The main object of this paper is to show how Darwinian sexual selection theory can be used to explain the probable evolution of song in passerine birds. I believe that sexual selection may well be the most important evolutionary force affecting both the design and functions of songs. Furthermore, there are two kinds of sexual selection and they have led to the evolution of two quite different kinds of basic song.

Intrasexual selection is where males first compete among themselves, and the winner either wins access to females, or to some resource such as territory which is an essential prerequisite for obtaining a female. This is indirect female choice, as the female selects the male indirectly through his possession of a territory. It should lead to the evolution of songs modified primarily for a territorial function.

Intersexual selection is where the female chooses the male directly on some physical or behavioural attribute, and this should lead to the evolution of songs modified primarily for female attraction.

A CASE HISTORY

To illustrate the main idea, we will consider the case of Acrocephalus warblers which I have been studying for many years in Europe, but which also breed in Japan. The first clue that sexual attraction is an important function of song came from studies on the seasonal rhythm of song production. In most species song output decreases after pairing, and in one, *A. schoenobaenus*, it ceases altogether. This was confirmed by playback experiments, when the mated male would still defend territory by aggressive behaviour - but did not sing back at all. It seems that song in this species is only used for female attraction and not for territorial defence.

Another clue that sexual attraction is the main function comes from detailed sonographic analysis of song structure. The songs of *A. schoenobaenus* are long, complex and variable. Each male has a repertoire of notes or elements which can be used to build songs. In each song he selects a few elements and repeats and combines them in a certain way. As each male has about 30 different element types in his repertoire, he can compose a vast number of different songs, never repeating the same one exactly. Although any one song only contains a few element types, the total

---

1 A summary of an invited lecture given to the Ornithological Society of Japan at Ueno Zoo on 5 July 1981.
number of elements can be over 100 and the song can last over a minute in duration.

Fortunately males cycle through their element repertoires quite quickly, and it is possible to estimate repertoire size for each individual in a population. Repertoire size is a good measure of overall song complexity, and so it becomes possible to test a major prediction of sexual selection theory. Do males with more complex songs obtain a real advantage by attracting females first? All the males in a population were recorded, analysed, and the dates when they paired with a female were also noted. The results confirmed that males with the most complex songs attracted mates first, and those with simpler songs had to wait much longer. Clearly, direct female choice is exerting strong intersexual selection pressure upon male song structure.

The technique of estimating repertoire size is also of use when comparing different species. It has always been assumed that there would be more intense sexual selection pressure on males in a polygynous species. This is due to the obvious effect of a male pairing with many females and so leaving behind far more offspring than a monogamous male. In birds most species are monogamous, as both parents are needed to feed dependent young. In marshland however, insect food is superabundant and some cases of polygyny occur. In the genus *Acrocephalus* two species, *arundinaceus* and *paludicola*, are polygynous to varying degrees, but their repertoire size is small, and they sing relatively short, simple songs. In contrast, repertoire size is much higher in the four monogamous species, *schoenobaenus*, *melanopogon*, *scirpaceus* and *palustris*, and they sing long, complex and variable songs.

**INTERPRETATION**

How can we explain this result, which seems to be quite opposite to what sexual selection theory predicts? The answer lies in an understanding of the different behaviour and ecology of polygynous and monogamous species, and in particular what a female should look for when she selects a mate. The female of a monogamous species must select a high quality male to help her feed the young. Territories are often small in size, and both parents are needed to carry in food from some distance away. If a male deserted, then his own young would certainly starve to death. When a female selects a male, she must select him directly on some aspect of male quality. In a species which uses song for sexual attraction, the structure of the song itself may be the first indicator of male quality. Once males with more complex songs start to attract females more successfully, and so leave behind more offspring, then the runaway process of intersexual selection will eventually produce extreme complexity.

The female of a polygynous species is not so concerned with male quality directly, as with the quality of the territory he has obtained. The male has a high probability of deserting her after egg laying, and so she must be able to raise the young successfully on her own. To do this she needs a good territory which will supply sufficient food nearby, to ensure her young will survive. Polygynous males defend large territories, and the females can select males indirectly through the quality of their territories. If so, there is no direct pressure on the song structure to become more complex, and instead the song develops primarily as a territorial signal to repulse rival males. Intrasexual selection pressure will tend to produce shorter, simpler songs, and there may be
several reasons why these are best suited for territorial defence. They are less confusing as a specific signal, and more easily learned by rival males who then avoid that particular territory.

SUMMARY

In the extensive literature on passerine song, there has been much debate on whether the main function is territorial or sexual. Sexual selection theory provides a unifying conceptual framework which recognises the importance of both these functions which are not mutually exclusive. In Acrocephalus warblers the two different kinds of sexual selection pressure may have led to the evolution of two main types of song. Long, complex songs have developed primarily for sexual attraction and short, simple songs mainly for territorial defence. In each case, sexual selection is the main evolutionary force, and female choice acts either directly or indirectly to produce the optimal song structure for each species with its particular ecology and mating system. The ultimate goal of all singing behaviour is to directly or indirectly maximise the reproductive success of the individual.

REFERENCES


(Received 30 November 1981)