

Bird vocalizations as systems of communication¹

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(With eleven text-figures)

I believe all naturalists will agree that birds are the most vocal animals apart from man. But what is all this noise for? Obviously—for communication! (Thorpe 1961). This answer at once gives rise to a second question, namely, what are the special circumstances of bird life which render vocal communication pre-eminently valuable? After all birds have outstandingly refined and perfected visual powers including excellent colour vision; they show a wide and often spectacular development of plumage, obviously adapted for display and signalling purposes. Linked with these they have evolved a complex series of elaborately and precisely controlled display movements and postures, designed to exhibit to the utmost advantage, as signalling devices, almost every feather of these specific plumage patterns: so, with all this, where does the voice come in?

Sound production, coupled with the right degree of development and specialization of the organs of hearing, has certain intrinsic advantages over other communication methods. The methods of communication employed by animals are, of course, very various. Apart from the visual signals, displays and gestures just mentioned, odour trails and the marking of territory by excreta and the secretions of special glands are all common and widespread in the mammals and the social insects. Such methods may indeed have their advantages for strictly terrestrial animals. But for the mobile and active birds, so often nesting in trees or bushes and little in contact with the ground, they have little utility. Again much sex behaviour in mammals is initiated and controlled by sensitivity to special secretions, as with the dog seeking the bitch on heat. However, birds, being mostly aerial, have had no reason to develop the special secretions and high olfactory sensitivity found in mainly ground-living animals. So it is understandable that the birds should not have developed olfactory stimulation as a feature in their sex life [Thorpe, W. H., see chaps. 2, 5 and 6 in Hinde, R. A. (Ed.) 1972].

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Quite apart from the special needs of creatures which are airborne, active and largely arboreal, these above-mentioned methods of communication all have considerable general limitations compared with mechanical vibrations of a medium—especially the air—as signals. Spiders of course can obtain certain information as a result of perceiving the vibrations of the web, and rabbits signal by thumping the ground. But the great advantage of using airborne or waterborne vibrations, namely ‘sound’ as signals, is that sound carries far and fast and readily bypasses obstacles. There is also a great spectrum of frequency and intensity available for use. In terms of mechanical effort, sounds are extremely economical to produce, and—since sounds vanish as quickly as they are produced—the items of information do not accumulate so as to prevent the sending of further messages. So it is obvious why a language (and after all the communication systems of birds may legitimately and in a general sense be termed a language) if it is to achieve its full potentialities must be a language of sounds. But although the language of sounds has been brought to a high degree of development by the insects, the amphibia, the mammals and perhaps also by the fish (which would be expected, because a sound wave travels farther, for a given loss of amplitude, in water than in air, and also approximately four times as fast) the birds, again apart from man, have raised the language of vocalizations to a level not otherwise attained in evolution.

Granting all this we may ask the question, ‘What are the particular circumstances of avian life which render vocal communication so valuable?’ These can be briefly listed under two headings as follows: *A.* On the nesting grounds during the breeding season. Here the communication is primarily by song or its substitute call-notes in birds which have no song. *B.* On winter or off-territory feeding grounds, on migrations and in strange or hostile environments. For these purposes it is usually the call-notes which are involved rather than the song, but there is no doubt that there are many examples (e.g. Terns) where call-notes, besides constituting a series of signals widely and perhaps innately understood throughout the species as warning calls etc., can also contain sufficient individual elaboration to render them serviceable as individual recognition marks.

Included under group *A* above, we may list the advertisement, establishment and maintenance of territory. The establishment of the pair bond. The recognition of the mate and the ability to distinguish him or her from other individuals in neighbouring territories; and also, as often seems to be the case, to distinguish between various neighbouring individuals. Then when the young are hatched and moving about, and while parental care is still operative, it is clearly often important that the young should be individually recognizable by the parents and the parents by the young. It is doubtful how far this situation obtains in the nidicolous

and altricial species but there is clear evidence that in many of the nidifugous and precocial birds such individual recognition may be extremely important and may extend for a long time after the young are fully winged and active. Even though they may not require feeding, it can often be important for the young to be protected from the inclement weather, shepherded away from danger and introduced to the best feeding grounds and the most suitable types of food available in the general environment (Thorpe 1968).

Under the heading of *B* the following circumstances must be mentioned. For life during the winter and in feeding flocks, as indeed throughout the whole life-history, calls warning of predators or other dangers are perpetually required. Above all perhaps on migration is it undoubtedly valuable, on many occasions, that a flying group should keep together.

