some extent; but the wings were not held out from the body as in the Wing-spreading display. The female sat in this posture for several minutes, occasionally interrupting it to perform a few hurried and rather erratic preening movements (with tail-quivering). Then she flew down to the ground again and behaved as before.

Some of the Hoarse Notes she uttered on the ground were rather peculiar. They were softer than typical Medium Hoarse Notes, but not as soft as the Muffled Hoarse Notes of the captive male described above. They were also somewhat distinctive in tonal quality. Most of them could be transcribed by something like *Whoo-oo-oo whoo-oo-oo . . .* They sounded as if they might be intermediate be-

tween typical Medium Hoarse Notes and Whisper Notes.

Some of them seemed to be "spontaneous." Once, at least, the female uttered a burst of such notes, accompanied by preening movements, when the male was silent and almost certainly out of her sight.

Both birds became less active by the middle of the morning, without having performed anything else in the way of pairing or other sexual or partly sexual patterns.

By next morning, their behavior had changed slightly. They came fairly close together occasionally, and even flew and landed together once or twice. The female performed very few Bill-up Tail-up displays with Wing-quivering. The male uttered songs or song-like patterns less frequently than before. Neither bird uttered Short Hostile Notes in the period (four hours in the early morning) that I watched them.

The most interesting incident of the day occurred rather late in the morning, when the male, who had been feeding near the female on the ground, flew up into a nearby tree. The female remained on the ground and assumed a Fluffed Hunched posture, more or less similar to the one assumed on the preceding day. Then she attacked and chased a Blue-black Grassquit (*Volatinia jacarina*). After the chase, she stood in a Fluffed Hunched posture again, facing in the direction of the male, and then lifted and quivered *one* wing (see Figure 1c). This Single Wing-raising was reminiscent of the asymmetrical wing-raising of male *Ramphocelus* tanagers before and/or after some copulation attempts.

The only conspicuous change in the behavior of the birds during the next four days was that they gradually spent more and more time close together. On the seventh day after the female was first seen on the male's territory, they spent as much time close together as most mated birds which have maintained the same pair-bonds for years. Their pair-formation seemed to be completed, and they suddenly began to perform new behavior patterns.

Copulations and Associated Patterns. The birds whose pair-formation is described immediately above also provided me with my best observations of later sexual behavior.

They both began to perform nest-building patterns early in the morning of the day their pair-formation seemed to be completed. The female started to peck at and pick up leaves and twigs on the ground shortly after dawn. At the same time, she uttered many Short Hostile Notes and bursts of Soft Chatter. Then she flew up, carrying a large leaf in her bill, and went to a potential nest site. After this, she rejoined the male, and the two birds fed side by side, occasionally performing some of their usual displays (e.g., mutual Medium Hoarse Notes, and Bill-up Tail-up patterns by the female). Then the male started to pick up nest

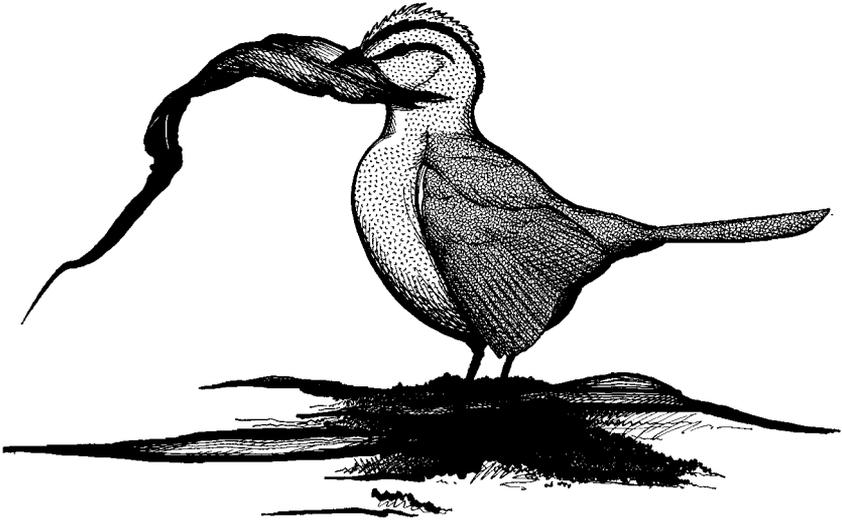


Figure 6. A posture sometimes assumed by birds picking up nest material.

