Study of altitudinal and geographical song variation, and interspecific interaction among *Phylloscopus* warblers in the Himalayas

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WILDLIFE SCIENCE



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2014

DECLARATION

I hereby declare that the thesis entitled "**Study of altitudinal and geographical variation, and interspecific interaction among *Phylloscopus* warblers in the Himalayas**" submitted for the award of the degree of Doctor of Philosophy in Forest Research Institute University, Dehradun, is a record of original research work done by me under supervision of Dr. G.S. Rawat, Professor, Wildlife Institute of India and Dr. Trevor Price, Professor, University of Chicago, USA, and it has not formed the basis for the award of any other degree or diploma. I also declare that the thesis embodies my own work, observation and analysis and in that respect, the investigation appears to advance knowledge in the subject.

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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.

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Chapter 1
Introduction

1.1 Background

1.1.1 Avian vocalizations, their studies and applications

Sound is the predominant form of communication among many groups of animals and particularly in birds. Insects, frogs, mammals and birds use vocal signals to attract mates and defend territories (Rogers and Kaplan 2000, Gerhardt and Huber 2002, Marler and Slabbekoorn 2004). Bird songs have attracted people for very long time as they find many references in music and literature. In 1773 Hon. Daines Barrington established song learning in birds by hearing song of a wren emanated by a captive Goldfinch; and in 1789, Gilbert White described how a single species (willow wren) could be separated into three separate species by their songs (Catchpole and Slater 2008). Marler (1952) found that song could vary from place to place in chaffinches. Such studies were limited in depth by the absence of recording equipment and analysis tools. The scientific study of bird song was triggered in 1950s by the introduction of sound spectrograph (Thorpe 1954). Recent technical advances in the form of small, easy to use sound recording equipment and availability of computer based, easy to use, sound analysis tools have made bird vocalization studies far less logistically difficult compared to 1950s when recording equipment used to be heavy and recordings were sent to laboratories for making spectrograms.

Birdsong is solely used in communication and therefore it is called a signal and it is generally accepted that communication has occurred when the signal modifies the behaviour of the receiving bird (Catchpole and Slater 2008). There are several theories regarding evolution of communication in animals. Earlier it was thought that communication benefits both the sender and the receiver, but nowadays communication is viewed more a result of conflict rather than cooperation between sender and receiver. In cases where cooperation is involved the signals will be evolved to be relatively quiet and inconspicuous such as alarm calls in the presence of predators, but in cases where interests of sender

and receiver conflict, there will be evolutionary arms race between manipulation by the sender and 'sales resistance' by the receiver as in case of rival territorial males (Krebs and Dawkins 1984). Sales resistance may occur among rival males but there are stronger reasons for it to be in females. It is now generally accepted that females have been selected for fine discrimination of male songs, because if a female chooses a male of wrong species or of inferior quality it will result in reduced breeding success (Catchpole and Slater 2008). Signals may impart reliable information from sender to receiver or the information may be less than reliable. The reliability of a signal requires that there is correlation of some aspect of the signal and some attribute of the signaler. According to Zahavi (1975) only honest signals should evolve. i.e. signals should be costly to produce so that it is difficult for a weak animal to produce signals to bluff the receiving rival or mate. It also costs the receivers to assess the signals and if the costs of getting extra information are quite high compared to benefit gained, the receiver may accept cheaper and less reliable signals sent by signaler (Dawkins and Guilford 1991).

Sound communication is one of the preferred modes of communication among birds, which seems to have many advantages over other modes of communication (Catchpole and Slater 2008). Birds, in general, have poorly developed olfactory system and rely upon visual and audio signals for communication, though a few group of birds such as oceanic petrels have relatively well developed sense of smell and some forest vultures use smell to locate food (Rajchard 2007). Visual signals have several disadvantages in poor light and also in their inability to propagate through or around objects e.g. in dense vegetation. Sound travels in all directions and can penetrate dense vegetation. It can also travel long distances. Sound is produced only when it is required and large amount of information can be transmitted rapidly and efficiently through the sound channel (Catchpole and Slater 2008). Energy spent in singing depends on the intensity of sound produced by a singing bird, and singing was traditionally thought to consume a significant part of energy but recent studies do not support this view (Catchpole and Slater 2008).

Sound in birds is produced by the syrinx, which is equivalent of larynx in humans. Songbirds or Oscines in the order Passeriformes, together with parrots and hummingbirds, have highly developed syrinx enabling them to produce some highly complex sounds, and these are the only group of birds that learn their songs. The song production begins in the brain. The songbirds, parrots and hummingbirds have forebrain structures for producing learned vocalizations, whereas all other birds use only basal brain structures for vocal production and their vocalizations are innate (Jarvis 2004).

Making permanent recording of bird songs is essential part of any scientific study of bird song. Any sound recording gear needs a recorder, microphone and a headphone. There have been great advances in recording technology from heavy and costly open reel recorders to cheaper cassette recorders, digital audio tape recorders, solid state recorders and hard disc recorders. Bird recording equipment has benefited by use of commercial voice recorders used for human voice, as birds and humans share much of the frequency range. New recorders are very small, relatively cheap, and easy to use, and offer great quality (refer to http://macaulaylibrary.org/field-recording for field recording techniques and the equipment). Once recorded, sound can easily be transferred to computers, and can be analyzed using sound analysis software, such as Raven Pro, as developed by Cornell Laboratory of Ornithology. These technological advancements have promoted not only bird and other animal sound research but also encouraged many people to take up nature and animal recording as a hobby resulting in large archives of animal, particularly bird sounds such as Macaulay Library at Cornell Laboratory of Ornithology in Cornell University, USA, Xano-canto Foundation (http://www.xeno-canto.org/) and Project AVoCet (http://avocet.zoology.msu. edu).

Bird sounds are increasingly used in avian research and conservation. Counting birds in forests and in any dense vegetation is not possible without in depth knowledge of bird sounds, and hence bird research and monitoring programs use bird sounds in various ways. Birdsong playbacks can play important role in species recovery programs, e.g. by augmenting captive breeding by playing tape

recorded conspecific sounds, controlling bird populations by playing sounds and censusing birds using playbacks of conspecifics (Gaunt and Mccallum 2004). Bird song studies also find use in neurobiological investigations and studies on speciation and evolution.

Vocalizations are regularly being used in defining species limits in birds, often together with genetic studies (Alström and Olsson 1995, Helbig et al. 1996, Alström and Olsson 1999, Alström et al. 2007, Alström et al. 2008, Alström et al. 2010, Saitoh et al. 2010). Many new species of birds have been discovered making use of bird sounds (Alström and Ranft 2003). Avian vocalizations have been of great use in the discovery of new species, assessment of taxonomic rank of allopatric taxa under the biological species concept and in phylogenetic analysis (Alström and Ranft 2003). Several new species have been discovered based on their vocalizations, and many sibling species are likely to be discovered in future with further analysis of vocalizations (Alström and Ranft 2003). As allopatric taxa cannot be adequately evaluated for their species status under the biological species concept, they are increasingly studied with the aid of comparative vocalizations, and several new taxa have since been elevated to species rank (Sibley and Monroe 1990, Parker 1991, Price 1996, Peterson 1998, Alström and Ranft 2003). This has been particularly so in the genus *Phylloscopus* (Irwin et al. 2001, Alström and Ranft 2003, Martens 2010).

1.1.2 Bird vocalizations, their characterization (syntax and frequency–time parameters) and analysis

Bird vocalizations are generally divided into songs and calls. Songs are generally long, complex vocalizations produced by males in the breeding season. However, both males and females, especially in the tropics, are known to sing throughout the year. Even in the temperate regions birds start singing much before breeding season and also after breeding, in the autumn (Catchpole and Slater 2008). Calls are generally simpler vocalizations. The distinction between songs and calls may sometimes get blurred but the concept seems to be useful. According to Catchpole and Slater (2008, page 8):

> *"Calls tend to be shorter, simpler and produced by both sexes throughout the year. Unlike songs, calls are less spontaneous and usually occur in particular contexts which can be related to specific functions such as flight, threat, alarm and so on..., there are obvious areas of overlap between simple song and complex calls, and plenty of exceptions to the criterion we have presented. But in general, ornithologists and ethologists recognize these distinctions and continue to find them useful."*

Majority of the songbirds have more than one version of their species song and each version is called a song type (Catchpole and Slater 2008). Number of song types in a bird's song is called song repertoire size. A complete rendition of song, which will be called whole song hereafter in the text, consists of repeated song units in certain way for a particular bird species, these units belong to certain song types and will be referred to as song to distinguish such units from whole song. The smallest unit of a song is an element or note.

Sound once recorded can conveniently be studied by sound analysis software. Sound waves are represented by amplitude and frequency and their temporal variation. Sound analysis software illustrates these features as the main output in the form of sound spectrogram, which is often called sonagram, sonogram or spectrogram. Throughout this thesis I use the term spectrogram. A spectrogram is a frequency time plot of sound, which visually illustrates sound parameters e.g. minimum frequency, maximum frequency and bandwidth. In case of avian vocalizations, notes (or elements) make the smallest unit, which is shown as continuous trace on spectrogram (Catchpole and Slater 2008). These notes rendered in different combinations make a song. Often the most important component of sound analysis studies is arrangement of these notes in song (syntax) and the frequency-time characteristics of the notes, note groups and songs. For example, a song may consist of all different notes or repetition of a few notes (syllables) in certain way, similarly notes differing in shape on spectrogram have different frequency-time pattern and therefore sound differently. With practice it is easy to read spectrograms to infer the sound they

represent, e.g. high and low pitch sounds can be inferred by high and low frequency traces on spectrogram.

Sound analysis mostly involves study of syntax and frequency-time parameters of songs, notes and note-groups. The syntax can be visually read from spectrograms and frequency-time parameters can be measured. The data so generated can be analyzed using statistical programs.

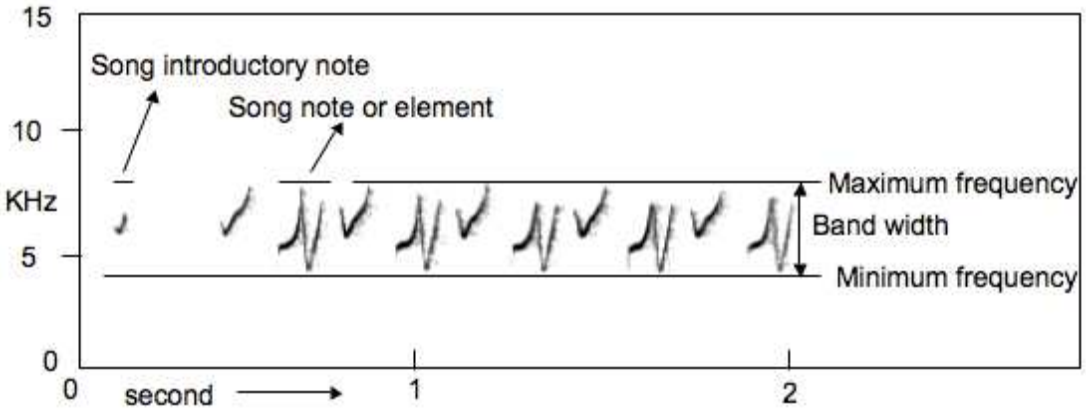

Figure 1.1 A spectrogram of a *Phylloscopus reguloides* song from North Bengal, India. The song consists of one introductory note and 10 other notes, which are repetitions of two note group (syllable). The song has three distinct notes, including introductory note.

1.1.3 Geographical variation in bird song

Bird species vary enormously in their songs, some sing with a single simple song whereas others have very large repertoires and quite complex songs (Kroodsma 2004).

Geographical variation in animal traits is often believed to trigger speciation processes (Price 2008). Mating ornaments and displays are primary examples of such traits that are involved in mate recognition and mate selection (Podos and Warren 2007, Price 2008). Geographical variation in mating signals and mate recognition systems can potentially facilitate assortative mating and reproductive isolation, leading to speciation. The 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

(Catchpole and Slater 2008). The geographical variation in bird song may arise as a consequence of vocal learning, habitat matching, genetic adaptation or social adaptation (Catchpole and Slater 2008, Price 2008).

Songs vary across species from simple to highly complex. Over half of all bird species, i.e. songbirds, the hummingbirds and the parrots, learn their songs from conspecifics but they may also improvise; the other species sing relatively simple innate songs (Catchpole and Slater 2008). Geographical variation is most obvious in the species that learn songs (Price 2008). Many of these species have populations divided into song dialects. Most studies of geographical variation have primarily been concerned with formation of dialects (Podos and Warren 2007, Price 2008), but more recently there has been much interest in how ecological factors, including the acoustic environment and body size and shape, affect song evolution. For example, Derryberry (2009) showed vegetation structure and bill size affect variation in song of White Crowned Sparrow, *Zonotricha leucophrys,* and Slabbekoorn and den Boer-Visser (2006) showed how song frequency of great tits, *Parus major,* has been modified to avoid masking by city noise.

Most songbirds learn their songs from conspecifics, which according to a limited number of studies could be their fathers as in case of Darwin' finches or territory neighbours as in case of indigo buntings and saddlebacks (Catchpole and Slater 2008). For many species, song learning is mostly during early period of their life, within first year, called sensitive phase, when birds are especially receptive to song stimuli and memorize songs readily, but there are exceptions e.g. in Canary learning continues much later in life and hence is an open-ended learner. Young birds, given choice, have preference for learning conspecific songs. The studies of song development by Marler (1976) and Konishi (1965a, 1965b) led to development of 'auditory template model' of song learning. According to this model young birds have innate crude 'template' defining approximate characteristics of their own species song, and during sensitive phase the birds develop exact template by memorizing songs matching this template (Catchpole and Slater 2008).

Birds vary in number of song types they have in their vocabulary. This number, which is called song repertoire size, may vary from a single song to more than 1000 songs. In species singing a single song type, it is common to have same song in the neighbors, but in species which have large repertoires, neighboring birds may share only some (or none) of their songs. There are extremes in neighbors song-sharing patterns, some birds share their entire repertoire with neighbors as in English populations of the corn bunting and village indigobird, whereas others share more with distant individuals than with neighbors, but the commonest pattern is probably where birds on adjacent territories share some songs (Catchpole and Slater 2008). Thus songs can vary between individuals between neighboring groups which might potentially interact or interbreed and also between populations, several kilometers apart, whose individuals are unlikely to meet each other, the variation called microgeographic and macrogeographic (Mundinger 1982, Catchpole and Slater 2008) respectively. The variation is most obvious in songs but it can also be at the level of syllables or notes that comprise them. Because of this, variation in notes may be much less than variation in songs as in the cases of Swamp Sparrow and Indigo bunting all the songs are made up of limited number of note types (Swamp sparrow, Marler and Pickert 1984, Indigo bunting, Baker and Boylan 1995). Thus, perhaps the variation at the level of notes is not unlimited and species are capable of producing certain note types only (Catchpole and Slater 2008). Geographical variation is most striking in the species with single song type or very small repertoire, where it is frequently found that change is not gradual but sudden switch from one dialect to other e.g. in White-crowned sparrow and Corn bunting (Catchpole and Slater 2008). Geographical or topographical barriers, habitat changes or colonization events are the likely causes for dialect formation, where populations with separate song traditions meet (Catchpole and Slater 2008).

Songs evolve by drift and selection as other phenotypic traits (Podos et al. 2004, Podos and Warren 2007, Price 2008). Podos et al. (2004) have summarized song evolution into five scenerios- cultural drift, genetic drift, cultural selection,

natural selection and sexual selection-under drift and selection, which are not necessarily mutually exclusive.

Cultural drift: It refers to chance variation of song, due to copying errors and founder effect, which has been considered to be main cause for simpler songs on islands and initial stages of dialect formation (Podos et al. 2004).

Genetic drift: Song memes may change due to random changes in genetic loci responsible for anatomical, physiological and neural mechanisms that underlie development and production of vocalizations, and that may happen when vocalizations are produced at or near limits determined by above mechanisms.

