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Many animals communicate using sound. The sounds involved are often short and simple calls, like the croaking of frogs or roaring of lions. But they may be much longer and more elaborate, and are then usually referred to as ‘song’ by analogy with those produced by humans. Some examples are the marvellously evocative songs of humpback whales, and birdsong with its great diversity. As technology enables humans to listen more closely to a variety of kinds of animal vocalization, we recognize more and more species as singers. For example, scientists have only recently discovered that mice sing ultrasonic songs, several octaves above the human hearing range (Holy and Guo, 2005). Many composers have been inspired by animal sounds, most frequently those of birds (*see* Birdsong), but also whales, frogs, insects, and others (Doolittle, 2008).

Whether or not the sounds produced by non-human animals should be classed as music is a more complex issue. It may be useful to consider such questions as why animals sing; what parallels can be drawn between human and animal singing behavior; what sonic or structural similarities exist between human and animal song; and whether an understanding of non-human animal songs might shed light on the origins of the music of the animal species *Homo sapiens*. The emerging field of zoomusicology deals explicitly with this sort of question (Mâche, 1983; Martinelli, 2002, 2009). Scholars in a variety of fields, both scientific (Fitch, 2006) and musical (Rothenberg, 2005, 2010, 2013; Taylor, 2008, 2011) contribute to this ongoing discussion.

The use of sound as a means of communication for animals has several advantages. As with human language, much detailed information can be packed into a short sequence of sound signals, and these travel rapidly through air or water in all directions, by day or night, little affected by obstacles. Other modes of communication are usually less efficient. Smells diffuse slowly and largely downwind; they cannot be rapidly changed. Visual signals move at the speed of light and can be quickly altered, but they are disrupted by obstacles in their path and usually depend on light, so are of little use in a dense environment or at night. Given these considerations, it is not surprising that sound is the channel of communication most often employed for complex animal signals, particularly when it is important that the signal covers the widest possible area.

Simple animal sounds, such as call notes, can convey a variety of messages. Examples are the calls used by members of a flock to maintain contact, or the alarm signals produced by certain animals when they spot a predator, which lead others to ‘freeze’ or seek cover. Some such calls are ‘referential’, like words in a language. Thus a vervet monkey (*Cercopithecus aethiops*) has different calls for eagle, snake, and leopard, and other vervets hearing these calls behave appropriately (Seyfarth, Cheney, and Marler, 1980). To the snake call they look down and approach with caution, to the eagle one they rush from the trees and into the thickets, while to the leopard alarm they run up into trees. The three calls might as well be words representing these three different kinds of animal. Such instances, however, appear to be rare. Most animal communication is believed to be affective

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rather than referential, representing emotional states rather than particular objects in the outside world, and in this respect many consider it to be more akin to music than to language. Further, the elaborate songs of some birds, in which each individual may have several hundred or even thousand different phrases, do not appear to convey many different messages. It seems that this variety has evolved for its own sake to convey the same message in many different and perhaps more persuasive ways, rather than because there are different messages to transmit.

## Bird Song

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The singing animals which have been most extensively studied are songbirds (scientifically known as oscine passerines, in the order *Passeriformes*) from temperate zones. Although most species of birds are quite vocal, most of the birds with complex songs are songbirds. Songbirds must learn their songs: they will not be able to sing their species song unless they can learn from other members of their species. (Birds from two other orders, parrots [*Psittaciformes*] and hummingbirds [*Trochiliformes*], must also learn their vocalizations, but they do not tend to produce the complex, stereotyped songs that passerines do.) The degree to which learning shapes passerine song varies, with some species only able to learn their species song from adult members of their species during a very narrow window while young, and others able to learn any song to which they are exposed, and to keep learning throughout their life.

