Bird Song: Beyond Species Recognition

In every bird song there is much more than meets the ear

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INTRODUCTION

ONE OF THE MOST admired characteristics of bird behavior is song. Few people can help but marvel at the beauty and complexity of avian vocalizations. For many birders, recognition of the species while it is singing forms the extent of their experience with song. There are, however, other interesting features of song which can be observed in the wild if one is aware of them. The purpose of this paper is to discuss a few of these features of bird song using familiar North American birds as examples. It is hoped that this will aid the amateur ornithologist in gaining a deeper appreciation of bird song while adding more enjoyment in the field.

WHY DO BIRDS SING?

BEFORE DISCUSSING some of the various features of bird song, it is necessary to understand several of the functions of bird song. Basically, song is used in competition between males for territory and in attraction and stimulation of females for breeding. Lemon (1977) has described song as an "acoustic flag", as a flag indicates ownership of property and the identity and location of the owner.

A territory can be thought of as any defended area (Noble 1939). The need to establish a territory comes from competition between males for valued and limited resources such as nesting sites, food, access to females and shelter from predators. Some means of indicating territorial ownership must be used. Colonial seabirds with relatively small, open territories can usually defend their area with face-to-face confrontation and aggression. This may be impossible or at least inefficient in terms of time and energy for species with larger territories, especially when vegetation obscures the bird's view. The use of song to indicate ownership seems to be much more efficient. Song can penetrate over or through vegetation, reach several individuals at once and convey a wide variety of information through differences in loudness, frequency and various aspects of song timing.

There is much evidence for the territorial function of song. It occurs in boundary disputes of many species and many individuals sing only within their defended area. A number of experiments have been done in which a tape recorder is used to "playback" songs to residents (Falls 1969). In these playback experiments, the resident often becomes quite aggressive towards the sound source, the loudspeaker. In other experiments, birds have been removed from an area and loudspeakers are placed in their territories. The areas in which song is played are taken over much less rapidly by other males than in areas in which no song is played (Krebs *et al.*, 1978). Finally, neighboring males can often be heard to countersing with one another. This is suggested to be an aid in maintaining the territorial *status quo* (Lemon 1968). In general, it is accepted that song does play a role in maintaining territory although the degree of dependence on song varies with the habitat and availability of alternative means of advertising ownership (Falls 1978).

In some species it appears that song has the additional function of attracting and stimulating females. In both the White-throated Sparrow *(Zonotrichia albicollis)* and the Brown Towhee *(Pipilo fuscus)*, singing is significantly reduced or even ceases after a male pairs with a female (Wasserman 1977, Marshall 1964). Wasserman (1977) also found with the White-throated Sparrow that if he removed the female from the male after pairing, the male would once again begin to increase his singing. Other examples of this courtship function of song will be revealed below.

GEOGRAPHICAL VARIATION

IF ONE TRAVELS across North America, one finds variations in morphological traits of some species such as plumage color in the Song Sparrow

Yellow-headed Blackbird in song. Photo/Helen G. Cruickshank.

(Melospiza melodia). Bird song can also show patterns of geographical variation. This variation can be on a large scale such as differences in songs of Cardinals *(Cardinalis cardinalis)* in Minnesota and Arizona or on a smaller scale (microgeographic variation) such as differences found in a few kilometers. Species that display this microgeographic variation in song can be said to possess *dialects:* neighboring birds have songs more similar to each other than to those of distant birds (Krebs and Kroodsma 1980). There are two possible distributions of these dialects. First, we may see groups of birds within a population singing similar songs. Thompson (1970) and Payne *et al.* (1981) have documented this in the Indigo Bunting *(Passerina cyanea)*. Groups of two to five males that share songs are common throughout one population in Michigan. The second possible dialect system involves isolated populations of one species in which each population has evolved a different form of the species' song. One of the best studied examples of this is that of the White-crowned Sparrow *(Zonotrichia leucophrys)*. The work of Baptista (1975, 1977), Baptista and King (1980), Lein (1979) and Heinemann (1981) has shown that separate populations along the west coast of North America and on an "island" of forest habitat in the plains of Alberta have different songs. Baptista (1977) has also found that some of the dialects are arranged like the first dialect system described above where once isolated populations have made secondary contact. Some of the birds on the borders are even "bilingual"!