Cultural selection: Songs with features more effective in the process of communication, both in the context of interactions between adults and imitation by juveniles, may be favoured by selection. For example songs with low frequencies and slow repetition rate evolve frequently in forested habitats, because of their better propagation in such habitats (Podos and Warren 2007). According to habitat matching hypothesis geographical variation in a species occurring in different habitats may evolve in the process of acoustic adaptation, wherein different features of song, e.g. frequency, note repetition are differentially propagated in different habitats (Catchpole and Slater 2008). Kirschel et al. (2009) showed that habitat variation in the green hylia changes its song.

Natural selection: Natural selection may facilitate vocal divergence via species interactions, in which site specific, population specific and species specific songs are favored as hybrid songs are selected against. For example local adaptation (or genetic adaptation) hypothesis employed to explain maintenance of song dialect boundaries is based on natural selection.

Natural selection can also indirectly affect song evolution if mechanisms (anatomical, physiological or neural) of song development and production are affected by natural selection. For example selection for feeding morphology, i.e.

large beaks, constrains Darwin's finches in producing trills (Podos and Nowicki 2004). Similarly in White-crowned Sparrow selection for beak morphology (in addition to habitat variation) was shown to account for some of the variation in song structure (Derryberry 2009).

Sexual selection: According to theory of sexual selection more effective song variants are retained over evolutionary time and female preference evolves with male trait evolution (Andersson 1994, Podos et al. 2004). Sexual selection can vary both in intensity and target (Price 2008). The course of sexual selection is often haphazard with different parameters favoured in different lineages, and divergent pathways of sexual selection may result in signal divergence in offshoot populations (Podos and Warren 2007). Resource abundance and dispersion can influence intensity of sexual selection. For example seasonal abundance of resources in the north has been attributed to high sexual selection on song resulting in their complexity and elaboration in *Phylloscopus trochiloides* (Irwin 2000). Resource dispersion can give rise to divergent mating systems, which result in different intensities of sexual selection. For example clustered resources have been associated with lekking mating system, where sexual selection by female choice is intense.

Habitat matching, genetic adaptation and social adaptation are the functional explanations offered for formation and maintenance of dialects. According to habitat matching hypothesis geographical variation in a species occurring in different habitats may evolve in the process of acoustic adaptation, wherein different features of song, e.g. frequency, note repetition are differentially propagated in different habitats. Genetic adaptation hypothesis suggests that birds benefit by mating with individuals from the same population as themselves as this avoids break-up of co-adapted gene-complexes, thus favoring local adaptations (Catchpole and Slater 2008). Social adaptation hypothesis posits that dialects may form and persist if individuals benefit from learning songs of their neighbors as this enables them to interact more effectively. According to another theory, epiphenomenon hypothesis, dialects may be functionless byproduct of

vocal learning and they may arise by inaccurate copying of songs (Podos and Warren 2007, Catchpole and Slater 2008).

Dialects are often thought to originate through some form of cultural drift or divergence simply through cultural mutation turnover, and in many cases divergence through these processes provides the best explanation for song variation (Koetz et al. 2007, Price 2008). However, studies, which search for environmental correlates of songs, focus on adaptive explanations driving song change. For example, in the Greenish warbler, *Phylloscopus trochiloides*, songs are longer and more complex to the north (Irwin 2000, Irwin et al. 2001). Irwin (2000) considered this may be a result of (1) increased intensity of sexual selection, or reduced costs of singing in the north (as expected from the food flush described above); (2) a shift in focus from male competition where territories are more dense in the south to female choice in the north; (3) a result of increased habitat complexity in the north or (4) more intense sexual selection resulting from the need for rapid establishment of territories in the more seasonal northern environment (see also Read and Weary 1992, Catchpole and Slater 2008, Botero et al. 2009). It is difficult to distinguish these alternatives with correlative studies, but here I use a neglected approach, and that is to investigate altitudinal, as well as geographical variation in songs.

In this study I investigate geographical variation in the songs of two species of *Phylloscopus* warblers at all scales, and explore the meaning of geographical song variation to birds by studying inter-population song-recognition by using intra-specific playbacks. I also explore altitudinal variation in bird song (see below).

1.1.4 Altitudinal Variation of Birdsong

Bird distributions along altitudinal gradient in the Himalayas show turnover of species with the change in physical and biological environments. Bird species combinations and assemblages are often very distinct and unique to each altitudinal belt (Rashid 2006, Acharya et al. 2011, Price et al. 2011). Most bird species breeding in Himalayas show substantial altitudinal distribution range exceeding more than 1000 m in most cases. The vegetation itself changes with

altitude, and several taxa show altitudinal replacement of congenerics up the Himalayan montane system. Some prominent examples include *Phylloscopus* leaf warblers (Price 1991), parid tits, nuthatches, fulvettas, yuhinas, chats, and flycatchers (Price et al. 2011). The birds encounter gradual change in their environment, both physical and biological, along their altitudinal span, and the change should be getting more evident at the extremes. Environment variation can bring change is song variables, for example, Kirschel et al. (2009) showed that environmental variables (elevation, and tree cover) and ambient noise by insects affected variations in song frequency of Green Hylia populations in Africa. Besides, ecology can potentially influence song structure by change in morphology because morphological variations can bring about vocalization variations as in case of Darwin's Finches (Podos and Nowicki 2004, Podos and Warren 2007). Price (1991) found intra-specific morphological variation within warbler species breeding along altitudinal gradient in Kashmir, indicating the possibility of song variation.

As far as I am aware no studies of altitudinal variation of songs within species have been undertaken. However, altitudinal variation has been studied across finch species (Badyaev 1997, Snell-Rood and Badyaev 2008). Snell-Rood and Badyaev (2008) found that species breeding at lower altitudes have more elaborate songs. They attributed the altitudinal differences to the presence of a harsher climate at higher altitudes, resulting in high cost of maintenance and consequently less intense sexual selection. If this is the case, then some of the alternative hypotheses for the evolution of song complexity can be rejected. For example, higher elevations are likely to be more seasonal environments, but seasonality has been thought to promote song complexity (Botero et al. 2009).

1.1.5 Interspecific interactions among altitudinal replacements

With altitude environmental factors, as well as vegetation structure and composition also changes. In the Andes, Terborgh (1971) identified physical and biological environment, competitive exclusion and ecotones as the factors explaining altitudinal distribution pattern of birds. Approximately one third of distributional limits were attributed to interspecific competitive exclusion

(Terborgh 1971, Terborgh and Weske 1975). Robinson and Terborgh (1995) using heterospecific playbacks found that interspecific aggression among morphologically similar bird species drives habitat selection along a successional gradient in Amazonian forest. Using heterospecific playbacks Jankowski et al. (2010) recently showed similar interspecific aggression as a spacing mechanism in closely related Andean birds along elevational gradient.

However, no study to my knowledge has yet been taken up to find out interspecific competition based on song recognition as a spacing mechanism in closely related Himalayan species.

1.2 Old World leaf warblers as a model

The genera *Phylloscopus* and *Seicercus* are non-monophyletic, but if combined together they form monophyletic group, or clade (Olsson et al. 2005) and a family Phylloscopidae (Old World leaf warblers) has been suggested for the group based on molecular genetic evidence (Alström et al. 2006).

These insectivorous birds are quite small in size weighing from 4.5 to 12 grams (Ali and Ripley 1987). Most of the species are greenish or brownish above and yellow or off-white below. These birds are very active almost constantly moving on the small branches and twigs in the foliage of trees or shrubs. Many of the species are long distance migrants, whereas some of them move little during winter.

Phylloscopus warblers in general have been widely investigated as a model for song evolution and speciation, because song appears to be the prime species isolating mechanism. Many species differ very little in plumage color, and the species are abundant and easy to study (Thielcke 1983, Irwin 2000, Päckert et al. 2004, Bairlein et al. 2006, Päckert et al. 2009, reviewed in Price 2010, Martens 2010).

With more than 70 species, this lineage represents one of the most speciose and morphologically least differentiated group (Helbig et al. 1995, Bairlein et al. 2006) inhabiting forested areas mostly in Eurasia and some regions of Africa (del Hoyo et al. 2006). The Himalayas are the centre of species diversity for the Phylloscopidae (Price 2010) where local species diversity is a maximum (Price 2010; Ghosh-Harihar and Price 2013). Vocalizations are often the best clues for identification of species in this group. Many *Phylloscopus* species occur in high densities, comprising up to 40% of all birds present in some areas (Price et al. 2003) and males are highly vocal during breeding season while defending their territories (Martens 1993), offering good opportunity for field study of this group. Great diversity of species and their general abundance has made the *Phylloscopus* a suitable model for studying ecology and speciation (Price et al. 1997, Martens 2010, Price 2010). Study themes relate to the topics including the high number of sympatric breeding species, the evolution of breeding distributions with special emphasis on the Himalayan avifauna, molecular genetic aspects of evolution and ecological differentiation, species swarms, and cryptic species, the association of habitat and song characteristics, links between vocalisations and phylogeny, radiation versus molecular genetics and bioacoustics, phylogeography and the evolutionary timescale of *Phylloscopus* radiations in the Sino-Himalayan region, determinants of northern and southern range limits, morphology and ecology along an altitudinal gradient, evolution of ecological differences in breeding and non-breeding seasons, correlates of wing morphology with foraging behaviour and migration distance, phylogeny versus ecological diversification and the evolution and age structure of a ring-species and on species limits using bioacoustics and genetics (Alström and Olsson 1990, 1992, 1995, 1999, 2000; Alström et al. 1992, 1997, 2006, 2008, 2010, 2011; Olsson et al. 1993, 2004, 2005; Irwin 2000; Päckert et al. 2004, 2009; Alström 2006; Martens 2010).

1.3 Objectives of the study

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.

1.4 Structure of the thesis

The thesis has been divided into six chapters. In addition to introductory first chapter (present chapter) there are five more chapters. The second chapter gives details of study area, fieldwork and vocalization terminology used. Chapters 3-5 form the core of the thesis. Chapters 3 and 4 are independent chapters on *Phylloscopus xanthoschistos* and *Phylloscopus reguloides* respectively. Each chapter gives a detailed account of song of the respective species including whole song, song repertoire, song-sharing, song repetition rate/singing variety, song syntax, introductory note, frequency time parameters, notes in the song and geographical variation, song complexity and song recognition both intraspecific and interspecific. Chapter 5 is about interspecific interactions among altitudinally replacing *Phylloscopu*s warblers using playbacks. Chapter 6 provides synthesis and conclusions of the study. This chapter summarizes the findings of the study including the similarities and differences found in song patterns of *P. xanthoschistos* and *P. reguloides* and their variations.

Chapter 2
Study area, field methods and vocalization terminology

2.1 The study species and their distribution in the Himalayas

Both the intensively studied species (*Phylloscopus xanthoschistos* and *P. reguloides*) have a breeding distribution in most of the Himalayas and in the North-eastern Hills of India, and hence it was attempted to cover as many areas in the distributional range as was logistically feasible. Other closely related species, wherever they happened to occur, were also studied in the same areas for inter-specific interaction. Areas in neighbouring Nepal and Bhutan were not taken up, but adjacent areas selected in India probably fill the gap. For example, Nainital in the west is close to western Nepal, and Sikkim and North Bengal are close to eastern Nepal and western Bhutan, whereas Eaglenest sanctuary is close to eastern Bhutan. In total 15 study areas were selected ranging from Jammu in the west to Arunachal Pradesh in the east. Out of these 15 areas, 13 areas fall in the Himalayas and the rest two in the state of Meghalaya in the North-eastern Hills. The location of study sites is shown in Fig 2.1 and the site coordinates and other details are given in Table 2.1.

2.2 Selection of study sites

Study sites were selected so as to cover wide range of breeding distribution of the intensive study species and closely related altitudinally replacing *Phylloscopus* species. All the Himalayan states in India and one in the North-east India were covered. The selection of sites within the states was determined based on my previous knowledge of occurrence of the species, accessibility of the area and the logistics available. As far as possible I attempted to select areas that provided a good altitudinal gradient, though a few of the sites did not. Some of the study sites had both the focal study species and closely related altitudinal replacements in the same area whereas few had only one species (see Table 2.1)

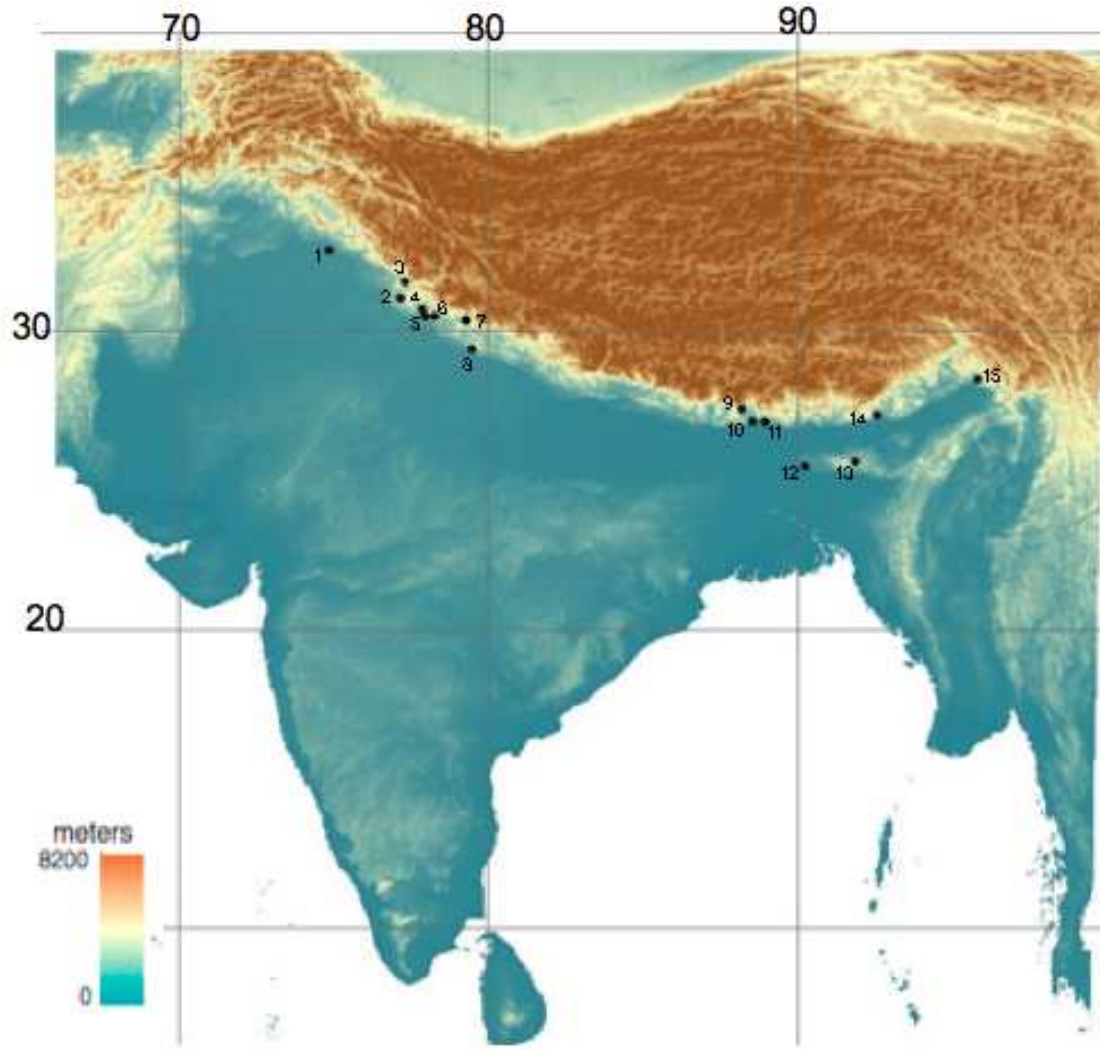

Figure 2.1 Approximate location of study sites spread from Jammu in the northwest to Arunachal Pradesh in the southeast (see Table 2.1 for site codes and other information)

Table 2.1 Study sites, geographical coordinates, study species and vegetation types.

