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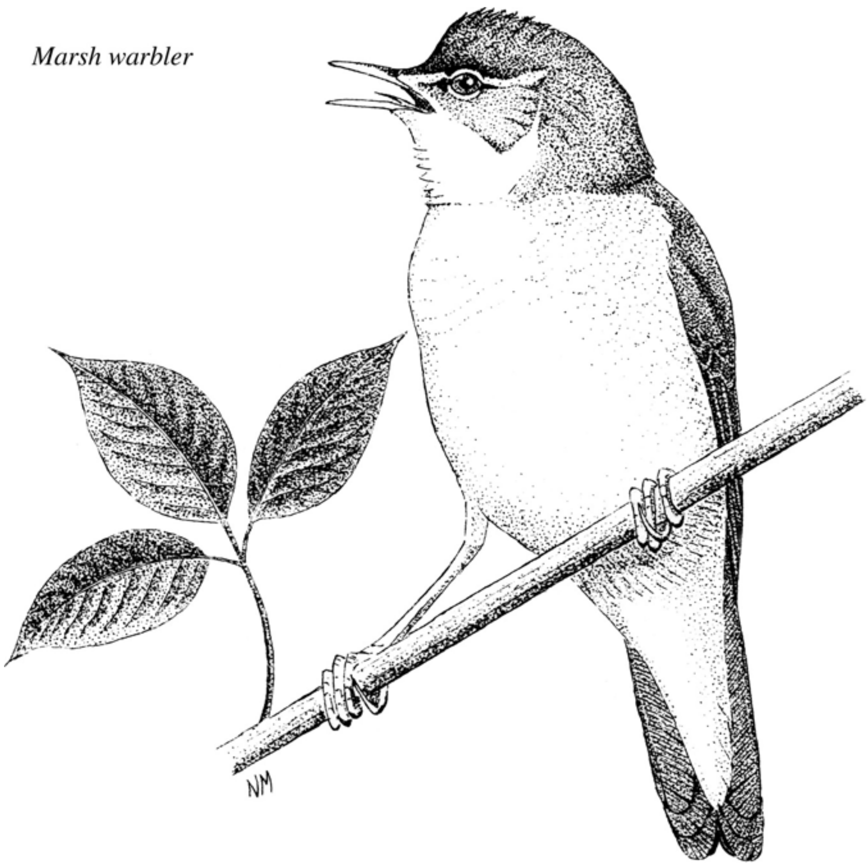
CHAPTER ONE

THE STUDY OF BIRD SONG

Marsh warbler



And your bird can sing
John Lennon *Popular song*

1.1 Introduction

This chapter is a brief introduction to the theory, terminology and techniques used in the scientific study of bird songs. Although everyone may assume that they do know what a bird song is, how does it differ from the other sounds that birds make? There are calls, notes, syllables and phrases to consider – and what are repertoires? Before we start using these words, it is just as well to define them and become acquainted with a terminology which can be confusing. Only then can we move on to consider the role of song in the lives of birds and to review the many studies that have attempted to shed some light upon it. Animal communication is a rapidly expanding field, and at this early stage it is also useful to consider some of the recent theoretical background. For example, what is 'communication' and how do we know it has occurred? What is 'information' and who benefits from sending and receiving it? What are 'signals' and why is sound transmission particularly effective? Finally, recording, analysing and experimenting with sounds is a highly technical field, currently being revolutionised by the use of computers at various points. We will also attempt to give the reader just a brief introduction to some of the more important techniques and any recent developments. But first, let us set the current study of bird song in its historical context.

1.2 History

Clearly, from references to it in music and in literature, particularly poetry, people have been interested in bird song for a very long time. But its detailed scientific study is a comparatively recent phenomenon. One reason for this is that making a permanent record of it, as we now do routinely on tapes or discs, was not easy until half a century or so ago. Song can be so rapid and complicated that only with such a permanent record that could be slowed down, repeated and analysed in various ways, is it possible to make a serious study of many aspects of it.