material and utter Short Hostile Notes and Soft Chatters. This seemed to stimulate the female to do the same thing (again). Both birds continued to pick up nest material, rather sporadically and at fairly long intervals, for a considerable time. The male apparently always dropped his material almost immediately after picking it up; but the female sometimes carried leaves to the same potential nest site as before. The male sometimes, but not always, accompanied her on these trips.

Both birds tended to utter particularly long series of Short Hostile Notes and/or Soft Chatters when they were "wrestling" with particularly large and awkward pieces of nest material. Their Short Hostile Notes and Soft Chatters sometimes seemed to intergrade; but series of intermediate notes were less common than either of the two extreme types. Both birds also tended to assume a slightly distinctive posture when handling pieces of nest material. This was much like an ordinary Fluffed Hunched posture, except that the head was held higher and the Crest-raising was more extreme (see Figure 6). At the same time, they tended to perform Wing-trembling. This was rather similar to Wing-quivering, but the wings were not raised, and the actual trembling movements were of much smaller amplitude than typical Wing-quivering movements. I think that both birds always maintained this posture and continued Wing-trembling when they uttered Short Hostile Notes and/or Soft Chatters.

The first copulation was seen the next morning (the eighth or ninth

day after the beginning of pair-formation). After a brief period during which the birds fed and handled nest material as on the previous day, the male flew toward the female (who was in a tree at the time), landed on a branch a few feet away from her, hopped toward her very rapidly, mounted her, and copulated almost immediately. There was very little preliminary display by either bird. One of the birds (probably the male) uttered a couple of Medium Hoarse Notes as the male flew toward the female, and the female assumed a Bill-up Tail-up posture with Wing-quivering (and presumably Whisper Notes) just as the male mounted. She continued this display after he mounted, until he began actual copulatory movements. The copulatory movements of both birds resemble those of most other passerines. The copulation was apparently successful. The male flew straight away from the female as soon as copulation was finished, landed on a branch about 10 feet from her, and immediately performed a few bill-wiping movements. The female resumed the Bill-up Tail-up posture with Wing-quivering for a few seconds after the male left, and then stopped and also performed bill-wiping.

After this first copulation, the two birds performed more sexual patterns later the same morning and on several successive days. Their behavior did not change much during this period. It was also very much like the behavior of the same male and his previous mate just before she began to incubate. Only a few of the reactions in this phase of the breeding cycle need to be described.

The male repeatedly approached the female in a more or less excited-looking manner, without subsequently attempting to mount her. (References to "the female" in the following paragraphs refer to both the first and second mates of this male, unless specifically noted otherwise.) Sometimes the male simply "froze" in a crouch or hunched posture, with some fluffing and/or ruffling, as soon as he got close to the female. When this occurred, he usually remained motionless for some seconds or minutes, and then resumed normal unritualized activities. (His postures during these freezes were quite variable. The posture shown in Figure 1a was one of the more common types. It is a crouch posture with fluffing of the breast and belly feathers as in typical Fluffed Hunched postures.) More often, the male would start to hop around very rapidly when he got close to the female. His hopping was usually accompanied by extreme Crest-raising and Belly-ruffling, and often combined with vigorous but apparently unritualized bowing movements. Some of his bowing movements included a lateral component, and might be described as irregular pivoting. Between hops or bows he sometimes stood, momentarily, in a rather extreme erect posture with Crest-raising and Belly-ruffling and his tail raised higher than usual (see Figure 5b).

He frequently pecked at nest material before approaching and hopping and bowing near the female. Sometimes he actually picked up nest material and held it in his bill throughout the hopping and bowing. At such times, he tended to utter Short Hostile Notes and/or Soft Chatters.