S. N.	Site	State	Study Species *	Vegetation @	Lati-tude	Long-itude
1	Patnitop-Ramban	Jammu and Kashmir	*Px, Po*	12C1c, 9C1b	32.69	74.86
2	Shimla-Nahan	Himachal Pradesh	*Px*	9C1b	31.09	77.18
3	Banjar-Jalori	Himachal Pradesh	*Px, Pr, Po*	9C1b, 12C2b, 12C1c, 14C1a	31.62	77.35
4	Chakrata	Uttarakhand	*Px, Po*	9C1b, 12C1c	30.7	77.87
5	Mussoorie	Uttarakhand	*Px*	9C1b, 12C1c	30.48	78.01
6	Dhanaulti	Uttarakhand	*Px, Po*	9C1b, 12C1c	30.48	78.30
7	Kedarnath	Uttarakhand	*Pr, Po*	12C1, 12C2b, 14C1,15E1	30.49	79.21
8	Nainital	Uttarakhand	*Px, Po*	9C1b, 12C1	29.37	79.49
9	Yuksom-Tsoka	Sikkim	*Px, Pr*	8B/C1, 9C1b, 11B/C1, 12/C3(a), 13/C6	27.36	88.21
10	Singalila-Senchal	West Bengal	*Pr, Pt*	11B/C1, 12/C3(a), 13/C6, 15C1	27.05	88.30
11	Samsing	West Bengal	*Px, Pc*	3C/C3b, 8B/C1	26.93	88.57
12	Nokrek	Meghalaya	*Px*	8B/C2	25.45	90.27
13	Shillong	Meghalaya	*Px, Pr*	8B/C2, 9/C2	25.62	91.90
14	Eaglenest	Arunachal Pradesh	*Px, Pr, Pc*	1B/C2, 8B/C1, 11B/C1, 12/C3(a)	27.13	92.60
15	Mehao	Arunachal Pradesh	*Pc, Px, Pr*	1B/C2, 8B/C1, 11B/C1, 12/C3(a)	28.345	95.88

*Abbreviations: *Px*: *Phylloscopus xanthoschistos, Pr*: *P. reguloides, Po*: *P. occipitalis, Pc*: *P. cantator, Pt*: *P. trochiloides*

@ Vegetation Types (following Champion and Seth 1968); 1B/C2: Upper Assam Valley tropical evergreen forest, 3C/C3b: Moist mixed deciduous forest, 8B/C1: Himalayan subtropical wet hill forest, 8B/C2: Khasi subtropical hill forest, 9C1b : Himalayan chir pine forest, 9/C2: Assam subtropical pine forest, 11B/C1: East Himalayan wet temperate forest, 12C1: Lower Western Himalayan temperate forests, 12C1c: Moist deodar forest 12C2b: West Himalayan Upper oak- fir forest, 12/C3: East Himalayan moist temperate forest,12/C3(a): East Himalayan mixed coniferous forest, 13/C6: East Himalayan dry temperate coniferous forest, 14C1a: West Himalayan sub-alpine high level fir forest. 15C1: Birch-rhododendron scrub forest,15E1: Dwarf Rhododendron scrub

Biogeographic coverage of the study sites

Rodgers and Panwar (1988) divided India into ten biogeographic zones based on similar ecology, biome representation, and community and species distributions. The study species are distributed in the Himalayas and the North-east India biogeographic zones of India. Biogeographic zones have further been divided into biotic provinces. The Himalayas biogeographic zone has four biotic provinces on east-west Himalayan axis namely the North-west Himalayas, the West Himalayas, the Central Himalayas and the East Himalayas, and the study species occur in all the provinces. The North-east India biogeographic zone has two biotic provinces, Brahmaputra valley and Assam hills, and it is only in the later biotic province that the study species have breeding distribution. North-east India biogeographic zone represents the transition zone between the Indian, Indo - Malayan and Indo - Chinese biogeographic regions (Rodgers and Panwar 1988). Assam Hills and Eastern Himalayas though fall into distinct biogeographic zones but have contiguity with hill chain connecting eastern Himalayas to Meghalaya via Patkai and Naga Hills and Barail Hill range. The study sites represent all the biogeographic provinces where study species breed (see Table 2.2 below).

Table 2.2 Study sites and biogeographic provinces (see text).

S.N.	Sites	Biotic Province
1	Patnitop-Ramban, Banjar-Jalori	2A: The North-West Himalayas
2	Shimla-Nahan, Chakrata, Mussoorie, Dhanaulti, Kedarnath WLS, Nainital	2B: The West Himalayas
3	Yuksom-Tsoka, Singalila-Senchal, Samsing	2C: The Central Himalayas
4	Eaglenest WLS*, Mehao WLS	2D: The Eastern Himalayas
5	Nokrek NP*, Shillong	8B: Assam Hills

* WLS – Wildlife Sanctuary NP – National Park

2.3 Description of study sites

Patnitop - Ramban area in Jammu: This is the westernmost area covered under the study. Out of the two in-depth study species only one, *P. xanthoschistos,* is distributed in the area, besides *P. occipitalis* that was studied for interspecific playback response. Vegetation at Patnitop is dominated by deodar (*Cedrus deodar*a) and nearby lower altitude areas have chir pine (*Pinux roxburghii*). Ramban is lower altitude area with chir pine as dominant vegetation. This site will be referred as Patnitop-Ramban further in the text.

Banjar-Jalori area in Himachal: This area falls in Kullu Valley of Himachal Pradesh. It will be referred as Banjar - Jalori in short. Here three study species - *P. xanthoschistos*, *P. reguloides* and *P. occipitalis* are distributed on same mountain slope. The vegetation is conifer dominated. Chir pine and ban oak (*Quercus leucotricophora*) species are replaced by deodar, blue pine (*Pinus wallichiana*), spruce (*Picea smithiana*), fir (*Abies pindrow*) and kharsu oak (*Quercus semicarpifolia*) as we gain altitude. For the purpose of *P. reguloides* this area also includes close by Sarahan area.

Shimla-Nahan Road in Himachal: This area is along Shimla-Nahan road in Himachal Pradesh and will be referred as Shimla-Nahan further in the text. This road had much less traffic and passes through good forest where *P. xanthoschistos* breeds. Here, *P. xanthoschistos* recordings were made in the forest along the road at the intervals of about 5km or more. The vegetation was mainly dominated by pure chir pine stands and moister areas had broadleaved trees.

Chakrata area in Uttarakhand: Chakrata area is in western Uttarakhand and it includes areas close to Chakrata and Kanasar and along Chakrata-Kanasar road. Conifers and oaks dominate the vegetation. Chir pine, blue pine, deodar, fir and spruce are the main conifer species, and ban oak, moru oak (*Quercus floribunda*) and kharsu oak are the oak species distributed here. *P. xanthoschistos* and *P. occipitalis* are the study species distributed here.

Mussoorie and Dhanaulti areas in Uttarakhand: These areas are located close to Dehradun, situated in lesser Himalayas in the state of Uttarakhand. The vegetation is dominated by *Pinus roxburghii, Cedrus deodara, Quercus leucotricophora* and *Q. floribunda*. *P. xanthoschistos* and *P. occipitalis* occur here. Mussoorie and Dhanaulti have been treated separately.

Kedarnath Wildlife Sanctuary area in Uttarakhnad: Tungnath, Chopta and Kanchula Kharak areas were covered in Kedarnath Wildlife Sanctuary. This will be referred as Kedarnath WLS area further in the text. Here the vegetation is dominated by conifer and oak species, whereas rhododendron bushes occur in the higher reaches close to Tunganath. *Cedrus deodara* and *Pinus wallichiana* occur in Kanchula Kharak area, which is replaced by *Picea smithiana* and *Abies pindrow* in the higher areas. Similarly *Quercus floribunda* near *Kanchula Kharak* is replaced by *Quercus semicarpifolia* above Chopta. *P. reguloides* and *P. occipitalis* are the study species distributed here. *P. reguloides* occurs higher up from some distance down of Chopta to tree line near Tunganath. *P. occipitalis* occurs in between Kanchula Kharak and Chopta.

Nainital area in Uttarakhand: Here the fieldwork was done along the Nainital - Vinayak road, in Kilbiri - Pangot area and at Nainital Botanical Garden. The main species of interest was *P. xanthoschistos*, though *P. occipitalis* did occur in higher areas on Nainital - Kilbiri road as well as in higher areas close to Vinayak. The vegetation was largely dominated by mixed broad-leaved forest and *Pinus roxburghii* was dominant in the Nainital Botanical Garden area.

Yuksom-Tsoka area in Sikkim: This area falls within and near Kanchenjunga National Park of Sikkim. The fieldwork was carried out at and near Yuksom, Sachin and Tsoka. All the three areas are along and near popular Yuksom-Dzongari track in the park. Yuksom area is lowest in altitude (below 2100m), Sachin area is in between (2200-2350m) and Tsoka is the highest among the three (above 2500m, and was covered up to about 3000m). Yuksom area has broadleaved and pine forests, whereas Sachin is dominated by broad-leaved vegetation. Tsoka area has conifer dominated vegetation with deodar, Himalayan

hemlock (*Tsuga dumosa*), fir *and* blue pine. *P. xanthoschistos* was observed at and below Yuksom, and it goes along the trail to Sachin some way, and also up to the monastery whereas *P. reguloides* occurs at and above Yuksom, and up to and little beyond Tsoka. This area will be referred as Yuksom-Tsoka in the text.

Singalila National Park and Senchal areas in North Bengal: Singalila National Park is located in the North Bengal part of West Bengal state along Nepal border. The fieldwork was undertaken along Sandakphu track which starts at Maneybhanjan near Darjeeling at about 2100m and reaches nearly 3700m at Sandakphu. *P. reguloides* and *P. trochiloides* (nominate race) are distributed here. Here the vegetation is dominated by conifer species near Maneybhanjan (mainly deodar) and before reaching Sandakphu (fir, spruce and blue pine) with dense broad-leaved forest in middle altitudes at and near Gairibas. The highest areas here have a number of rhododendron species.

Senchal area is the other area close to Darjeeling below popular tourist destination Tiger Hill. Here altitude covered was between 2000-2300m. The vegetation is dominated by broadleaved species. *P. reguloides* is distributed here. These areas will be referred as Singalila-Senchal further in the thesis.

Samsing area in North Bengal: Samsing area is in the lower reaches of Neora Valley National Park. Here, field study was carried out below 1500m. The area has broad-leaved, largely evergreen forest. *P. cantator* and *P. xanthoschistos* are distributed here. The area will be referred as Samsing in short.

Nokrek National Park area in Meghalaya: Nokrek National Park is located in western Meghalaya in Garo Hills. This site will be referred as Nokrek in short. Here, the vegetation comprises dense broadleaved forests within the National Park and degraded areas dominated by bamboo growth in the vicinity. This area includes the highest area in Garo Hills with altitude reaching more than 1400m. *P. xanthoschistos* is the study species distributed here.

Shillong Plateu - Nongkhyllum Sanctuary in Meghalaya: This area falls in Khasi hills of Meghalaya State and includes the highest area in Meghalaya close to state capital of Meghalaya, Shillong, and nearby Nongkhyllem Wildlife Sanctuary. Shillong Plateu is a popular tourist spot in Meghalaya and has good forest cover. The fieldwork was carried out in the forest on the left side of Shillong Peak road few kilometers before reaching the peak. The vegetation is largely broad-leaved interspersed with pine, and pure pine stands. *P. xanthoschistos* and *P. reguloides* are the species of interest distributed here. One morning was spent in Nonkhyllum sanctuary, which has tropical evergreen forest. This site will be referred as Shillong further in the text.

Eaglenest Sanctuary area in Arunachal Pradesh: Eaglenest wildlife sanctuary and nearby areas located in western Arunachal Pradesh are much visited sites by birders. The sanctuary and adjoining areas have wide altitudinal range from about 400m to 3000m. A motorable unmetalled winding road passing through the sanctuary provides easy access to forest areas at altitudinal gradient from about 400m to 2700m and only areas close to the road are easier to access. *P. cantator*, *P. xanthoschistos* and *P. reguloides* are the study species distributed here. The vegetation changes from tropical evergreen to wet temperate as we go up the road. The adjoining areas of the sanctuary in the northern aspect are in rain shadow and chir pine *Pinux roxburghii* is common in such areas from about 2000m downwards in vicinity of Tenga valley. The area will be referred as Eaglenest in the text.

Mehao Sanctuary in Arunachal Pradesh: This area falls in Dibang Valley district of eastern Arunachal Pradesh. Like Eaglenest Sanctuary, here also altitude varies from about 400m to more than 2600m. *P. cantator*, *P. xanthoschistos* and *P. reguloides* are distributed here, in the order of increasing altitude. The vegetation is broadleaved forest in lower areas that gives way to mixed conifer forest in the higher areas. A road passes through the sanctuary and adjacent area covering large altitudinal range from foothills to about 2600m. This site will be referred further as Mehao in short.

2.4 Fieldwork at study sites

The fieldwork consisted of recording songs and carrying out playback experiments. Songs of P*. xanthoschistos* and *P. reguloides* were recorded for both studying geographical and altitudinal song variation and for using recordings in intra and interspecific playback experiments. *P. cantator, P. occipitalis* and *P. trochiloides* songs were mainly recorded for carrying out inter-specific playback experiments. Intraspecific playback experiments were carried out for *P. xanthoschistos* and *P. reguloides* populations, and interspecific experiments were carried out between closely related altitudinal replacements i.e. *P. cantator*, *P. xanthoschistos*, *P. occipitalis*, *P. reguloides* and *P. trochiloides*. Time and date of each recording was registered in the digital recorders, which were mostly used, and additionally spoken at the end of a song recording itself. Playback time and other details were recorded in the field books used for recording playback observations. Fieldwork was normally taken up in the early morning hours from about 5.00 am to 10.00 am, but was occasionally extended to later in the day wherever time available in the morning hours was reduced due to rain. Recording and playback experiments were undertaken along existing paths and roads in forests, and human induced background noise was avoided as far as possible.

2.4.1 Recording of vocalizations

Songs were recorded using Telinga Pro6 and Pro5 microphones with a Marantz PMD 671 and sony PCM-D50 solid state recorders and occasionally with Sony PCM-D1 digital audio tape recorder. All the recordings were made in wav file format with 16 bit resolution and 44.1 KHz sampling rate. For each recording, I noted altitude, date and site. Whenever possible I recorded up to about 5 minutes long songs of *P. reguloides* and up to about 10 minutes long songs of *P. xanthoschistos*, and avoided individuals where there was a great deal of background noise.

2.4.2 Playback Experiments

Playback experiments were carried out to test the significance of geographical song variation in populations of *P. xanthoschistos* and *P. reguloides* and also to investigate interspecific playback responses between closely related *Phylloscopus* warblers. A Saul Mineroff Speaker and Ipod Nano player were used for playbacks. I made wave files of clean recordings of 2-5 minutes length, with the amplitude of each recording brought to similar level. I undertook playback experiments in the mornings in good weather conditions, avoiding windy and heavy overcast conditions. The volume of speaker and player was set for sufficiently loud sound comparable to sound level produced by a typical bird. For each playback location I recorded date, time, and altitude. I used local songs as controls, except for some controls which were from close sites e.g. at Singalila-Senchal and Shillong sites a few songs from Yuksom-Tsoka and Nokrek respectively were used as controls. I first played an experimental tape to each male for 5 minutes and noted response for each minute. Each minute I recorded the response as no response, mild, moderate or strong response (i.e. a score of 0, 1, 2 and 3 respectively; see Table 2.3) based on the approach of the bird to the speaker and behavioural observations. I then played back a control tape of a local song. However if response to the experimental tape was very strong, I did not play back a control, reasoning that the response to the control would be strong also. Pseudo-replication has been found a design fault common in playback studies (Kroodsma 1986 and Kroodsma et al. 2001), it was minimized in the present study by using many different experiment and control recordings at each site.