Some interesting work was done before that time. The Hon. Daines Barrington wrote a letter to the President of the Royal Society in 1773 recounting a variety of observations he had made. He established the existence of song learning, for example, because he heard the song of a wren emanating from a house he was passing and, knowing how difficult such birds were to keep in captivity, knocked on the door out of curiosity, only to discover that the singer was a captive goldfinch. Presumably this bird had been exposed to wren song at some stage and had picked it up. At around the same time, in 1789, the great English parson and naturalist Gilbert White described how birds previously known as willow wrens could be separated by their songs into three separate species. These we now call the willow warbler, the wood warbler and the chiff-chaff. Those with a good ear were also able to detect that birds had repertoires of songs and study the way these were strung together into sequences, as Craig (1943) did with eastern wood pewee song, or that song could vary from place to place, as found by Marler (1952) for the chaffinches singing in different glens in the Scottish highlands.

The depth of such studies was severely limited, not just by lack of the possibility of recording, except latterly on wax drums, but most importantly by the lack of analytical equipment. The real revolution came with the invention of the sound spectrograph, first used to provide a visual representation of song by Thorpe in 1954. Such equipment was not cheap, and therefore its use was somewhat restricted, but it still led to a huge growth in studies of song. Today, equivalent visualisations of song, together with many other forms of analysis, can be carried out using a variety of computer packages at a fraction of the cost. The detailed study of bird song is within the scope and budget of many laboratories and even amateurs: as a result the subject is advancing with great strides. Thanks to these very powerful techniques, there are now few areas of animal behaviour research that have not been illuminated by studies of bird song.

1.3 Some basic theory

1.3.1 Signals and communication

When a bird sings, it produces a sound which serves to communicate with other members of the same species. Because the song is a special structure used solely in communication, we call it a signal. But how do we know whether communication has occurred? It is generally held that if the signal modifies the behaviour of the receiving animal then we can infer that communication has taken place (Slater 1983c). For example, if we play back a tape recording of a male great tit song to another male, we may cause the second male to respond by approaching the speaker and displaying aggressively. As the song appears to have modified his behaviour, we are entitled to conclude that communication has occurred. This is a somewhat restricted definition of communication, as it relies upon a behavioural response and thus excludes passive signal detection by the receiver. For example, if we repeated the experiment on another great tit and obtained no response, it may be that the great tit had heard the song but decided for some reason not to respond. Such behaviour may often occur, so we must temper our definition with caution and also be sure to carry out a number of experiments before we draw any firm conclusions.

Although it may be relatively easy to demonstrate that communication takes place, it is much more difficult to suggest why it has evolved. Early theories emphasised the benefits that might accrue to both the sender and the receiver (e.g. Smith 1977) and saw communication as a sharing of information between individuals to their mutual advantage. Modern ethologists are much more inclined to view communication as the outcome of conflict rather than cooperation between sender and receiver.

Krebs & Dawkins (1984) examined how different kinds of signals may result from the benefits that accrue to senders and receivers. Sometimes, cooperation rather than conflict is involved, and they suggest that a system which benefits both receiver and sender would give rise to the evolution of relatively quiet, inconspicuous signals. For example, a great tit may give an alarm call to warn its fledglings that a sparrowhawk is approaching. The call should be loud enough to reach the fledglings but not loud enough to reach the hawk and give away the position of the caller. To be able to hear the call, the fledglings should develop sensitive hearing, and so a coevolutionary process will lead to the production of calls that are 'cost-minimizing conspiratorial whispers'. The fascinating story of the evolution of alarm calls, and their possible detection by predators, will be discussed in detail later in the book.

But where the interests of sender and receiver conflict, as in a territorial dispute, there will be a different kind of coevolution. Here, Krebs & Dawkins (1984) suggest that there is an evolutionary arms race between 'manipulation' by the sender and 'sales resistance' by the receiver. The male great tit this time sings as long and loud as he can manage, simply to force his message across. As we will see in later chapters, loudness and repetition are a particular feature of the songs of males when defending their territorial boundaries. Although sales resistance may occur among rival males, there are even more compelling reasons why females should be wary of male signals. If a listening male makes a mistake, he may just waste energy in a display or a fight, but if a listening female chooses a male of the wrong species, or one of inferior quality, she may pay a severe penalty in reduced breeding success. We will also see in later chapters that there is now considerable evidence that females have been selected for fine discrimination of both quantity and quality of male songs.