The female occasionally responded to such approaches by assuming a Bill-up Tail-up posture, performing Wing-quivering, and uttering Whisper Notes. More often, she ignored the male and continued with whatever she had been doing before he approached. She assumed Bill-up Tail-up postures with Wing-quivering and Whisper Notes relatively more frequently when the male approached her in a less excited manner with Medium Hoarse Notes or no display at all.

She also performed Bill-up Tail-up and Wing-quivering patterns occasionally when the male was not approaching her. In some cases, such displays were associated with (usually following) periods of sitting in a more or less extreme Fluffed Hunched posture, pecking at and picking up nest material, performing tail-quivering, and/or uttering Short Hostile Notes. Sometimes the female performed what was either extreme Wing-trembling or slight Wing-quivering (without raising of the wings) while she sat in a Fluffed Hunched posture. Sometimes she tried to approach the male after she had sat in a Fluffed Hunched posture and/or carried nest material for some seconds. The male seldom responded to such approaches, and she usually performed bill-wiping movements when he failed to respond.

I know that the birds copulated fairly often in part of the period I watched them, but I never got a good view of any copulations except the one described. The birds always retired to dense cover before beginning their other copulation attempts. I could hear Whisper Notes during such attempts, and catch glimpses of some of the movements involved; but that was all. Such copulation attempts did *not* usually follow immediately after hopping, bowing, and carrying nest material by the male. They seemed to be preceded by nothing more than a few Medium Hoarse Notes, by one or both birds, or absolutely no display at all.

The male performed one combination of displays, once, when he was mated to his first female, which I never saw again. He landed on the ground, a considerable distance from the female (also on the ground), uttering Soft Chatter notes as he came down and for a few seconds after landing. Then he began to utter W and CH Notes in alternation. Occasionally he would also raise one wing and quiver it. This was rather like the Single Wing-raising of the female described above, but the male did not usually lift his wing far above the level of his back. He did not always raise the same wing; but he did not seem to alternate right and left wings in any regular manner. His wing-raising was partly synchro-

nized with the accompanying notes, insofar as it usually began as he uttered a W Note. He continued this performance for some minutes; but it did not seem to induce any reaction, and he eventually stopped without further display. The whole performance was reminiscent, in some respects, to the Upward Wing-quivering and Dawn Calling of male Brown-capped Bush-tanagers.

The second female began nest-building "in earnest" approximately an hour and a half after she first copulated with the male. This nest-building was rather different from the nest-building described above. It was much faster and more sustained. The female made numerous trips back and forth, collecting nest material and carrying it to the nest site almost without pause. Surprisingly, the site to which she carried the material during this intensive building was not the site to which she had carried material earlier, nor even near the first site. The nest at the second site was completed in a few days. The male did not help the female in the building of the real nest. (He still carried nest material occasionally, when he approached her and hopped and bowed; but this seldom occurred when she was building or very near the nest.)

I did not see much of the behavior of other Green-backed Sparrows in the phase of the breeding cycle in which copulations and nest-building occur. The little that I did see appeared to be similar to the behavior of the birds described above.

Discussion. It may be possible to identify the usual causes and functions of some of the partly or primarily sexual reactions and associated patterns of Green-backed Sparrows by analyzing their forms, and the circumstances in which they occurred and the effects they produced during the encounters described above.

Muffled Hoarse Notes are so similar to Medium Hoarse Notes in sound and some other respects that they must be produced by similar motivation. They may be direct expressions of both the same hostile motivation as Medium Hoarse Notes and some additional sexual tendency (the latter affecting the sound of the notes instead of, or in addition to, the orientation of the birds uttering the notes). Soft Chatters may be produced by an analogous combination of some sexual tendency and the hostile motivation usually producing Short Hostile Notes.