Two main reasons have been proposed to explain most temperate-zone songbird songs, and there is good evidence for both of them (Catchpole and Slater, 2008). A clue is provided by the fact that song in these birds is produced primarily by males, and occurs most frequently during breeding season. At this time, males of most songbird species (and females of a few) fight for territories. They often have duels in song across territorial boundaries and, if the birds involved have repertoires of multiple songs, each tends to match the song of the other as they sing. A male redwinged blackbird (*Agelaius phoeniceus*) that cannot sing suffers more intrusions on to his territory (Smith, 1979). If a male great tit (*Parus major*) is removed from his territory, the territory will be less rapidly invaded if recordings of great tit song are played from loudspeakers within it (Krebs, 1977). Such evidence points to song having a role in rival repulsion. Repelling rivals with song may also explain why some birds sing a number of distinct song types, for this enables them to match different intruders. Many such birds sing the same song several times in succession before moving on to the next and, unless countersinging with a rival, they will often cycle through their whole repertoire before returning to the first song (e.g. the chaffinch, *Fringilla coelebs*: Slater, 1983).

The need to repel rivals may explain why many birds sing multiple song types, and why they may repeat each song several times, but it does not account for the extreme elaboration of song found in many other species. Here a likely explanation lies in the second proposed reason why animals sing: that it attracts mates. In the case of temperate songbirds, it is usually males who sing to attract females. Males of many species stop singing once they are mated (e.g. the sedge warbler, *Acrocephalus schoenobaenus*: Catchpole, 1973), and song increases enormously if a male loses his partner (e.g. the great tit: Krebs and others, 1981). In several species song has been found both to attract females (Eriksson and Wallin, 1986) and to stimulate them to build nests and lay eggs (Kroodsma, 1976). One might suppose that a simple song labelling the male as belonging to his species, so that only the right females are attracted, would be sufficient. This may be so in some species, where a simple little song fulfils that function. But in other species females are known to be most attracted by males with more

elaborate songs or large repertoires of different songs (Catchpole, 1980; Eens, Pinxten and Verheyen, 'Male Song', 1991). The message of each sound is the same: 'I am a male in breeding condition'; but the male that can say it in the most varied way is more attractive to females and thus most likely to be successful in leaving his genes to the next generation. In such birds, unlike those with small repertoires, it is much less common for the same song to be repeated several times consecutively, for the main message is variety itself (Slater, 1981).

The sedge warbler is a good example of a bird with a large song repertory (Catchpole, 1976). Each male's song is composed of relatively few elements (the smallest unit of song construction, seen as unbroken lines on the spectrogram) but these are combined to make a complex whole. At the start, two elements alternate; then numerous others are introduced in quick succession in the middle of the song. Two of these are then selected to alternate in the closing section. These two then introduce the next song, which starts after a brief pause. This way of combining a small repertory of elements leads to an almost infinite number of possible songs, but just how varied they are depends on the number of elements that a male has: the effectiveness of a male in attracting and stimulating females depends on his element repertory. Males with a large repertory both attract females earlier in the season and stimulate them to mate more effectively (Catchpole and others, 1984).

Unlike the sedge warbler, nightingales have fixed repertoires of song types, each of which is near identical every time it is produced (Todt and Hultsch, 1996). But the repertory itself is very large, usually consisting of over 200 different phrases. A bird tends to cycle through its repertory, though it misses out many of the phrases each time it goes through the sequence; thus the same phrase rather seldom occurs twice in close succession, but will often recur after some 70 or 80 others. What the nightingale seems to be doing, as is the sedge warbler but in a different way, is maximizing the variety of its output.

One dramatic aspect of song learning in many birds is mimicry, the copying by one species of another. A well-known example is the European starling (*Sturnus vulgaris*) in which each bird, in addition to the distinctive whistles and rattles that make up its species-specific song, will incorporate the songs of several other species (Eens, Pinxten, and Verheyen, 'Organisation of Song', 1991). However, the most remarkable case must be that of the marsh warbler (*Acrocephalus palustris*), a small European bird which migrates to East Africa in the autumn. Adults cease to sing before their chicks hatch, but the young birds learn the sounds of many other species from Europe and Africa during their first winter and incorporate them into a song which, while of distinctively marsh warbler patterning, is largely or entirely based on mimicry (Dowsett-Lemaire, 1979). On average, a male marsh warbler mimics some 77 other species. It is not known why birds mimic, but it seems to be a way of building up a varied repertory. It appears to be easier for birds to copy the sounds that they hear than to generate variety by improvisation.

