

The Institute of Biology's
Studies in Biology no. 115

Vocal Communication in Birds

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General Preface to the Series

Because it is no longer possible for one textbook to cover the whole field of biology while remaining sufficiently up to date, the Institute of Biology has sponsored this series so that teachers and students can learn about significant developments. The enthusiastic acceptance of 'Studies in Biology' shows that the books are providing authoritative views of biological topics.

The features of the series include the attention given to methods, the selected list of books for further reading and, wherever possible, suggestions for practical work.

Readers' comments will be welcomed by the Education Officer of the Institute.

1979

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Preface

Man has always been fascinated by the elaborate and often very beautiful vocalizations produced by birds. Writings of the early naturalists, as well as poets and philosophers, concentrated upon the descriptive, aesthetic and musical aspects of songs. During the late 1950s, advancing technology resulted in the development and use of equipment which at last put the subject on to an objective, scientific basis. Since then, interest and research into all aspects of vocal communication in birds has continued to expand, and for this reason I have had to be selective rather than comprehensive in compiling this short introduction to the subject. In doing so, I have favoured studies which are analytical and functional rather than merely descriptive, and in particular I have tried to emphasize the experimental approach both in laboratory and field. The underlying theme of the book is not only to show how birds communicate with their vocalizations, but also to suggest wherever possible why they have been selected for during evolution. In spite of considerable advances in recent years, the central problem of why birds have evolved such complex and varied vocalizations remains one of the most interesting, challenging and elusive questions in the field of animal communication.

London, 1979

C. K. C.

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1 The Communication System

Although most people would probably agree that animals communicate with one another, there is rather less agreement about how and why they do it, and sometimes a tendency to compare the world of animal communication with that of human language. *Communication* is rather a difficult term to define, but in general it is the process whereby the behaviour of one animal alters the probability of some behaviour in another. During communication, information is passed between animals by signalling, but it is not enough to merely detect the signal. For the scientist to establish that communication has really occurred it must also be shown that the signal has in some way altered the behaviour of the recipient. SMITH (1965) has also pointed out that there is a clear distinction between the message contained in the signal and its actual meaning to a recipient. The message may remain constant, but its meaning may vary with context and receiver. For example, many birds sing in territory, but whereas the song means 'keep out' to a rival male it means 'come in' to a female. Most traditional views of animal communication emphasize the sharing of information between individuals to their mutual advantage. A more recent view, put forward by DAWKINS and KREBS (1978), is that during evolution the signaller has been selected to manipulate and exploit the behaviour of other individuals to his own advantage. Any communication system must have a sender, a signal, a medium and a receiver, and the general principles underlying communication apply to all animals. In this book we will be dealing with only one type of communication – acoustic – in one group of animals – birds. Although they use other methods to produce sounds, those produced by their vocal apparatus are some of the most complex known in any animal group, including humans. Whether bird *vocalizations* are in any way analogous to human *language* is extremely doubtful, but they do represent the evolution of an extremely sophisticated communication system which we are only just beginning to understand.

1.1 Sound production

Sound waves are alternating changes in the pressure of the medium, which is normally air. The height, or *amplitude*, of sound waves are measured in microbars, but a more familiar unit which measures sound volume is the *decibel* (dB), a logarithmic scale of pressure ratios. *Wavelength* measures the distance in millimetres of one complete wave alternation or cycle, and the number of cycles per second is known as the *frequency*. Frequency is normally measured in units of thousand cycles or

kiloHertz (kHz), and gives an indication of how high or low sound is pitched.

