Acoustic Communication in Birds

Differences in Songs and Calls, their Production and Biological Significance

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The article highlights the biological significance of songs and calls in birds. The structural diversity of songs and its relevance for social behaviour are described. Acoustic communication plays an important role in the life of birds and has proven useful in establishing phylogenetic and evolutionary relationships among species.

Communication is an integral part of animal behaviour. Birds communicate with each other primarily by means of visual and vocal signals. Elaborate or cryptic plumage, brightly coloured bare skin, wattles, tail, beak and feet are used in communication, with or without accompanying acoustic signals. Sound is an ideal method for communication over long distances. Acoustic signals seem to be produced only when required, and sound can be used to transmit a large amount of information efficiently.

Vocal signals play an important role in the life of birds in a variety of aspects like pair maintenance, parent-offspring interactions, cohesiveness among flock or family members, and threat situations. The sound spectrogram (graphic representation of a sound also known as sonogram) technique is a well-established method to characterize acoustic signals on the basis of their frequency, duration and amplitude (*Box* 1). In many birds, the features of acoustic signals have been used as species signature to infer phylogenetic and evolutionary relationships. These detailed features of acoustic signals tend to be similar in closely related species and to be more divergent in more distantly related ones. In some species, vocal signals can also be used as a tool in population size estimation. Studies on the acoustic communication of bird species in India, however, have been rather

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Box 1. Important Terms used in Animal Communication Studies

Allopatric species: Species whose distribution ranges do not overlap.

Sympatric species: Species that occur in same place.

Sibling species: Reproductively isolated but morphologically similar or nearly similar species.

Oscine birds (Song birds): Species belonging to the order Passeriformes.

Posture: Still-body show generally performed by male birds using elaborated/ornamented feathers e.g. tail posture of magpie robin.

Display: Generally used for bodily actions e.g. courtship dance in birds.

Call: These are brief sounds with simple acoustic structure produced for immediate requirement such as contact, alarm and threat.

Syrinx: Sound producing organ of birds.

Phonation: Production of sound.

Song: Elaborated vocalizations generally produced by male birds.

Spectrogram: Graphic representation of sound (frequencies vs time).

Strophe/phrases: Structural units of the songs, made up of elements.

Amplitude: Loudness of the sound, measured in decibels (dB).

Frequency: Sound is a wave form. Number of waves/cycles per second is known as frequency of sound, which is measured in Hertz (Hz).

few as yet. Only a few Indian species, such as Oriental magpie robin *Copsychus saularis*, Red-vented bulbul *Pycnonotus cafer*, Black-headed starling *Sturnus pagodarum*, Hill myna *Gracula religiosa* and Greenish leaf warbler *Phylloscopus trochiloides*, have been studied in detail. (*Figure* 1 and *Box* 2).

Figure 1. (A) Brahminy starling Sturnus pagodarum males sing for mate acquisition and when a predator approaches close; both sexes produce threat calls. (B) Oriental magpie robin Copsychus saularis usually sings from exposed branches of trees to facilitate widespread transmission of the song.

Box 2. Oriental Magpie Robin

Songs, calls and visual displays of the Oriental magpie robin have been studied in detail. In northern India, this species breeds between May and August raising several broods. During this period, males sing complex and melodious songs in their respective territories for the advertisement of territories and mate acquisition. Six types of calls namely territorial calls, emergence and roosting calls, threat calls, submissive calls, begging calls and distress calls are also part of their vocal repertoire. In addition, individuals have been reported to use escape calls and anger calls occasionally. A Kumar and D Bhatt have found that this bird also uses a number of visual signals for communication. Display flights with complex songs and tail postures are used by male birds to attract females. Along with highly varied songs, the males perform various courtship ceremonies involving stretching of head forward and downward in front of females, spreading of tail feathers, left-right movement of neck, stretching of beaks skyward and other actions that eventually lead to mating. When an intruder arrives in the territory of a male, the territory owner shows threatening posture and produces threat calls. Nestlings and fledglings use a begging display with wing quivering, when demanding food. In addition, one type of resting and three types of sleeping postures have also been observed. It is interesting that the females also sing solo or duet songs for the synchronization of the reproductive process. The Oriental magpie robin is an excellent model to study the patterns of geographic and individual variation in songs, evolutionary aspects of song complexity, and the developmental, anatomical and neurobiological aspects of phonation.

Songs, Calls and Terminology

Vocal signals in birds are usually divided into calls and songs. However, the distinction is arbitrary and different authors use different terms for the same categories of signals. The following criteria can be used for the classification of vocal signals.