Although female birds in temperate regions rarely sing, they play an active role in shaping the direction in which song evolves. In species where females selectively mate with males with more elaborate songs or larger repertoires, this drives the development of ever more complex songs, through the process known as 'sexual selection' (Charles Darwin, 1871). There are also some temperate songbird species in which both males and females sing, including European robins (*Erithacus rubecula*), redwing blackbirds (*Agelaius phoeniceus*), starlings (*Sturnus vulgaris*), and others (Langmore 1998). In some of these cases, the female as well as the male defends a territory,

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singing to ward off intruders. In at least one temperate passerine species, the Alpine accentor (*Prunella collaris*), both males and females sing to attract mates (Langmore, Davies, Hatchwell, and Hartley, 1996).

Though female song is somewhat of a rarity in temperate region birds, it is quite common in tropical Passeriformes (Morton, 1996; Langmore, 1998; Slater and Mann, 2004). In a number of these species, mated pairs sing duets. In some species, such as the Slate-Coloured Boubou (*Laniarius funebris*), the duetting pair appears to sing to jointly defend their territory (Sonnenschein and Reyer, 1983). Duetting may also enhance pair-bonding between members of a pair (Slater and Mann, 2004), or help coordinate care of young (Langmore, 2004). In at least one non-passerine tropical species, the black coucal (Voigt and Goymann, 2007), the usual sex roles are reversed, with females singing more complicated songs to attract males. Female black coucals also defend territory, while males build nests and care for the young.

An unusual case is that of the plain-tailed wren (*Pheugopedius euophry*), native to the Andes, which sings in 'choruses' of up to seven birds, with all males singing one part and all females singing the other (Mann, Marshall-Ball, and Slater, 2003). The choruses interlock so tightly that a casual listener might mistake it for one bird singing. Here it is believed that neighboring birds are mutually defending their territory against rivals.

## Mammal Song

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While there are more than 4000 species of song-learning Passeriforme birds, vocal learning appears to be much rarer among mammals. So far it has been recognized in humans, whales and dolphins (Payne and McVay, 1971; Guinee and Payne, 1988; Janik and Slater, 1997), some species of bats (Esser, 2003; Knörnschild et al., 2009), phocid (earless) seals (Ralls, Fiorelli, and Gish, 1985), and possibly in mice (Holy and Zhongsheng, 2005; Arriaga, Zhou, and Jarvis, 2012) and elephants (Poole et al., 2005). Some other vocally communicative mammals, such as wolves, may learn to alter their vocalizations to communicate different things to their conspecifics, but do not learn the vocalizations themselves. It is interesting to note that gibbons – lesser apes native to Southeast Asian rainforests – sing complex duet songs, famed for their musical sound, but they do not learn these songs. A gibbon raised in isolation will still sing the correct song for its species, and a hybrid offspring will produce a hybrid song (Geissman in Wallin, Merker, and Brown, 2001). Our closest primate relatives, the great apes (bonobos, chimpanzees, gorillas, and orangutans) are not known to be vocal learners.

Mammalian song often occurs for the same reasons as song in birds. One of the best known, most complex mammal songs, that of the humpback whale (*Megaptera novaeangliae*), for example, is believed to function in male-male competition, with females listening and gathering information about which males they prefer (Herman et al., 2012). The song of the humpback whale is not unlike that of the nightingale in its patterning, with a series of themes through which each animal cycles, although here each theme tends to be repeated several times (Payne and McVay, 1971). Remarkably, all the humpbacks in a population share these themes, yet the songs change during the singing season. The themes gradually morph into new themes, while old versions may be dropped (Payne and Payne, 1985). Cultural change is a notable feature of learnt vocalizations in songbirds (and of course in humans) as well as in whales. However, the whale example is unusual in that changes take place within a single

season, with each animal modifying its song in synchrony with the rest of the population. Bowhead whales, too, sing complex songs which change throughout the season (Tervo et al., 2011), though these have so far been less studied.