In cases where the control was played, I subtracted the score on the experiment from the score on the control to get the differences in responses. These difference scores were analyzed to find geographical variation in song recognition in *P. xanthoschistos* and *P. reguloides*, and interspecific aggression among altitudinally replacing closely related *Phylloscopus* warblers.

Table 2.3 Playback response scoring

Category	Response	Score
Strong	Directional movement toward speaker: Bird approached speaker <5m, and/or flew over speaker at less than 5m distance.	3
Moderate	Directional movement toward speaker: Bird approached speaker >5m and<10m, and/or flew over speaker at the same distances more than three times	2
Weak	Directional movement toward speaker: Bird approached speaker >10m and<15m, and/or flew over speaker at the same distance less than three times.	1
No response	Bird did not come closer to speaker, did not show directional movement towards speaker, did not fly over speaker	0

2.5 Vocalization terminology

I have generally followed the terminology adopted by Catchpole and Slater (2008). I define common terms used for vocalizations of both the species, *P. xanthoschistos* and *P. reguloides* here, also describing how to count, measure or estimate them wherever it is not obvious (also see Figure 1.1 in Chapter 1).

Song note (Element): A continuous trace of a bird vocalization on the frequency time axis is called a note or element. I use the word note, and not element, in the thesis. The number of notes is visually counted on a spectrogram by counting such traces separated by inter-note spaces.

Song: Vocalization of generally one to two second duration that is separated by other such vocalization by more than a 2 second time interval. A song consists of notes and inter-note intervals generally arranged in taxon specific order.

Whole song: Continuous rendition of songs lasting from a few seconds to more than 15 minutes. Whole song consists of both songs and inter-song intervals.

Introductory note: Initial note of a song separated by next note by much more inter-note time interval than time interval between other successive notes. Introductory notes are found in many species and they have been attributed to an alerting function, when compared with the rest of the song, which has message component (Richards 1981). In the species discussed by Richards (1981), the introductory note is typically a pure tone whistle, but in *P. xanthoschistos*, *P. reguloides* as well as other *Phylloscopus* warblers (*personal observations)* this is not the case. *P. xanthoschistos* uses multiple introductory notes preceding different songs and in some populations (e.g. in Sikkim) they run into song*. P. reguloides* has a typical hook-shaped introductory note.

Song type*:* The arrangement of notes in a song (syntax). Together with note form, this distinguishes one song type from another.

Syllable: Here it denotes note (element) group that occurs together and may repeat in a song.

Song-type sharing*:* Sharing of song types between individuals, defined as $2s/(x+y,)$ where s denotes number of song types held in common, and x and y are the repertoire size for each individual.

Repertoire size*:* Number of song types in the whole song of a bird.

Song rate*:* Number of songs produced per minute, calculated for a sequence of songs from the beginning of the first song to the beginning of the last song, divided by time. Any break of more than 10 seconds was considered the end of a whole song.

Eventual variety and immediate variety*:* Songs sung in a way that bird repeats a song type few times before switching over to another song type is called eventual variety, in contrast to immediate variety where a song in a sequence has different song type before and after it (Catchpole and Slater 2008). *P. xanthoschistos* sings with eventual variety in contrast to *P. reguloides,* which

sings with immediate variety (chapters 3 and 4). Generally a *P. xanthoschistos* with 5 song types in its repertoire, for example, sings its whole song in ….aaaabbbbbbbccccddddddeeeeeaaaaaabbbbccccccddddddeeeeeaaaaaa……
pattern, where a, b, c, d and e are song types; here song types are repeated in serials and different song type serials are rendered in a fixed order.

Song-repetition rate: Average number of songs of a song type sung by a bird before the bird switches to another song type.

Total notes: Total notes in a song including the introductory note.

Distinct notes: All the distinct note types in a song, with repeated note types counted only once.

Minimum frequency, maximum frequency, central frequency, bandwidth and song length: These are frequency and time measures of the selected sound, e.g. note, syllable or song. Whereas minimum and maximum frequencies are the lowest and highest frequencies of the sound, the central frequency estimates the frequency that divides the sound into two intervals of equal energy. Bandwidth is difference of minimum and maximum frequency of a sound as measured on a spectrogram window. Song length and note length are the durations of respective sound features. The above sound parameters were measured on a spectrogram window of Raven Pro 1.3 software by selecting the desired sound window and placing the cursors at minimum and maximum values of frequency and time, using brightness and contrast features for accurate placement. Central frequency is much less susceptible to measurement errors due to inaccurate selection of sound window of song spectrogram e.g. placing minimum and maximum frequency bars, hence central frequency does not often change with minor errors in measuring minimum and maximum frequencies.

Frequency measurements made on spectrogram window by placing cursor are often not very accurate (Zollinger et al. 2012) because of smudge of spectrogram lines, particularly when amplitude versus frequency studies are involved. But in

this study amplitude measurements are not involved and amplitudes of recordings were similar. So I do not visualize significant inaccuracy in measurements, and any bias in the measurements will be distributed uniformly across all the data.

Chapter 3

Geographical variation in the song of the Grey-hooded Warbler *Phylloscopus xanthoschistos*

3.1 Introduction

Here I investigate song variation across the range of the Grey-hooded Warbler *Phylloscopus xanthoschistos***,** a very active small olive warbler about 8.5 cm in size (Rasmussen and Anderton 2005). The bird is overall yellowish in coloration, lighter on the underparts, dull greenish yellow on the upperparts, giving a *Seicercus* like impression (Martens 2010). This insectivorous bird feeds mainly in middle and upper storey of trees, often hovering and sallying (Rasmussen and Anderton 2005, Ghosh-Harihar and Price 2013). The species is resident in the outer range of the Himalayas from North Pakistan to Arunachal Pradesh and North-east Indian Hills (Rasmussen and Anderton 2005) and also extends to north, west and south-west Myanmar (Martens 2010) where it breeds between 900 and 2700m and winters in the foothills up to 2000m (Rasmussen and Anderton 2005). The bird breeds in evergreen, open broadleaved, and coniferous forests, and winters in forest, secondary growth, scrubs and orchards (Ali and Ripley 1987, Grimmet et al. 1998, Rasmussen and Anderton 2005).

3.1.1 Systematics and Taxonomy

P. xanthoschistosis is a member of the family Phylloscopidae (Alström et al. 2006) and belongs to White-tailed Leaf Warbler (*Phylloscopus davisoni*) species complex, comprising of *P. davisoni*, *P. xanthoschistos*, *P. ogilviegranti* and *P. hainanus, w*hich have Sino-Himalayan distribution (Olsson et al. 2005, Päckert et al. 2009, Martens et al. 2011). The *davisoni* complex is similar to the *P. reguloides* complex in distribution pattern, evolutionary history and, north-to-south coloration gradient (Martens et al. 2011). *P. xanthoschistos* is closest to *P. davisoni*, which has abutting distribution in the east and southeast of distributional range of *P. xanthoschistos* (Olsson et al. 2005, Päckert et al. 2009,

Martens et al. 2011). It is also close relative of the much more studied Greenish warbler, *P. trochiloides* (Johansson et al. 2007, Price 2010).

Within the Indian subcontinent Ali and Ripley (1987) recognize four subspecies- *albosuperciliaris*, *xanthoschistos*, *tephrodiras* and *flavogularis* (Figure 3.1) based on subtle differences in colour, but taxonomy is confused (Per Alström pers. communication). I studied song samples from all subspecies (Table 3.1).

3.1.2 Song of *P. xanthoschistos*

According to Martens et al. (2011) territorial songs of the species in *P. davisoni* super species group to which *P. xanthoschistos* belongs, are complex with many different and strongly modulated element types in the individual verse. Syllable repetition in song is rare in the group but exceptions are *P. davisoni sensu stricto* and *P. ogilviegranti* (*disturbans* ssp. only), which have regular song patterns with syllable repetition (Martens et al. 2011).

Previous work on *P. xanthoschistos* has investigated the song syntax of the Nepal subspecies (nominate *xanthoschistos)*, based on 11 recordings from Nepal (Päckert et al. 2004). As described by Päckert et al. (2004) this subspecies sings a series of discrete song types of irregular and complex structure, including highly modulated notes. The song types have an introductory note followed by rest of the notes arranged in one of 5 syntax types. Four of the syntax types are arrangement of notes in ABAB, ABCABC, $_{A}B^{C}{}_{A}B^{C}$, ABABCC, where subscripts and superscripts indicate shift in frequency. The fifth syntax type (87% of all songs described) is a complex jumble either without, or with very little, repetition (Table 4 of Päckert et al. 2004). Päckert et al. (2004) did not consider the arrangement of song types within the whole song.

3.1.3 Study sites

The study areas, in general, have been described in Chapter 2. Here I give details in the context of the study species *P. xanthoschistos*.

Jammu: Here fieldwork was carried out close to Patnitop and Ramban, both on Jammu-Srinagar highway. At Patnitop, the fieldwork was carried out at and near Patnitop, along Jammu road and along Nathatop road. At Ramban the fieldwork was undertaken along and near a road on the left bank of Chenab.

Shimla-Nahan: I carried out fieldwork along Shimla-Nahan road, mainly on the much less used diversion road from Shimla - Chandigarh highway to Nahan. Here I stopped regularly after a few minutes to get good sample of *P. xanthoschistos* songs along gradually descending road.

Banjar-Jalori: Here *P. xanthoschistos* occurs mainly from Gibi village downwards along the very steep Banjar-Jalori road, whereas higher areas have *P. occipitalis and P. reguloides*. The fieldwork was carried out near Gibi and a few kilometers along the descending road to Banjar town.

Chakrata: At this site fieldwork was undertaken along Chakrata-Kanasar road, and near Chakrata town.

Mussoorie: Fieldwork was carried out along Rajpur-Mussoorie road, Gilori Power House road, and in Hathipaon - Cloud-end area.

Dhanaulti: Fieldwork was carried out along Mussoorie-Dhanaulti road, Dhanaulti-Kaddu Khal road and at and near Dhanaulti town.

Nainital: Here the fieldwork was carried out in and near Nainital town (particularly Nainital Biological Park) and along Nainital-Kunjakharak road-mainly near Nainital, Pangot and Vinayak.

Samsing: At this site fieldwork was undertaken near Samsing, particularly along Machuki- Neora Valley National Park track.

Yuksom-Tsoka: Here fieldwork was undertaken in the vicinity of lower boundary of Kanchenjunga National Park at Yuksom. The areas covered include Yuksom town, Monastery road, Jorthang road and Yuksom-Tsoka track.

Eaglenest: Here fieldwork was taken up within Eaglenest Wildlife Sanctuary along Khellong-Bompu road, near Eaglenest Wildlife Sanctuary at Lama Camp, and along Lama Camp-Tenga road.

Nokrek: At this site fieldwork was carried out along the walking track inside Nokrek National Park, Daribokgre village - Nokrek National Park track and along Daribokgre-Tura road.

Shillong: Shillong Plateu area has good forest cover. The fieldwork was carried out in the forest few kilometers before Shillong Peak, along both sides of a stream on the left of climbing Shillong Peak road.

Mehao: Here fieldwork was carried out along Sally Lake –Mayodia Pass road, upto Tiwari Gaon in Mehao Wildlife sanctuary area.

3.2. Methods

Fieldwork was undertaken from 2007 to 2010 during the breeding season (April-June, except on 30th March at Shimla-Nahan and on 4th July at Mussoorie) (Table 3.1). I visited 13 sites across the Himalayas (Figure 3.1) and Northeast Hills. Fieldwork consisted of recording birdsongs and carrying out playback experiments.

Table 3.1 Study sites: *P. xanthoschistos* subspecies distributed, duration of fieldwork, geographical coordinates and altitude, and vocalization material analyzed for each site are given in the table.

Site	Subspecies	Dates	Lati-tude	Longi-tude	Altitudinal range (m)	Song material analyzed *				
						N^1	N^2	N^3	N^4	N^5
Jammu	*albosuperciliaris*	9-12 May 2009	32.69	74.86	755-2100	42	21	13	8	161
Shimla-Nahan	*albosuperciliaris*	30 Mar 2008	31.09	77.18	770-1970	41	21	7	1	215
Banjar-Jalori	*albosuperciliaris*	31 May and 4 Jun 2010	31.62	77.35	1635-1835	32	10	6	-	77
Chakrata	*albosuperciliaris*	1-2 June 2008	30.70	77.87	1805-2285	34	17	9	2	94
Mussoorie	*albosuperciliaris*	22 Jun and 4 July 2009	30.48	78.01	1190-2075	24	12	7	2	89
Dhanaulti	*albosuperciliaris*	2-4 and 7 Apr 2009	30.48	78.30	2040-2415	28	14	8	3	108
Nainital	*albosuperciliaris*	30 Apr-5 May 2010	29.37	79.49	1350-2410	46	25	24	8	229
Yuksom-Tsoka	*nominate*	3-6 and 27-28 May 2007	27.36	88.21	1365-2000	40	20	14	9	111
Samsing	*nominate*	4-6 May 08	26.93	88.57	730-1650	40	20	17	7	108
Nokrek	*tephrodiras*	18-20 April 09	25.45	90.27	1010-1385	40	20	13	6	106
Shillong	*tephrodiras*	22-24 April 2009	25.62	91.90	500-1850	22	11	6	4	52
Eaglenest	*nominate*	06-26 April 2008	27.13	92.60	780-2140	104	52	24	13	231
Mehao	*flavogularis*	26-29 April 2009	28.345	95.88	500-1790	28	14	9	5	59

*N^1: Songs analysed for frequency time parameters and number of notes, N^2: Individual recordings used for frequency time parameters and number of notes, N^3: Individuals analyzed for song rate and song-repetition rate, N^4: Individuals analyzed for repertoire, and N^5: Number of Song types analyzed for note repetition and introductory note in song

