

A SPECTROGRAPHIC ANALYSIS OF THE VOCAL REPERTOIRE OF THE AFRICAN VILLAGE WEAVERBIRD

By NICHOLAS E. COLLIAS

The object of this report is to make a contribution toward the understanding and objective portrayal of the vocabulary of a passerine bird. In 1953, the author, together with a specialist on human linguistics (Collias and Joos, 1953), published a report on the spectrographic analysis of the vocalizations of chickens. There seems to have been no previous spectrographic study of the vocal repertoire of a bird. Since that time the acoustic spectrograph has become quite widely used as an instrumental aid to the study of animal sounds and communication. However, most authors dealing with birds have largely restricted their attentions to the detailed analysis of song patterns. Quite recently, Poulsen (1958), working in Denmark, has presented a spectrographic study of the calls of the Chaffinch (*Fringilla coelebs*), using Marler's (1956) names of the calls as based on an intensive field study in England. The paper by Marler emphasizes song analysis, but it does not include spectrograms of some of the calls. Gompertz (1961) in Britain has described the vocabulary of the Great Tit (*Parus major*) using spectrographic analysis.

There are many other excellent studies of bird vocalizations, but those studies either lack spectrograms or else illustrate only a few of the calls of a species spectrographically. This article is not intended to be a comprehensive review of such papers but rather is a report of an attempt to cover the entire vocal repertoire of a species of bird with the aid of spectrographic analysis. A general classification of animal sounds from the viewpoint of communication and of function in the natural life of the animal is available (Collias, 1960).

The present report is based on a nine-months' field study of the eastern Congo race, *graueri*, of the common Village Weaverbird (*Textor cucullatus*) in Africa (Collias and Collias, 1959) and especially on observations of a breeding colony of the West African race, *cucullatus*, held in aviaries on the campus of the University of California at Los Angeles over a period of several years. In general, there was not much difference between the calls of these two races. The spectrograms accompanying this report are all based on tape-recordings made in California.

A brief abstract of some of the results has been published (Collias, 1961). This investigation has been supported by Grant G-9741 from the National Science Foundation and Grant 1623 from the University of California at Los Angeles. My wife, Elsie, helped in many ways, particularly by raising a young weaverbird used in the study. I am indebted to my colleague Thomas R. Howell for a critical reading of the manuscript and to W. R. Fish for advice on recording techniques.

MATERIALS AND METHODS

Some three dozen birds were secured from West Africa through the courtesy of Jean Delacour, who also kindly advised on methods of aviary construction and maintenance of the birds. Later, Gérard Morel generously sent us additional birds from Senegal, which were needed for replacements. Robert Constable was also helpful with advice on aviary construction and care of the birds, while Wayne Hansus gave us an African acacia tree (*Acacia* sp.) in which our colony became successfully established, built nests, and raised young. The birds were fed on a standard parakeet seed mixture, lettuce, mealworms and crickets, with grit and cuttlebone always available. Richard Burrows

helped take care of the birds during the main part of the study, and I am indebted to him for the recording on tape of call number 6.

The tape recorder used to record vocalizations was an Ampex Model 910, used with an Electro-Voice 666 dynamic microphone and operated by a 12-volt battery, with a DC-converter, enabling me to use the recorder inside the large (16 × 16 × 30-foot) aviary, free from any external power source. The vocalizations were recorded on tape at 7½ inches per second.

The spectrograms of each call were made on a "Sonograph," Model-R, manufactured by the Kay Electric Company. From three to a dozen or more examples of each call were so reproduced. Spectrograms of every call were made with both narrow and wide-filter, emphasizing precision with respect to either the harmonic or the temporal structure of the call, respectively. Spectrograms of each call were also made at both normal and half-speed, essentially the same general structure being revealed in either