Finally there are some situations common to *A* and *B*, namely communications in darkness or bad visibility, communications in dense vegetation and communications amongst colonial nesters, especially dense colonies of sea birds, where nothing less than the great elaboration and precision of which auditory communication methods are capable is likely to provide the necessary refinement and individually recognizable multiplicity of signals.

A very significant example of the way in which call-notes are often adapted to the particular function that they serve is provided by the call-notes used by various passerine families that give warning of danger from predators. Marler (1955) has shown how such notes are specialized in their acoustic structure for the particular type of predator encountered. Thus in finches, chats, warblers, thrushes and wrens, detection of an enemy on the ground or perched in a tree (e.g. a weasel, a hawk or an owl) results in the birds giving repeated loud calls of extremely brief duration but covering a great frequency range. Call-notes of this structure usually sound more or less click-like or tick-like to our ears. They are often given in a situation in which it is presumably advantageous for the bird concerned to draw attention to this particular danger and to warn others of its exact location. Thus we get what is known as the mobbing response of many small birds to a perched owl in which they stand around at a fairly safe distance and chatter at the enemy. The result is to attract neighbours to join in the mob. Now it has been shown that this type of call has the characteristic of being very easily located—not only by bird ears but by our own; for loud click-like sounds are quickly and readily referred to the right direction and roughly to the right distance.

When however danger is from a flying predator in the air above, e.g. hawk, or an owl, then the threat is immediate and the danger great. So far from making itself conspicuous the threatened bird dives into the

nearest shelter and gives a type of call which starts and stops gradually and maintains a fairly constant pitch somewhere around 7 kHz. Other birds hearing these calls likewise fly to shelter and repeat the same calls from their hiding-places. The point that first strikes the human observer on hearing these calls is that they are extremely difficult to locate. This is due in the first place to the fact that they lack the characteristics previously mentioned which make localization easy. But besides this there is another reason. A bird employs the same methods as we do to locate the origin of a sound. These consist of comparisons between the sound as received by the two ears involving three different types of data: (1) phase difference, (2) intensity difference and (3) time of arrival. Phase difference is most likely to be valuable at low frequencies: for instance, the data become ambiguous when the wavelength is much less than twice the distance apart of the ears. Intensity differences are most valuable at fairly high frequencies and the differential effect on the two ears is due to the 'sound shadow' cast by the head of the listening bird. Sound shadows only become important when the wavelength approximates to the diameter of the obstruction. Differences between the time of arrival of the sound at the two ears will, of course, be more obvious the larger the distance apart of the ears. But calculations suggest that sounds about the frequency of 7 kilohertz are likely to be maximally difficult to locate for the ears of a bird of medium size—say a hawk or an owl. This frequency is too high for effective binaural comparisons of phase difference and too low for there to be enough sound shadow perceptible by the ears. Thus the *seet* call of the male chaffinch probably gives no clues as to its location either by phase or intensity difference. This leaves only the third method, the appreciation of binaural time differences; and just because the sounds begin and end gradually or imperceptibly, no clues for time difference are supplied. So it appears that the alarm-calls of quite a number of passerine families, uttered when a predator threatens, are both physically and physiologically far more precisely adapted to their function than anyone would have supposed previous to Marler's work.

One of the most interesting results of recent studies of bird behaviour has been the discovery of the desirability, one may even say the necessity, that parents should learn to recognize their young individually and the young their parents. Even in nidifugous species, where the young move about and may scatter soon after hatching, this individual recognition is often crucial. This implies of course both individual distinctiveness and the ability to learn and respond appropriately to individual differences. Indeed when we consider the problem of reproduction and survival faced by birds such as many species of gulls, terns, gannets, penguins and so on—birds which nest in very dense colonies and obtain their food during the nesting period in rather restricted areas of sea or

coastline near their colony—we can at once see a number of ways in which such abilities for individual recognition could be advantageous. Without it the feeding of the young, at least as soon as they become mobile, could be a very wasteful process. Hordes of young would be competing for food from each individual adult as it returned to the colony; with the result that the strongest, the most fortunate, the most mature or the quickest, would obtain ample food and many others would starve. And those which did survive would be no better fitted to take their place as adult members of a colony-nesting species. In the circumstances of colony nesting the eugenic need is for selection to operate so that adults which ensure that their own young are fed are at a selective advantage without, thereby, decreasing the chances of other young in the assemblage. This is the *sine qua non* of social life.