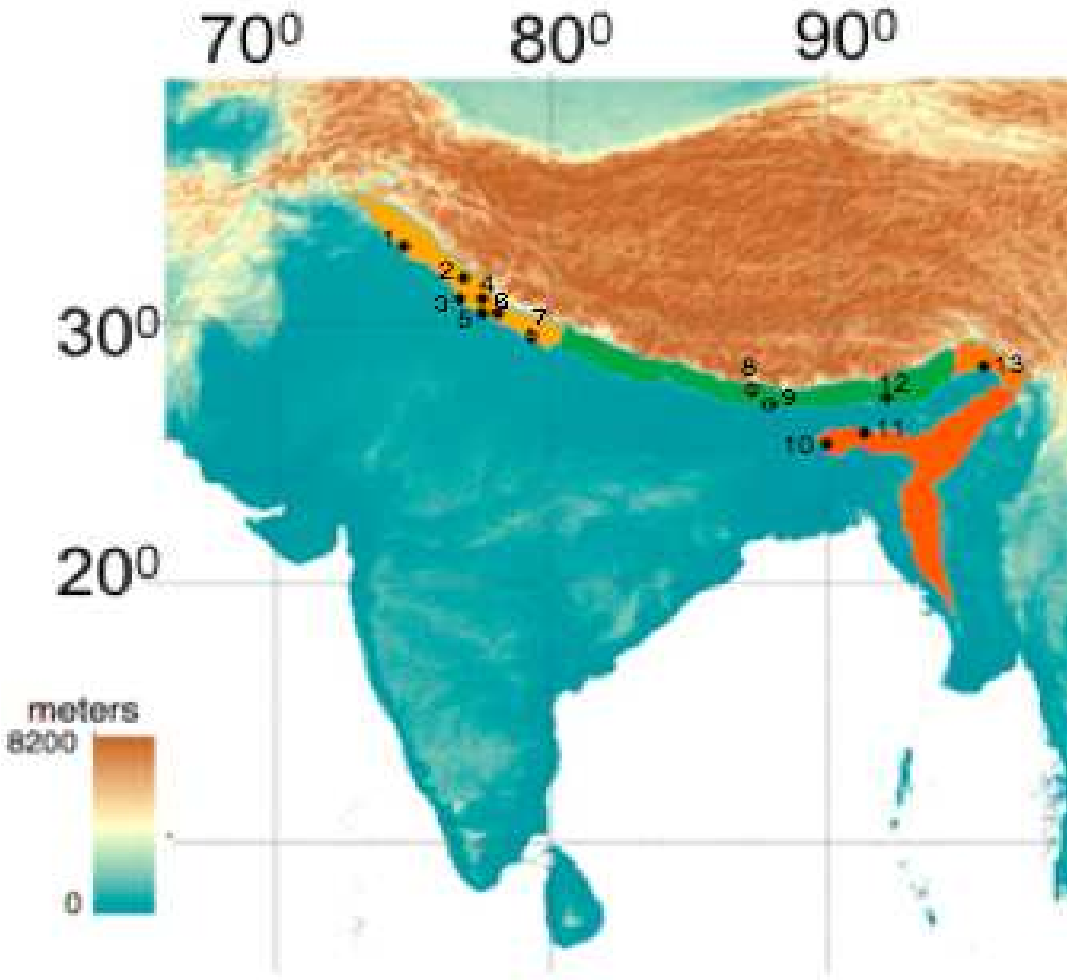

Figure 3.1 Topographical map of India (based on Price et al. 2011) indicating locations of study and approximate distributions of the 4 subspecies of *P. xanthoschistos* (see Table 3.1)**.** Site codes, 1: Jammu, 2: Shimla-Nahan, 3: Banjar-Jalori, 4: Chakrata, 5: Mussoorie, 6: Dhanaulti, 7: Nainital, 8: Yuksom-Tsoka, 9: Samsing, 10: Nokrek, 11: Shillong, 12: Eaglenest and 13: Mehao. Colour codes, light orange: *albosuperciliaris*, green: *nominate*, orange: *flavogularis* and red: *tephrodiras*

3.2.1 Birdsong recording

Birdsong recording methodology is given in Chapter 2. I attempted to record long songs up to 10 minutes and longer as *P. xanthoschistos* sings with eventual variety, and therefore needs longer recordings to capture repertoire size. Table 3.1 gives number of recordings, used in analysis, for different study sites.

Besides birdsongs, ambient noise was recorded at two sites, one in the west – Chail sanctuary and nearby areas in Himachal Pradesh, and the other in the east - Eaglenest sanctuary in Arunachal Pradesh, in 2011 breeding season. To make ambient noises comparable same recorder and microphone with same settings, as given below, were used.

Ambient noise recording: Ambient noise was recorded using Sony PCM-D50 recorder and Sennheiser me 66 shotgun directional microphone fitted with wind protection foam, suspension and handle. Limiter and microphone attenuation switches of the recorder were set to off position, and manual recording level was fixed at mark 6. The microphone was connected to the recorder and was held parallel to ground on vertically stretched right hand while recording. Four recordings of about 15 seconds duration were made in four horizontal directions at each point. Ambient noise was recorded at 10 points in Eaglenest sanctuary in Arunachal Pradeh and at another 10 points in Chail sanctuary and nearby areas in Himachal Pradesh.

3.2.2 Playback Experiments

Playback experiments were carried out to test the significance of geographical variation in *P. xanthoschistos* songs. I also investigated inter-specific playback responses among congeners (see Chapter 5). Methodology used for playback experiments is given in Chapter 2. To avoid pseudo-replication, as many different recordings as possible were used; both for experiment and control (see Table 3.2).

3.2.3 Analysis

3.2.3.1 Definitions of terms used: I have defined general vocalization terminology in Chapter 2 (also see Figure 2.2). However, terminology relating to certain peculiar aspects of *P. xanthoschistos* vocalization is defined here.

Table 3.2 Playback experiment summery: Details of intra-specific playback experiments among *P. xanthoschistos* populations (A) and inter-specific playback experiments among altitudinally replacing *Phylloscopus* species (B).

A: Intra-specific playbacks				
Site	**Playback experiments**	**Experiment recordings**	**Control experiments**	**Control recordings**
Chakrata	7	6	6	4
Dhanaulti	2	2	1	1
Nokrek	9	9	9	5
Patnitop-Ramban	6	6	2	2
Mussoorie	4	3	3	3
Nainital	9	8	5	5
Himachal	5	5	1	1
Shillong	1	1	1	1
Eaglenest	2	2	1	1
Total	45	42	29	23
B: Inter-species playbacks*				
Species pairs	**Playback experiments**	**Experiment recordings**	**Control experiments**	**Control recordings**
Px - Pr	12	9	10	6
Px -Pc	5	5	5	4
Pr -Px	6	6	6	6
Po -Px	4	2	4	3
Pc -Px	5	3	5	4
Total	32	25	30	23

* Song of first species played to the second species separated by dash. Abbreviations, *Px: P. xanthoschistos, Pr: P.reguloides, Pc: P. cantator, Po: P. occipitalis*

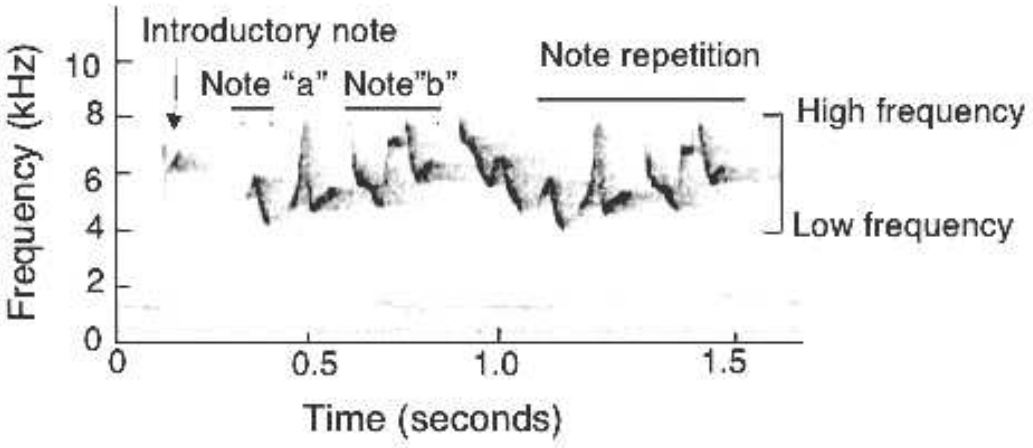

Figure 3.2 Spectrogram of a typical *Phylloscopus xanthoschistos* song (from Samsing) showing some of the terms used (see definition of terms used).

Note: continuous trace of a bird vocalization on frequency time axis, or where time interval between continuous traces is less than 0.02 seconds. Generally the notes were continuous and separated (see note "a" in fig 3.2). However, some tracings involved abrupt frequency shifts, which were instantaneous or separated by few ms (see note "b" in fig 3.2). In the latter cases I classified tracings separated by less than 0.02 second as part of the same note. The frequency shifts in short intervals could possibly be due to sound production switching from one syrinx to another without involving mini-breaths (Hartley and Suthers 1989, 1990, Suthers et al. 2004, Suthers and Zollinger 2004). On the other hand, mini-breaths seem to require more than 0.02 seconds observed, and separate notes. Figure 3.3 shows how intervals separate into three classes, which define notes and introductory notes (see below).

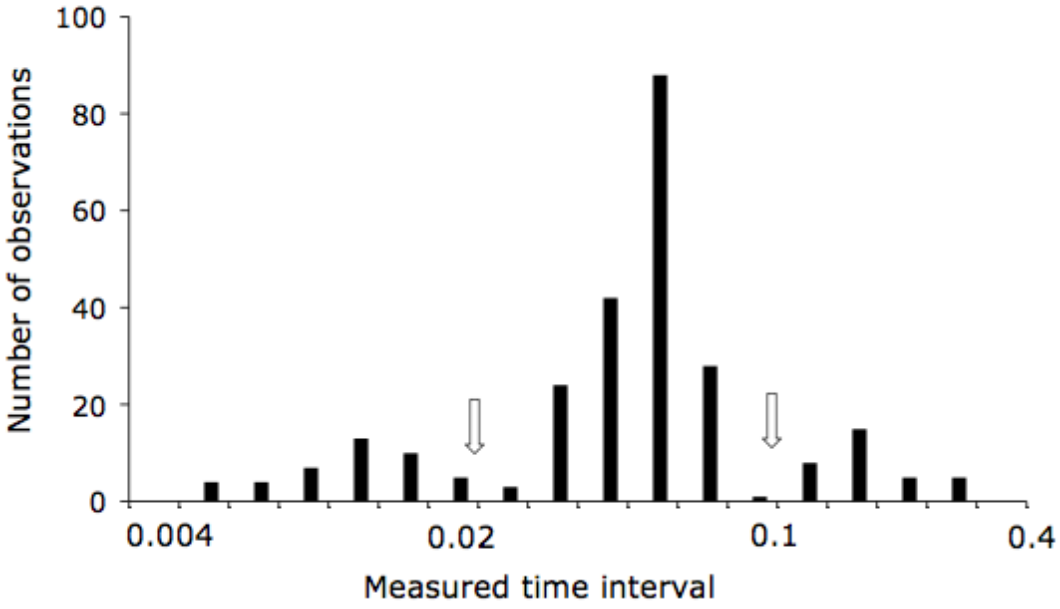

Figure 3.3 Frequency distribution of time intervals (log transformed) within a song for 32 different song types from *P. xanthoschistos* (8 from each of the subspecies) combined. Time intervals fall into three groups. Right: intervals separating and thereby defining introductory notes (>0.1 second). Left: intervals considered to be part of the same note (<0.02 second). In the center intervals are between song notes.

3.2.3.2 Selection of recordings for analysis: For song analysis, recordings with minimal background noise were selected. Some recordings included two males, as identified based on song intervals, and I did not use these for "whole song" analysis. I preferably used long recordings to compare whole song variation (e.g. in number of song types sung) between populations, but used both long and short recordings to characterize song parameters such as frequency.

3.2.3.3 Identification of song types: Spectrograms of *P. xanthoschistos* song were made using Raven Pro 1.3 software. Default settings (Hann, 512 samples, 3 dB Filter Bandwidth 124 Hz, 50% overlap, 86.1 Hz) were used. Songs were visually matched on Raven Spectrogram window for labeling them as different song types. Several studies (Nowicki and Nelson 1990; Baker and Boylan 1995) including one on *Phylloscopus trochiloides* (Irwin 2000) have found perfect agreement between quantitative measurements of song types and visual classifications. I compared song types across all birds at a site. No song types are shared between sites.

3.2.3.4 Whole song parameter analysis: Repertoire size, song rate, song repetition rate, and song sharing for selected populations were estimated.

1. Song repertoire estimation: Botero et al. (2008) have reviewed the three methods, simple enumeration, curve fitting and capture–recapture, used for estimating repertoire size and they found that presentation style of vocalization is very important consideration when attempting to estimate repertoire size. As noted, *P. xanthoschistos* sings its song types with eventual variety, i.e. it generally sings with whole series of one song type and then switches to another song type and so on. As has been observed in the case of the Chaffinch (*Fringilla coelebs*) (Catchpole and Slater 2008) one sequence of song types i.e. aaaaaabbbbccccccddddddddeeeee……is often followed by the same sequence of song types in the same order. But in *P. xanthoschistos*, in minor variation, rarely the last song of a serial is preceded by first song type of the next serial i.e. aaaaaababbbbb…… pattern, instead of aaaaaaabbbbbb…... occurs.

A bird will repeat one song type from 2.2 to 10.8 times (mean 4.8, N=157) before switching to the next, and thus a whole sequence of song type serials will follow, and after a complete run of song types sequence, new sequence with song type serials in the same order will follow. For example if a, b, c, d, e, and f are song types in a bird's song repertoire, two runs will be aaaabbbbccccccddddeeeeffffffaaabbbbbbbbccccccddddddeeeeffff. Hence number of song types in a complete sequence before repetition begins, can give good estimate of repertoire size e.g. 6 in the preceding example. However, there are a few exceptions. In 68 birds which had at least one complete run of serials and at least one serial repeated, there were 643 combined song types in first run, or an average of 9.59 song types per bird. 445 serials after the first run (including 1 with 4 runs, 1 with 3 runs, 16 with 2 runs and the rest 50 with 1 run completed) added 11 new song types (contributed by only six birds - 5, 2, 1, 1, 1 and 1 new song types) or 0.02 song types per serial on average. This suggests that including only first run sequences underestimate population averages by a trivial amount. Hence repertoire size can be reasonably estimated by number of song types in first run, which will not be appreciable under estimation.

Figure 3.4 shows a plot of number of song types versus number of songs examined for all whole songs in which the first (or upto third subsequent) song type is repeated (N = 68). Conventionally the complete repertoire is considered to have been obtained when saturation has been reached i.e. when recording more songs adds no more song types which in Figure 3.4 is only reached at approximately 75 songs. Hence the analysis above suggests less than one song type per bird is missed. The figure shows all whole songs in which the first song type (or rarely upto third subsequent) was repeated at a later stage in the song. This means that the whole songs with short intervals between recurrences of the first song type are included even when they had relatively few songs recorded in total and part of the appearance of low saturation reflects this bias in the data collection.

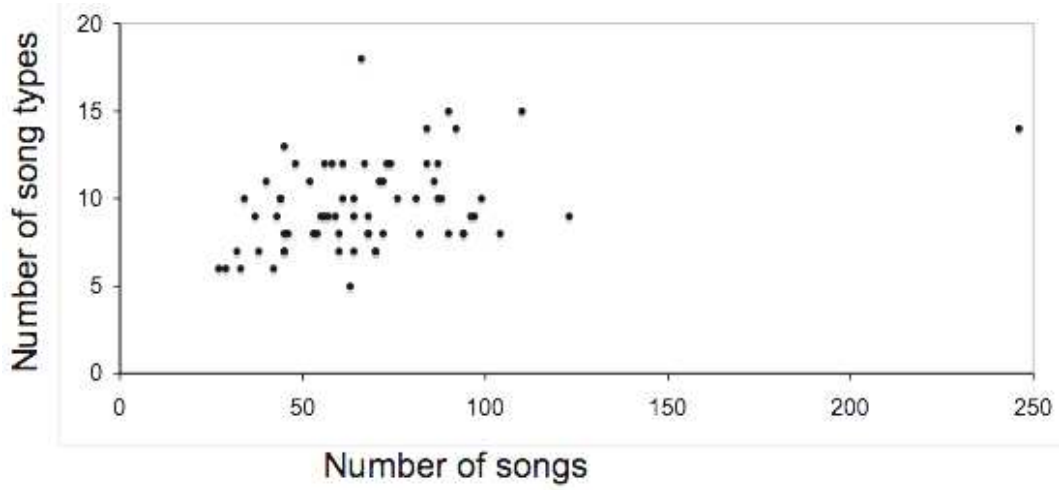

Figure 3.4 Number of distinct song types encountered against number of songs recorded for an individual, for all sites combined. Only songs that had the first (or up to third subsequent) song type repeated are included.

An average of 68.91 songs were studied per individual for repertoire estimation (range 27-246 songs, N=68 individuals). Across sites the number of songs used for repertoire estimation per individual studied did not vary ($F_{11,56} = 0.81$, $P = 0.63$).