Physical characteristics: Vocalizations uttered in a single articulation and generally made up of a single element (an element is a continuous sound, preceded and followed by a silent gap) with few exceptions (i.e. complex calls that are made up of more then one type of element) are known as calls (*Figure 2*). In contrast, a typical song may include a continuous series of strophes or phrases (group of elements either similar or dissimilar in structure). In other words, songs are long, complicated sounds, whereas calls are relatively short and simple.

Biological functions: On the basis of behavioral context, signals of birds can be classified into songs and calls (with few exceptions such as territorial calls, courtship calls, etc.) Generally,

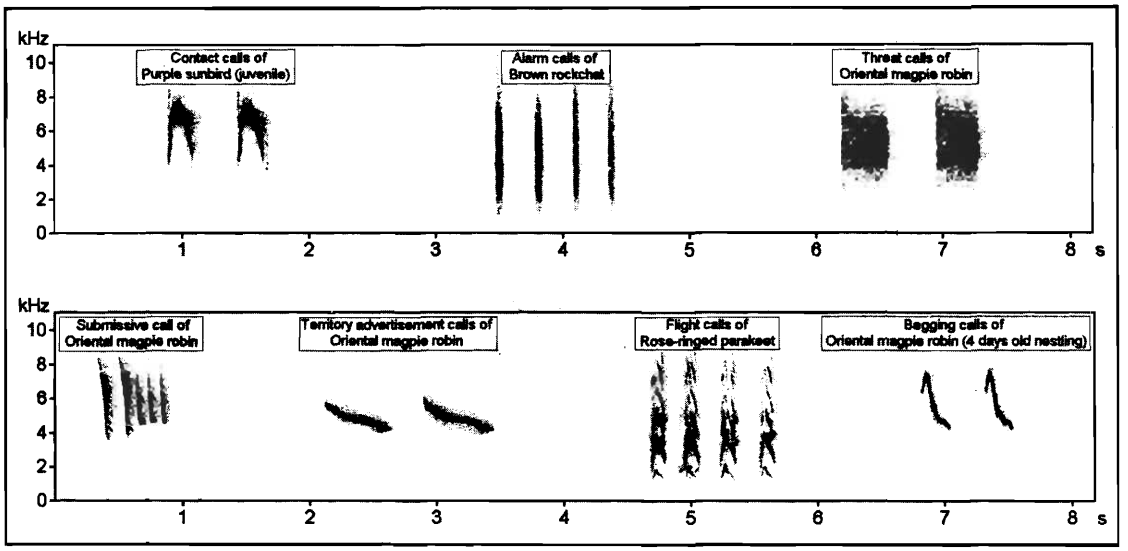

Figure 2. Different types of calls in birds.

birds use songs for territory advertisement and mate acquisition (*Box* 3), whereas calls are given in specific contexts such as contact, mating, threat, begging, flight and alarm (*Figure* 2 and 3).

Anatomical basis of phonation: On the basis of structural differences of the 'voice-box' or syrinx, birds can be classified into songbirds and non-songbirds. The tympaniform membranes of the syrinx are responsible for phonation, when tensed by associated muscles (*Figure* 4). The muscles can be extrinsic, originating and inserting on the trachea, or intrinsic, at any rate inserting on the syrinx, and originating either on the trachea or on the syrinx itself. In non-songbirds only two pairs of extrinsic muscles exist, whereas songbirds can have 5-7 pairs.

Neurobiology of phonation: The songbirds have a specific pathway and some centres in their brains, which play an important

Box 3. Biological Functions of Bird Songs

1. Mate acquisition.
2. Territory establishment and defence.
3. Species, sexual and individual recognition/identification/ discrimination.
4. Synchronization of reproductive processes.
5. Mate guarding and prevention of cuckoldry.