Tschanz, summarizing in 1968 nearly 10 years of work, was a pioneer in his demonstration that young guillemots (*Uria aalge*) learn to react selectively to the call of their parents and that, during the first few days of life, the parents similarly recognize their own young. Indeed there is some evidence that the young while still within the egg may learn to respond to and recognize some aspects of the sounds produced by the adults. There has long been considerable reason for suspecting that in some terns and gulls also (Beer 1970) the adults can recognize their mates and young and the young their parents, by call alone. Thorpe and his co-workers (Thorpe 1968; Hutchison, Stevenson & Thorpe 1968; and Stevenson *et al.* 1970) have studied two species of terns in this respect, the Sandwich Tern (*Sterna sandvicensis*) and the Common Tern (*Sterna hirundo*) and have found that the so-called 'fish call', uttered by the parent when returning to its young with food, has just the kind of structure required to provide auditory data for individual recognition. In the forty different individuals from which it was possible to obtain a series of samples of the 'fish call', each bird had a call measurably distinct from all the others and the successive calls given by any one bird were extraordinarily similar. Each call lasts only half a second or less but within this half-second there are three phases and each of these phases is different from the others and characteristic of the individual which gives them, in a combination of qualities. Thus we can measure independently the duration of the segment, the number of pulses in a segment, the lowest and highest frequencies displayed and the change with time in the distribution of the principal frequencies. Yet with all these individual characteristics present the 'fish call' is still a good diagnostic feature for the species. In the case of the Sandwich tern for instance it seems probable that the duration and number of pulses in the third segment are used to identify the individual's call and also that the frequency changes during the passage of the second segment contribute to this. On the other hand the first segment of the call does not show individual

differences of the same degree and it is likely that the first segment is primarily of importance for indicating the species and the last two more specialized for determining the individual. And all this information is conveyed in a call lasting as I have said half a second or less and the individual segment perhaps enduring for no more than a fifth of a second. Sensitivity to changes in auditory stimulation of such extremely brief duration are of course quite beyond the capacity of the human ear. But there is now a considerable amount of evidence showing that the temporal sensitivity of the bird ear is better than ours by a factor of about ten. And indeed if we slow down tape recordings of these 'fish calls' of the terns to about 1/4 speed we find that we can begin to distinguish these important individual differences. That the terns themselves can indeed do this has been shown by Thorpe and his co-workers (Stevenson *et al.* 1970) in the Common tern. He found that the chick at 4 days of age while quite unresponsive to a playback of calls of other members of the colony, responds immediately on being played the returning call of one of its own parents. The response is a sudden alert, 'cheeping', turning and walking towards the loudspeaker. So it seems that the call of the returning parent, the Common tern, carrying food, is quickly learnt and responded to by the individual young concerned. If we may put this in blatantly anthropocentric terms it appears that this call is in effect saying 'Here is Mum [or here is Dad] with food'.

There is also a great deal of information available regarding the specialization of songs, as distinct from call-notes, for individual recognition. For my discussion of this I shall restrict myself to a particular case, namely that of antiphonal song or duetting as a new topic and one particularly appropriate to this volume as mainly relevant to tropical species.

I first encountered the duetting of tropical bird species on my first visit to a tropical forest environment, namely that at Barro Colorado, Panama, in 1932. There I encountered the spectacular duetting of the Marbled Guiana Quail (*Odontophorus guianensis panamensis*). I also then learnt of the duetting propensities of the tropical American wrens. A lengthy visit to Tanganyika in 1939 reinforced my interest in duetting but the time was still far too early for careful study since the tape-recorder had yet to be invented. Not until 1962, during a study visit to Uganda, did I have the opportunity to record African birds for myself, and I at once became fascinated and astonished at the constancy and precision of duetting in the genera *Laniarius*, *Cisticola*, *Cossypha* and *Trachyphonus*; and realized the possibilities of study, now for the first time opening out, as a result of the development of portable tape-recorders linked with the use of the sound spectrograph. Thus commenced a research project which was to last over 10 years (Thorpe 1972). As a result of my own work and of a survey of the now extensive literature I can state that there are 32 or more families of birds in which duetting—

that is either simultaneous or alternating song—is known to occur between the mated males and females. Within these families there are something of the order of 120 species which have been noted as duettists in this sense and of these 120 nearly 100 are tropical. In fact precise duetting or antiphonal singing as a means of maintaining contact between male and female is extremely rare outside the tropics.