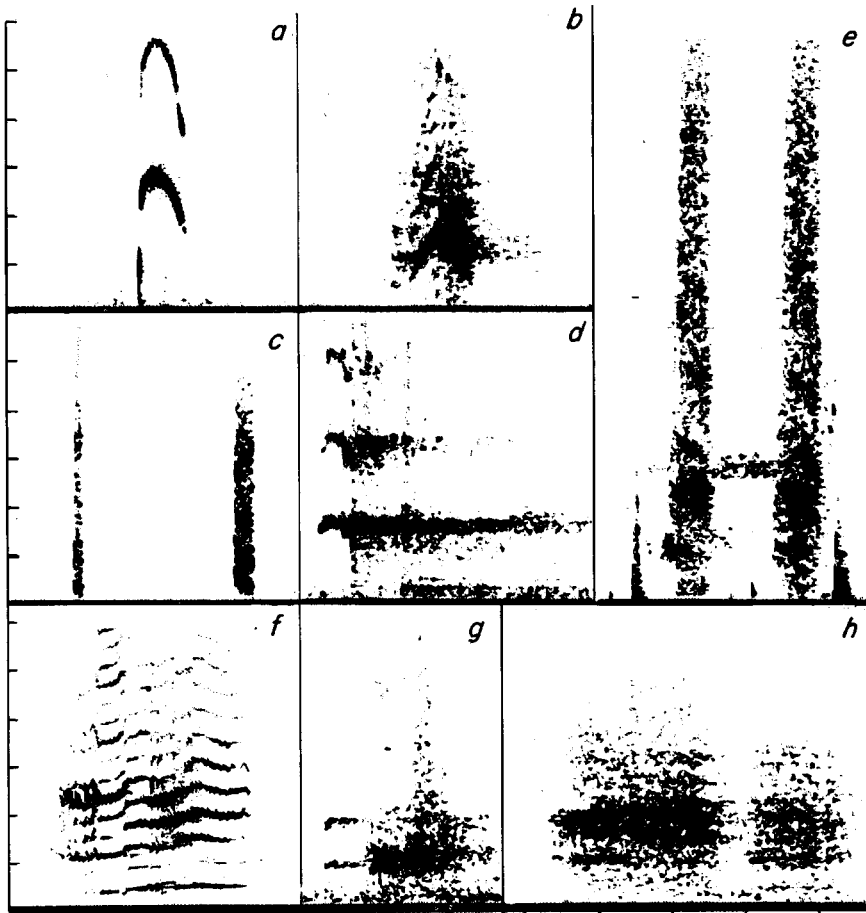


Fig. 1. Spectrograms of calls of generalized nature uttered by the Village Weaverbird (*Textor cucullatus*). Vertical scale, cycles per second with 2 kc. for each graduation; horizontal scale, time in seconds with 0.1 second for each graduation. Each call is depicted at half-normal speed and at narrow filter. See text for details.

case. For economy of space, and to bring out clarity of pattern, only spectrograms made with the narrow filter setting and at half-speed are here reproduced (figs. 1, 2).

DESCRIPTION OF CHARACTERISTIC VOCALIZATIONS

The Village Weaverbird is a very sociable and vocal species, and, in nature as in our aviaries, the crowded colonies of this gregarious breeder are seldom silent. It has some 15 different calls, each used in a more or less different situation, as characterized beyond.

Two main groups of calls may be recognized primarily on the basis of generalized versus specialized use. The calls of a generalized nature are given in similar situations to the corresponding calls in many other species of birds (Collias, 1960) and under situations not necessarily related to the nest or to the immediate vicinity of the nest. Calls of this group, numbers 1 to 8 in the following list, tend to have relatively simple structure, as indicated by their spectrograms (fig. 1), with the exception of the high-intensity distress call (fig. 1*f*). Calls numbers 9 to 15 are more specialized in relation to the complex nesting habits of the species, and these calls often have a complex spectrographic structure (fig. 2). With the exception of song, these specialized calls represent types of calls found in fewer species than the generalized calls of the first group.

The different calls are described under convenient verbal headings, with special reference to the physical structure of each as objectively portrayed in its spectrogram. The usual situations eliciting each call are also characterized. It is, of course, evident that for crucial evidence of the function of each call, play-back tests with specialized equipment would be desirable for this large and somewhat separate problem.