The Bill-up Tail-up patterns of Green-backed Sparrows are similar to the "soliciting" patterns of many other species of passerine birds in form, and are probably strictly homologous with them; but they are certainly not purely sexual, and possibly not even predominantly sexual. The fact that they are performed most frequently by females in the initial stages of pair-formation, and are frequently associated with escape movements, suggests that they are produced when both escape and sexual tendencies are activated, possibly when both tendencies are strong but

escape is preponderant. Some relatively weak attack tendency may be activated in conjunction with the escape tendency; and the sexual tendency involved may be either pairing or copulatory. The Bill-up Tail-up postures with the tail raised particularly high and without Wing-quivering movements or Whisper Notes are probably produced when the escape tendency is relatively stronger than when the more common Bill-up Tail-up postures with both Wing-quivering and Whisper Notes are produced.

All the Bill-up Tail-up patterns may function as appeasement.

The Fluffed Hunched posture may be little more than an "intention movement" or low intensity indication of the Bill-up Tail-up posture, produced by similar but slightly weaker motivation. It is rather similar to the "fluffed" postures of many other passerine birds (see, for instance, Hinde, 1955) in form, and may also function as appeasement.

Wing-trembling may be an analogous low intensity indication and/or a partly inhibited form of Wing-quivering. The drooping of the wings during Fluffed Hunched postures may be a low intensity indication of Wing-quivering and/or Wing-trembling.

The irregular bowing and pivoting movements of males are obviously produced by conflicting tendencies to approach and escape from the female; but the nature of the approach tendency involved remains obscure. It could be aggressive and/or sexual.

Some of the nest-building movements in copulatory situations may be performed as "substitutes" for more direct copulatory behavior. If so, they may be strictly comparable to such reactions as the feeding of the female by the male and mutual preening performed by mated birds of many other species in similar circumstances.

Some bill-wiping in sexual situations may be a reaction to thwarting. (It may be a reaction to any one or all of several different kinds of thwarting. Green-backed Sparrows perform bill-wiping movements in a great variety of situations, when almost any type of behavior is suddenly stopped or interrupted.)

General Comment

All or almost all of the displays of Green-backed Sparrows seem to be more or less strictly homologous with displays or associated unritualized patterns of Crimson-backed Tanagers. The display behavior of Green-backed Sparrows, as a whole, is certainly more like the corresponding behavior of Crimson-backed Tanagers than is the display behavior of the species of *Chlorospingus* that have been studied. Most of the displays of Green-backed Sparrows that are homologous with displays of Crimson-backed Tanagers are very similar to the latter in form and occur in similar sequences with similar frequencies, while many of the displays of

bush-tanagers that are probably homologous with displays of both Green-backed Sparrows and Crimson-backed Tanagers are distinctly different from the latter in one or more features.

The similarities between the displays of Green-backed Sparrows and Crimson-backed Tanagers may be an indication that the two species are closely related. It seems unlikely that such similarities could be convergent adaptations to similar factors of the external environment, since the two species differ in both habitat preference and general social or gregarious tendencies, and other tanagers and finches living in the same areas have more distinctive display behavior.

The principal difference between the display repertory of the Green-backed Sparrow and that of the Crimson-backed Tanager is that the former includes a larger number of distinct types of display than the latter. Adult Green-backed Sparrows have approximately 22 types of display or partly independent components of display in their repertoires, while adult Crimson-backed Tanagers, by the most generous assessment, can hardly have more than 18 types of display or partly independent components of display.

This is not a contradiction of the preceding statement that almost all the displays of Green-backed Sparrows are homologous with patterns of Crimson-backed Tanagers. Two or more displays of Green-backed Sparrows may be homologous with the same, single, display of Crimson-backed Tanagers (e.g., the Short Hostile Notes and CH Notes of Green-backed Sparrows, both of which seem to be homologous with the Short Hostile Notes of Crimson-backed Tanagers). Some displays of Green-backed Sparrows may (also) be homologous with unritualized patterns of Crimson-backed Tanagers.

The fact that Green-backed Sparrows have more different types of display than Crimson-backed Tanagers may be correlated with the difference between the general social habits of the two species. Green-backed Sparrows are much less gregarious than Crimson-backed Tanagers, probably because (or partly because) they are more aggressive than Crimson-backed Tanagers. (I have certainly seen more overtly aggressive reactions between neighboring pairs of Green-backed Sparrows than between Crimson-backed Tanagers under natural conditions.)