2. Song rate: Song rate was calculated for long selected whole songs, within which longest song serials without more than 10 sec inter song intervals were selected. If such a song serial has n song types rendered in dt time, measured from beginning of 1st song type to the beginning of n+1 the song, the song rate will be n/dt.
3. Song repetition rate: Total number of songs in five complete serials of song types, assuming the first serial to be incomplete, were counted and divided by five to estimate song repetition rate for a particular whole song. For example aaabbbbccccddddeeeffffgg sequence has five complete song type serials having 18 songs, and hence song repetition rate is 18/5 = 3.6.
4. Song type sharing: For estimates of song type sharing, birds with 6 or more song types recorded were included to get good sample size. Sharing is over only short geographical scales (see results) and only 3 sites were studied where sufficient individuals were recorded in a local neighborhood (along a road). The average number of song types recorded

from birds used in this analysis was similar in each location (Table 3.1). Song sharing was plotted against altitudinal separation, and the pattern compared across locations (Figure 3.5).

3.2.3.5 Song type parameter measurements: I measured (a) minimum frequency, (b) maximum frequency, (c) bandwidth, (d) central frequency and (e) song length, and recorded number of total and distinct notes from the song spectrograms. All the above measurements were made on Raven Pro 1.3 spectrogram (Hann window, 512 samples, 3 dB Filter Bandwidth 124 Hz, 5.80 ms time resolution, frequency grid spacing 86.1 Hz) window enclosing the spectrogram by cursors, and using brightness and contrast settings for placing the cursors. Zollinger et al. (2012) addressed the potential errors associated with frequency measurements by visual inspection because frequency cut offs, particularly sweeps, can not be exactly determined because of smudge of frequency band. I used clear recordings and biases, if any, are constant across all song spectrograms analyzed. For each site I measured more than 24 song types (but only one song per song type) from each of the sites except Shillong, where 22 song types were measured. Generally two song types were selected from one individual. In a few cases sufficient recordings were not available, and more than two songs were measured from the individual recording. I measured frequency-time parameters using Raven Pro 1.3 default settings, and counted visually syntax parameters, i.e. number of total and distinct notes.

3.2.3.6 Introductory notes: Although I found no song type sharing between populations (even those such as Sesni and Lama in Eaglenest that were only a few kilometers from each other), I noticed that introductory notes do not vary as much with distance, and there was introductory note sharing among various populations. All the introductory notes were labeled for each site, and they were visually matched for sharing among sites. I used shape of the note spectrogram as the main criterion used for comparison, and small frequency shifts were not considered. I also found that some notes that were introductory in some songs mostly from the southeast appeared as the second note after an original

introductory first note in other songs from the northwest. Populations were compared for this feature of the song.

*3.2.3.7 Analysis of ambient noise***:** Ambient recordings were analyzed using Raven Pro 1.3 software. Ambient recordings of 10 second duration, upto 12 Khz in frequency, were used for finding average power in the ambient noise. There were 4 such recordings used for each point, pertaining to four directions. Thus 40 measurements of average ambient power for 10 points in the southeast and northwest were made.

3.2.3.8 Statistical Analysis: I transferred all the data to spreadsheet, Microsoft Excel, and then analyzed using JMP (SAS Institute 2000. JMP 4.0. Cary, North Carolina: SAS Institute). Analysis involved summary statistics, F test, regression analysis, principal component analysis (PCA), and non-parametric Mantel's and Kruskal - Wallis tests. Non-parametric tests were done where normality of data was questionable. P values are shown upto two decimal places and I have generally chosen significance level at $P \leq 0.01$ for the analysis to be more conservative and aso because often multiple parameter tests are involved.

3.3 Results

Here I first describe aspects of the whole song and geographical variation of its parameters. This is followed by description of song types, their classification and variation with latitude, longitude and altitude. Introductory notes are described in the last section.

3.3.1 Whole song

3.3.1.1 Song repertoire: P. xanthoschistos sings with singing style approximating eventual variety with repetition of song type serials in cyclic pattern which pertains to standard cluster types, eventual variety of Botero et al. (2008) with cyclic pattern of appearing of clusters.

Table 3.3 Whole song parameters of *P. xanthoschistos.* Repertoire size does not vary significantly among sites, but song rate and song repetition do. Mean repertoire size varies from 8 to 12 song types. None of these whole song parameter means show latitudinal and longitudinal variation. There is no altitudinal trend of these parameters for the combined data.

Site	Repertoire size (mean ± s.e.)	Song rate (mean ± s.e.)	Song repetition rate (mean ± s.e.)
Patnitop-Ramban	9.75±0.88	10.78 ± 0.64	5.40 ± 0.36
Banjar-Jalori	-	11.52 ± 1.08	5.27 ± 0.91
Shimla-Nahan	12.00	13.63 ± 0.6	4.46 ± 0.34
Chakrata	11.00±1.00	10.98 ± 0.68	4.28 ± 0.28
Mussoorie	8.00±0.00	10.20 ± 0.77	6.83 ± 0.87
Dhanaulti	9.33±1.33	11.78 ± 0.45	4.13 ± 0.25
Nainital	9.13±0.95	10.62 ± 0.44	5.09 ± 0.34
Mehao	10.60±1.33	12.04 (0.64)	4.02 (0.24)
Yuksom-Tsoka	8.33±0.65	10.34 ± 0.38	5.03 ± 0.32
Eaglenest	9.69±0.63	11.9 ± 0.49	4.38 ± 0.20
Samsing	10.43±0.69	11.33 ± 0.55	5.07 ± 0.30
Shillong	10.25±2.63	11.16 ± 0.46	3.73 ± 0.26
Nokrek	9.50±1.23	11.08 ± 0.33	4.74 ± 0.42
F statistic	$F_{11,56}$ = 0.57, P=0.84	$F_{12,144}$ = 1.85, P=0.05	$F_{12,144}$ = 2.94, P=0.001
Kruskal Wallis test	$\chi 2$ = 8.84, d.f. =11, P = 0.64	$\chi 2$ = 21.50, d.f.=12, P=0.04	$\chi 2$ = 25.02, d.f.=12, P = 0.01
Regression of site means with latitude	R^2= 0.01	R^2= 0.13	R^2= 0.01
	P= 0.72 , N=12	P= 0.23, N=13	P= 0.70, N=13
Regression of site means with longitude	R^2=0.0002	R^2=0.21	R^2=0.002
	P= 0.96, N=12	P= 0.12, N=13	P= 0.87, N=13
Regression of pooled data with altitude	R^2=0.0076	R^2=0.01	R^2=0.00
	P=0.49, N=65	P=0.17, N=148	P=0.99, N=148

Note: For sample sizes by site and for site coordinates see Table 3.1. The sites are given in the order of decreasing latitude. Numbers of sites for pooled data are 12, 13 and 13 for repertoire size, song rate and song repetition rate respectively.

For individual birds repertoire size ranges from 5 to 18 and across sites, the number of mean number of song types per individual varied from 8 to 12, the mean repertoire for the combined data being 9.81 (sd = 2.98, N = 68). Repertoire sizes for individual sites are given in the Table 3.3. Repertoire size variation among sites is not statistically significant (P > 0.5, both for F test and Kruskal-

Wallis test). There is no significant geographical variation of mean repertoire size (Table 3.3).

3.3.1.2 Song rate: Individual song rate of *P. xanthoschistos* varied from 7.4 to 17.4 songs per minute. The mean song rate across sites ranged from 10.34 to 13.63 songs per minute with combined population mean of 11.25 songs (s.d. = 2.09, N = 157) and it differed significantly among sites (see Table 3.3). But no significant clinal variation of site mean was detected (Table 3.3).

3.3.1.3 Song repetition in whole song: Song repetition for individual whole songs ranges from 3 to 8.6 songs per song type, if we exclude one bird at Mussoorie with 10.8 repetitions. Site mean of song repetition varied significantly across sites from 3.73 to 6.83 songs per song type (see Table 3.3) with mean value of 4.82 (s.d. = 1.42, N = 157) for all populations combined. Song repetition does not show significant variation with latitude and longitude, when site means were regressed separately with each of them. Song repetition shows negative correlation with repertoire size but the correlation is not strong ($R^2 = 0.05$, $P < 0.05$).

All the above three whole song parameters did not show any altitudinal trend when combined data was regressed with altitude. Also for individual sites these parameters do not show significant altitudinal trend, except that at Nokrek, song repetition decreases with altitude ($R^2 = 0.48$, $P < 0.01$, N = 13), which deserves further study.

3.3.1.4 Song-type sharing: Song-type sharing among neighbours and nearby individuals is common, but many individuals, even neighbours do not share any songs. The sharing is confined to a distance extending few kilometers only, and it decreases with distance between individuals (see Figure 3.5). I did not come across any song-type sharing among populations studied at different sites. Even birds separated by more than 5 kilometres in Himachal Pradesh, along the Shimla-Nahan road, were found not sharing song types.

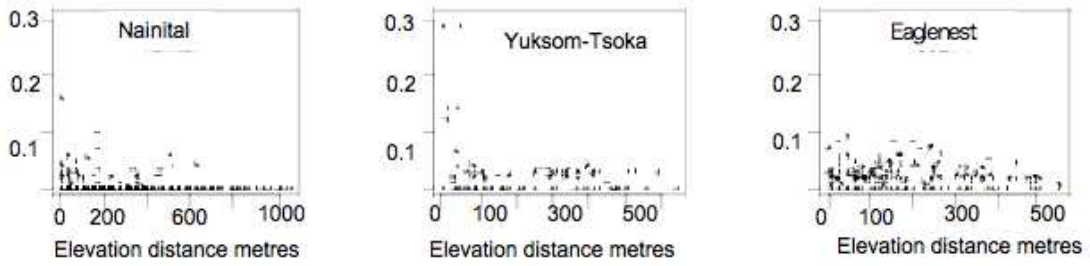

Figure 3.5 Proportion of song types shared as a function of altitudinal separation. Statistics are: Eaglenest (east), R = -0.13, N = 19, P = 0.18 (by Mantel test); Yuksom-Tsoka (east), R = -0.27, N =14, P = 0.04; Nainital (west), R = -0.2, N = 24, P = 0.0009.

3.3.2 Song syntax and song parameters

3.3.2.1 Syntax of P. xanthoschistos *song types: P. xanthoschistos* song types generally consist of an introductory note, separated from the rest of the song by an inter-note interval, which is larger than the other inter-note intervals (Figure 3.3). Introductory note in *P. xanthoschistos* is quite variable unlike in *P. reguloides*, and even in a whole song different song types may have different introductory notes. In some songs (e.g. from Yuksom-Tsoka) the first note of the rest of the song is identical to the introductory note (Figure 3.6, panels "m"). In northwestern populations, the song after introductory note may start with an introductory note of southeastern populations (Figure 3.6, panel "n"). Further details of introductory notes have been dealt separately below.

As noted in the introduction, Päckert et al. (2004) recognized five syntax types from one subspecies in Nepal. The present study covered all four subspecies across a wide geographical range, with correspondingly greater variety. Accordingly, I propose the following categorization of songs (excluding the introductory note).

(i) Regular note repetition (abcabc.., abcdab...,etc*):* 2-6 distinct notes followed by repetition of the one or more notes in the same sequence. Generally if the number of distinct notes is between 2 and 4, the whole sequence is repeated 1-2 times. If the number of distinct notes in the song is more than 4, then only the first or the first few notes in the sequence are repeated.

(ii) No note repetition: When distinct notes number from 5-7, usually no notes are repeated. This is generally the case in the western populations.

(iii) Irregular note repetition: In this type of repetition one or more notes do not follow pattern mentioned under first type. There may be patterns such as abcbc, abcdecde, abcdebf, abcdabe, abacda, abcdae and abcdaefg (see Fig 3.6). In addition, patterns may end with a unique note repeated twice as pointed out by Päckert et al. (2004) e.g. abcc and abacc. One song type with abccc pattern was also recorded in Nainital area.

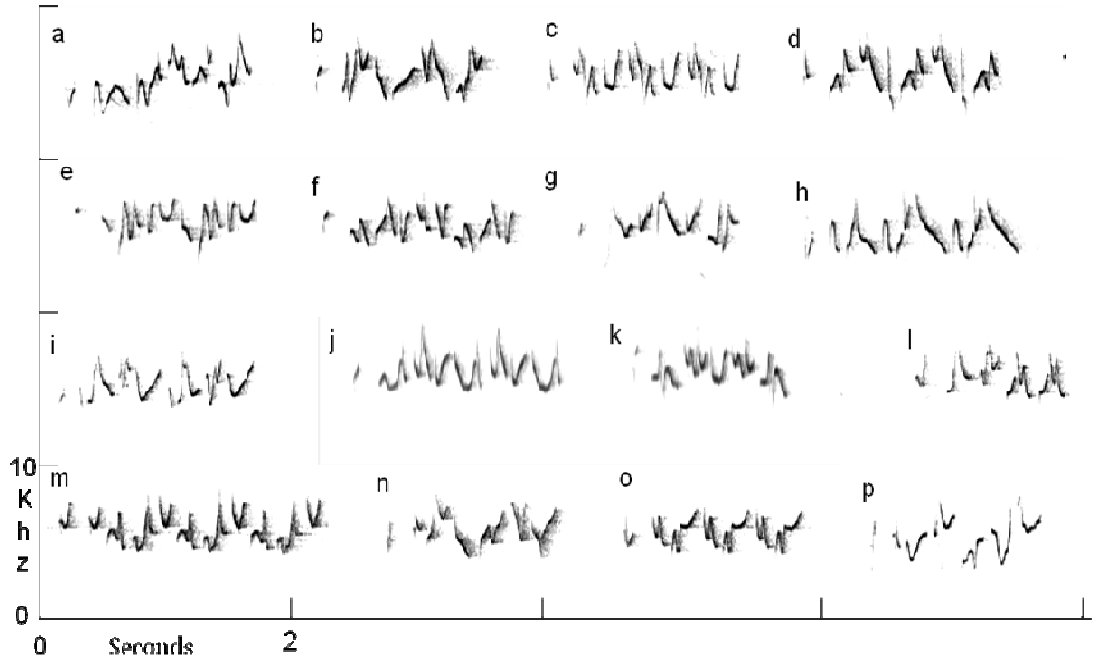

Figure 3.6 Spectrograms from *Phylloscopus xanthoschistos* indicating the range of variation. (a and b) No note repetition (a) Himachal, west and (b) Arunachal, southeast. (c) Two note repetition (Arunachal, southeast) (d) Three note repetition (Arunachal, southeast). (e) Four note repetition (Arunachal, southeast). (f) Five note repetition (Arunachal, southeast). (g-l) Unusual motifs of note repetition: *abcbd* (Jammu, northwest) (h) *abacdacd* (Arunachal, southeast) (i) *abcdaefd* (Meghalaya, southeast) (j) *abcdbcd* (Arunachal, southeast) (k) *abcba* (Arunachal, southeast) (l) *abcdd* (Uttarakhand). (m) Song illustrating introductory repeated as the second note (Yuksom-Tsoka, southeast): this pattern was only commonly observed in Yuksom-Tsoka and Chakrata in Uttarakhand. (n) Song where second note is identical to an introductory note in the southeast (Patnitop-Ramban, west). (o,p) a typical eastern (Eaglenest, Arunachal) and northwestern (Shimla-Nahan, Himachal) song placed together to illustrate the greater complexity in syntax and bandwidth of northwestern songs.

Most of the songs belong to first two types, and third type songs are rare. First type songs are predominantly in the southeast and very rare in the extreme northwest, whereas second type songs occur as a rule in the west, with rare exceptions. Third type songs may be found with very few numbers in both east and west, and could possibly be subsongs rendered by juveniles. Table 3.4 also shows a difference in populations in the number of repeated notes in the song.

Table 3.4 Song syntax differences across sites (see also Figure 3.6). See Table 3.1 for site coordinates. Northwestern (northern) populations (first seven) rarely repeat notes in song, whereas southeastern populations (last six) have high note repetition in song. Northwestern populations have very high proportion of different introductory notes (from southeast) running into their songs (i.e. making first note of a song after an introductory note), whereas in the southeast it is rare except at Nokrek. Some populations, particularly Yuksom-Tsoka and Samsing populations in the southeast and Chakrata population in northwest, have same introductory note repeating and running into song (see "m" in Figure 3.6).