Of the 32 families mentioned there are some 9 in which antiphonal song at its highest development has been produced. By this we mean alternating or precise unison song between the paired male and female given with high precision and used even when the birds cannot see each other. The result of this is that distance, intervening vegetation etc., offer little or no obstacle to mutual recognition and the maintenance of contact. These 9 families are: Megapodidae, Phasianidae, Rallidae, Formicariidae, Troglodytidae, Turdidae, Sylviidae, Laniidae and Meliphagidae. It soon became clear that the most attractive African genus with which to begin work was *Laniarius* and *L. aethiopicus* the most promising species for our purpose. Accordingly the brief summary which I shall give here concerns this species almost exclusively. Before proceeding further however, one point should be made: that is that the term duetting includes four varieties of dual song namely, (a) antiphonal, (b) polyphonic, (c) unison and (d) overlapping (polyphonic). These four examples are illustrated by Fig. 1. Three separate populations

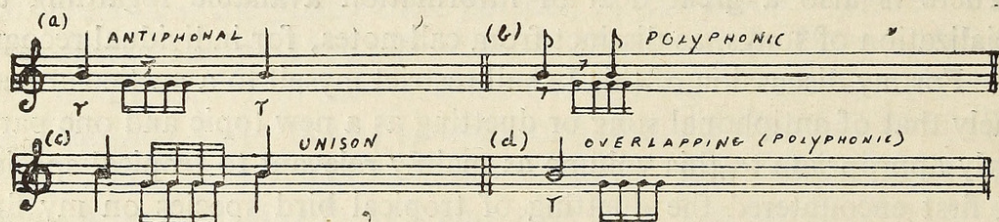


FIG. 1. Types of duet singing. [N.B.—The contributions of the two birds are distinguished by the notes of one having the tails up and the other down. Thus in (c) where all the notes are shared each note has two tails, one up the other down.]

of the race *major* of this species were studied in East Africa, two of them in Kenya separated by about 240 km and one in SW. Uganda separated from the nearest Kenya population studied by about 700 km. Vocalizations consist of antiphonal singing between the members of the mated pair, the male usually, but not necessarily, being the leader. On occasion the birds may sing the whole of a given pattern in exact synchronicity. We also found that either bird alone can sing the whole duet pattern by itself. As Figs. 2-8 will show, these song duets comprise attractive little tunes, even striking the European listener as of considerable musical quality with a clear harmonic relationship. The device of one bird singing the whole duet pattern by itself when the other happens to be

absent, seems to be used as a means of calling an absent mate back to his or her territory. It was also shown that while there are many duet patterns common to most, if not all, pairs in a given area, the repertoire of each pair is likely to be distinct from that of its neighbours and the