Birds produce sounds in many different ways, clapping the wings together, snapping the bill, and of course the well-known drumming of woodpeckers. Interesting as these sounds are, they are still relatively primitive compared to those produced by their vocal apparatus, the *syrinx*. The *syrinx* contains special membranes which, due to the passage of air forced over them, vibrate and so generate sound waves. Humans and other mammals produce sounds from the larynx situated at the top of the trachea, but in birds the *syrinx* is much lower at the junction of the two bronchi. There is considerable variation in *syrinx* structure, but passerine birds, which include the oscines or true song birds, have the most complex of all. The *tympaniform membranes* are situated on the bronchial walls and vibrate as air is forced over them in each bronchial lumen. Several pairs of syringeal muscles act to control membrane tension and thus vary the quality of sounds produced. The most obvious differences between this system and a mammal larynx is that there are two quite separate sound sources, one in each bronchus. That the two sources might produce separate sounds has long been suspected, as two harmonically unrelated sounds which clearly overlap in time have been detected on the sonagram (see § 2.2) traces of several species. NOTTEBOHM (1971) was able to confirm this experimentally on the chaffinch (*Fringilla coelebs*) by severing the right or left hypoglossal motor nerves which supply the right and left sides of the *syrinx*. Birds which have the right side denervated and are allowed to recover lose only one or two elements from the song, whereas those denervated on the left side lose practically all the elements leaving only one or two (Fig. 1-1). It seems that although each side

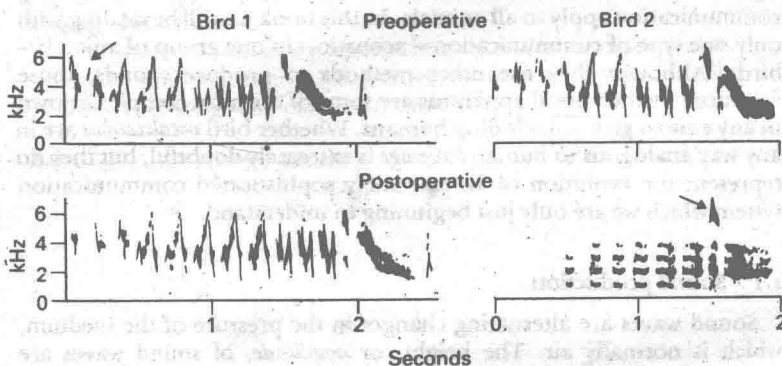


Fig. 1-1 Two male chaffinches shared the same song type, then bird 1 had the right hypoglossus cut and lost one song element (arrowed) while 2 had the left hypoglossus cut and lost all but one element (arrowed). (The unstructured sounds in 2's song are a result of airflow through the denervated bronchus.) (From NOTTEBOHM, 1971.)

normally produces a part of the complete song, the left side predominates and is responsible for most of it. This *lateralization* of control has since been confirmed in other species, but to what extent the intact bird synchronizes or independently controls output from both bronchi during normal singing is unknown. It is now thought that this lateralization may extend to the central nervous system (CNS) where attempts are being made to investigate the central control of vocalizations. If it does, there is an intriguing parallel with the control of human speech where cerebral dominance by one hemisphere also occurs.

1.2 Hearing

The outer ear of birds is not very obvious, due to the absence of an external pinna. This is thought to be for aerodynamic reasons, although bats which also fly usually have a large external pinna. The opening of the *external auditory meatus* is protected by feathers which, although they may hinder hearing, to some extent are essential to reduce wind noise during flight. The meatus conducts sound to the *tympanic membrane* or eardrum which vibrates due to changes in pressure. The middle ear transmits these changes mechanically to the inner ear. In birds this is done by a single bone, the *columella* unlike the three ear ossicles of mammals. The columella is held by ligaments against an oval window to the fluid-filled *cochlea* of the inner ear. It is here that sensory hair cells act as the final transducers of mechanical vibrations into nerve impulses. The cochlea is a tube which has a much folded roof, the *tegmen vasculosum*, which covers the *basilar membrane*. Pressure changes cause the basilar membrane to vibrate and the sensory hair cells to discharge nerve impulses to the brain. It has long been suspected that different sound frequencies excite different regions of the basilar membrane. In birds, the length of the cochlea and basilar membrane is much shorter than in mammals, which may mean that the CNS plays a more important role in frequency perception. The frequency range to which the ear is sensitive varies from species to species, but the area of maximum sensitivity generally appears to be between 1 and 4 kHz (Fig. 1-2), much the same as in man. Early methods of determining frequency ranges relied solely upon behavioural audibility curves obtained in conditioning experiments. Later techniques used cochlear potentials, and now potentials can be recorded from the *cochlear nuclei*, groups of neurones in the brain itself. KONISHI (1970) has applied this technique to several species, and found that the threshold curves obtained closely match those found by earlier behavioural studies (Fig. 1-2). His neurophysiological studies have also confirmed that birds cannot hear high (*ultrasonic*) frequencies beyond the audible range of humans, above about 20 kHz. Although birds do produce ultrasonic sound (THORPE and GRIFFIN, 1962), it is of low intensity and always associated with audible sounds. MOSS and LOCKIE (1979) have recently shown that capercaillies (*Tetrao urogallus*) produce very low (*infrasonic*) frequencies