So far, we have assumed that the signals transmitted give reliable information from sender to receiver. At this stage, we should mention that the word 'information' is used in two different ways. Technically, information theory considers it to be 'a reduction in uncertainty' about the sender's future behaviour on the part of the receiver. In other words, information is said to have passed from sender to receiver when the sender's behaviour becomes more predictable to the receiver (Halliday 1983). When information is transmitted between birds, it is generally about something quite precise, such as species, sex, identity, likely next action, and so on. There are some grounds for expecting that receivers will be selected to detect unreliable or false information. Zahavi (1979, 1987) has suggested that only signals which are honest indicators of size, strength or motivation should evolve. One reason for this is that many signals are costly to produce, and so it is difficult, for example, for a smaller, weaker animal to cheat or bluff the receiver into accepting it as a larger, stronger rival or mate.

The view that, because of costs incurred by the sender, evolution has generally favoured 'honest advertising' in communication has now become widely accepted. However, Dawkins & Guilford (1991) have pointed out that receivers also pay costs when assessing signals. If the costs of long, detailed assessment are high in relation to the value of the extra information gained, then receivers might settle for cheaper, less reliable signals. If so, the receiver may be open to being bluffed, cheated and manipulated to the sender's advantage. In their review, Krebs & Davies (1993) suggest that such coevolutionary arms races between sender and receiver may have two different end-points. In one, the outcome is the evolution of honest signalling, but in the other we may find unreliable signals have evolved as one animal attempts to manipulate the behaviour of the other. Recent developments in this field have also been reviewed by Maynard Smith & Harper (2003), and by Searcy & Nowicki (2005), who focus particularly on the evolution of reliability and deception, using bird

Table 1.1. A comparison of difference sensory channels of communication

	Acoustic	*Visual*	*Chemical*	*Tactile*
Nocturnal use	Good	Poor	Good	Good
Around objects	Good	Poor	Good	Poor
Range	Long	Medium	Long	Short
Rate of change	Fast	Fast	Slow	Fast
Locatability	Medium	Good	Poor	Good
Energetic cost	Low	Low	Low	Low

Modified from Alcock 1989.

song as a key example. The latter point out that reliability requires there to be a correlation between some aspect of the signal and some attribute of the signaler that the receiver benefits from knowing about. Hence the receiver benefits from assessing the signal rather than ignoring it. Deceit requires not only that the correlation between signal and attribute be broken, but that the signaler benefits from that breakdown. Searcy & Nowicki (2005) present a detailed review of this complex area and discuss how opinions about the prevalence of reliability and deception in animal communication have changed over the years.

The apparent coevolutionary arms race between senders and receivers involves many different aspects of communication, which we will be considering throughout this book. It is important to emphasise that we will not just consider the signal (song) itself, but how it is transmitted through the environment, how it is perceived by receivers and, in particular, how males and females react to both natural and experimental signals.

1.3.2 Why sound?

Sound is only one of several channels of communication that are open to birds, and the advantages and disadvantages of the different channels have been summarised in Table 1.1. In general, birds have rather a poorly developed olfactory system, and so this method is less important than the main channels of sound or vision. This contrasts with mammals, where olfaction is a very important method of communication. Olfaction is rather less important to humans, as their tiny noses indicate, and, like birds, humans rely particularly upon sound and vision. There is no doubt that visual signalling is of great importance to birds, as indicated by their elaborate plumage and coloration and as seen in their eye-catching visual displays. What then are the particular advantages of sounds, especially when compared to visual signals?

Visual signals have several disadvantages, for example in darkness or poor light. But bad conditions for visual signalling can occur at any time in dense habitats such as forest or reeds and when animals move out of view behind objects. Try looking for a small bird as it moves through the canopy. Now you see it – now you don't! But if it calls or sings you can always hear it, long after it moves out of sight. Sound travels in all directions, it can penetrate 'through' or 'round' objects, and it travels over long distances. Sound is an ideal method for communicating over long distances, and although birds also call softly to each other, their songs are often loud and can carry for several kilometres. How natural selection may have acted to 'shape' song structures for optimal transmission through different habitats is one of many topics we will discuss later in this book.