1. *Hunger-distress chirp* (fig. 1*a*, 1*b*).—The typical cry given by a baby bird begging for food emphasizes high frequencies and drop in pitch of each note. At one day of age (fig. 1*a*) this vocalization contains clean-cut harmonics extending at ordinary intensity above 20 kc.; only the lower two harmonics are illustrated. By the 18th day of age the call is much more strident, with a wide, diffuse spread of frequencies, resulting in a smudged spectrogram (fig. 1*b*). These records are of a hand-raised young weaverbird; figure 1*b* was taken 8½ hours after the young bird was last fed. Intimate and daily association with this individual suggested that this call note, or one sounding identical to our ears, was also given in a number of situations in which hunger played no obvious role, but in which the common element could perhaps be characterized, somewhat subjectively, as "distress." For example, in addition to giving this call when it was hungry, our young bird gave this chirp: (1) when it fell off its perch, (2) when "frustrated" in its attempts to obtain some object that it was obviously trying to get, such as a piece of string just outside its cage, (3) when one of us walked away from its cage after sitting quietly beside the cage for some time, and (4) when flying out of its cage and apparently unable to find a place to land. This was noted at the time the young bird was developing the ability to fly.

2. *Contact notes given while perched* (fig. 1*c*).—The spectrograms of two soft notes uttered by a 23-day-old hand-raised weaverbird just as it received food (mealworm or grain) are illustrated. At a very early age this call is given after the bird receives food and apparently is projected by conditioning to a later age as the bird gains experience with feeding situations. This call is quite possibly analogous to the "pleasure notes" of baby chicks, which function as contact notes and are also given by hungry chicks on receiving food (Collias, 1960). This sound could be described as a light, soft *stuck!*. Another situation in which this call was given was when the bird was hopping around on my wife's lap, pulling and biting at her dress. The bird also gave similar calls at times when exercising by flying back and forth in its cage.

As the spectrogram shows, the contact note differs strikingly from the hunger-distress call in being very brief in duration, in its abrupt onset, and abrupt termination, and in its emphasis on low frequencies. The strongest frequencies are below 2 kc., whereas the distress call has little energy below 2 kc. However, like the distress calls, the contact note tends to show some drop in pitch of the stronger frequencies, but this tendency is not nearly so extreme as in distress calls. The two notes illustrated give a good idea of the extremes of variation in duration of individual contact notes. This variation is small.

3. *Flight contact notes*.—Adult weaverbirds give spectrographically very similar contact notes while perched and while flying. However, in the flight notes, as revealed by the spectrogram, the stronger frequencies tend to average somewhat higher in frequency (mostly above 2 kc.) than is true of contact notes given while the bird is perched. The flight notes also sound to our ears slightly different from the contact notes given when a bird is not flying, and we designated the flight contact note as a sharp *chick!*, instead of the *tsuck!* that seemed to us a closer imitation of the perch contact note. No spectrogram is reproduced here of the flight contact note since it is so little different from the perch contact note; furthermore, the spectrogram of the flight call tends to be obscured by that of the accompanying wing-beats.

4. *Low-intensity alarm cry (fig. 1d)*.—A loud, rather sharp series of chirps are given when the observer approaches an aviary containing birds reared in the wild, or steps out of a blind, or when some unaccustomed sound, like the hissing of an air hose, suddenly impinges on the birds, or when the birds are being transferred to some strange place. The chirps given may be repeated but are well spaced, often coming as much as a second or more apart. The spectrogram, of a single chirp, shows the typical duration and frequency of alarm chirps. Each chirp is much greater in duration than any of the contact notes and lays emphasis on higher frequencies but does show some harmonic structure.

5. *High-intensity alarm cry (fig. 1e)*.—When a man moves suddenly and rapidly toward the birds, or climbs the colony tree, or when a hawk dives at the colony, or when a very intense abrupt sound occurs, such as a gunshot, sneeze, blowing of an automobile horn or slamming of a door, the birds immediately give a series of very rapidly repeated, very harsh and quite loud, brief notes, sounding to us like a harsh chatter, —*kik!-kik!-kik!-kik!-kik!-kik!* and so on. The spectrogram reveals an extremely wide spread of frequencies (over 20 kc. when the sound is reproduced at normal intensity) of each note, with most of the energy being concentrated at high frequencies (4 to 6 kc.), compared with other call notes. With the exception of the hunger-distress cries, other calls of the Village Weaverbird have little or no energy above 12 kc. Each individual note of this alarm cry is rather brief (0.05 to 0.07 seconds), as many as three notes being uttered per second, although none of these notes is so brief as the ordinary contact notes of the species.

