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ANNIVERSARY ESSAY

Fifty years of bird song research: a case study in animal behaviour

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The growth of bird song research over the past half century has been catalysed by both technical and theoretical advances. The study of mechanisms has largely moved to the neurobiological level, where work on bird song has blossomed. At the behavioural level, development and function have been the prime foci of attention, and I briefly review the advances in these two areas. But, looking forwards, the well is far from dry: I suggest a few topics on which I expect that papers will appear in the journal in the next few decades.

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Looking at the first few volumes of the *British Journal of Animal Behaviour*, as it was called when it first appeared in 1953, makes quite a contrast with the last few. Most of the early articles in the journal were descriptive rather than experimental, those that did ask questions were largely about mechanisms, and such theoretical discussion as there was concerned instinct and the first rumblings of discontent about Lorenz's theories. There was little about communication in general or bird song in particular, an abstract on chaffinch song by a very young Peter Marler being an exception. The President of ASAB, W. H. Thorpe, wrote the Editorial to Volume 1. He was then best known for his work on learning in insects; the first of his seminal papers on song learning in birds would not appear until the following year.

Work described in recent volumes is almost entirely experimental, underpinned by the rich body of theory that has been developed in the intervening decades. This, and I would argue most notably the concept of inclusive fitness (Hamilton 1964) and the ramifications extending from it, have led to much of the research described now being either at the functional end of the spectrum, or at least placed firmly in a functional and evolutionary context. Many of the papers concern communication, powered especially by the current interest in sexual selection and mate choice; some 25 contributions in the last three volumes (over 5%) deal with bird song.

In this essay I would like first to consider some of the advances that have led this area of research to prosper as it has. Then I shall look at some of the achievements of the past 50 years, focusing on development and function

as the two areas of greatest impact. Finally, I shall discuss a few topics where I feel that the fruit is ripening and will be picked in the years ahead.

TOOLS FOR THE TRADE

Bird song is a wonderful topic for attacking a wide variety of questions in animal behaviour and that realization, together with changes in theory over the past few decades, has undoubtedly boosted studies in this area. But technical advances, even more than theoretical, have been responsible for opening up new possibilities in the study of song. The introduction of the sound spectrograph, originally used by Thorpe (1958) in his study of chaffinch, *Fringilla coelebs*, song development, undoubtedly gave huge impetus to the field. This equipment made it possible to describe and measure sounds, and its successors have enabled the manipulation of them, in a degree of detail hard to achieve for other aspects of behaviour. Thorpe's classic study led the field to blossom. Similarly, the study by Nottebohm et al. (1976), which first applied neurobiological techniques to the mechanisms underlying song and its development, was another seed that has germinated to produce a huge tree. I would argue that the two main paradigm shifts in bird song research have stemmed from these papers. But paradigm shifts are not single-handed affairs (my bird song database includes over 2000 references): Thorpe's torch has been carried on, most notably by Marler and his colleagues on several small-repertoire species (see Marler 1997 for a recent review) and by Todt and his group on the nightingale, *Luscinia megarhynchos*, with its large repertoire of song types (see Todt & Hultsch 1996). Similarly, the neurobiological revolution that Nottebohm instituted, and has continued to lead, has been joined by

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many others whose findings have built up an impressive edifice (see, for example, the recent review by Brainard & Doupe 2000).

It would be easy to list many other technical advances that have spurred on the field. To me some of the most impressive have been the innovative techniques recently applied to understanding how the syrinx (the bird's sound-producing organ) works. It seemed remarkable enough that a bird would sing with a thermistor in each of its bronchii (Suthers et al. 1994), but subsequent papers have been based on endoscopic pictures of the syrinx in action (e.g. Larsen & Goller 1999, 2002). Such technical feats have shown that birds do not produce sounds in a way that the study of their cold anatomy had suggested: while the system is complex and many issues are unresolved, sound generation seems to depend more on vibration of the labia and lateral tympaniform membranes than on the medial tympaniform membranes as thought earlier.