Some odontocetes (toothed whales), including dolphins and belugas, are also vocal learners, with highly complex, varied vocalizations. Their vocalizations are not usually called song by scientists because there is no stereotyped song which is repeated, but rather a variety of flexible sounds which are combined in different ways. Female sperm whales learn series of clicks, called 'codas', which vary according to their 'clan'. Although these codas don't sound much like what we usually think of as music, they are culturally transmitted (Rendell et al., 2012). Odontocete vocalizations appear to serve a variety of functions, including individual identification and group bonding.

## Music

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Can we say that animal songs are 'music'? This depends to a large extent on how we choose to define 'music' (*see* Music), and is not something that can be answered with a simple yes or no. Certainly there are surface similarities. Many animal sounds are rhythmic, such as the trill of a stridulating grasshopper. Others consist of fairly pure, steady-pitch, flute-like sounds, such as the whistles common in many birdsongs. However, this sort of surface similarity does not necessarily point to similarity in meaning or function. Energy efficiency alone might predict some of these features. A regular rhythm is shown by a mechanism operating at its resonant frequency, and this is where the energy cost is least. Concentrating all the energy in a narrow frequency band to produce fairly pure sounds is also economical, as such sounds carry farther. Concentrating calls at a particular frequency or tempo also helps broadcast species identity, essential both for attracting mates and for repelling rivals.

It is not difficult to find examples of more complex features that also have parallels in both human music and animal song. For example, certain species of animals make similar choices of interval to humans. Tropical boubou shrikes (*Laniarius aethiopicus*: Thorpe, 1972) and musician wrens (*Cyphorhinus arada*: Doolittle and Brumm, 2012) both favor consonant over dissonant intervals. Musician wrens also use musical 'motifs' – distinctive patterns of duration and contour that recur at different pitch levels within a song (Doolittle and Brumm, 2012). Humpback whale songs, too, share some structural elements with many kinds of human music. Humpback whales often start or end different phrases with the same subsection, a feature that has been likened to rhyming (Guinee and Payne, 1988). It has been suggested, somewhat speculatively, that the common features of successive themes may help the whales to memorize the long sequence of sounds that they sing, as rhyming, or parallel phrase structure, is known to do in humans.

At a more general level, it has been pointed out that similar sounds in different animals may very often convey similar messages (Morton, 1977). For example, deep and gruff sounds tend to be aggressive and hostile while pure and high ones are more affiliative and friendly. Probably there are two factors involved. First, only large animals can make deep sounds, so the deeper the sound the more intimidating it will be to smaller individuals, who would be well advised to retreat rather than risk a fight. Secondly, to be easily understood by other individuals, signals should be as distinctive as possible (the so-called 'principle of antithesis': Darwin, 1872). Probably, friendly signals that are pure and high have come to contrast maximally with hostile ones simply to preclude confusion. It may be more than just by analogy, then, that deep, loud, and ponderous sounds tend to be aggressive and threatening in

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both animal communication and human music. This is one aspect of music and animal song that may have a shared evolutionary origin. Humans and some other species may also use similar patterns of sound to express different levels of emotional arousal. A study of the song of the Arabian babbler (*Turdoides squamiceps*), for example, suggests that the rules underlying their call sequences when they are excited and when they are calm are equivalent to those used to convey calm or excitement in musical counterpoint (Cohen, 1983).

Rhythmic entrainment – the ability to produce sounds to coordinate with an external rhythm – has long been considered a uniquely human ability. In recent years, however, entrainment has been found in several non-human species, including sulphur-breasted cockatoos (*Cacatua galerita leonora*; Patel et al., 2009), budgerigars (*Melopsittacus undulates*; Hasegawa et al., 2011) and California sea lions (*Zalophus californianus*; Cook et al., 2013). This is one music-related feature that humans may also share with some other primate species, at least to a limited degree. Chimpanzees (*Pan troglodytes*) have recently been found to be able to synchronize tapping with a rhythm they hear (Hattori, Tomonaga, and Matsuzawa, 2013).