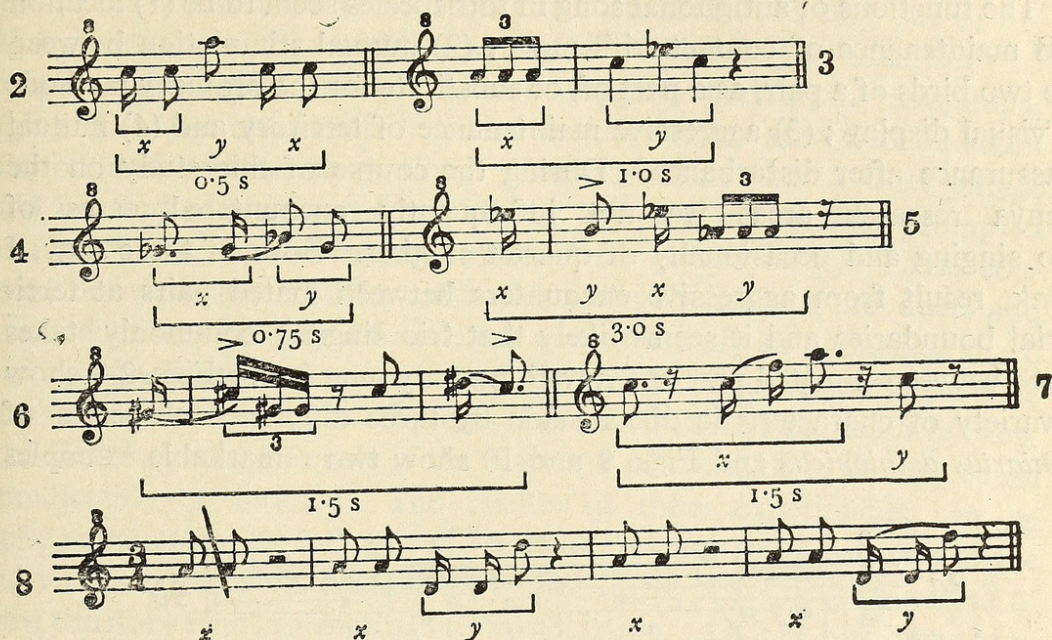


FIG. 2. *Laniarius aethiopicus sublacteus*, Vipingo, Kilifi, Kenya, Dec. 1954. N.B.—All the illustrations are given at approximately scientific pitch (middle 'C' = 256 c/s). Unless otherwise stated, as here, all the figures refer to race *major* (Thorpe & North 1965). N.B.—The figure 8 above the treble clef symbol indicates that all that follows should be read as one octave higher than would otherwise be the case, e.g. middle 'C' becomes 512 c/s. 'x' & 'y' = the two birds.

FIG. 3. *L. aethiopicus*, Dundori, Nakuru, Kenya, 17 Mar. 1964 (Thorpe & North 1965).

FIG. 4. *L. aethiopicus*, Kabale, Uganda, 15 Feb. 1962 (Thorpe & North 1965).

FIG. 5. *L. aethiopicus*, Meadow Point, Lake Nakuru, Kenya, 17 Mar. 1964 (Thorpe & North 1965).

FIG. 6. *L. aethiopicus*, Hippo Pool, Lake Nakuru, Kenya, 17 Mar. 1964. Note that this is a rather more elaborate duet than the previous ones. The contribution of the two birds is not indicated in this case since it seemed to vary a good deal (Thorpe & North 1965).

FIG. 7. *L. aethiopicus mossambicus*, San Martino, Mozambique Coast (C. Haagner). The timing in this example is very precise but the bar length might vary between 0.75 and 1.5s (Thorpe & North 1965).

FIG. 8. *L. aethiopicus mossambicus*, San Martino, Mozambique Coast (C. Haagner). This is a duet with a more complex time pattern. Bar length 1.5s (Thorpe & North 1965).

individual repertoire and to some extent also the individual voice quality can be used as a means of individual recognition by the birds. The vocal repertoire is worked out and developed between the two members of a mated pair and isolated birds seem unable to produce any complexity of vocalization patterns. Studies of captive birds have shown that the

crowding of the birds, particularly if they cannot see one another, leads to great temporary elaboration of duet patterns; and there is some evidence that in crowded areas where territories are small, duet patterns are more complex than in regions where the population is sparser.

The functions of antiphonal song in this species seem to be (1) location and maintenance of contact with mate; (2) mutual stimulation between the two birds of a pair, as a part of, or substitute for the ordinary methods of visual display; (3) aggressive maintenance of territory and (4) mutual reassurance after disturbance. During the course of this study on the Kenya research areas we not infrequently encountered cases of trio singing and occasionally of quartet singing. Both of these may, I think, result from aggressive encounters between mated pairs at territorial boundaries and it seems likely that trio singing commonly takes place between a mated pair and a well-grown young one. Figs. 2-8 show a variety of characteristic duets made by three different subspecies of *Laniarius aethiopicus* and Figs. 9 and 10 show two remarkable examples

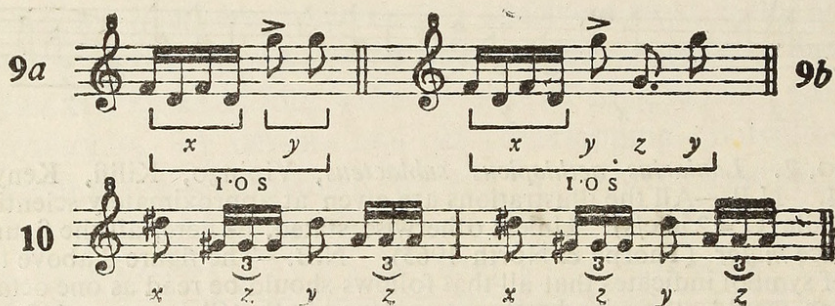


FIG. 9 (a, b). *L. aethiopicus*, Lake Bunyoni, Kabale, Uganda, 14 Feb. 1962. *a*, represents a duet pattern heard as a very long, precisely timed series. During one considerable stretch of this series a third bird 'z' joined in. It was far away from the others but nevertheless inserted its single note remarkably accurately. *b*, it tended to intervene in every second duet of 'x' and 'y' (Thorpe & North 1965).