At a less complex level, the simple facts that male birds will respond to playback of song by approaching the loudspeaker, calling and singing (Brooks & Falls 1975), and that females (especially with an oestrogen boost) will often respond with a copulation solicitation display (King & West 1977), have led to a spate of studies on responses to song. A large number of such experiments have now been conducted, demonstrating clearly the differences in response that birds have to different stimuli, for example to the songs of neighbours and of strangers. The design of many such experiments was criticized by Kroodsma (1986, 1989), to considerable controversy (see McGregor 1992). While some of his aspirations for experimental design were more exacting than is realistic, Kroodsma was certainly right to highlight the dangers of pseudoreplication, and this message has been largely taken on board. But the assumption that bird song playback experiments were in some way uniquely bedevilled by this problem is incorrect and harmful: tests of a drug using samples from a single production batch do not necessarily generalize to any other batches either. The self-criticism of bird song research in this respect could well be emulated by many others.

SONG DEVELOPMENT

Thorpe was not the first to study song learning. Barrington (1773) showed clearly that cross-fostering could lead birds to learn the song of the wrong species, a linnet, *Acanthis cannabina*, that of a skylark, *Alauda arvensis*, for example. But only the precision of the sound spectrograph has permitted experiments to reveal the full subtlety of the interactions involved in the development of song. While song is learnt, typically the breadth of that learning is limited so that young birds end up producing only the song of their own species. It is one of the most impressive examples of how nature and nurture interact during development.

Early models of song development saw young birds hatching with a rough idea (or crude template, to put it more correctly) of what their own species' song was like (e.g. Konishi & Nottebohm 1969; Marler 1970). Other

songs failed to match this and were not learnt but, when the birds heard their own species' song, the template was honed to an exact one which they then attempted to match with their output when they began to sing themselves. In several of the species first studied, the process of song memorization was limited to a sensitive phase early in life, in some cases ending a good period before the bird began to sing itself.

Subsequent work has shown the need to amend this model in various ways as more detailed studies of song development have been carried out (see, for example, the recent description of how song emerges from subsong in zebra finches, *Taeniopygia guttata*, by Tchernichovski et al. 2001). The sensitive phase varies considerably between species, being completed before their first winter in some (e.g. marsh wren, *Cistothorus palustris*: Kroodsma 1978), but extending into adulthood in others (e.g. indigo bunting, *Passerina cyanea*: Margoliash et al. 1994). Its duration and timing may depend on the young bird's precise experience (e.g. Jones et al. 1996), although the extent to which it is modified by social interaction, as argued for example by Baptista & Petrinovich (1984), is a matter of some controversy (Nelson 1997). In addition to the role of other birds as sources of learnt material, it has been found that they may influence selection of the material used when the young bird starts to sing. In many species young birds learn a wide variety of song elements which they produce in subsong (e.g. swamp sparrow, *Melospiza georgiana*: Marler & Peters 1982). However, their full song is based on a more limited range: they may reject songs that fail to match those of neighbours with whom they interact (e.g. field sparrow, *Spizella pusilla*, Nelson 1992), or they may preferentially retain those that females find attractive (brown-headed cowbird, *Molothrus ater*: West & King 1988). This procedure has been called 'action-based learning' by Marler & Nelson (1993).

Despite these findings it is not the case that tutoring is simply a matter of getting conditions right and a young bird will master whatever song it is exposed to. Particular species may be limited in the range of sounds that they produce, and may be incapable of copying ones outside that range (e.g. swamp sparrow: Marler & Pickert 1984; see also Podos 1997). Young birds may also be especially prone to focusing on and learning the sounds of their own species. For example, fledgling white-crowned sparrows, *Zonotrichia leucophrys*, chirp more in response to playback of white-crown song than to that of other species, suggesting that it is, even at this early stage, a more salient stimulus to them and thus one that attracts their attention (Nelson & Marler 1993); they even show a preference for their own subspecies over others (Nelson 2000). The presence of the introductory whistles of white-crown song also serves as a cue for vocal learning: provided these whistles are present young birds learn alien sounds that follow and would normally be rejected (Soha & Marler 2000). Birds trained with isolated phrases will also reassemble them into the species-specific sequence, again implying some constraint on the form of song (Soha & Marler 2001).