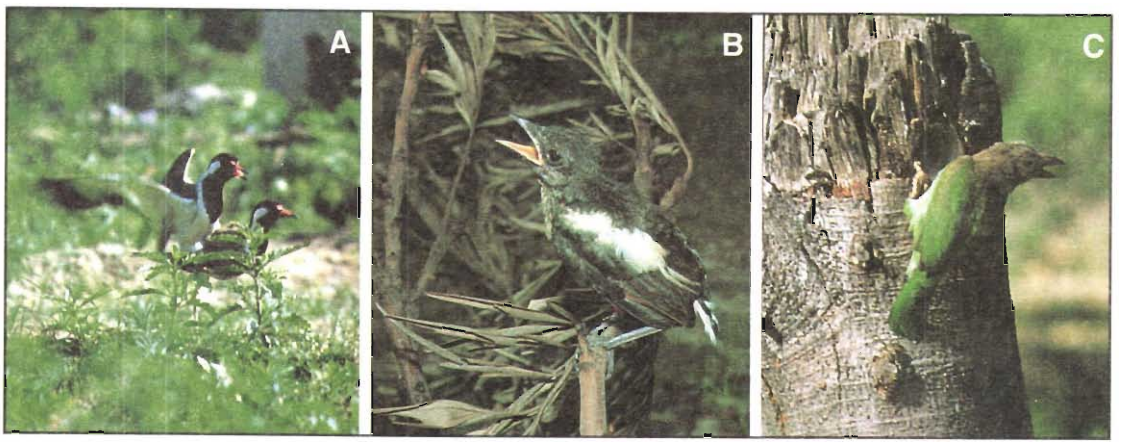

Figure 3. (A) The male Red-wattled lapwing Vanellus indicus rapidly utters, Tit...tit...tit... call during courtship. Males in most avian species produce courtship vocalizations to synchronize the process of mating. (B) Fledgling of Oriental magpie robin Copsychus saularis giving contact calls. Nestlings/ fledglings of most avian species use contact/begging calls. (C) Brown-headed barbet Megalaima lineata produces a song phonetically rendered as Turrrr..rr.. r...tur..tur..tur..tur... throughout the breeding period.

role in the production of songs. This is a complex pathway composed of clusters of neurons called nuclei or centres and axons from these, projecting to other nuclei. There are as many as nine separate nuclei, most of which are in the forebrain.

In some cases, non-songbirds do produce relatively simple, repetitive and low frequency vocalizations (usually 0.5 to 2.0 kHz frequency range) for mate acquisition. In fact, these vocalizations should not be treated as true songs but are, nevertheless, often commonly referred to as songs e.g., the songs of doves, barbets, nightjars and cuckoos.

Production of Songs and Calls

The syrinx is the organ that produces vocal signals in birds. It is located at the junction of trachea and bronchi (*Figure* 4). The sound is generated by tympaniform membranes (TM), situated

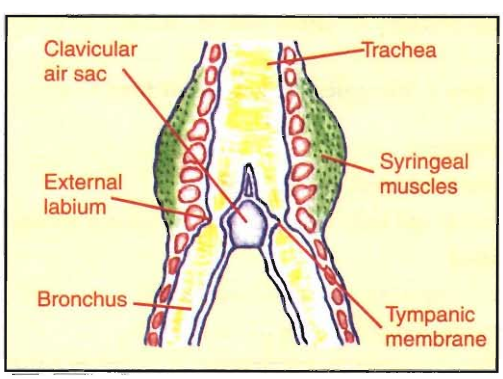

Figure 4. Anatomical view of the syrinx of a songbird (modified from Catchpole and Slater, 1995).

on the medial walls of the bronchus, and is due to the pressurized flow of air from bronchi to trachea. When the air is forced from lungs to trachea through bronchi, the TM vibrates and produces sound waves. The frequency of signals is based on the vibrations of the TM and the amplitude is controlled by the pressure of air. The length of trachea and syringeal muscles also influence the flow of air and the characteristics of the sound.

The structure of the syrinx varies markedly among bird species. However, its basic anatomy is considerably consistent in songbirds. Cartilaginous rings at the caudal end of the trachea and semirings at the cranial end of each bronchus are modified and surrounded externally by several pairs of syringeal muscles. The syrinx of songbirds contains two potential sound sources at the cranial end of each bronchus. The duplex nature of this vocal organ has an important role in the production of song. It gives songbirds the ability to control sound production independently on each side of the syrinx, thereby significantly increasing potential complexity of song in a way that is not available to most classes of vertebrates. Some birds also use the muscles of throat, as well as bill movements for the production of properly shaped signals.

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Diversity in Singing Behaviour

Singing behaviour in birds is highly diverse (*Figure* 5), and song characteristics in bird species may also vary temporally and spatially. Many species, such as thrushes and chats, sing only during the breeding season, whereas others, such as bulbuls, sing throughout the year. In some species, only males sing, while in others, females also sing, either singly or in duets with males. Female song has been reported in many species such as European robin *Erithacus rubecula*, Northern cardinal *Richmondena cardinalis*, White-crowned sparrow *Zonotrichia leucophrys*, Red-winged blackbird *Agelaius phoeniceus* and Oriental magpie robin (*Figure* 6A, *Box* 2). The major functions of female song include territorial defence, prevention of polygyny, attracting males, and coordination of breeding activities.