FIG. 10. *L. aethiopicus*, Dundori, Nakuru, Kenya, 3 Apr. 1964. A remarkable trio. All three birds were in the same tree. Note that bird 'x' gave a D sharp every 2 s and bird 'y' a D sharp every other 2 s whilst bird 'z' gave a G sharp and an A natural every other 2 s in alternation (Thorpe & North 1965).

of trio singing in the field. Vocalizations of this species were of course studied by the usual methods of physical analysis using a sound spectrograph but since the notes of which the duets are composed are so pure and precisely pitched ordinary musical notation gives a much better and equally accurate picture of the songs than does the sound spectrograph and is accordingly used here.

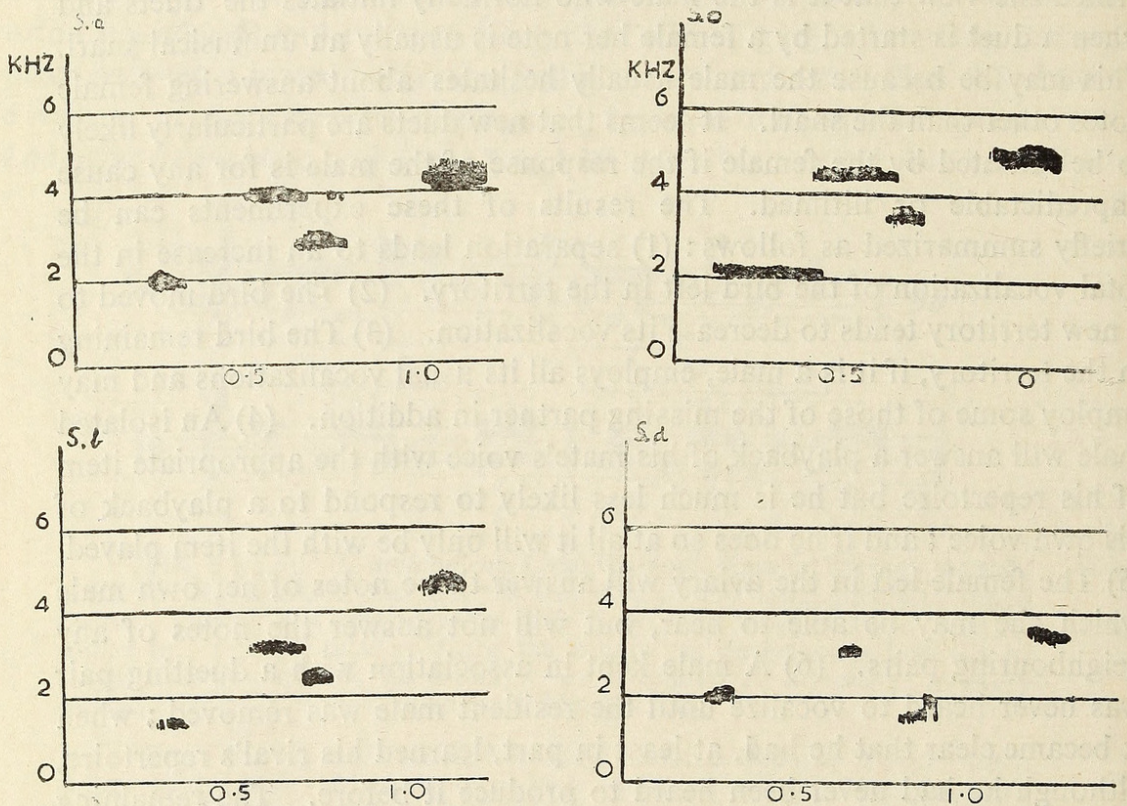
In addition to studies in the field on this species and others also studied during a period of four years in large tropical aviaries at Madingley, Cambridge, England, this work confirmed the field observations that the birds have exact control of the timing, pitch and overall rate