One might inquire into the reason for the marked difference in patterning of the low- and the high-intensity alarm cries. Possibly the reason for the brevity of the individual notes in the latter call is that there is no time in an emergency situation for call notes of longer duration to be given. Indeed, we have noticed in Africa that when suddenly surprised by a hawk the colony may sometimes immediately dive into protecting cover without giving any alarm cries.

One effect of this alarm cry is to stop the noisy, persistent cheeping of hungry nestlings.

6. *High-intensity distress call (fig. 1f)*.—When a Village Weaverbird is held in the

hand and is not accustomed to this situation, it often utters a loud, prolonged strident squawk, which the spectrogram shows has numerous harmonics of broken or quavering pitch. It is not the fundamental that is strongest, but, as in the spectrogram shown, it is first the sixth and later the fourth harmonic, that is, the emphasis in this call is on the higher frequencies, as in the case of alarm cries generally. Each squawk may rise a little in pitch but ends with a drop in pitch or has a harsh ending.

7. *Low-intensity threat sound* (fig. 1g).—A deep, "blackbird-like" note, *chuck!*, often given repeatedly, is uttered when a Village Weaverbird discovers or is given some object related to its normal requirements, such as a mealworm, grasshopper, lettuce, fresh nest materials or even fresh water. We observed that our hand-raised weaver in some of these situations was likely to peck and bite at us if we subsequently attempted to remove an object, perhaps some tidbit, just given. Presumably, the call may be a challenge, announcing readiness to defend some possession.

On one occasion, a three-foot king snake (*Lampropeltis getulus*), that had previously entered the aviary and swallowed one of the birds, was caught and later was returned to the aviary in a glass aquarium. The birds generally ignored it, but when it was held in the aquarium next to two brood nests containing nestlings, the male weaverbird came nearer and gave low-intensity threat sounds repeatedly and much more frequently than it did when the observer did not have the snake. This test was repeated some half-dozen times with the same results. When the snake was held in the hand in the tree, the male weaverbird would silently dive at it, striking at the snake's head.

The spectrogram demonstrates that the low-intensity threat is a quite prolonged note with an emphasis on relatively low frequencies and that the call starts and fades out gradually, the latter properties, in particular, being in marked contrast to the contact calls. The low-intensity threat sound differs from the alarm cries of the species in the emphasis of the former on relatively low frequencies.

8. *High-intensity threat sound* (fig. 1h).—When a dominant male chases a subordinate male on the wing, a single, very harsh snarl or "growl" is often heard. This call is rarely given under other circumstances, although we have heard male Village Weaverbirds give it in Africa whenever they chased a female Didric Cuckoo (*Chrysococcyx caprius*) away from the colony tree. This species of cuckoo is a persistent brood parasite of the Village Weaverbird.

The spectrogram indicates that the high-intensity threat sound resembles the low-intensity threat in its gradual onset and gradual termination and, as compared to most other calls, in emphasizing low frequencies. But it differs from the low-intensity threat in being more prolonged and in that the strongest frequencies are not quite so low. It differs from the low-intensity alarm cry in being harsher and in lacking much energy above 6 kc.

9. *Male song* (fig. 2a, 2b).—Only the male sings in this species. He may sing directly toward another male, or to his own mate in her nest. The song is the most complex and the longest of the various vocalizations in the repertoire of the Village Weaverbird. Beginning with a series of brief and variable notes, the male terminates the song with one or two, generally two, prolonged buzzes. This buzz is the longest and one of the most characteristic notes of the species, although it should be added that a buzz is also typical of the song of many other species in the subfamily of true weaverbirds (Ploceinae). The only other call given by the Village Weaverbird that resembles the terminal buzz of the song is the high-intensity threat or growl, which the buzz resembles in its gradual onset (first buzz) and termination (second buzz). The prolonged nature of this call has a considerable component of strong, low frequencies. But the buzz differs

in being even longer (as much as a second in length), in being somewhat pulsed, and in its much more complicated patterning which contains high as well as low frequencies.