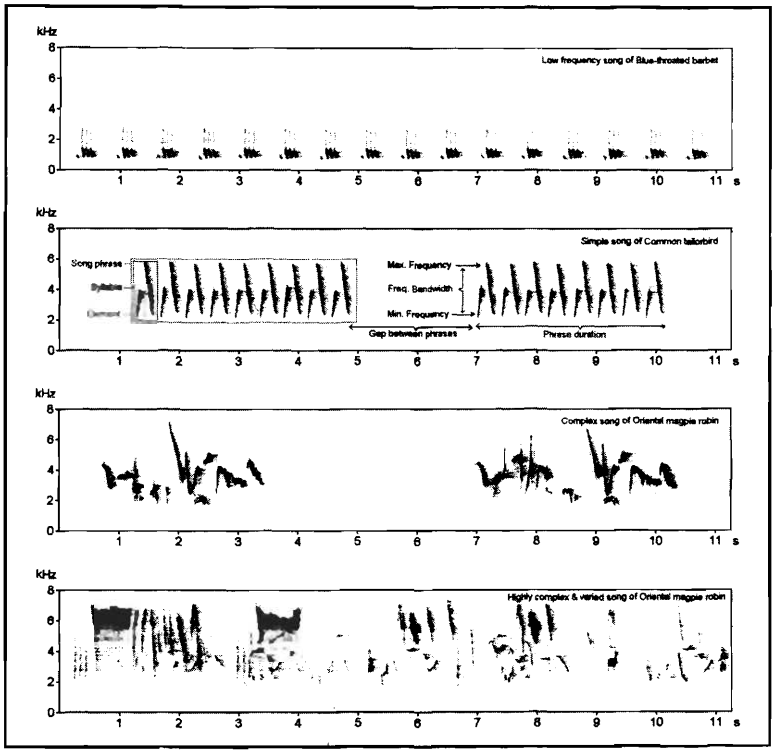

Figure 5. Different types of songs in birds and measurement of variables. (A) Low frequency song of Blue-throated barbet Megalaima asiatica probably used for mate acquisition. This stereotyped vocalization consists of phrases made up of syllables having two types of elements. (B) Simple song of Common tailorbird Orthotomus sutorius made up of stereotyped song phrases without structural variations in elements. (C) Complex song of Oriental magpie robin consisting of different types of phrases/ strophes separated by silent gaps. Males use this song for territory advertisement. (D) Highly complex and varied song of Oriental magpie robin. Males are observed using this song for mate acquisition. This song is made up of different types of elements uttered continuously in a song bout.

In some cases, the male and female both sing at the same time often with precise temporal coordination. This phenomenon is known as '*duet singing*'. Often, they sing stereotyped and inte-

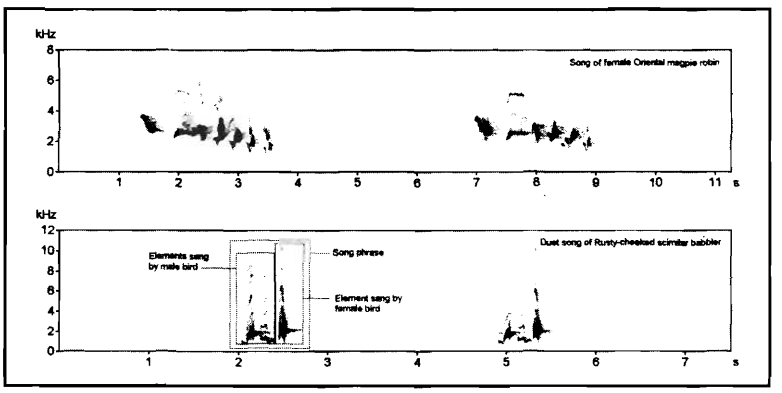

Figure 6. (A) Song of female Oriental magpie robin consists of phrases similar to male song. (B) Antiphonal song of Rusty-cheeked scimitar babbler Pomatorhinus erythrogenys. In a song phrase, the first two elements are sung by the male and last element is sung by the female.