at which they produce their duets. The pitch control is certainly accurate to a semitone and often consistent to a quarter-tone; although whether the Shrikes 'deliberately' control their pitch to this degree of fineness is not absolutely clear. Work in aviaries and in some simple separation experiments confirm the view arrived at from field work that one of the major functions of the imitative ability of the birds is to establish and strengthen the social bonds. It also suggests that social antiphonal singing is in the nature of a mutual display which serves to maintain cohesion and ensure recognition. The possibility that a duet phrase could be used as a personal 'name' by one bird for another prompted us to carry out separation experiments with paired birds. These confirmed the view that it is the male who normally initiates the duets and when a duet is started by a female her note is usually an unmusical snarl. This may be because the male usually hesitates about answering female notes other than the snarl. It seems that new duets are particularly likely to be initiated by the female if the response of the male is for any cause unpredictable or illtimed. The results of these experiments can be briefly summarized as follows: (1) separation leads to an increase in the total vocalization of the bird left in the territory. (2) The bird moved to a new territory tends to decrease its vocalization. (3) The bird remaining in the territory, if it is a male, employs all its usual vocalizations and may employ some of those of the missing partner in addition. (4) An isolated male will answer a playback of his mate's voice with the appropriate item of his repertoire but he is much less likely to respond to a playback of his own voice; and if he does so at all it will only be with the item played. (5) The female left in the aviary will answer those notes of her own male which she may be able to hear, but will not answer the notes of any neighbouring pairs. (6) A male kept in association with a duetting pair was never heard to vocalize until the resident male was removed; when it became clear that he had, at least in part, learned his rival's repertoire, although he had never been heard to produce it before. The remaining female would respond to this though she would not respond to strangers.

Thus the overall picture shows that these duet patterns are worked out between members of a mated pair as soon as their formation is established and that the repertoire of any one pair, while it will certainly include a number of vocal patterns which are common to other pairs in the district or other districts, is nevertheless sufficiently individual to the pair concerned to render its recognition by voice alone quite simple. Thus antiphonal singing seems to be fully explicable as a highly effective method for maintaining contact between known individuals in an environment of dense vegetation.

In conclusion it is illuminating to consider the situation amongst the 40 species and 153 subspecies of the genus *Cisticola* (Grass warblers). Out of this great assemblage the superspecies *Cisticola hunteri*, comprising

four species, contains the only ones for which there is as yet evidence for antiphonal singing. It seems likely that these four, *hunteri*, *chubbi*, *nigriloris* and *discolor* are duettists, although there is no firm evidence concerning the last of them. They are all birds of dense grass vegetation above an altitude of 1500 metres ; ascending in one case to over 4300 metres. The songs are normally a duet, presumably started by the male ; but trio singing, quartet singing and elaborate communal singing among pairs are well established in one species and probable in the others. There is evidence for both individual and geographical differentiation between song patterns and the accuracy of timing is on occasion phenomenal. In one instance with *Cisticola chubbi*, the mean



Vertical scale : kilohertz
Horizontal scale : Time in seconds

FIG. 11. Traced sonograms showing only the musical tones in the duets of *Cisticola nigriloris* and their transposition. S.a, S.b, S.c, and S.d are four duets recorded from a single pair by STJERNSTEDT. a, b, c & d. Consistent pitch patterning with transposition in the Mbeya Mountain pair (Thorpe 1972).

reaction time of approximately 400 milliseconds was consistently maintained to a standard deviation of around 3 milliseconds : that is about 1/8 of the error which a human being would show under similar circumstances (Thorpe 1963). The speed and precision of the response timing is almost as impressive as this in some of the Shrikes including *Laniarius aethiopicus* and particularly the superspecies *Laniarius barbarus*. *L. barbarus* and *L. erythrogaster* have been particularly carefully studied in this respect,

the second species by ourselves in tropical aviaries as well as in the field (Thorpe 1972). But to return to *Cisticola*, while the function of multiple singing is not understood there is good evidence that individual recognition can be based on vocal characteristics. It is suggested that at the high altitudes in which these birds are found, persistence of dense mist and cloud may well be responsible for the survival value of well developed vocal communications. Fig. 11 (Thorpe 1972) shows another intriguing characteristic of the songs of *Cisticola nigriloris* where the pitch patterning is highly precise but has, an unusual feature of bird songs, a precise transposition in the middle of the song.

In conclusion it may be said that although a great deal has been learned about antiphonal song in recent years it is clear that a vast number of further examples wait to be elucidated and that they are most likely to be found in inhabitants of tropical vegetation.

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