Singh, P. (2014). Study of altitudinal and geographical song variation, and interspecific interaction among Phylloscopus warblers in the Himalayas. Wildlife Institute of India. Dehradun, Forest Research Institute, Dehradun.

Summary

Sound is predominant mode of communication among birds and has advantages over visual communication, particularly where habitats are dense. Bird vocalizations are usually categorized into calls and songs. Calls are short, simpler and often monosyllabic vocalizations, which are used by both male and female birds, whereas songs are long, complex vocalizations, occurring in long spells with diurnal rhythm and generally produced by the male in the breeding season. Birdsong is an important species and mate recognition signal whose main functions have been recognized as mate attraction, mate stimulation and rival repelling. Birdsong is classified into whole song, which is song bout usually lasting several minutes and consisting of smaller song units, classified as a "song" or phrase, which are separated in whole song by inter-song intervals. Songs are made of the smallest vocalization units, called notes, separated from each other in a song by much smaller time interval than inter-song interval. Single notes or a group of notes arranged in a sequence repeat in songs of some birds, and these repeating units are called syllables. Songs are classified into song types based on notes and their arrangement in a song. In many birds songs begin with a note separated from other notes by more time-interval than between other notes of the song. This note is called introductory note of a song, and it is associated with alerting the receiver about the message to follow.

Species vary greatly in birdsong e.g. the repertoire of song types they sing, singing style (repeating a song type few times before switching to new type called eventual variety or switching to new type without repeating called immediate variety), number of songs rendered per unit time i.e. song rate, arrangement of notes in a song i.e. song syntax, number of notes in a song type, and also in frequency and time parameters e.g. minimum frequency, maximum frequency and bandwidth.

In many species songs vary from one place to another, called geographical song variation. Geographical variation in birdsong is most obvious in the species that learn songs. Over half of all bird species, i.e. songbirds, the hummingbirds and

the parrots, learn their songs from conspecifics or improvise; others sing innate songs. Geographical variation in mating signals and mate recognition systems can potentially facilitate assortative mating and reproductive isolation, leading to speciation.

Song variation within a species can be at micro geographical scale as in the sharp dialect boundaries or it may be macro-geographical, gradual between populations many kilometers apart. Many species have populations divided into song dialects. Most studies of geographical variation have primarily been concerned with formation of song-dialects, but more recently there has been much interest in how ecological factors, including the acoustic environment and body size and shape, affect song evolution.

Besides role of birdsong among the individuals of a species, birdsong also plays role in interspecific interactions particularly among closely related congeners. Birds respond to conspecific sounds and to the sound of closely related taxa with which they compete for territories. Competitive exclusion has been found an important spacing mechanism among altitudinal replacing congeners in Andes. Recent experiments in the Central American mountains in Costa Rica using interspecific playbacks of closely related elevational replacements have directly tested that song mediates interspecfic aggression among these species; species respond to congener playbacks either moving away from the speaker or approaching the speaker. It is not known whether similar spacing mechanism exists in Himalayas.

Leaf warblers, *Phylloscopus* species, are among the most common species in the Himalayas. They though look similar but have distinct songs and calls. These species are very vocal in breeding season. They are quite popular as subject of study among researchers and have been studied for their ecology, systematics and taxonomy, and speciation.

I studied geographical song variation in two leaf warblers i.e. Grey-hooded Warbler, *Phylloscopus xanthoschistos* and Blyth's Leaf Warbler *Phylloscopus*

reguloides. These species occur in the Himalayas and North-east Hill States of India. *P. xanthoschistos* has four subspecies breeding in India whereas *P. reguloides* has two to three subspecies based on different classifications. The objectives of my study were:

1. To study altitudinal and geographical variations in songs of *Phylloscopus xanthoschistos* and *Phylloscopus reguloides* along the Himalayas.

2. To examine the role of interspecific aggression in habitat selection among four closely related *Phylloscopus* warblers along altitudinal gradients using song playbacks.

I carried out fieldwork at 15 sites across Himalayas (including two localities in the Northeast state of Meghalaya) covering all subspecies of the two species. The fieldwork included recording of songs of *P. xanthoschistos* and *P. reguloides* and to carry out playback experiments, both intraspecific and interspecific. Intraspecific experiments were carried out to know the significance of geographical song variation, and the interspecific experiments for finding out interspecific aggression among closely related *Phylloscopus* species. As far as possible different recordings were used for experiment and control playbacks to avoid pseudoreplication..