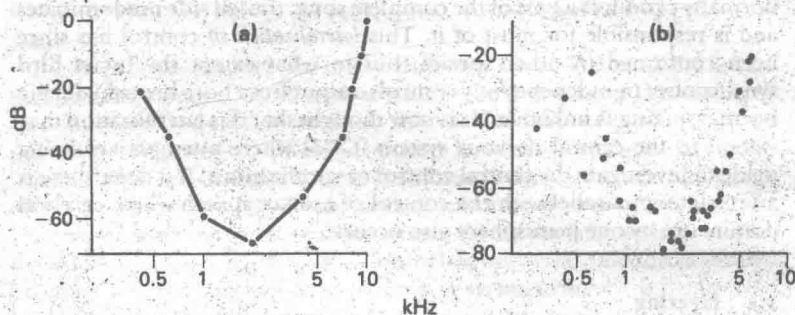


Fig. 1-2 A behavioural audibility curve (a) compared to neural thresholds (b) obtained from the brain of a starling (*Sturnus vulgaris*). (From KONISHI, 1970.)

inaudible to humans, below 40 Hz, but there is as yet no evidence that they can hear it themselves.

It has already been mentioned that the avian cochlea is much shorter than in mammals, but it is also broader and contains more sensory hair cells per unit length of basilar membrane. Another difference is the extensive folding of the tegmentum vasculosum which is thought to have a damping effect bringing the system to rest more quickly. It has often been suggested that such design might well improve the temporal resolution of sounds which follow one another quickly. Even cursory examination of sonagrams shows that birds usually produce as many as ten distinct syllables per second, and also extremely rapid frequency modulations. Evidence will be presented in later chapters to show that birds are quite capable of discriminating between such minute variations particularly in the temporal patterning of calls and songs. Neurophysiological evidence of high temporal resolution of sounds has been obtained by KONISHI (1969) from the cochlear nuclei of the brain. Single clicks were resolved with intervals between them of only about 2 ms and sometimes less. Behavioural evidence has now been obtained by WILKINSON and HOWSE (1975) who trained captive birds to discriminate between double and single clicks for a food reward. They could still resolve double clicks as two separate sounds when the click interval was as small as 2 milliseconds. Such powers of resolution are way beyond those of most mammals including man, and it does seem that birds are capable of communicating with sounds on a much faster time scale than humans.

2 Methods and Techniques

There are many different levels at which the investigation of vocalizations can proceed. The first step is to find a singing bird and be able to hear it clearly. By listening carefully and taking detailed notes, the early naturalists were able to describe many important features and characteristics of the different species' vocalizations. However, subjective descriptions based upon memory and recorded in verbal shorthand are of little use to the modern scientist, who needs to make an accurate record of the vocalizations. Tape recordings can be repeatedly analysed by modern electronic equipment to reveal the precise details of vocalization structure for comparison and further study. It may also give clues as to function, a hypothesis can be set up, and a series of experiments planned to test it. These may involve captive birds in the laboratory or playback experiments on natural populations in the wild.

2.1 Sound recording

The recording equipment must satisfy the following criteria. It should be of high quality for later laboratory analysis of recordings, and yet be light, portable and robust for work in the field. With the advent of solid-state physics and miniaturization, there is now a reasonable choice of such equipment, some of it specially designed with the above requirements in mind. A battery-operated tape recorder with an adequate *frequency response* and high tape speed is essential to capture the rapid frequency modulations mentioned earlier.

Selection of the correct type of microphone is extremely important, and for most work a *dynamic microphone* is best. Several are now designed specifically for outside work and so are suitably robust as well as being sensitive and responsive to the frequency ranges described earlier. Since they mostly have low impedance, long cables can be used if necessary to connect with the tape recorder input. There are only two ways of getting close enough to obtain a good quality recording: positioning the microphone near the singing bird at the end of a long cable, or using a parabolic reflector and microphone some distance away.