Other advantages stem mainly from the rapid and transient nature of sound communication. A song or call is only produced when needed, and large amounts of information can be transmitted rapidly and efficiently through the sound channel. There might perhaps be one disadvantage if, as has sometimes been suggested, singing is very costly in terms of energetics. A song has to be 'made' each time it is produced, and some birds sing thousands of songs per day. However, recent evidence suggests that this is not the case and that song is comparatively cheap to produce compared, for example, with the cost to a bird of hopping or flying around its cage (e.g. Oberweger & Goller 2001, Ward *et al.* 2004). It does therefore seem that the many advantages of sound communication rather easily outweigh its costs. Birds, like humans, are intensely vocal creatures, and communication by sound has come to play a central role in their lives.

1.3.3 Songs, calls and terminology

Bird vocalisations can be divided into songs and calls. The distinction is both traditional and arbitrary, but as these terms are still retained in the literature we must attempt some clarification. There is also a taxonomic reason for the distinction. One particular group, the oscines, were originally separated from the rest of the order Passeriformes, primarily on the number and complexity of their syringeal muscles. As these birds generally produced more complicated sounds or 'songs', the oscines became known as 'the true songbirds'. But, as we will see later, the differences between oscines and sub-oscines may have more to do with how they learn their songs (and the underlying brain structure) rather than with the actual complexity of their vocalisations.

As this book is largely devoted to the study of songs, it is only fair that we should attempt a definition. In general, 'songs' tend to be long, complex, vocalisations produced by males in the breeding season. Song also appears to occur spontaneously and is often produced in long spells with a characteristic diurnal rhythm. But to these features there are innumerable exceptions. Especially in the tropics, it is common for females to sing as well as males, and both sexes may do so throughout the year even though breeding only occurs during a restricted period (e.g. Langmore 1998). Even in temperate regions, song may occur well before egg-laying and there is also often a bit of a resurgence in the autumn. In the European robin, for example, song may be heard in every month of the year and in the winter it is produced by both males and females singing on separate territories (Lack 1946). However as far as complexity is concerned, it is not easy to generalise and, as we shall see in Chapter 8, species differ enormously in how varied their songs are. There are even songbirds that appear not to 'sing' at all, but the simple 'cheeping' of a male house sparrow on a rooftop may fulfil the same function so that it is, in effect, a very simple song.

What then are calls? 'Calls' tend to be shorter, simpler and produced by both sexes throughout the year. Unlike songs, calls are less spontaneous and usually occur in particular contexts which can be related to specific functions such as flight, threat, alarm and so on. As with the house sparrow example, there are obviously areas of overlap between simple song and complex calls, and plenty of exceptions to the criteria we have presented. But in general, ornithologists and ethologists recognise these distinctions and continue to find them useful. Why the oscines have evolved such complex songs, and a special brain pathway to learn them, is one of the central themes of this book.

Having stated that one of the main characteristics of most songs is their complexity, we have a number of other categories and units to define. Most birds have more than one version of their species song, and some have many. For example, most male chaffinches have more than one version of their song and will repeat one several times in a bout of singing, and then