grated songs, in which both sexes exchange notes in such a regular way that unless the listener is standing between the singing birds, he may think that only one bird is singing. In some species such as Black-headed gonolek, *Laniarius erythrogaster,* and Rusty-cheeked scimitar babbler, *Pomotorhinus erythrogenys*, the male produces one element and female another in a simple alternating system called '*antiphonal singing*' (*Figure* 6B). Duets can involve songs, calls or non-vocal sounds such as bill chattering of storks and drumming of woodpeckers (*Box* 4). Duets are often accompanied by coordinated visual displays in many species such as Cuban grassquit *Tiaris canora*, Spotted morning thrush, *Cichladusa guttata,* and Oriental magpie robin. In some cases, known as '*chorus singing*', more than two birds of a family or flock are involved in singing, such as in the Australian magpie, *Gymnorhina tibicen*, a communal breeder in which both males and females join in the chorus.

It is believed that birds sing their songs most intensively at dawn because this is the time of the day when these songs propagate

Box 4. Non-vocal Acoustic Signals

Some birds produce non-vocal acoustic signals using their beaks, wings or tails. Woodpeckers are well known for hammering on dead limbs using their beaks. The male Great spotted woodpecker *Picoides major* drums on dead wood branches 500-600 times per day to attract a female for courtship. The pattern and frequency of drumming varies from species to species. Playback experiments show that females respond only to their own species drumming. The drumming is used both in pair formation and territory advertisement. Some species produce sounds by clapping their mandibles together; for example, White storks *Ciconia ciconia* use it for pair maintenance, and most owl species use it as a threat display. Several members of the grouse family make audible noise by stamping their feet on the ground during courtship. Tails can also be used for producing mechanical sounds. The Common snipe *Gallinago gallinago* produces a two-second burst of drumming or bleating by specially modified outer tail feathers. In some species, non-vocal sounds are produced by the wings. Male wood pigeons and nightjars produce a loud 'clap' by beating their wings together during their aerial courtship display. In many species, certain feathers of the wings are specially modified for sound production. In the Woodcock *Scolopax minor*, three outer wing feathers are remarkably narrowed and stiffened, so that when they are spread during courtship flight, air rushes through them producing vibrations with a high pitched whistling sound. The same type of feather adaptation is found in the wing feathers of certain ducks, bustards, doves, hummingbirds, cotingas and manakins.

Bird vocalizations are highly variable. In some species each male has only a single, simple and stereotyped song, which he repeats monotonously over and over again. On the other hand, some species have two to several hundred types of phrase in their songs.

most effectively (up to 20 times better than at midday). Some birds show a marked peak of singing activity around dawn and, if individuals of different species join in, it is often termed the '*dawn chorus*'. A relatively low second peak of singing is also observed at dusk before roosting (sleeping) in many birds such as in Reed warbler *Acrocephalus scirpaceus* and Sedge warbler *A. schoenobacnus*. Some species use calls instead of song in their roosting chorus. Crows, mynas, bulbuls, sparrows are known for their prominent roosting chorus.

Bird vocalizations are highly variable at all levels from within an individual to between species on regional, local and individual scales (*Figure* 5). Regional variations in song are often termed '*dialects*' as they resemble in many ways the regional variations found within human languages. In birds, the repertoire of songs varies enormously. In some species such as in White-crowned sparrow *Zonotrichia leucophrys,* each male has only a single, simple and stereotyped song, which he repeats monotonously over and over again. On the other hand, some species have two to several hundred types of phrase in their songs. Catchpole has suggested that a male Sedge warbler may never repeat exactly the same sequence of notes twice during the course of its life. This is because each song is extremely long and complex and made up of different types of elements or notes. Why is the song so complex in some bird species? If the main function of song is mate attraction and territorial defense, then perhaps individuals develop more complex songs to gain some selective advantage, through the process of sexual selection. However, it is not easy to answer such evolutionary questions.

In European starling *Sturnus vulgaris*, Great reed warbler *Acrocephalus arundinaceus* and the Aquatic warbler *A. paludicola,* the males with large repertoires of complex songs are usually also in better condition. Females may, therefore, be obtaining high-quality mates by choosing on the basis of song complexity. In many birds, complexity levels of songs are species specific, while some others develop this using other ways such as duetting (described earlier) and mimicry (imitation of songs and

calls of other species). However, in most cases, birds learn only the song of their own species. A few species, such as mockingbirds, European starlings, drongos and leafbirds, can copy the songs of other species to increase song complexity.

In addition to the calls and songs, birds also exhibit some other fascinating acoustic adaptations. For example, species living in dark caves, such as the Cave swiftlet *Collocalia linchi* from Indonesia and the Oilbird *Steatornis caripensis* from South America, use echolocation (like bats) to navigate.