The *parabolic reflector* has undoubtedly made the collection of good quality recordings much easier, and is indispensable to the modern recordist. It consists of a shallow dish, which when pointed at a distant sound source reflects the sound waves and concentrates them to a focal point. The microphone is positioned facing into the dish at the focal point (Fig. 2-1) and so receives the greatly amplified sound. The reflector also makes the system more directional and selective by cutting down on

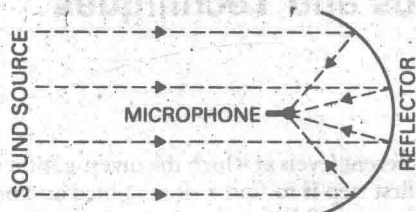


Fig. 2-1 Diagrammatic representation of a parabolic reflector to show the positioning of a microphone at the focal point of sound-wave reflection.

unwanted side noise so improving the signal-to-noise ratio of the whole system. The dish can be accurately directed on to the sound source either by sight, or by wearing headphones and acoustically monitoring the sound input. Dishes come in a variety of sizes, the larger the more powerful, and are made of either aluminium or fibre glass for lightness. They have some disadvantages in wind, and overall frequency response is far from uniform, but generally the advantages more than compensate. An excellent review of different recording techniques and equipment has been published by GULLEDGE (1977).

2.2 Sound analysis and sonagrams

The cathode-ray *oscilloscope* can be used to display recorded sound as a series of waves on the screen. These can be photographed at intervals and then measured to determine frequency and amplitude. There are, however, a number of disadvantages in analysis by oscilloscope, mainly due to the rapid rate of frequency and amplitude modulation in bird vocalizations. To be sure that all the changes are detected, minute sections, measured in fractions of a second, must be displayed and photographed one after the other, before a composite song can be constructed and studied. Oscillographic methods are better suited to the study of sounds which remain fairly constant and for this reason are most often used in the study of insect sound communication.

The development of a special *frequency spectrum analyser*, called a *sonagraph*, revolutionized the study of bird vocalizations. Its potential was soon realized by Thorpe, who was the first to use it extensively on passerine songs. Now available in a variety of forms and with various accessories, its basic principles remain the same. The sonagraph records on a magnetic drum a short sample of about 2.5 seconds of the sound to be analysed. It is then rapidly scanned by being revolved and replayed over 500 times through a filter which is gradually tuned to higher frequencies. As this is done, a dark trace is produced on sensitive white paper which is also revolved on a cylinder connected to the drum. The main result of this is to produce a graph of frequency against time,

but amplitude is also represented as the darker the shading the greater the amplitude. The trace is called a *sonagram* and may be stored as it is, traced, photocopied or photographed and a great deal of information obtained later by measurement. The main criticism levelled at the sonograph is that if incorrectly calibrated, used or interpreted, it can give misleading information, but this surely applies to any scientific instrument. Another criticism is that by displaying in detail the extensive minutiae of frequency variations, it actually confuses by giving too much information. This rather curious criticism can be remedied by simplifying the final trace, and obscuring the finer details of harmonic structure and amplitude variations by Indian ink. Many feel that such a simplified trace, which merely shows frequency range and modulations in uniform black, gives sufficient information, particularly for illustrations in books. The main advantage of sonagrams is that they really do give the reader a picture of what sounds are like, and after a little practice even a novice is able to read them with far greater ease than learning musical notation. By actually presenting an objective representation of the recorded sound itself, the sonagram also renders obsolete the necessity to resort to inadequate phonetic descriptions. Although sometimes useful for field ornithologists there are very real dangers of placing any reliance upon these for serious scientific research. In her book, JELLIS (1977) points out how field guides in different countries give remarkably different phonetic descriptions for the same species. The call of the golden oriole (*Oriolus oriolus*) is given as 'weela-weeo' in England, 'tuolio' in France and 'dudelio' in Germany. Upon actually hearing the call from a wild golden oriole for the first time she felt that none of them had given her much help in identifying it. In looking at a sonagram for the first time the reader may experience a similar feeling, and so at this stage here are a few useful hints as to the interpretation of some common vocalizations shown in Fig. 2-2. All these sounds are found in the songs of one single male sedge warbler (*Acrocephalus schoenobaenus*), and are the units, or building blocks, from which songs are constructed. There is considerable variation and disagreement among scientists as to the correct terminology to use, and they are often referred to as notes or syllables. For the sake of convenience and consistency in this book all sub-units within songs will be called *elements*.