It may be more advantageous for very aggressive birds to perform a great variety of displays than it would be for less aggressive birds of otherwise similar habits. Very aggressive birds run a greater risk of becoming involved in contact fights, and suffering physical injuries, unless their aggressiveness is controlled in some way. As their aggressiveness is presumably advantageous in some respects (since it has been developed in the course of evolution), it cannot be controlled simply by being reduced. The development of a variety of displays may be an

alternative method of control. It may be "easier" to keep a dispute from "getting out of hand" by performing many different types of display, each of which probably conveys a slightly different signal, than by repeating a relatively small number of different types of display, each of which conveys a less precise signal. The more precise the signals, the less chance there is of a fight developing by mistake.

Very aggressive birds may also experience strong motivational conflicts more frequently than do less aggressive birds of otherwise similar habits. As strong motivational conflicts usually produce displays, very aggressive birds might be expected to display more frequently, on the average, than less aggressive birds. (I observed too few Green-backed Sparrows and Crimson-backed Tanagers to be able to make quantitative analyses of the whole display behavior of the two species; but my observations would suggest that Green-backed Sparrows do, in fact, display more frequently than Crimson-backed Tanagers in at least many situations.) It may also be more advantageous for birds which display very frequently to perform a great variety of displays than it would be for birds which display less frequently. If nothing else, habituation to relatively infrequent repetitions of a large number of different types of display may be less rapid than habituation to more frequent repetitions of a smaller number of different types of display. Habituation may be disadvantageous, in most cases (but certainly not in all—see above), simply because it reduces the strength of the signal effects of displays.

In an earlier paper (Moynihan, 1960), I suggested that highly gregarious species of birds tend to express a relatively larger proportion of their hostility by display than less gregarious species of birds. Green-backed Sparrows and Crimson-backed Tanagers are not necessarily exceptions to this general rule. It is possible that Crimson-backed Tanagers express a larger proportion of their hostility by displays than do Green-backed Sparrows, even though (or if) they actually display less frequently than do Green-backed Sparrows, as their total hostility may be less.

The fact that highly gregarious species may tend to have fewer distinct types of displays than less gregarious species of otherwise similar habits does not mean that the display repertoires of highly gregarious species will always tend to be reduced or simplified. Some aspects of the biology of some highly gregarious species, such as the habit of breeding in colonies, may favor the opposite tendency, i.e., the elaboration of display repertoires. This will be discussed in a later paper.

The frequent redirection of some of the hostile displays of Green-backed Sparrows may be another adaptation to minimize some of the disadvantageous effects of aggressiveness. Hostility redirected upon a mate is less likely to lead to a contact fight than hostility directed toward an opponent.

ACKNOWLEDGMENTS

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SUMMARY

This is primarily a study of the hostile and sexual displays of Green-backed Sparrows.

Their purely or predominantly hostile displays include Short Hostile Notes, a variety of Hoarse Notes, several Ruffling patterns, Wing-spreading, and (possibly) Gaping.

Their partly or primarily sexual displays include Plaintive Notes, a variety of songs or song-like patterns, Muffled Hoarse Notes, Soft Chatters, Bill-up Tail-up postures, Fluffed Hunched postures, Wing-quivering, Wing-trembling, and (probably) manipulation of nest material.

All or almost all of the displays of Green-backed Sparrows seem to be homologous with displays or associated patterns of Crimson-backed Tanagers (*Ramphocelus dimidiatus*). This is probably a reliable indication that the two species are rather closely related. The display behavior of the Green-backed Sparrow, as a whole, is more like the corresponding behavior of the Crimson-backed Tanager than is the display behavior of the species of *Chlorospingus* that have been studied.

The principal difference between the display repertory of the Green-backed Sparrow and that of the Crimson-backed Tanager is that the former includes a greater number of different types of display. This may be causally related to differences in the general social behavior of the two species, i.e., the fact that Green-backed Sparrows are more aggressive than Crimson-backed Tanagers.

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