Value of Communication Studies

The study of songs and calls enriches our knowledge regarding the communication value of these signals in birds, and places this research at the interface of neurobiology, animal behaviour, and ecology. Vocalizations are also useful in classification, for designating new species, assessment of taxonomic rank, and phylogenetic analyses. Study of bird song is very useful in species identification. Some morphologically similar species such as warblers and cuckoos can easily be identified by their vocalizations. For example, the Eurasian cuckoo *Cuculus canorus* and Indian cuckoo *C. micropterus* are very similar in appearance but their songs are quite different. In the Indian cuckoo, the song phrases are composed of four elements, while the Eurasian cuckoo always sings phrases made up of two elements (*Figure* 7). The loudness of songs also varies significantly between these two species.

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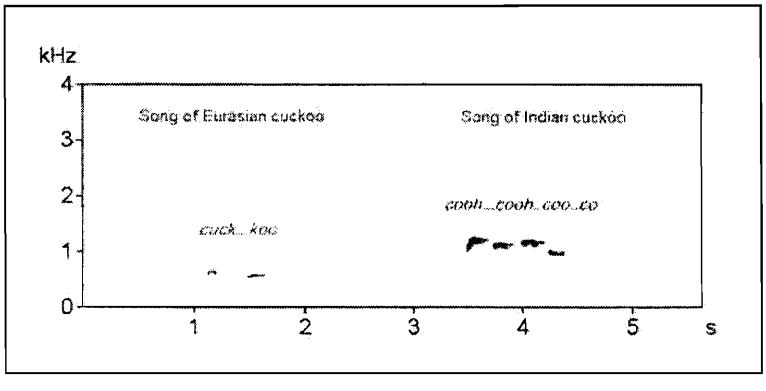

Figure 7. Structural variations in the song of Eurasian cuckoo Cuculus canorus and Indian cuckoo C. micropterus.

In some birds, alterations in the acoustic features are indicators of increased noise levels in environment. Recent studies indicate that songbirds lose their original features of songs in noise-polluted environment.

Many new species have been discovered only due to differences in vocalizations from other species. For example, the Cryptic warbler *Cryptosylvicola randrianosoloi* was first detected in 1992 in Eastern Madagascar by its voice. In many cases, taxa have been upgraded from the rank of subspecies to species or even from colour morph to species; for example the North American Western grebe *Aechmophorus occidentalis* and Clarks' grebe *A. clarkii* were previously considered to be colour morphs of the same species. The Willow flycatcher *Empidonax traillii* and Alder flycatcher *E. alnorum* were formerly considered to be conspecific, but later on it was found that they differed in vocalizations, that they do not respond to playback of each other's songs and are partly sympatric. In playback experiments, usually males respond more strongly to conspecific songs as compared to heterospecific songs, however interspecific aggressions are also reported in some temperate congeneric species.

Recording and playback of vocal signals is frequently used to attract birds to the observer so that they may be identified visually or to attract them towards mist-nets (nets made up of thin nylon threads used in bird-trapping). Playbacks are also used as aural stimuli during bird census to increase the detectability of a given species or to survey otherwise secretive or nocturnal species such as owls and nightjars. The identification and census of migratory species are also possible with the help of acoustic analysis of calls produced by them during migration at night.

In some birds, alterations in the acoustic features are indicators of increased noise levels in environment. Recent studies indicate that songbirds lose their original features of songs in noise-polluted environment. In Britain, traffic noise has rendered many of the birds tone-deaf, turning their beautiful songs into harsh cackles. Birds in the affected areas have harsher songs, with fewer notes and tones. They are also less successful in establishing territories and finding mates. The Golden oriole *Oriolus oriolus*, Wood warbler *Phylloscopus sibilatrix*, and Hawfinch *Coccothraustes coccothrautes*, all highly endangered, are among the worst affected.

Conclusion

Songs and calls are a fascinating aspect of bird biology. Many neurobiologists, ethologists and ecologists are using bird songs as a model to understand various aspects of phonation, sexual selection and behavioural ecology of birds. Unfortunately, in the Indian subcontinent, these types of studies are not common. Many Indian species are waiting for a proper study of their acoustical characterization. Therefore, there is a need to fill up this gap through active research and characterization of vocal repertoires of Indian species, an effort that will help understand bird behaviour and ecology, and possibly their taxonomy as well.

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