Animal Communication: Timing Counts

Collective signalling in animals has fascinated biologists for a long time. A recent study on Australian songbirds sheds new light on the function of highly coordinated avian duets.

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From a bird calling in the tree tops to a whale singing in the depths of an ocean, the astounding variety of vocal repertoires and the ways in which animals use them have fascinated laymen and scientists alike. Most animals that use sounds to communicate do so singly, broadcasting their songs or calls to others. But in some species, a group may join together in a chorus or members of a pair may produce a duet. The sounds that different animals contribute are not necessarily coordinated in any way (for example [1,2]), but can sometimes be strikingly so, as is the case in many of the choruses and duets found in birds (Figure 1). Such collective signalling is particularly interesting, because the interplay between the single components produced by different individuals can form a new quality, which, in turn, may act as a signal itself. This sort of meta-parameter could be formed by the particular phrases that individuals combine (for example [3]) or the temporal patterning between the individual contributions of the collective signal.

Duets are much commoner and easier to analyse than complex group displays and have evolved independently in a wide variety of taxa, including primates and birds (reviewed in [4]). Among birds, they occur in 200-odd species around the world, the overwhelming majority of them in the tropics [5]. Few people who have had the chance to hear birds duet fail to be amazed by the stunning precision with which they can perform. The male and female of a pair often fit their sounds together so precisely that it is hard to believe it is not just one bird singing. Many studies have been carried out on these elaborate vocal displays over the past 30 years [6], but no clear picture has yet emerged as to how and why birds duet, and our understanding of this fascinating form of animal signalling is still surprisingly patchy.

One particularly intriguing idea is that the overall temporal precision of the duet may improve with the duration of the pair bond, because achieving such a high degree of song coordination between partners is likely to take time and investment. Thus, well-coordinated duets may signal pair stability or commitment between the duet partners [7,8]. Several studies have examined this idea since it was put forward more than a quarter of a century ago, but none could find evidence for it. Levin [9] found that bay wrens (*Thryothorus nigricapillus*) whose mates had been removed sang with as close precision with their new partners as they did with their long-established mates. A similar result was obtained by Marshall-Ball and co-workers [10] for the closely related plain wren (*Thryothorus modestus*): pairs that had been together for two years or more were found to sing with the same degree of coordination as pairs formed only recently.

New data from a common Australian bird, however, suggest that duet precision does reflect pair bond strength. In a study on magpie larks (*Grallina cyanoleuca*), reported recently in *Current Biology*, Hall and Magrath [11] show that the temporal coordination of duets improves with pair duration. The duet of magpie larks consists of an alternation of male and female song notes. But the precision of the duet may vary: in highly coordinated duets, the male and female alternate their notes in a rapid succession, but in poorly coordinated duets the notes do not fit precisely together and often overlap. Hall and Magrath [11] found that magpie larks sang more precisely coordinated duets the longer they had been paired. In the first week of their partnership, fewer than half the duets were highly coordinated; but after a year or more, the pairs sang over two thirds of their duets in precise coordination.

Like many birds, magpie larks use their songs as a signal during territorial disputes, and most interestingly they respond to these differences in duet coordination when challenged by a rival pair. When Hall and Magrath [11] played back duets with different levels of coordination to territorial pairs, they found that the males sang more songs in response to highly coordinated duets with no overlap between song notes than to playbacks in which at least a third of the notes overlapped. The authors suggest that more precisely coordinated duets are perceived by male magpie larks as a more threatening territorial display, and thus the birds respond more strongly. As established pairs of magpie larks are more likely to sing well coordinated duets than newly mated birds, the precision of temporal patterning could signal the duration of their pair bond and thus the quality of their coalition and their ability to cooperate.

It remains to be shown just what is the cooperative benefit for precise temporal coordination of duets — for both intruding birds and the territorial pair. If birds with more coordinated duets are more likely to take over territories, then signalling their greater ability would be a benefit for the intruders. In addition to analysing the responses of territorial males to such duets, it would also be interesting to investigate just how territory holders duet in response. Perhaps more precise duets are better in territorial defence as well, so that it pays territory owners to cooperate in this way also. Addressing these issues may reveal whether duet coordination is sexually selected, and so give us a better understanding of the selective forces that led to the evolution of avian duets.