I analyzed 157 whole songs, and 521 song types (two from one bird) of *P. xanthoschistos* from 13 sites for whole song parameters and frequency-time parameters respectively. Besides 1640 song types were examined for song syntax features and introductory notes. In case of *P. reguloides* 132 whole songs and 159 song types (one from one bird) were analyzed from 7 sites. The songs were analyzed using Raven Pro 1.3 sound analysis software. Repertoire size, song rate and song repetition rate and song sharing were the whole song parameters, and minimum frequency, maximum frequency, bandwidth, central frequency, song length and number of notes in a song, were the song type parameters studied. All the different songs at a site were labeled different song types by visually matching their song spectrograms for notes and their

arrangements within a song, songs varying merely in number of repetition of same syllables (note-groups) were not considered to be different song types. Whole song and song type data were transferred to spreadsheet for statistical analysis.

P. xanthoschistos sings with eventual variety, repeating a song type, on an average, from 3.73 to 6.83 times across sites. Mean repertoire size across sites varies from 8 song types to 12 song types, and mean song rate for sites varies from 10.20 to 13.63 songs per minute. No significant geographical pattern was found in these whole song parameters.

One feature that is common in both the species is that they share song types between immediate neighbours. The proportion of shared song types between birds reduces with distance, and no common song types were found between study sites. In case of *P. xanthoschistos* it was found that birds separated by about 5 km distance were not sharing any song types.

The songs of *P. xanthoschistos* and *P. reguloides* begin with an introductory note. *P. reguloides* song was found to have typical hook shaped introductory note, a v-shaped note, being rare except at Shillong site in Meghalaya. In contrast *P. xanthoschistos* has a set of different introductory notes at each site. These notes vary from site to site and some of the notes are shared between sites. The pattern of sharing is not correlated with geographical distance in all cases, for example some introductory notes are shared between Nokrek in Meghalaya, Mehao in east Arunachal Pradesh and Shimla-Nahan in Himachal Pradesh, and these notes are not found in some close by sites e.g. in Eaglenest in west Arunachal Pradesh.

An important discovery during the course of my research on *P. xanthoschistos* introductory notes is that some of the introductory notes of eastern populations are found in the songs of western populations, appearing as first note of their song after introductory note. In this way total number of distinct notes in the songs of northwestern populations increases making the song more complex.

The same introductory note is also repeated as the first note of the rest of the song in some populations e.g. Yuksom in Sikkim and Chakrarta in Uttarakhand but it is not as common as the first pattern.

P. xanthoschistos sings across sites within minimum frequency (mean ± s.e.) ranging from 2494 ± 66 to 3476 ± 106 Hz, maximum frequencies ranging from 8493 ± 103 to 9196 ± 71 Hz, with bandwidth ranging from 5017 ± 116 to 6424 ± 118 Hz, with number of distinct notes in the song ranging from 4.45 ± 0.21 to 6.63 ± 0.17, and song length varying from 1.19 ± 0.03 to 1.48 ± 0.04 seconds. Birds in northwest sing with higher bandwidth and more number of notes, which they rarely repeat in song, whereas birds in southeast sing longer songs with fewer notes, which they often repeat. Songs are more complex in the northwest as they have more distinct notes and higher bandwidth.

A total of 139 song playback experiments were carried out including 91 intraspecific playbacks among *P. xanthoschistos* and *P. reguloides* populations and 48 inter-specific playbacks. Playback results show that there is strong response to the inter-population playbacks i.e. the songs of one population are well recognized by the other populations. This indicates that song divergence is not enough for affecting reproductive isolation. But there was very poor inter-specific playback response among altitudinally replacing *Phylloscopus* warblers except between *P. xanthoschistos* and *P. reguloides*.

P. reguloides, unlike *P. xanthoschistos* sings with singing style that is close to immediate variety, so that in this species song types rarely repeat. *P. reguloides* was found to have much lower repertoire size, repertoire site means ranging from 3.06 to 3.48 song types per bird. The birds sing with mean song rate for sites ranging from 6.39 to 7.81 songs per minute. No significant geographical pattern in these whole song parameters was detected.