In sonagrams, the axis is frequency, measured in kiloHertz (kHz). As frequency approximates to pitch, the higher the noise is, the higher it appears on the trace. The time scale along the abscissa is usually in seconds. Perhaps the most common sound people associate with birds is a whistle. If you make a short whistle of constant pitch, it will appear as a pure, *unmodulated frequency* on the sonagram, a fairly straight horizontal band (a). A whistle which starts at a higher frequency and drops to a lower one is said to be *frequency modulated* and appears as a slope (b). If more rapid modulations are introduced as in a slow (c) or fast (d) vibrato, they will be shown on the sonagram. A completely different sound is the harsh

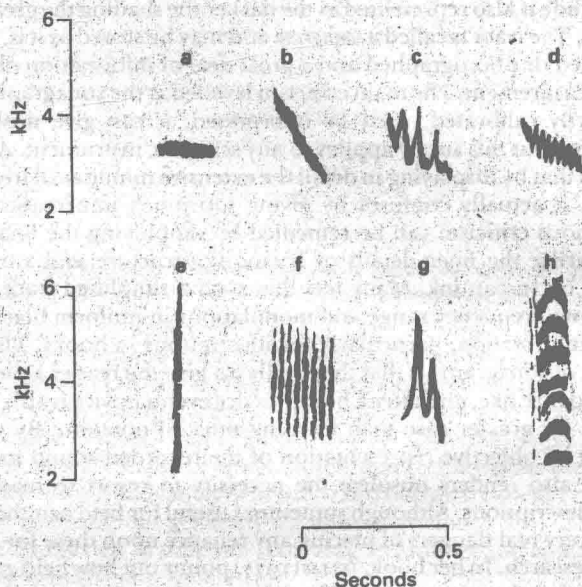


Fig. 2-2 Sonagrams of some different sounds (elements) produced by a male sedge warbler and described in the text.

noise produced when a wide frequency spectrum is used. A short burst of wide frequency noise results in a single click (e) and if several occur close together a harsh buzzing or rattling is produced (f). Frequency modulations can occur in a wide variety of complex forms and many will be encountered later, but (g) for example sounds rather like a chirp. Another complication is when a sound which has a low *fundamental frequency* also has higher frequencies which occur as multiples of the fundamental. These are called *harmonics* and in the example here (h) result in a rather gruff barking noise.

There are a number of new instruments which have appeared since the sonagraph. The *melograph* plots only the main or fundamental frequency as a single line, but also plots amplitude beneath. A *continuous frequency spectrum analyser* can now quickly produce sonagram-like traces on an oscilloscope screen. These can be photographed every few seconds to greatly speed up what has been a much slower process on the orthodox sonagraph.

2.3 Experiments

Many laboratory experiments are concerned with the role of *auditory feedback* in the development of song. Young birds are often taken from the

nest and then raised by hand in aviaries away from other birds. A better, but more difficult form of acoustic isolation, is to hatch and raise the young in special sound-proof chambers. These ensure more complete control of the acoustic environment, and often have built-in microphones and speakers for various experiments. Drastic experiments to remove auditory feedback altogether, involve deafening young birds after hatching by cochlea removal. The results of these methods will be discussed in Chapter 5, but important as laboratory experiments are for song development, they tell us little about the functions of song in the wild.