Song learning remains a topic of particular interest because of the interplay between nature and nurture that

it reveals. It is also a prime case of imitation. While there have been occasional attempts to argue this away (see [Whiten & Ham 1992](#)), on the grounds that vocal learning is an easier skill than visual imitation, the discovery that some birds are at least as good as many primates in copying motor skills ([Heyes & Ray 2000](#)), may set this argument on its head. Perhaps the generic skills that vocal learning has given birds equip them well for other forms of imitation (see [Moore 1992](#)).

THE FUNCTIONS OF SONG

[E. O. Wilson \(1975\)](#), in his ‘dumb-bell model’, predicted that animal behaviour would be swallowed up by neurobiology at one end and sociobiology at the other. As far as song is concerned he has been largely right but only if, as sociobiologists are prone to do, one ignores development. The neurobiology of song would take an article in itself (and a different author!). But an immense amount of energy has also gone into understanding the functions of song.

The impetus for this study has come from theoretical considerations. In the 1950s it is probably true to say that most ethologists thought that ‘good of the species’ and ‘good of the individual’ arguments were alternative ways of expressing much the same thing. [Wynne-Edwards \(1962\)](#) did a service by challenging that view, and papers by [Hamilton \(1964\)](#) and others led to recognition of the importance of kin selection and the primacy of inclusive fitness. For communication it became clear, as put most strongly by [Krebs & Dawkins \(1984\)](#), that animals would signal only if it was to their own advantage. It was not primarily about cooperation and helping others, but about influencing them for the individual’s own ends.

On the face of it, generating a large number of decibels from an exposed perch on the top of a tree is not the most obvious way of enhancing one’s inclusive fitness. The energy costs of song do not appear to be great ([Oberweger & Goller 2001](#)), but time is expended, and predation risks must also weigh against the behaviour unless there are substantial gains to pit against them. These gains appear to be two-fold. Song repels rivals, as shown most elegantly by [Krebs \(1977a\)](#) on great tits, *Parus major*, in what has become the classic paper on bird song function. Song also attracts females (e.g. flycatchers, *Ficedula* sp.: [Eriksson & Wallin 1986](#)) and stimulates them (e.g. canaries, *Serinus canaria*: [Kroodsmma 1976](#)). The balance between the two functions of rival repulsion and mate attraction probably differs between species, and this may account for some of the diversity of singing styles they show ([Slater 1981](#)).

The form of song, the rate of singing and many of its other features, may also convey more subtle information, for example on how good a parent a male will be ([Greig-Smith 1982](#)). Songs may also indicate male quality in several other ways (see review by [Searcy & Yasukawa 1996](#)). Females have sometimes been found to prefer some phrases to others (e.g. [Vallet & Kreutzer 1995](#); [Forstmeier et al. 2002](#)); these may be ones that are difficult to produce so that only males of high quality can master them. [Nowicki et al. \(2002\)](#) have also recently

shown a preference in female song sparrows, *Melospiza melodia*, for songs that have been accurately copied, which may be another cue to male quality. Repertoires have been a particularly challenging topic. There now seems little doubt that large ones, which may include hundreds or even thousands of song types, have arisen through sexual selection by female choice ([MacDougall-Shackleton 1997](#)). In various species larger repertoires are more attractive and stimulating to females (e.g. sedge warbler, *Acrocephalus schoenobaenus*: [Catchpole et al. 1984](#); [Buchanan & Catchpole 1997](#)). Evidence as to why it benefits females to respond in this way is also coming forward. The most frequent suggestions have been that only high-quality males can afford large repertoires because the necessary brain space is costly ([Gil & Gahr 2002](#)), or because parasites ([Buchanan et al. 1999](#)) or developmental stress ([Nowicki et al. 2000](#)) affect the capacity to produce a variety of songs.