It is of interest that the song also resembles the high-intensity threat in the general type of situation in which it is given. Singing is most frequently heard in formalized

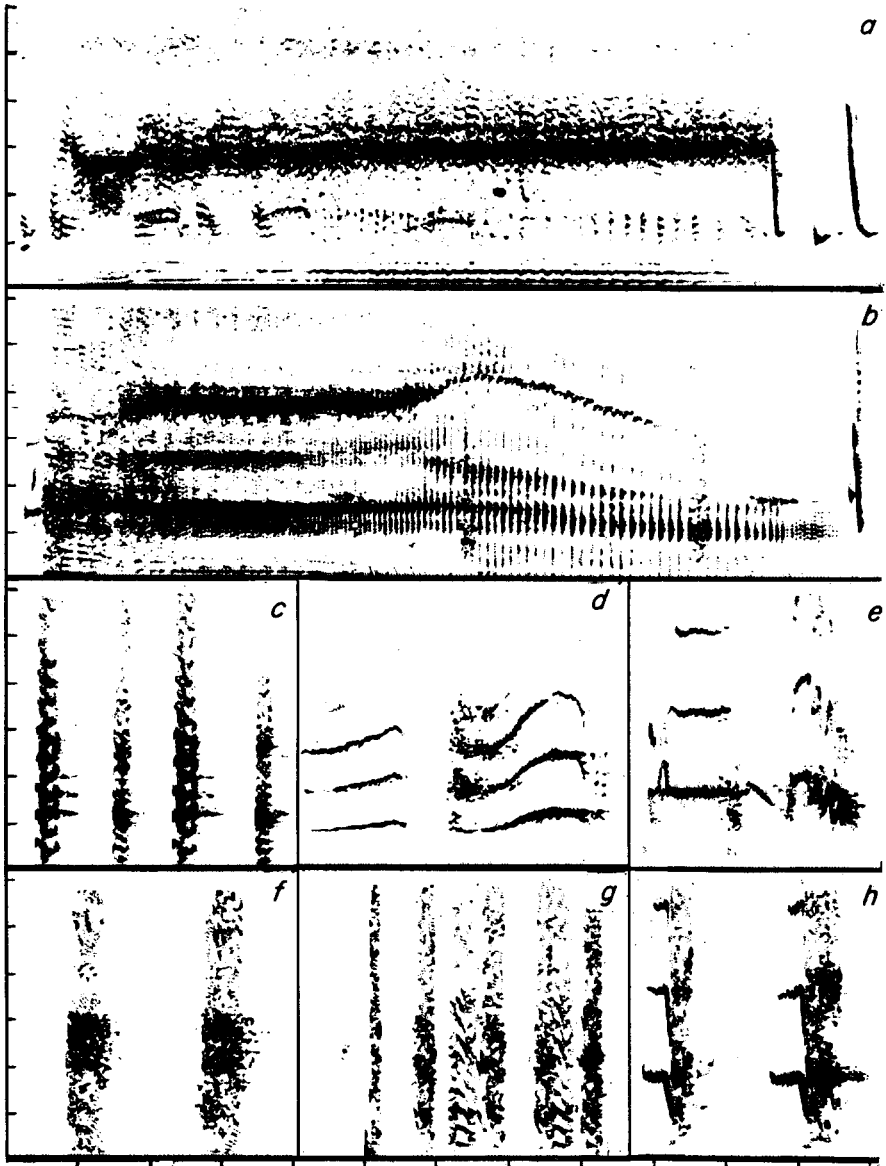


Fig. 2. Spectrograms of vocalizations of the Village Weaverbird specialized in relation to the complex nesting habits of the species. Vertical scale, cycles per second with 2 kc. for each graduation; horizontal scale, time in seconds with 0.1 second for each graduation. Each vocalization is depicted at half-normal speed and at narrow filter. See text for details.

territorial boundary disputes between males, as well as in the course of disputes over dominance relations away from the territory. Not infrequently, a song bout will be interspersed with a sharp exchange of pecks and may culminate in a violent fight, with both birds grappling one another with their feet, biting and pecking at the head of the opponent. The general situation that stimulates singing differs somewhat from that in which the high-intensity threat or growl is given. Although the latter seems almost always to be directed at a subordinate bird, the song is often heard from a subordinate male defending his territory against a male that ordinarily dominates on neutral ground. A dominant male as a rule merely chases a subordinate intruder out of his territory without a formalized song contest.

