

INTRODUCTION

Bird songs are among the most beautiful, complex sounds produced in the natural world and have inspired some of our greatest poets and composers. Whilst biologists are equally impressed, their curiosity is also aroused. How and why has such an elaborate form of communication developed among birds? Charles Darwin was one of many who struggled to attempt an answer, and the elaborate songs of male birds such as nightingales clearly influenced his thinking as he developed the theory of sexual selection. Since then, biologists from many different disciplines, ranging from molecular biology to ecology, have found bird song to be a fascinating and productive area for research. The scientific study of bird song has made important contributions to such areas as neurobiology, ethology and evolutionary biology. In doing so, it has generated a large and diverse literature, which can be frustrating to those attempting to enter or survey the field. At the moment, the choice is largely between wrestling with the original literature or tackling advanced, multi-author volumes. Although our book is aimed particularly at students of biology, we hope that our colleagues in different branches of biology and psychology will find it a useful introduction. We have also tried to make it accessible to the growing numbers of ornithologists and naturalists who increasingly want to know more about the animals they watch and study.

The literature on bird song has seen rapid growth in the sheer number of publications, at least 1000 more in the 12 years since our first edition. The subject has also had its share of controversies. We have tried to do justice to the field without being too partisan and without burdening the reader with too many citations. We hope that our many friends and colleagues will excuse our omissions, especially where the examples we have chosen might have been from their favourite bird, but were not.

In our efforts to achieve a balanced view and widen our expertise, each chapter has been read by one or more experts in each particular area, and we are extremely grateful to them for their considerable help. We have not always followed their advice, and we cannot guarantee that they will be pleased with the result, but we do know that the book has gained immensely from their efforts. We remain grateful to those who read chapters in the first edition for us: Patrice Adret (2 and 3), Luis Baptista (3), Paul Handford (9), John Krebs (2), Bob Lemon (8), Peter McGregor (6), Anders Møller (5) and Bill Searcy (7) and Haven Wiley (4). We also thank those who have read the revised versions in this edition: Henrik Brumm (1, 4 and the reference list), Diego Gil (5), Michelle Hall (8), Rob Lachlan (9), Stefan Leitner (2), Peter McGregor (6), Katharina Riebel (3) and Bill Searcy (7). In addition, many of our immediate colleagues and respective research groups have answered questions and helped with discussion and clarification of numerous issues. Finally, we thank Karen Johnstone, who carefully redrew the figures for the first edition, Nigel Mann for his delightful vignettes, and Martin Griffiths of Cambridge University Press for seeing the book into print for us.

We are both ethologists, and so it is no coincidence that the book is structured around the four questions that Tinbergen prescribed. We start with causation, continue with development, and then move on to function and finally to evolution. Therefore, although the book has many 'themes and variations', it is very much about the biology of bird song. We hope that it illustrates what the scientific study of bird song has contributed to biology in the past, and what exciting developments it may hold for the future. A comparison of this edition with the last one will illustrate just how rapid progress has been in the past decade: in several places it has even been necessary to introduce new sections to take account of this.

Chapter 1 is an introduction to some basic theory, terminology and methodology. In Chapter 2 we attempt to summarise the dramatic and exciting recent advances made by neurobiologists, perhaps the biggest growth area in the whole field. This chapter centres upon the complex neural circuits concerned with song but also deals with sound production, hearing and perception. Chapter 3 deals with the development of song in the individual. Most birds learn their songs during a sensitive period early in life. The intricate interplay between the genetic and environmental factors involved has made the study of bird song a classic example of

behavioural development. Chapter 4 investigates the problems of sound transmission through the environment and illustrates how different habitats may have shaped the evolution of songs. Song structure can also give important information regarding the location and distance of the singing bird.

Chapter 5 considers the context in which song occurs: who does the singing and when? Is there really a dawn chorus, and why is this the best time to sing? Chapter 6 concentrates upon males and emphasises recognition of species, mates, offspring and territorial neighbours. Territorial defence appears to be an important function of bird song. Chapter 7 switches to the female and emphasises the role of song in sexual selection and female choice. Female attraction appears to be another main function of male song. In Chapter 8 we survey the extraordinary richness and variety of bird song and deal with complexities such as repertoires and duets. It searches for patterns and trends and offers some ideas concerning the evolution of such complexity. Finally, Chapter 9 ventures further along the evolutionary path and considers variation in both time and space. How do songs vary from place to place, do dialects exist, how do songs change as they are transmitted across generations?

To some of these questions this book may provide the answers, but to answer others we will have to wait for another generation of biologists. We hope that they will find investigating the biology of bird songs to be as fascinating, challenging and rewarding as we have done.