It has sometimes been suggested that variations in song may provide a marker of kinship, an attractive idea given the importance that kin recognition may play in various aspects of behaviour. For example, if males learn their songs from their fathers, then females could use them as a cue to avoid mating with close relatives. This may indeed be the case in Darwin’s finches, *Geospiza* sp., in which males do learn their songs from their fathers, and females avoid mates who sing like their fathers, although not in their first breeding year when they breed late and have limited choice ([Grant & Grant 1996](#)). However, in this respect, Darwin’s finches appear something of an exception: in most other species that have been studied song learning occurs primarily after independence from the parents and is thus unlikely to provide a cue to kinship ([Slater & Mann 1990](#)).

KEY QUESTIONS FOR THE FUTURE

There are few areas of animal behaviour that the study of bird song has not illuminated in the last 50 years and, albeit very selectively, I hope I have illustrated some of these. I would like to finish by considering some current trends and future prospects to show that the cornucopia is not yet empty.

Females and Song

Song by females and the effects of male song on females have been two of the main growth areas of study in the past few years. The former has been a comparatively neglected topic because much of song research, indeed much of most research, is carried out in temperate regions of the world where female song is, at least relatively, rare ([Morton 1996](#)). On the other hand, females often sing in the tropics, and may also join in with males in more or less sophisticated duets (e.g. [Levin 1996](#); [Hall 2000](#)). Even in temperate regions it is probably commoner than often assumed, and certainly deserves more study ([Langmore 1998](#)). The reasons why females sing, and the significance of duetting, remain matters of debate.

The response of females to the songs of males was for long neglected because of the difficulty of studying it in the field. While males interact with each other repeatedly throughout the season, the attraction of a mate may be the work of an instant. Radiotracking female great reed warblers, *Acrocephalus arundinaceus*, has, however, suggested how they sample among males before making their choice (Bensch & Hasselquist 1992); once mated they obtain extrapair fertilizations from neighbouring males with larger repertoire sizes than their own mate, and this appears beneficial as postfledging offspring survival correlates with paternal repertoire size (Hasselquist et al. 1996). In the laboratory, work on female preferences using copulation solicitation has been supplemented by the use of operant techniques (e.g. Riebel et al. 2002), which are a tool of great potential. Just how the songs of males are adapted to attract and stimulate females is a rich seam that is only just starting to be mined. Similarly, while we know much about song learning in males, with some exceptions (e.g. Clayton 1990), we still know little about how female preferences develop.

The Neurobiology of Repertoires

Studies of the behavioural mechanisms underlying song, once a major issue, have tended to decline as the neurobiological study of bird song has expanded. The neurobiologists have answered some fundamental questions about the brain mechanisms concerned with song learning, storage and production, but these questions would not even have been asked without the basic behavioural information in the first place. The complexity of song organization and sequencing has been well described for many species. Songs are often very much equivalent 'alternative motor patterns' (Hinde 1958), with the choice between them following clear rules (Slater 1983). Behavioural data such as these provide a challenge to neurobiological explanation. How birds select between songs may yield secrets on the broader issue of how animals decide what to do and when to do it.

Why do Songbirds Learn their Songs?

On present evidence, vocal learning has a surprisingly discontinuous distribution (Janik & Slater 1997), although within the groups of birds that show it (parrots, hummingbirds and oscine passerines) it appears to be universal. The questions of why vocal learning is advantageous, and why it occurs in some groups and not others, remain to be satisfactorily answered. Given that it has been found throughout those groups that do show it, perhaps the question of why it occurs is best split in two. First, there is the historical question of why it arose in the first place, which it may have done before the evolution of anything that we would call 'song'. Second, once it evolved, why did it persist, despite the highly varied roles that song plays in the lives of different species? In view of the great differences in song between species, one functional theory (e.g. learning matches to neighbours or learning matches to transmission characteristics of

habitat) seems unlikely to account for all (Slater 1989). For this reason, the possibility that, once learning had evolved, species showing it got caught in a 'cultural trap' does seem an attractive one (Lachlan & Slater 1999). But this question continues to be a challenging one and, again, one of likely significance beyond the world of bird song. Social learning has recently become an active field of study (e.g. Heyes & Galef 1996): bird song is a prime example of this phenomenon and one that may shed light on the advantage to animals of learning from others in other contexts as well.