P. reguloides, except at Banjar-Jalori site in Himachal Pradesh, sings with typical song syntax: an introductory note followed by repetition of syllables of two to four notes, three note repetition is the most common pattern except at site

Shillong in Meghalaya, where two note repetitions is more common. One of the significant finding is that in Himachal Pradesh *P. reguloides* have distinct song syntax features. Here instead of single typical song syntax, birds sing songs with five different syntax types. These extra song syntax types have not been reported in *P. reguloides* at any other site, except that one has been reported extralimitally in *P. reguloides assamensis* from Myanmar. Syntax features of Himachal *P. reguloides* resemble song syntax of sister species *P. claudiae* and *P. goodsoni*, both occurring in China.

P. reguloides sings across sites within minimum frequency ranging (mean ± s.e.) from 3327 ± 88 to 3453 ± 93 Hz, maximum frequencies ranging from 8316 ± 121 to 8510 ± 115 Hz, with bandwidth ranging from 4874 ± 115 to 5306 ± 234 Hz, with number of distinct notes in the song ranging from 3.48 ± 0.15 to 4.13 ± 0.14 and with song length varying from 1.61 ± 0.03 to 1.82 ± 0.05 second. Song parameters of *P. reguloides* do not show significant geographical variation from northwest to southeast. Inter-population playback experiments show song recognition between different populations, though there is less recognition between Himachal and rest of the populations.

Interspecific playbacks among altitudinal replacements involving *P. cantator, P. xanthoschistos, P. occipitalis, P. reguloides* and *P. trochiloides* did not detect interspecific aggression, except between *P. xanthoschistos* and *P. reguloides*. Hence it appears that interspecific aggression, based on song recognition, may not be the only factor responsible for spacing of all close congeners along altitudinal gradient. There may be visual signals involved in interspecific aggression and other factors like environmental variation with altitude, vegetational ecotones and diffuse competition may be important in determining species distribution limits along altitude. Unlike in the mountains close to equator in Central America and the Andes where interspecific aggression has been found common spacing mechanism, Himalayan system has much more seasonal climate, and many altitudinal replacements may not be interacting in non-breeding season, which may perhaps reduce interspecific aggression.

Both the species were found to have complex songs in the northwest but the complexity is achieved in different ways, by increasing within song complexity in *P. xanthoschistos* and by increasing inter-song complexity in *P. reguloides*. There are many hypotheses for correlating song complexity with latitude, some are based on higher sexual selection in the north and others are based on sound transmission in noisy environment. Four complementary hypotheses can explain the detected pattern: Climatic variability and unpredictability hypothesis, transmission in noisy environment hypothesis, seasonal food flux in the northwest and more male-male competition. According to a hypothesis by Botero et. al (2009) climatic variability and unpredictability leads to elaboration of songs because high cognitive ability is required in such environments and complex songs add to cognitive ability. Himalayan avifauna is considered to be immigration avifauna: Himalayas were under cold and dry conditions during the last glaciation maximum and there were no habitats for the warblers. Immigrated taxa might have experienced more variable and unpredictable climatic conditions in the western Himalayas leading to development of more complex songs.

According to transmission in noisy and species rich environment hypothesis, birds in these environments sing simpler and repetitive songs. Songs of *P. xanthoschistos,* which occur in lower areas compared to *P. reguloides,* are eventual in variety, and within *P. xanthoschistos* songs in the southeast, which is noisier, repeat syllables, whereas in the northwest they rarely do so. According to seasonal food flux hypothesis, food is abundantly available in seasonal environments during breeding time reducing cost of singing, but according to a recent study the food is lower in the northwest (Ghosh 2013). According to male-male competition hypothesis birds in high-density areas sing shorter songs because there is more male-male competition in such areas. Bird density in *P. xanthoschistos* has been found comparable in east and west, but the songs are significantly longer in the east rejecting the hypothesis. In *P. reguloides,* the density is higher in the east but song length does not vary from northwest to southeast, and hence the male-male competition hypothesis is not supported in this case too. *P. xanthoschistos* has more species rich environment in the

southeast, and that explains its simpler songs in the east according to sound transmission hypothesis.

Occurrence of atypical songs in *P. reguloides* in Himachal Pradesh has been explained by six complementary hypotheses. These are based on meeting of *P. reguloides* from Himachal with sister species *P. claudiae* in winter and learning its songs, selection for more cognition in northwestern population because of variable and unpredictable climate, character displacement in the habitat where it has overlapping distribution with its close relative *P. occipitalis*, greater migration distance and greater sexual selection in Himachal population, selection for simpler and shorter songs in the higher density southeast environment and therefore complex songs once common in common ancestor were selected against in the southeast, and lastly it may be that Himachal population is more phylogenetically distant from rest of Himalayan taxa.