Site	Song types analyzed	Note repetition in song (%) of song types			Introductory notes in song	
		None	Regular	Irregular	% same introductory note repeated	% different introductory note in song
Patnitop-Ramban	161	96	0	4	0	35
Banjar-Jalori	77	90	0	10	0	51
Shimla-Nahan	215	95	1	4	0	65
Chakrata	94	90	2	7	14	37
Mussoorie	89	96	0	4	0	30
Dhanaulti	108	96	1	3	1	22
Nainital	229	93	3	3	0	19
Mehao	59	37	43	20	2	0
Yuksom-Tsoka	111	63	32	5	50	5
Eaglenest	231	16	67	17	0	9
Samsing	108	19	62	19	22	7
Shillong	52	6	92	2	0	7
Nokrek	106	3	92	5	0	31

An important aspect of *P. xanthoschistos* song is its variable introductory note, which is described next.

3.3.2.2 Introductory notes in P. xanthoschistos *song:* As stated above *P. xanthoschistos* song has a number of different introductory notes, which vary in shape and frequency (see Fig. 3.7 below).

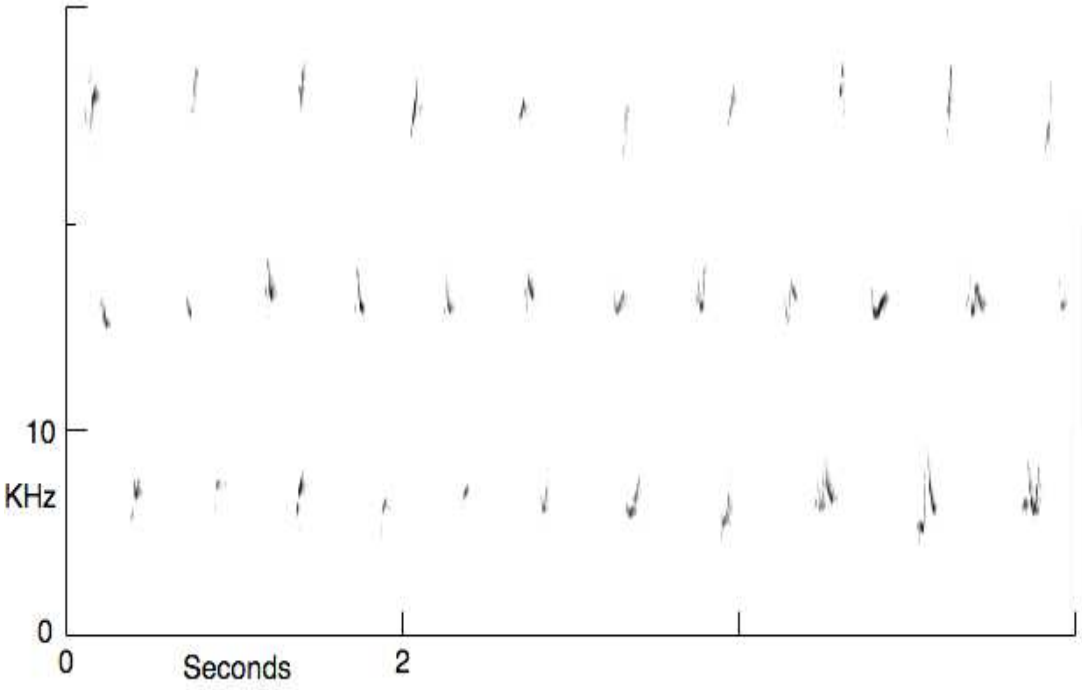

Figure 3.7 Representative introductory notes. *Upper row:* Shimla-Nahan (northwest). *Middle and lower rows*: Yuksom Tsoka and Eaglenest (southeast).

Unlike song types which are not shared over a few kilometers, introductory notes are shared even among populations several hundred kilometers away. But the sharing is not always more among the populations close to each other. For example, some introductory notes are shared among Mehao, Meghalaya, Himachal and Jammu populations (i.e., up to 2000 km apart) whereas some populations not very far apart share very few notes, for example Chakrata and Himachal populations (see Table 3.5).

Notes of the same form as introductory notes are found in the rest of the song. This happens in two ways i.e. when first note in the rest of the song is the same as the preceding introductory note or the first song note is different introductory

note usually from other populations (see Figure 3.6, spectrograph "m" and "n"). The former is common in Samsing and Yuksom-Tsoka whereas later is prevalent in western populations making as high as 65% of all song types at Shimla-Nahan in Himachal Pradesh (see Table 3.4)

Table 3.5 Introductory note sharing among different populations of *P. xanthoschistos*. Numbers within parentheses indicate number of introductory notes in different populations. Values along and up of leading diagonal show fraction *2xcommon notes/sum of notes in two populations*, where as numbers below diagonal are actual number of notes shared. Light green shading is for sharing index less than 0.2, and light blue shading is for greater than 0.4 sharing index.

	Mehao (8)	Eaglenest (14)	Shillong (4)	Nokrek (5)	Samsing (12)	Yuksom-Tsoka (16)	Nainital (13)	Dhanaulti (12)	Mussoorie (10)	Chakrata (17)	Shimla-Nahan (13)	Patnitop-Ramban (16)
Mehao (8)	1	0.09	0.33	0.31	0.2	0.08	0.19	0.1	0.22	0.08	0.48	0.5
Eaglenest (14)	1	1	0.11	0	0.54	0.46	0.59	0.46	0.42	0.52	0	0.07
Shillong (4)	2	1	1	0.22	0.4	0.3	0.35	0.13	0.14	0.19	0.12	0.1
Nokrek (5)	2	0	1	1	0	0	0.11	0	0	0	0.22	0.29
Samsing (12)	2	7	3	0	1	0.57	0.56	0.33	0.45	0.48	0	0.07
Yuksom-Tsoka (16)	1	8	3	0	8	1	0.62	0.36	0.38	0.54	0	0
Nainital (13)	2	8	3	1	6	9	1	0.4	0.23	0.41	0.08	0.14
Dhanaulti(12)	1	7	1	0	4	5	5	1	0.55	0.48	0	0.07
Mussoorie (10)	2	5	1	0	5	6	3	6	1	0.52	0	0.08
Chakrata (17)	1	8	2	0	7	10	6	7	7	1	0	0
Shimla-Nahan (13)	**5**	0	1	**4**	0	0	1	0	0	0	1	0.69
Patnitop-Ramban (16)	**6**	1	1	**3**	1	0	2	1	1	0	11	1

3.3.2.3 Frequency and time parameters: *P. xanthoschistos* sings across sites within minimum frequency ranging (mean ± s.e.) 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 second (see Table 3.7). The central frequency which divides song energy into equal halves ranges from 5603 ± 53 to 6019 ± 38 Hz across sites.

The principal component analysis (PCA) shows that the first four principal components (PCs) of the frequency and time parameters explain 88% of total variation (Table 3.6). Correlations of the PCs with original song parameters are shown in Table 3.6. PC1 positively correlates with bandwidth (this captures positive and negative correlations with maximum and minimum frequency respectively) and distinct notes in the song, and is negatively correlated with song length and total notes. That implies that songs with high PC1 score are shorter, but have wide frequency span, and high number of distinct notes, and are therefore more complex. High bandwidth and high number of distinct notes represent more information content in the song, and hence are good measures of song complexity (Irwin 2000; Irwin et al. 2008).

Table 3.6 Principal component correlations with original parameters of *P. xanthoschistos* song and variance explained by each component.

	PC1	**PC2**	**PC3**	**PC4**
Minimum frequency	**-0.76**	-0.13	0.53	0.06
Maximum frequency	0.54	0.43	0.51	-0.29
Central frequency	0.10	0.12	**0.84**	0.05
Bandwidth	**0.91**	0.34	-0.12	-0.21
Song length	-0.46	**0.79**	-0.20	-0.13
Total notes	-0.50	**0.79**	-0.08	0.15
Distinct notes	0.48	0.22	0.05	**0.84**
% Variance explained	34	23	19	12
Note: Boldface indicates correlation >0.7				

PC2 is positively correlated with song length and total notes, i.e. birds with high PC2 scores sing longer songs. PC3 is positively correlated with central frequency, maximum frequency and minimum frequency. Birds with high PC3 scores sing with higher minimum and maximum frequencies, reflecting upward frequency

shift of song bandwidth. PC4 is strongly correlated with the number of distinct notes in the song. Songs with high PC4 score have more distinct notes but unlike birds with high PC1 scores (which also sing with more distinct notes) do not sing at high maximum frequency and with wide bandwidth.

Table 3.7 Frequency-time parameters and number of notes for different sites. Mean values are given with standard errors (see Table 3.1 for sample sizes). F statistics and Kruskal-Wallis test (χ^2 values given in the bottom rows show significant differences among sites for all measurements). Superscripts indicate P values, and *** means P<0.0001. See Table 3.1 for site coordinates.

Site	Minimum Freq. Hz	Maximum Freq. Hz	Central Freq. Hz	Bandwidth, Hz	Length, seconds	Total notes	Distinct notes
Patnitop-Ramban	2834 ± 88	8925 ± 66	5849 ± 44	6091 ± 128	1.29 ± 0.03	6.43 ± 0.18	6.31 ± 0.19
Banjar-Jalori	3044 ± 68	9181 ± 66	5940 ± 63	6137 ± 101	1.29 ± 0.03	6.66 ± 0.17	6.63 ± 0.17
Shimla-Nahan	3180 ± 93	9017 ± 79	5952 ± 62	5837 ± 119	1.19 ± 0.03	6.56 ± 0.16	6.39 ± 0.15
Chakrata	2514 ± 73	8938 ± 69	5842 ± 48	6424 ± 118	1.33 ± 0.02	6.44 ± 0.13	6.35 ± 0.15
Mussoorie	2632 ± 91	8945 ± 71	5861 ± 68	6313 ± 116	1.37 ± 0.03	6.33 ± 0.16	6.29 ± 0.18
Dhanaulti	2666 ± 88	8971 ± 84	5716 ± 49	6306 ± 121	1.3 ± 0.02	6.07 ± 0.13	6.07 ± 0.13
Nainital	2494 ± 66	8914 ± 61	5799 ± 42	6420 ± 94	1.28 ± 0.02	6.24 ± 0.12	6.13 ± 0.11
Mehao	3073 ± 111	8855 ± 70	5712 ± 63	5782 ± 132	1.27 ± 0.03	6.57 ± 0.17	5.71 ± 0.22
Yuksom-Tsoka	3126 ± 91	9196 ± 71	6019 ± 38	6070 ± 124	1.34 ± 0.03	6.85 ± 0.20	5.50 ± 0.17
Eaglenest	3323 ± 60	8977 ± 43	5925 ± 27	5654 ± 76	1.41 ± 0.02	6.96 ± 0.14	4.68 ± 0.10
Samsing	3414 ± 88	9003 ± 74	5975 ± 42	5589 ± 117	1.47 ± 0.03	7.43 ± 0.19	5.23 ± 0.20
Shillong	3476 ± 106	8493 ± 103	5732 ± 65	5017 ± 116	1.45 ± 0.05	8.00 ± 0.28	4.45 ± 0.21
Nokrek	3234 ± 73	8800 ± 69	5603 ± 53	5565 ± 94	1.48 ± 0.04	8.38 ± 0.24	4.55 ± 0.13
F (12,508)	15.65***	4.59***	6.32***	11.15***	8.27***	12.48***	24.72***
χ^2, d.f.=12	149.20***	45.69***	68.32***	108.96***	83.17***	103.49***	197.71***
[c]Mean, N=521	3040 ± 27	8957 ± 20	5858 ± 14	5917 ± 34	1.35 ± 0.01	6.86±0.06	5.59 ± 0.05

[c]Mean: Combined mean, when all site data is combined.

3.3.2.4 Song variation with latitude, longitude and altitude: P. xanthoschistos shows significant variation in song syntax and frequency time parameters across sites (see Table 3.7). Part of this variation is due to geographical and altitudinal trend in the song parameters. Regression analysis results of the principal components on latitude, longitude and altitude are given below in Table 3.8.

Table 3.8 Regression of Principal component (PC) site means with latitude and longitude, R^2 and P values shown, N=13.

		Mean (PC1)	**Mean (PC2)**	**Mean (PC3)**	**Mean (PC4)**
Latitude	R^2	**0.71**	0.23	0.01	**0.76**
	P	**<0.001**	0.10	0.71	**0.0001**
Longitude	R^2	**0.58**	0.04	<0.01	**0.57**
	P	**<0.01**	0.52	0.99	**<0.01**

Latitude and longitude are highly correlated for *P. xanthoschistos* study sites (R^2 = 0.77, P < 0.0001) and hence to separate latitudinal effects from longitudinal effects is not possible.

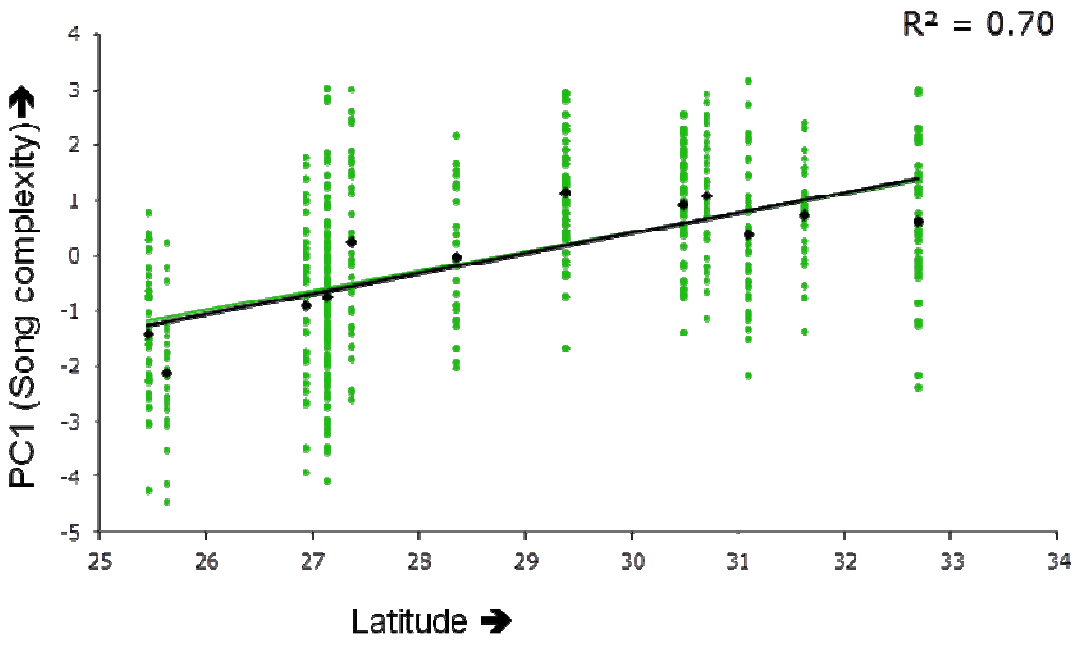

Figure 3.8 Plot of PC1 scores with latitude, with line of regression (green colour), showing song complexity increase in the west. Black points are PC1 site means and black line is regression line of PC1 means with latitude (R^2 = 0.70). PC2 and PC3 do not show latitudinal pattern but mean PC4 has significant correlation with latitude, reflecting use of more distinct notes in the west (Table 3.7).

Latitudinal variation: Site mean of PC1 scores is strongly correlated with latitude, which implies that song complexity increases towards the west (Figure 3.8): birds of the Western Himalayas sing with more distinct notes and a wider bandwidth (see Table 3.7). However, the Yuksom-Tsoka site in Sikkim in the east is an exception where birds sing with wider bandwidth, due to a very high maximum frequency of the birds there.

Mean values of individual song parameters when regressed with latitude and longitude corroborate the above finding: distinct notes, total notes (song length), bandwidth and minimum frequency show significant variation with latitude (see Table 3.9).