The most common type of field experiment now performed is the *playback experiment* where an extension speaker is placed in or near territory. It relies upon the well-known tendency of a bird in territory to defend it by showing aggressive behaviour towards the sight or sound of a rival male. Although models and preserved birds can also be used, the use of a recorded acoustic stimulus by itself has the advantage of removing other variables from the experimental design. If a strong *baseline response* to normal recorded song is elicited, then presumably the bird is recognizing and responding to specific features contained in it. Experiments can then proceed to investigate these by varying those features in a variety of ways. A series of pilot experiments will show how a particular species responds to playback and the most appropriate criteria can then be selected. For example, a typical response of a very reactive bird might involve immediately stopping any other behaviour, orientating towards the speaker, approaching it and finally even contacting it. It may also produce vocalizations and visual threat displays. At the simplest level, the response could be scored on an 'all or nothing' basis, but usually each of the different categories are scored separately. They can also be ranked, so that a bird which approaches the speaker scores more than one which merely orientates towards it, and so on. Useful as scoring methods are, they do involve subjective factors, and if possible the best method is to *quantify* responses by *objective measurements*. Ideally several different categories of behaviour should be measured, and this has been done in the example shown in Fig. 2-3.

Five categories were selected to measure the responses of ten male sedge warblers to 4 min of playback of their species song both before and after pairing (CATCHPOLE, 1977). *Latency of response* (a) was the reaction time measured from the start of the experimental song to the first movement of the whole bird towards the speaker. As can be seen, this increased significantly after pairing. *Time spent searching* within a 1 m radius of the speaker (b) was totalled and this showed a significant decrease after pairing. *Time spent singing* during the 4 min (c) showed the most dramatic change, as no males sang after pairing. The *nearest distance* each bird eventually approached to the speaker (d) was measured to within 1 m, and this also showed an increase. However, the *number of calls* given (e) showed a significant increase after pairing. We will not attempt to draw any conclusions from the experiment at this stage, but it does illustrate how

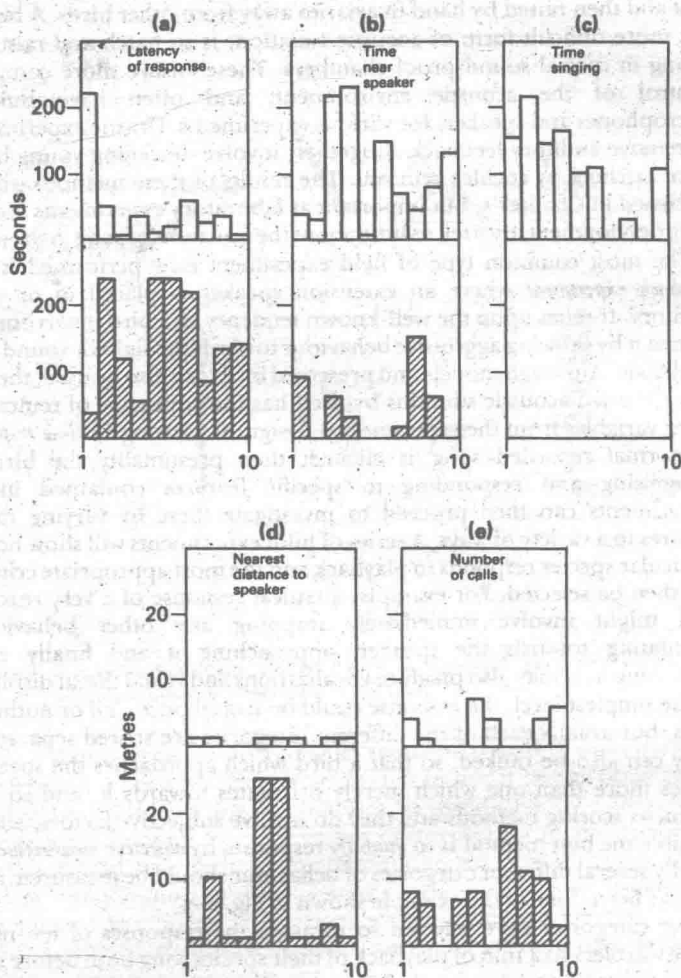


Fig. 2-3 Results obtained by using five different categories of response in the same playback experiment on ten male sedge warblers (1 to 10) before (unshaded) and after (shaded) pairing (From CATCHPOLE, 1977.)

different criteria and methods of measurement give different results. More sophisticated methods and measurements may involve several observers, the use of additional tape recorders and film cameras. Experimental design, categories of response, methods of measurement and appropriate statistical tests, should all be planned together to achieve meaningful results.