The spectrograms illustrate only the penultimate buzz (fig. 2*a*) and the terminal buzz (fig. 2*b*) that at once follows the penultimate buzz in a typical song. These spectrograms omit the variable and brief preliminary notes and phrases. In the first buzz there tends to be a slow and gradual rise in pitch, whereas, in the second buzz the pitch is at first sustained and then falls toward the end of the song. The first buzz contains wavering ill-defined harmonics, and the bird sings both high and low at the same time. Most of the energy is at 5 to 7 kc., and there are marked harmonics at 0.4 kc. and at 0.6 kc. In the second buzz there is a strong energy band at 2 to 3 kc. and another at 7 to 8 kc.

10. *Nest-material carrying call* (fig. 2*c*).—When returning to his nest with a strip of nest material, the male almost invariably keeps uttering a series of brief, relatively low-pitched, pleasant-sounding notes of rather light intensity, but readily audible from a short distance. At normal speed the call has an almost humming quality. The spectrogram of this very repetitive call shows that each individual note is only 0.02 to 0.04 seconds long. The different notes are given at a rate of three to six per second. Sometimes the male utters a single series of notes, and often, as illustrated in the spectrogram, there are two series of notes, each type of note alternating with the other. The nest-material carrying call closely resembles the perch contact call, and, in fact, in the case of young immature males is scarcely distinguishable to the ear, suggesting that it arises from this call in ontogeny. It differs in its typical form from the perch contact note in having a somewhat harmonic structure and in a tendency of some of the harmonics to ascend toward the terminus of each note.

11. *Male call announcing arrival of females* (fig. 2*d*).—In this species in central Africa, we observed that the males occupy the colony tree several weeks or more before the females appear. The males build the external shell of the nests, which the females may later accept, lining the interior, incubating the eggs, and doing most of the work of raising the young. When the females appear, there is wild excitement among the males, all of which display, or fly rapidly back and forth in their small territories. They give voice to peculiar cries which are very different from any of their other vocalizations and are rarely, if ever, given in any other type of situation than that announcing the arrival of visiting and inspecting females. This call also served to alert the observer to the renewed burst of activity in the colony.

Two examples of this call are illustrated in figure 2*d*. This vocal signal is characterized by its relatively clear harmonic structure, with a marked upswing in pitch and increase in loudness, although there is sometimes an abrupt drop at the end of the call. There are many fewer harmonics than is true of the brassy scream of the fear or high-intensity distress squawk, and in strong contrast to the latter the emphasis is on the lower harmonics, with the fundamental being the strongest in the male call announcing the arrival of a female.

12. *Nest-display call of male (fig. 2e)*.—When a female perches in or near a male's territory, he displays his most recently built, greenest nest to her. He hangs upside down beneath the bottom entrance of the nest, fluttering his widely opened wings and rotating his body in a more or less horizontal plane. At the same time he repeatedly gives voice to a double-noted utterance, that we named the *look! see!* call for our convenience. The whole display with its associated vocalizations definitely attracts the female. We have often seen a female wait until the male displayed the nest and then promptly enter and inspect the nest.

The nest-display call consists of a squeal, quickly followed by a descending, rapid trill. As the spectrogram reveals, the squeal is a quite sustained note about 0.15 seconds long with widely spaced harmonics. The fundamental at about 3.5 kc. is the strongest. The trill is only about 0.1 seconds long. This whole, double-noted attraction call is quite different from any of the other vocalizations of Village Weaverbirds, although it has a slightly chirping quality and is vaguely reminiscent of the low-intensity alarm chirp of the adult, of some of the chirping distress cries of the young, and of what we have called the "nest call of the female" (see beyond).

13. *Scold-chatter call of the male (fig. 2f)*.—After an inspecting female enters a male's nest, and especially if she pokes her head out of the nest as if to leave, the male owner of the nest gives a rolling series of brief and fairly harsh notes, while perched or hopping about in his territory. Sometimes these notes are run together into a compound note, although the usual rate of repetition varies from about 6 to 20 per second.

As the spectrogram clearly shows, most of the energy in the scold-chatter call is concentrated at about 4.0 to 6.4 kc. and there is little or none above 12 kc. In this respect the call differs strikingly from the otherwise quite similar high-intensity alarm cry (fig. 1e), which, as described previously, is particularly characterized by its extremely great range of frequency spread, from near the bottom of the frequency scale up to almost 24 kc.

We are not sure of the function of the scold-chatter call. Possibly it is a warning to other males and a type of territorial defense note, since neighboring males not infrequently will invade another territory in an attempt to prevent a female from entering the other male's nest.