How do these dialects form? At present, there are two postulated pathways which both depend on (1) the site at which young males learn their songs and (2) the dispersal patterns of the first-year birds. One pattern of dialect formation that has been suggested would involve young males learning songs from their fathers and/or neighbors around the nest and then returning to the same area of their birth to breed. As yet we do not have the detailed banding studies necessary to determine whether this occurs. The second model of dialect formation involves young males dispersing to some suitable habitat, not necessarily their natal area, and learning the songs from neighboring adult males. This may be useful to the young bird as it gives him the ability to countersing with his rivals. This probably occurs in many species but has been best documented in the Bewick's Wren *(Thryomanes bewickii)*. Kroodsma (1974) showed that young males gain independence from their parents at about 35 days of age and move an average of 1.2 kilometers away to set up a territory of their own. They then learn the songs of the surrounding adult males.

Kirtland's Warbler in song. Photo/O.S. Pettingill.

SONG REPERTOIRES

SOME BIRDS SUCH as the Chipping Sparrow *(Spizella passerina)* have a single song type which they repeatedly sing. Other species, however, have a repertoire of songs which range in size from two songs, as in the Black-throated Green Warbler *(Dendroica virens)*, to over fifty songs as in the Gray Catbird *(Dumetella carolinensis)*, the Mockingbird *(Mimus polyglottus)*, the American Robin *(Turdus migratorius)* and others.

The function of the various repertoires has long been a puzzle to ornithologists. Why is one song sufficient in some species while other species need many songs? We do not have the answers although some interesting hypotheses have been presented.

It is known that male birds use song to attract and stimulate females. Darwin (1871) suggested that song repertoires may be the vocal counterpart of the elaborate plumage and displays that males of various other species use to attract females. Where can we find evidence that song repertoires are the counterparts of these elaborate visual displays? First, it is known that a display is more elaborate when competition for females is more intense. Thus, if repertoires are used to attract females, the more complex repertoires should be found in situations where competition is most intense. In polygynous mating systems (one male with several females) there is stiffer competition for females than in monogamous mating systems. In comparing the closely related wrens of the family Troglodytidae, males of the polygynous species such as the Short-billed Marsh Wren *(Cistothorus platensis)* have larger repertoires than males of monogamous species such as the Bewick's Wren (Kroodsma 1977).

Repertoires may also function in territorial battles between males. Studies on the Great Tit *(Parus major)*, a European chickadee, and the Red-winged Blackbird *(Agelaius phoeniceus)* have shown that individuals with larger repertoires are more capable of territory defense and probably have better territories than individuals with smaller repertoires (Krebs and Kroodsma 1980, Yasukawa 1981).

How could repertoires be advantageous in male-to-male competition? One possibility was suggested by Charles Hartshorne (1956, 1973). He noted that it would be disadvantageous to have a territorial rival get used to or "habituate" to your "keep out" signal. He suggested that repertoires may have evolved as an "anti-monotony" device. If this were true, birds that were "nonversatile" singers, those possessing fewer than three song types, should be "discontinuous" singers (not rambling on and on) and birds that were "versatile" singers, possessing more than three song types could afford to sing much more often and continuously. To exemplify this point, consider the Chipping Sparrow which has one song type. It spends about 28% of its time singing and has an intersong interval of about 6 seconds. In contrast, individual Mockingbirds, which have well over fifty songs, spend about 74% of their time singing and have an intersong interval of about one second (Borror 1959, Reynard 1963, Wildenthal 1965). Of course there are many exceptions and intermediate cases but in general the anti-monotony principle appears to hold true (Kroodsma 1978). Other examples of this anti-monotony principle can be observed in the field. Note how the males of some species such as the Song Sparrow or Rose-breasted Grosbeak *(Pheucticus ludovicianus)* will sing the same song repeatedly until another male sings nearby. Upon hearing the second male, the original singer will usually switch song types. One problem with the anti-monotony hypothesis is that it does not explain why some birds have repertoires and others do not (see Krebs and Kroodsma 1980 for further discussion).