3 Calls and Communication

Bird vocalizations are traditionally divided into calls and songs, and although there are considerable difficulties in exactly defining the two terms, the distinction still remains a useful one. As a general rule, *songs* are long, more complex in structure and produced by males in the breeding season, whereas *calls* are short, simple and produced by both sexes throughout the year. As we will see later, there is still considerable debate as to the possible functions of songs, but for several reasons the functional interpretation of calls is less difficult and so provides a useful starting point.

3.1 The functions of calls

One reason why the functions of calls are better understood, is that they are given in quite specific *contexts* or during certain behaviour patterns. Any variation in calling rate, intensity, or sometimes the occurrence of an intermediate form, probably reflect underlying changes in motivation which may also be transmitted to other individuals. If a particular call is only given during territorial displays and fighting, it seems reasonable to assume it is an aggressively motivated threat call. Furthermore, if the call itself is seen to effect the behaviour of other members of the species, then it fulfils our criteria of communication, as well as providing additional clues as to function. Indeed, one characteristic of calls is that in many cases they do have an immediate effect upon the behaviour of other individuals. Calls can be thought of as expressing a tendency to behave in a certain way, and also transmitting that information to other individuals who upon receiving it may modify their behaviour accordingly.

By studying different calls in relation to behaviour, it has been possible to build up the total *vocabulary* of calls for many species. THORPE (1961) has tabulated data from several species and it can be seen (Table 1) that the size of call vocabulary varies considerably from species to species. Passerines, on average, have a rather larger vocabulary than other groups, but overall there seems to be an upper limit of about 15 different calls in any one vocabulary. In most cases there is room for at least one call for flight or aggression, but as many as three calls for different alarm and courtship situations. The young too have their own special calls, such as when begging food from their parents. The various categories presented by Thorpe in his summary give a good idea of the overall range and type of calls to be found in most bird vocabularies.

However, these categories are not comprehensive, and there are also

Table 1 The call vocabularies of various species. (From THORPE, 1961.)

Circumstances in which uttered	Herring gull	Fowl	Dove	Great tit	Chaffinch	Buntins	Blackbird	Whitethroat	Pied flycatcher	Wren	Song sparrow
Calls of adults											
Flight	.	.	.	+	+	+	+	+	.	.	+
Settling	.	.	+	+	.	.	.	+	.	.	.
Social (flock)	+(2)	.	+	+	+	+	+	+	+	+	+
Alarm 1	+	+	+	+	+	+	+	+	+	+	+
Alarm 2	+	+	+	+	+	+	+
Alarm 3	+	+	+	+	+	+	+
Flying predator	.	.	.	+	+	.	+	.	+	+	.
Ground predator	.	+	.	+	+	.	+	?	.	+	+
Distress scream	.	+	+	.	+	.	+	.	+	+	+(2)
Aggressive	+	+	+	.	+	+	.	+	+	+	+
Territorial	.	+	+	+	+	.	+
Courtship 1	.	.	+	+	+	+	+	+	.	+	+
Courtship 2	+	.	.	+	.	+	+
Courtship 3	+	.	.	+	.	+	.
Copulation	+	.	+	+	+	+	.	+	.	+	+
Nest-site	.	.	+	.	.	+	.	.	+	.	+
Mate feeding	+	.	.	+	.	+	.	?	.	.	.
Food	+	+
Roosting	+	?	.	+	.
Total	7	6	8	9	13	10	11	12	9	12	14
(or 15)											
Calls of young											
Pleasure	.	+
Distress	.	+	+	+	.	.	+
Distant begging	+	+	+	+	+	.	+
Close begging	+	+	+	+	+	+	+
Total	7	2	3	2	2	3	3	2	2	1	3
(or 18)											

calls which have more unusual and highly specialized functions. These may involve communicating with other species, *interspecific communication*, or using calls as a form of sonar, *autocommunication*. One particularly interesting example is shown by African honeyguides, such as the aptly named *Indicator indicator*, whose special calls and behaviour guide men and other mammals to the nests of wild honeybees. The nests, which would otherwise be inaccessible to the birds, are broken into by the larger animal, and the honeyguides can then feed on broken pieces of the comb. This symbiotic relationship appears to have developed originally between