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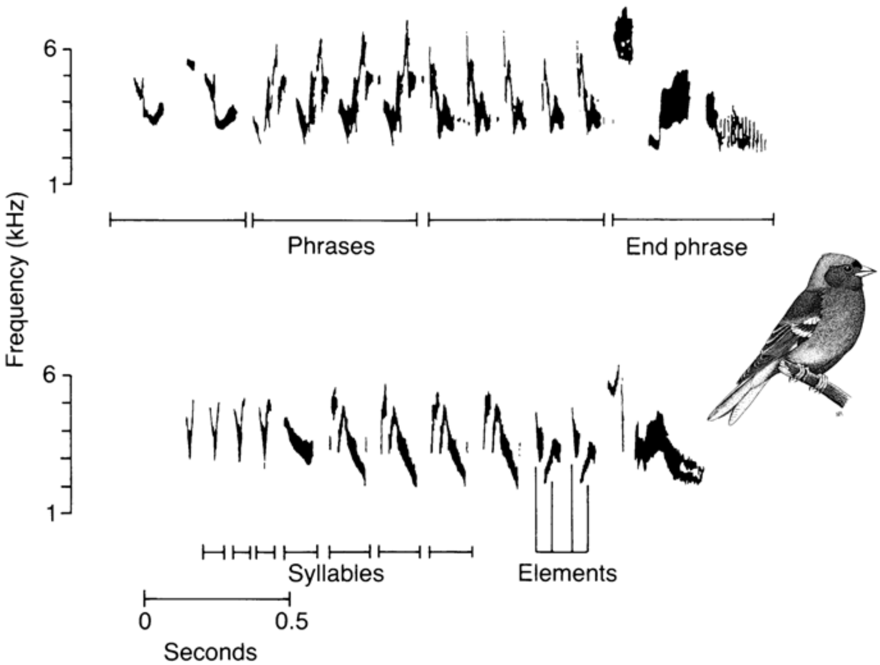

Fig. 1.1. Sonagrams of two different song types from the repertoire of a male chaffinch, also illustrating divisions into phrases, syllables and elements (from Slater & Ince 1979). As explained in Section 1.3.3, sonagrams are plots of frequency against time with the trace being dark where there is energy at that particular point, so giving a visual representation of the pattern of sound.

switch to another. Each version is called a song type, and the male chaffinch is said to have a repertoire of song types (see Fig. 1.1, and the more detailed discussion of repertoires in Chapter 8).

Moving our analysis to a more detailed level, we can also see that each chaffinch song consists of a number of distinct sections. These are called phrases, and each phrase consists of a series of units which occur together in a particular pattern. Sometimes, the units in a phrase are all different, as in the end phrase shown in Fig. 1.1. The units themselves are usually referred to as syllables. Syllables can be very simple or quite complex in their structure. When complex, they are constructed from several of the smallest building blocks of all, called elements or notes (but the latter is usually avoided because of its musical connotations). One definition of an element is simply a continuous line on a sonagram, as illustrated in Fig. 1.1.

Songs, syllables and elements can also be defined by the time intervals which separate them, intersong intervals are the longest, and so on downwards. Because of the great variety of form and structure in songs, individual workers often use and define their own terms, which may be slightly different from those given above. These can only serve as a general guide for this book, for there can be linguistic as well as technical problems with definitions. For example, in German there are two different words for 'song': 'gesang' means the song of a particular species, whereas 'strophe' means a particular delivery of a song. This last word is now often adopted in English to refer to a single rendition.

1.4 Some basic techniques

1.4.1 Observing

The very idea of 'observing sounds' seems like a contradiction in terms. However, if the main objective is to determine what possible functions a sound has, then this is where to start. Currently, it has become fashionable in many branches of modern biology to construct a hypothesis, perhaps even a model, and then test selected predictions by experiment. Naturally, this book is full of such examples, as experiments have played a leading role in the scientific study of bird sounds. But to formulate an appropriate hypothesis or model, a period of observation should first be undertaken. This should preferably be a thorough field study which relates the singing bird to its habitat, to its other behaviour and to its general life history.

The experimenter may have rather less enthusiasm for this phase, regarding the necessary field work as difficult, dull and somewhat old-fashioned. However, it is vitally important for several reasons. For example, it will provide an accurate source of basic information from which a proper hypothesis can be constructed. It should reveal such essential information as when, where and to whom the bird sings. The first clues as to the probable functions of song invariably come from simple, contextual observations in the field. Does a male sing only in his territory? Does he countersing against rival males? Does he stop singing when he has paired with a female? These are very basic questions, and their answers will help to give initial clues to function and will allow appropriate hypotheses to be formulated. Does the male sing only at dawn? Does he stop when his mate appears? Does he sing more in her fertile period? More precise questions such as these can also be answered by careful observations and may lead to the eventual design of suitable playback experiments to test more detailed functional hypotheses. Nor need the modern field worker feel too old-fashioned. The traditional note-book can be replaced by an electronic one, and a number of software packages will allow a full,