14. *Copulation call (fig. 2g)*.—Within two or three days after a female accepts the nest of a male, the two usually begin copulating, and a day or two after that the female begins to lay her eggs. Just prior to and during copulation a whirring note is given, apparently by either or both of the sexes. This call has a somewhat wooden and rolling quality and is of low intensity. Examination of the spectrogram shows that the call consists of a rapidly uttered series of very brief notes, each being only 0.01 to 0.05 seconds long. These notes may be run together, accounting for the whirring quality of the call. Most of the energy in the call lies between 1 and 7 kc. and the call has something of a harmonic structure. These two factors, together with the low intensity of the call, perhaps account for the fact that it is not unpleasant to our ears.

It may be added that when the female has small nestlings she often pauses just before entering the nest, assumes what looks like the typical precopulatory posture with wings vibrating, bend of the wings raised, and head and tail lifted a bit, while she utters a call very similar, if not identical, to the copulation call.

15. *Nest call of female (fig. 2h)*.—After a female accepts a nest, the male is largely excluded from entering it, although he may often peer up into the entrance. On such occasions the female within frequently utters a loud, rather high-pitched call of a somewhat squealing or "protesting" quality. We have no clear idea of its function, although

it possibly prevents the male from disturbing the female while she is lining the interior of the nest or when she is incubating. Upon hearing this call, the male generally leaves and never attempts to force his way into the interior.

As the spectrogram shows, this call of the female starts with a short, rather high and sustained note (a "squeal"), which then drops very abruptly in pitch, the remainder of the call being lost in a smudge. The squealing onset of the call is strongest at about 3.6 kc. with weaker harmonics at about 7.2 and 10.8 kc.

DISCUSSION

Remarks on terminology.—The study of vocal communication in animals is a particularly difficult field in which to avoid misinterpretations based on one's own subjective impressions and his identification with the subjects of study. Perhaps the best way to present a description of animal calls would be to label them call number 1, 2, 3, 4, and so on, using spectrograms to indicate the structure of each call and attempting to describe as impersonally as possible all of the various situations in which each vocal utterance is emitted. But even when this procedure is followed one may ultimately come to the conclusion that the common element in the various "objective" situations giving rise to a particular vocalization is often very difficult to characterize, except by means of such "subjective" human categories as distress, pleasure, alarm or threat (Collias and Joos, 1953). The important thing is, first, that this type of characterization be done after and not before detailed study of the various vocalizations of a given species. Second, such terms should not be taken too seriously, that is, they should not be considered as ends in themselves, thereby blocking further investigation, like the ambiguous term "instinct." One should investigate not whether a given sound is to be called a "distress" or "threat" sound, but he should describe the precise structure and the situation under which it occurs in nature and the function of the sound. The last should preferably be determined by deliberate experimentation, but quite often nature furnishes experimental situations that give some clue.

In the preceding paragraphs, some of the calls have been placed in what appear to be somewhat subjective categories. Perhaps some have been erroneously placed. But these labels were introduced deliberately only after the various calls had been observed some hundreds or thousands of times in a variety of situations, enabling the generalization implied by the terminology used to be suggested. Perhaps, with further study, it may be possible to describe more acceptably ("operationally") the common feature in the different situations associated with a particular vocalization as well as the range of variability in the latter.

Comparison between different vocalizations of the Village Weaverbird.—Another problem concerns the similarities and differences between the various vocalizations of a species of animal. Thus, comparison of the physical structure of the different vocal signals of the Village Weaverbird, in relation to the presumed function of these calls, leads to certain general statements: (1) Notes that are characterized by having a very brief duration include contact calls between different individuals and calls denoting uncontested possession of some object such as food or nest material. In contrast, the longest notes of the species include the high-intensity threat (or "growl") and the buzzing terminus of the male's song. (2) Calls with relative emphasis on the higher frequencies include particularly the distress cries and alarm cries. On the other hand, calls with relative emphasis on low-pitch include especially threat signals of different kinds and also the contact calls and the call given by the male when carrying nest material. (3) Descending frequencies characterize especially the high-intensity alarm cry and the

distress cries, whereas ascending frequencies are most marked in the call by the male announcing arrival of females and in the repetitive notes uttered by a male carrying nest material. (4) Finally, the harshest sounds given by the Village Weaverbird include the higher intensity signals of distress, alarm and threat. On the other hand, clear harmonics are present in the male call announcing arrival of the female and in the repetitive notes given by the male carrying nest materials.