Finally, one seemingly logical function of repertoires in both female attraction and male-to-male competition would be to reduce the "vagueness" in communication by having each song possess its own message or set of messages. Of course avian mental capabilities will limit this to some extent; birds cannot possess an elaborate language as man does although they do use different songs to mean different things. Lein (1972) found that the *"trees trees murm'ring trees"* song of the Black-throated Green Warbler correlated with a greater willingness to enter into a confrontation with a rival male than the *"sree sree sree sree tow tray"* song which is sung in periods when the bird is not in contact with another male. Similarily, the Chestnut-sided Warbler *(Dendroica pensylvanica)* has five different song types, each of which is used to indicate a different level of motivation in territorial encounters (Lein 1978). The Yellow-throated Vireo *(Vireo flavifrons)* has eight different song types. Smith *et al.* (1978) found that each of these was associated with different activities such as patrolling territorial boundaries, foraging away from the nest, approaching the nest or remaining in its vicinity. Why this vireo might have such a system is not yet understood.

Henslow's Sparrow singing. Photo/Phil Moylan.

MIMICRY

IT IS WELL KNOWN that some species of birds imitate the vocalizations of other species. Some species such as the Mockingbird are prolific mimics. Mimicry is rare in other species. As with repertoires, several hypotheses have been proposed to explain how mimicry aids the bird in continued existence and propagation.

In some species, it is believed that birds mimic other species to increase the size of their repertoires. Enlarged repertoires are then used as described above in competition for territories and females. The Mockingbird, one of our most famous mimics, is believed to fall into this category. There are many accounts of this bird's mimicking ability. For example, Townsend (1924) claims to have heard the songs of 55 different species in one hour.

In some birds, there is competition for resources (such as territories) with members of other species as well as with its own species. Mimicking the song of another species is thought to increase the efficiency of competing with this species for valued resources. One example of this can be seen in the Indigo and Lazuli buntings *(Passerina cyanea* and *P. amoena)*. In the areas where their ranges do not overlap, each species has its own set of notes that make up its "species specific" song. In the Great Plains where their ranges do overlap, there is much mixing or sharing of these notes to aid in interspecific territoriality (Emlen *et al.*, 1975). For example, one may find an Indigo Bunting with a song consisting of 75% Indigo notes and 25% Lazuli notes.

Several other species are reported to be mimics although the function of their mimicry is unknown. These include the Starling *(Sturnus vulgaris)*, Gray Catbird, Yellow-breasted Chat *(Icteria virens)* and the thrashers.

COUNTERSINGING AND DUETTING

THE TERM COUNTERSINGING refers to the behavior of one male repeating a song of a rival. This may occur many times and usually with many different song types. One probable function of this countersinging is that a resident can direct a "keep out" signal at a specific intruder. This apparently is the case in the Cardinal (Lemon 1968).

Duetting (more properly called Antiphonal Song) occurs when both male and female members of a pair cooperate in singing a song. Each member's contribution may occur in the form of phrases or individual notes. Duetting occurs in over 32 families of birds around the world, most of them tropical. In some species, duetting functions in strengthening the bond between mated birds. This occurs in the Common Grackle *(Quiscalus quiscula)*, Abert's and Brown towhees *(Pipilo aberti* and *P. fuscus)*, and probably in the Painted Redstart *(Setophaga picta)* and Canada Goose *(Branta canadensis)* (Wiley 1976, Marshall 1960, Marshall and Balda 1974, Collias and Jahn 1959). In the Bobwhite, Gambel's and California quails *(Colinus virginianus, Lophortyx gambelii, L. californicus)*, duetting functions to aid members of a pair in maintaining contact when they lose sight of each other (Stokes and Williams 1968). Finally, a pair may sing a territorial song. Lemon (1968) believes that this occurs in the Cardinal.

CONCLUSION

THESE ARE A FEW of the many interesting features of bird song which can be enjoyed by the birder on every field excursion. They are much easier to recognize if you know what to listen for, and it is hoped that this paper will guide the birder in delving deeper into the wonders of bird song. The study of bird song dialects, for example, has only just begun, and much can be learned by the amateur armed with inexpensive recording equipment.

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