In addition to these functional considerations, there are the

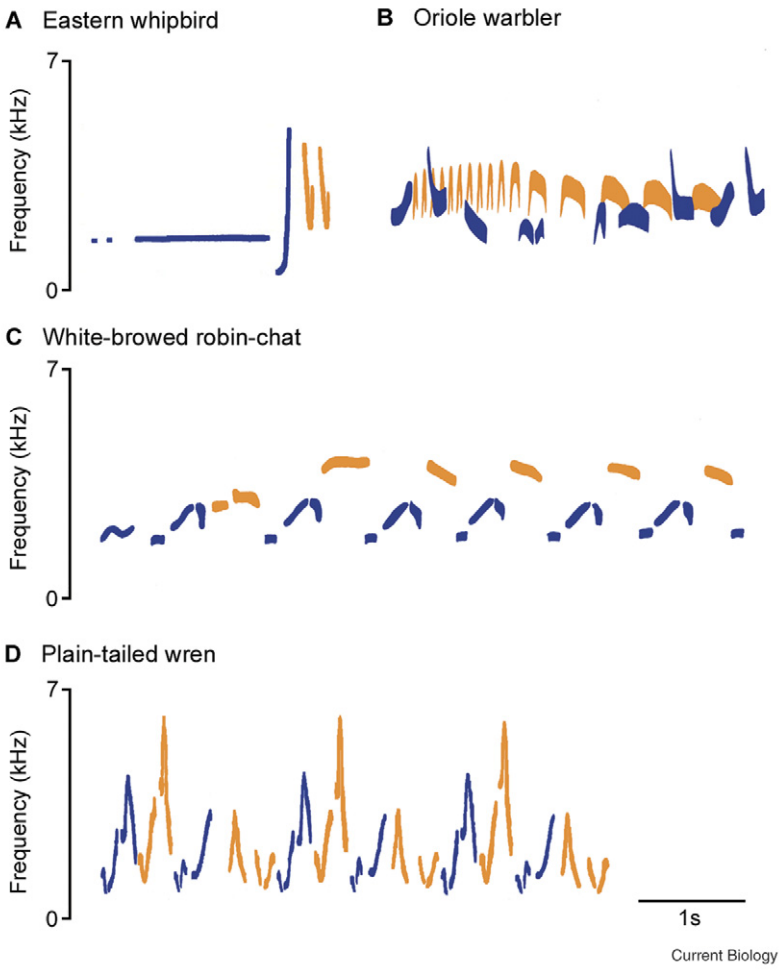

Figure 1. Avian duets and choruses.

The way in which birds sing collectively varies a lot between species (the male part of the song is illustrated in blue, the female in orange). (A) The duets of eastern whipbirds (*Psophodes olivaceus*) are of a stimulus–response type, where the female simply responds to the male phrase [4]. (B) The songs of oriole warblers (*Hypergerus atriceps*) are an example of duets with rather loose temporal association, in which the female overlaps the male part [16]. (C) Some species produce highly coordinated duets in which the members of a pair fit their notes precisely together, as for instance in the white-browed robin-chat (*Cossypha heuglini*) [17]. (D) The most complex type of collective singing yet found has been in the plain-tailed wren (*Thryothorus euophrys*), where males and females fit their parts precisely together and cycle through a very rapid succession of different phrases. On top of that, the male and female parts are not only sung by the two members of a pair, but can be produced by several males and females of a group, each sex singing closely in unison [18]. (Panels A and C adapted from [4] and [17], respectively.)

problems of just how birds achieve and detect duet coordination. It may be that the overlap of song notes is key here. Poorer temporal coordination between the duetting partners will lead to increased overlap between their vocalisations, and thus to mutual masking. The mitigation of signal masking is one of the major forces affecting the way in which birds sing [12]. In particular, it has been shown that songbirds can adjust the temporal pattern of their singing to avoid overlap with the sounds produced by other birds [13]. This suggests that the fundamental mechanism that duetting birds use to achieve their highly coordinated singing is widespread and also present in non-duetting species, which use it to avoid signal masking. On a proximate level, signal masking could explain why the magpie larks responded more strongly to the precisely coordinated duets: the highly coordinated playbacks may simply have been a stronger stimulus, because their components were not masking each other, so making the duet more intelligible.

Hall and Magrath's findings [11] clearly support the idea that duet songs function in territorial disputes. But duetting may also play a role within a pair, especially in mate guarding. Support for this comes from cases where birds respond more aggressively to solo songs of their own sex than to duets (for example [4,14,15]). This is the opposite of what one would expect in territorial defence, as two birds would be a greater threat than one. The confusing variety of evidence we have at present suggests that duetting may serve more than one function within a species and different functions between them. More studies such as that of Hall and Magrath [11] will help to reveal whether signalling pair bond strength is a more widespread phenomenon, and whether vocal coordination plays a role in the sexual selection of avian duets.

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