It is evident from perusal of the preceding list that Darwin's principle of antithesis applies to the vocalizations of weaverbirds, as in other animals (cf. Collias, 1960), since calls given in opposite types of situations tend to be opposites also in their physical structure.

Comparison of vocal communication in the Village Weaverbird and other birds.—The vocalizations of this species fall readily into the general ecological and functional classification of animal sounds previously published elsewhere (Collias, 1960), and similar categories have been used in this report. It may be worthwhile to point out, for example, some resemblances between vocal communication in the Village Weaverbird and another bird, the Domestic Fowl, the vocalizations of which have also been studied in detail (Collias and Joos, 1953). In both species, the distress chirp of the young bird is characterized by emphasis on descending frequencies. However, there is no very close resemblance in structure of the flock or brood contact notes of the young in the two species, except that in both instances the notes are relatively weak and briefer in duration than are the distress cries. The various attractive calls of a domestic hen to her chicks are soft, repetitive, brief and low-pitched, resembling in all of these respects the "copulation" call of the female weaverbird, which, as we have seen, is given not only during copulation but also just before a female with nestlings enters her nest. The alarm cries in both species are loud and harsh and emphasize the higher frequencies. However, in the weaverbird, the highest alarm cry consists of a series of very brief notes instead of being a prolonged scream as in the fowl. Threat sounds in both birds, as in many other species, are harsh and deep and are characteristically low-pitched, instead of high-pitched and shrill, as are the alarm cries. The song of the male weaverbird, like the crowing of the cock, is the longest and one of the most specific and harmonious sounds of the species.

Enough has been said above to bring out the probable generality of the types of vocal signals described, since the Village Weaverbird and the Domestic Fowl are very different kinds of birds.

Vocal communication and the principle of adaptive specialization.—In studying the various vocal signals given by each of a variety of species (Collias, 1960), a number of things become apparent. First, non-human species have a very limited vocal repertoire, often consisting of merely one to two dozen vocal signals. Second, this vocal repertoire is not so limited for most species as a casual perusal of the literature might suggest. Third, the vocal signals used are related to the living problems faced by each species, and paralleling the general adaptive specialization of each species is a corresponding specialization and diversification in the vocal signals used to aid the more specialized parts of its existence. As summarized elsewhere (Collias, 1960), Seton had noticed that the wolf uses a variety of special signals to aid its hunting, whereas Fitch described a correspondingly great diversification and specialization in the alarm cries of an animal that is much hunted, the California ground squirrel (*Citellus beecheyi*). More recently, we observed in a study of vocal communication and social behavior in the northern elephant seal (*Mirounga angustirostris*) during its breeding season that five of the eight vocal signals noted apparently represented different varieties of the

threat sounds so often used on its breeding grounds by this constantly bickering species (Bartholomew and Collias, 1962). But, interestingly enough, in association with its very large size and isolated breeding habitat, the elephant seal, at least in the breeding season, differs strikingly from many other species of animals in apparently lacking an interspecific alarm cry. At least we heard none, although these seals readily threaten a person.

Some 15 distinct calls have just been described for the Village Weaverbird. The most interesting thing, perhaps, about vocal communication in this species is that fully half of the different vocal signals are closely related to its highly specialized mating and nesting habits. In this respect, the Village Weaverbird provides a good example of the adaptive specialization as applied to vocal communication among animals.

SUMMARY

The African Village Weaverbird (*Textor cucullatus*) has at least 15 different calls, each used in a more or less different situation. The physical structure of these vocal signals is objectively characterized by use of sound spectrograms, and a description is given of the various situations eliciting each vocalization.

It is shown that opposite types of situations generally induce vocal signals having more or less opposite types of physical structure, illustrating Darwin's principle of antithesis in this species.

Comparison of the vocal signals of the Village Weaverbird with those of the Domestic Fowl and other birds brings out many similarities and helps generalize the functional categories used for the different vocalizations.

The principle of adaptive specialization is applied to vocal communication in animals, with special reference to the Village Weaverbird. Thus, half of the various vocal signals used by this species are closely related to its highly specialized mating and nesting habits.

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