The Rôle of Small Repertoires

Small repertoires of just a few song types are less easy to understand than large ones which, as discussed above, are likely to have evolved through sexual selection by female choice. By contrast small repertoires are often thought to have evolved primarily in a male-male context. Various theories of their function have been put forward. These range from the idea that they stop the listener from habituating (antimonotony, Hartshorne 1956), to the notion that they simulate the presence of more than one individual (Beau Geste, Krebs 1977b), to the suggestion that they avoid muscular fatigue (antiexhaustion, Lambrechts & Dhondt 1988). None of these ideas has received unqualified support, and the fact that many such species sing with 'eventual variety', singing each song type a number of times before singing the next, suggests that it pays the individual to get each message across before moving on to the next (Slater 1981). But why? Perhaps the most plausible hypothesis is that repertoires allow birds to match, or not to do so, when countersinging with neighbours (e.g. Beecher et al. 2000); this is less likely where the level of sharing is low, although birds may still 'match' with similar songs (Burt et al. 2002). Interactive playback has been an important recent technical advance which is helping us to understand just how individuals use their songs in relation to one another (e.g. Vehrencamp 2001). It helps to simulate the dynamic interchange between two birds which is a far cry from the stereotyped repetition of a single unvarying song type that traditional playbacks involved. It may give us the key to understanding why one song type is the norm in many species, whereas in others individuals usually have three or four (see data in Read & Weary 1992).

Species Differences in Singing Behaviour

One of the striking things about bird song is its remarkable variation between species. Repertoire size that ranges from one simple song type to several thousand complex ones is but a single example. But it also varies in many other ways: in whether one or both sexes sing, in seasonal and daily cycles, in the relation between song and the breeding cycle, in whether variety is immediate or eventual, and so on. Many species have now been studied and it is becoming increasingly feasible to use the comparative method to see how these features of singing link with other features of way of life. From the first efforts in

this direction, the answer does not seem to be simple (Read & Weary 1992). A great deal of judgement is also needed in deciding how species should be categorized and how the data should be framed. On repertoires, for example, should a species with a limited number of elements that are recombined to give a very large number of song types (e.g. willow warbler, *Phylloscopus trochilus*: Gil & Slater 2000) be scored at the element or song type level? It is certainly not satisfactory to look at some species at one level and others at another (Møller et al. 2000). But, these technical difficulties apart, with the increasing sophistication of the comparative method, and our rapidly growing knowledge of the lifestyles and singing patterns of different species, I would anticipate a spate of such studies. It is a topic of which the surface has barely been scratched.

Song and Interactions

As mentioned above, interactive playback is allowing a much more realistic approach to the relations between two males singing on adjacent territories. It is becoming apparent that the challenge males provide to each other is not just in what they sing, how much and how loudly, but in the way in which songs relate in time to each other, alternating or overlapping (e.g. Todt & Naguib 2000).

In various ways, even looking at interactions is an oversimplification. As shown with the alarm calls of chickens (Marler et al. 1986), birds may behave differently depending on whether or not they have an audience, and on the nature of that audience. Even where singing interactions are not involved, a male may use his songs differently in the presence of another male, a female and when on his own. This is most obvious in the growing number of species that appear to have songs that they use in different contexts, but it may also be an important, largely unexplored, issue in species where this is not the case.

A separate question is whether the influence of song spreads beyond pairs of interactants. The active space of song will often encompass many other individuals, and singing interactions may themselves involve more than two individuals, in relationships more akin to a network (McGregor & Dabelsteen 1996). Even where only two birds are singing, the form of their interaction may provide others with information about them. Evidence is beginning to accumulate that this 'eavesdropping' may indeed provide information to third parties (e.g. Peake et al. 2002).

CONCLUSION

In this short essay I have had to be very selective, and have obviously placed stress on subjects that interest me and ignored ones others may feel of prime importance. It is part of the richness of our subject that many different perspectives are possible. What I hope I have illustrated, however, is not only that the study of bird song has proved a particularly illuminating one over the past five decades, but that it will certainly also keep us busy in the next half century as well.

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