Behavioral parallels between human music and non-human exist too. Human music is a cultural activity: although all developmentally typical humans are born with the ability to make music, the kind of music they make depends on the culture they are born into. Song is a cultural activity for other vocal learning species as well: song will sound different depending on which conspecifics young learn their song from. Song-learning birds in geographically separated regions may thus sing in different ‘dialects’. There have even been cases of birds who travel between regions with different dialects being ‘bilingual’, singing the appropriate version of the song depending on where they are. Humpback whales in different ocean basins also sing different songs. In one case, a population of humpback whales on the East coast of Australia was observed to abandon their song for the song of two newcomers who had come from an otherwise unconnected population from the West coast of Australia (Noad et al., 2000).

Do all of these similarities mean that some animal song is music? Any parallel between human music and animal song as a whole is more likely to be by analogy than because of any shared musical ancestry with other singing animals. The most recent common ancestor between humans and birds was a reptile-like creature who lived about 200 million years ago which was unlikely to have communicated with complex vocalizations or to have learned its song, while our closest living relatives, the great apes, communicate more by gesture and facial expression than by sound. They have loud vocal displays, such as the ‘pant hoot’ of chimpanzees, but these are far from elaborate, stereotyped, or musical, and are not culturally transmitted. Vocal learning – an essential feature for any who consider music to be a cultural activity – has arisen separately in different parts of the animal kingdom; in the case of humans this was in the relatively recent past, since the time of the common ancestry with chimpanzees about two million years ago. Nonetheless, some aspects of musicality may have a shared evolutionary origin between two or more species. For example, the connection of sound with emotional state is something that could potentially have existed in the reptilian common ancestor of mammals and birds.

It has been suggested from time to time that the songs of some birds, whales, or other animals, which seem to us especially beautiful, may be more so than is strictly necessary for their biological function (Thorpe, 1961; Boswall, 1983). Could this indicate some sort of aesthetic sense, and that the animal takes pleasure in song for its own sake? Some candidate songs would be those of the song thrush

(*Turdus philomelos*), European blackbird (*Turdus merula*), superb lyrebird (*Menura novaeollandiae*), pied butcherbird (*Cracticus nigrogularis*), mockingbird (*Mimus polyglottos*), hermit thrush (*Catharus guttatus*), humpback whale (*Megaptera novaeangliae*), and various species of gibbons (*Hylobatidae*). It is difficult to test such ideas. Sexual selection is an open-ended process, which can lead to larger and larger song repertoires until other constraints, such as storage space in the brain, set limits. Where it is responsible, it is unlikely that song could be demonstrated to be more elaborate than sexual selection demanded. Likewise, where song functions to enhance pair- or group-bonding, a complicated song may be more effective. On the other hand, there is nothing incompatible between any functional explanations and either aesthetics or the enjoyment of song. But that is where the problem of testing comes in. Humans can tell us about their musical experiences; we can ask them about it and discuss their feelings and perceptions with them. When it comes to non-human animals, however, we have no access to their inner experiences, so the answer to that question can only be a matter of speculation. Of course this goes both ways. Even if a human says he or she is making music purely for enjoyment or other aesthetic or emotional reasons, the music may also be serving a biological or other function, which the musician may or may not be aware of. For example, a musician could perform a piece while being primarily conscious of the enjoyment or satisfaction they derive from playing it. But at the same time, they could be hoping that an audience member might find them attractive, establishing their membership in the group of people that understand or appreciate that sort of music, or establishing their proficiency relative to other practitioners of the same sort of music.

Although we are not able to answer definitively the question of whether some animal songs are music, it is clear that there are many overlapping features between many kinds of human music and many kinds of animal songs. In some cases, the songs of humans and non-humans overlap enough that we may be able to gain deeper understanding of animal song by combining traditional methods of biological inquiry with tools from music theory and musicological analysis, and deeper understanding of human music by looking at how it functions in a biological context.

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## See also

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