Table 3.9 Regression of mean values of song parameters with latitude and longitude (N = 13). R^2 values and significance levels (up to two decimal places) are shown.

		Minimum frequency	**Maximum frequency**	**Bandwidth**	**Song length**	**Central frequency**	**Total notes**	**Distinct notes**
Latitude	R^2	**0.43**	0.20	**0.53**	**0.57**	0.07	**0.66**	**0.88**
	P	**0.01**	0.12	**<0.01**	**<0.01**	0.38	**< 0.001**	**<0.0001**
Longitude	R^2	**0.47**	0.14	**0.52**	0.29	0.05	**0.40**	**0.70**
	P	**<0.01**	0.20	**< 0.01**	0.06	0.45	**0.02**	**<0.001**

Altitudinal variation: The effect of altitude is small but significant on song complexity (see Table 3.10 below), when all site data is combined. Within sites, I have little evidence that songs vary with altitude. However one site, Mussoorie, does appear to show an effect ($R = 0.61$, $P < 0.01$), which is worthy of further study. The altitudinal effect for the combined data could also be because *P. xanthoschistos* occurs higher in the west where birds have more complex songs.

Table 3.10 Result of the PC regression with altitude for the combined sites data. R and P values shown and N = 487. PC1 (song complexity) and PC4 (distinct notes) show significant association, but R values are very low.

		PC1	PC2	PC3	PC4
Altitude	R	0.32	- 0.01	- 0.06	0.10
	P	<0.0001	0.76	0.18	0.03

3.3.2.5 Song variation among subspecies: As expected from the geographical analysis, song parameters and PC scores differ significantly when analyzed at the level of the four subspecies of *P. xanthoschistos* (see Table 3.11). Subspecies *albosuperciliaris* (distributed from Jammu to Uttarakhand) has the most complex songs whereas *tephrodiras* (from Meghalaya) has the least complex (Figure 3.9), but longest songs (see Figure 3.9). The nominate subspecies (from Yuksom-Tsoka) sings with highest maximum frequency, whereas northwestern subspecies *albosuperciliaris* sings with the lowest minimum frequency. A plot of subspecies on PC1 and PC2 axes shows segregation of subspecies (Figure 3.9).

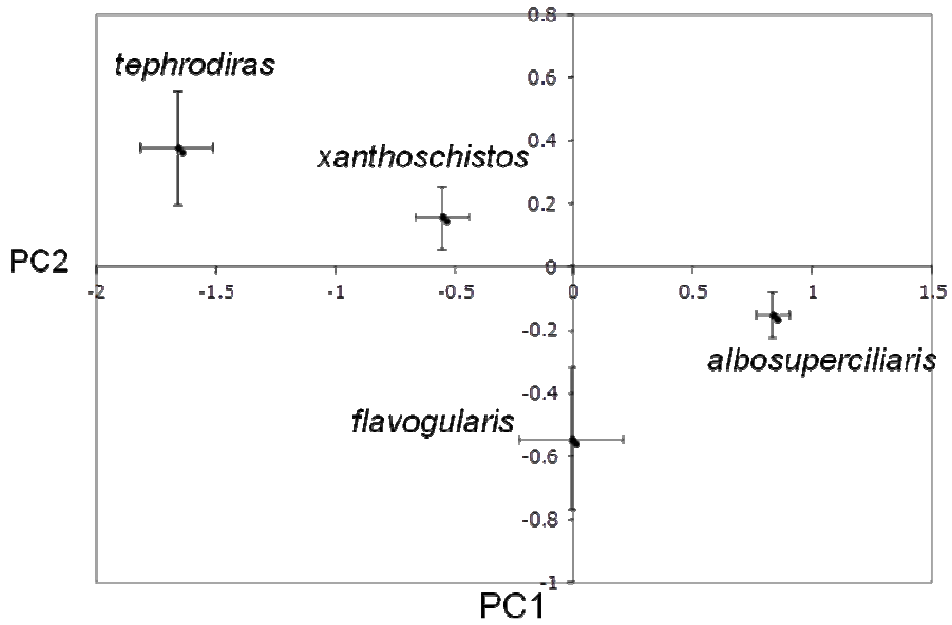

Figure 3.9 Four subspecies of *P. xanthoschistos* separating on PC1 and PC2 axes (means and standard error bars shown). PC1 axis indicates bandwidth and distinct notes, a measure of song complexity whereas PC2 is highly correlated with song length (see Table 3.6).

Table 3.11 Song parameter means (± s.e.) for *P. xanthoschistos* subspecies **(**Note boldfaced extreme values of minimum frequency, bandwidth, song length (total notes) and distinct notes in different subspecies). The sites sampled are Patnitop-Ramban, Banjar-Jalori, Shimla-Nahan, Chakrata, Mussoorie, Dhanaulti and Nainital for *albosuperciliaris*, Yuksom-Tsoka, Samsing and Eaglenest for nominate, Mehao for *flavogularis*, and Nokrek and Shillong for *tephrodiras* (see Table 3.1 and Table 3.7) All these parameters separate subspecies (P values <0.0001 for all parameters, by both an F-test and Kruskal Wallis test)

***P. xanthoschistos* Subspecies**	**N**	**Min. freq.**	**Max. freq.**	**Band-width**	**Song length**	**Cent. Freq.**	**Tot. note**	**Dist. note**
albosuperciliaris	248	**2772±35**	8977±27	**6205±45**	1.29±0.01	5853±20	6.4±0.1	6.3±0.1
xanthoschistos	184	3300±44	9030±33	5731±58	1.41±0.02	5956±20	7.0±0.1	5.0±0.1
flavogularis	28	3073±111	8855±70	5782±132	1.27±0.03	5712±63	6.6±0.2	5.7±0.2
tephrodiras	61	3332±61	8699±60	5367±81	**1.47±0.03**	5649±42	**8.3±0.2**	**4.5±0.1**

3.3.3 Song recognition

P. xanthoschistos individuals recognize songs of individuals of other populations of the species. Song recognition is also common among individuals of different subspecies. But, response to inter-specific playbacks between *P. xanthoschistos* and its three altitudinal replacements -*P. cantator*, *P. occipitalis* and *P. reguloides* was not detected or it was comparatively poor (Fig 3.10).

3.3.4 Ambient Noise

Ambient noise was found to be higher in the east, being 50±2 and 47±3 dB for Eaglenest in Arunachal Pradesh and Chail in Himachal Pradesh respectively.

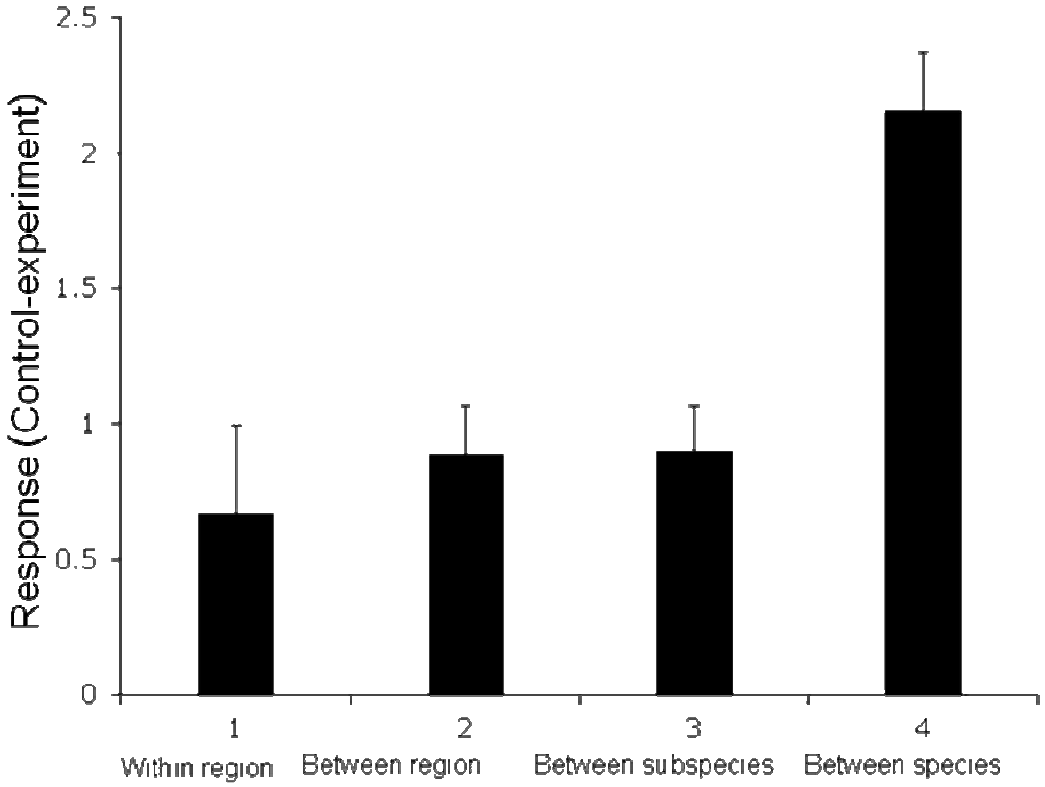

Figure 3.10 Playback responses within species- within region (0.67 ± 0.33, N = 6), between regions- southeast and northwest (0.89 ± 0.18, N =39), between subspecies (0.90 ± 0.17, N = 43) and between species (2.16 ± 0.22, N = 32). Details of interspecific responses are described further in Chapter 5.

3.4 Discussion

In the above dissection of *P. xanthoschistos* song I have described whole song, song syntax and frequency-time features of the species over large part of its distributional range. *P. xanthoschistos* sings in song bouts, whole songs, consisting of song types and inter-song intervals. It sings with characteristic song repetition, population mean repetition of song types varying from 3.73 to 6.83 times across sites (mean = 4.82, s.d. = 1.42 for combined data) before switching over to the next song type. The mean song repertoire ranges from 8 to 12 song types (combined data mean = 9.81, s.d. = 2.66). On an average it sings ranging from 10.34 to 13.63 songs per minute across sites with combined data mean of 11.25 songs per minute (s.d. = 2.09, N = 157). There is song sharing among the neighbours, which declines with distance, and there is no sharing among birds few kilometers apart. All the song types start with an introductory note, which

unlike in other species songs is quite variable. Variable song introductory note, geographical pattern of song complexity, song recognition and subspecific differences in song features are discussed below.

3.4.1 Variable introductory notes

A feature of the song of *P. xanthoschistos* is an introductory note, defined as an initial note separated from the rest of the song by distinct time gap (Figure 3.3). Spectrograms in Päckert et al. (2004) indicate that many species in the genus *Phylloscopus* begin with an introductory note, which can be in the form of modified calls (e.g., *P. schwarzi, P. armandii*), a short whistle (e.g., *P. cantator, P. ricketti*), or short hook (e.g., *P. reguloides*), but not all species have an introductory note (e.g. *P. collybita*, *P.trochiloides*, *P. trochilus, P. davisoni*, and *P. proregulus*). Although introductory notes occur in many species of passerine birds (Richards 1981), their role has not been well studied. In many species they have a narrow frequency range and relatively wide spacing that should lead to high detectability and be an alerting component, compared to the message in the rest of the song (Richards 1981). In the much-studied White-crowned sparrow *(Zonotrichia leucophrys)* the first part of the song is a pure tone whistle that is shared across the species (Soha and Marler 2000, Price 2008). In contrast, I have found that introductory notes in *P. xanthoschistos* are present in multiple forms and these notes are shared among different populations. The note is not a whistle, but may have an alerting function, e.g. by resembling aspects of the alarm call. The great variability in introductory form may have contributed to evolution of songs in the west, as I discuss further in a later section.

3.4.2 Geographical patterns of P. xanthoschistos song variation

Geographical variation occurs across all spatial scales. At the smallest scale song types completely turnover in a few kilometers, although individuals on adjoining territories share a maximum of 1/3 of all their song types (Figure 3.5). Notes are shared over longer distances than song types. I catalogued introductory notes and found that they are shared not only between closely placed populations, a few kilometers to 100 kilometers and more, but also between populations separated by more than 2000 kilometers, which can result in a disjunct

distribution of populations sharing introductory notes. For example, birds in Nokrek, Mehao, Shimla-Nahan and Patnitop-Ramban have some common introductory notes. It is unclear if this principle applies to notes within songs, but it has previously been shown in several species of birds that notes are more widespread than song type (Marler and Pickert 1984, Balaban 1988, Nelson et al. 2004).

The most striking finding is an increase of complexity with latitude: individuals sing over a higher bandwidth and with a greater number of note types at higher latitudes. An increase in song complexity with latitude appears to be a common pattern within bird species (Irwin 2000**,** Botero et al. 2009), but opposite has been observed in Arctic Warbler complex (Alström et al. 2011). The song types in the west rarely have repeated notes. They may have been derived from the east, which was thought to be a refuge during Pleistocene glaciations (Johansson et al. 2007, Price et al. 2011). A striking feature of the introductory notes is that the western songs appear to be built, or at least modified, by the movement of introductory notes into the rest of the song. This can happen either by repetition of the same song's introductory note, or the appearance of introductory notes from different songs. For example, introductory notes in Samsing, Yuksom-Tsoka and Eaglenest have been found internal to the song of the populations in the west e.g. Shimla-Nahan and Banjar-Jalori in Himachal Pradesh. Thus multiple incorporations of introductory notes into the song may have contributed to increased complexity in the northwest.

3.4.2.1 Existing hypotheses and observed patterns: Several explanations have been proposed for why song complexity should increase towards higher latitudes (Catchpole 1980, Wiley and Richards 1982, Irwin 2000, Mountjoy and Leger 2001, Brumm and Slabbekoorn 2005, Botero et al. 2009, Collins et al. 2009, Price 2013, Wiley 2013).

1. *Higher densities and short songs*: In the greenish warbler Irwin (2000), following Catchpole (1982) and Slater (1981), notes that densities are higher at lower latitudes and suggests that this leads to a greater

emphasis on male competition, which favours short songs (because males listen to and respond to each other). Singh and Price (in prep) report estimated breeding bird densities of *P. xanthoschistos* in surveys of 5ha plots in central areas of their altitudinal range of 1.4 pairs/ ha in east and 1.5/ ha in the west, which are similar and unlikely to be significantly different from each other. So, in case of *P. xanthoschistos* song length variation is not correlated with change in density.

2. *Seasonal environments, high food availability and high song complexity*: A second explanation is that food levels are higher in a seasonal environment, lowering costs of singing (Irwin 2000). This has often been applied to considerations of repertoire size, with large repertoire size thought to be an honest indicator of male quality (Gill and Gahr 2002); only high quality males are able to bear the costs of singing large repertoires. However, in *P. xanhoschistos* there is no variation in repertoire size across latitudes (Table 3.3). Hence if the food availability considerations apply to song complexity, then food levels for the species should be higher in the west. But food levels in general were found to be lower in *P. xanthoschistos* habitat in the west (Ghosh 2013). Hence the hypothesis is not supported by the present study.

3. *Climatic variability and unpredictability*: Botero et al. (2009) posit that climatic variability and unpredictability leads to elaboration of songs in Mockingbirds because high cognitive ability is required in such environments and elaborate songs develop in birds with higher cognitive ability. Himalayan avifauna is considered to be immigration avifauna: Himalayas were under cold and dry conditions during the last glaciation maximum, some 18000 years back, and there were no habitats for the warblers (Johansson et al. 2007). Immigrated taxa might have experienced more variable and unpredictable climatic conditions in the western Himalayas compared to the eastern, possibly leading to development of more complex songs.

4. *Singing in noisy environment* and signal redundancy: Finally, at lower latitudes, species diversity is higher and the sound environment more cluttered (in a preliminary study comparing two sites, Eaglenest in the

southeast and Chail in the northwest, ambient noise was found to be higher in the southeast, mean ± s.e. being 50±2 dB and 47±3 dB for Arunachal and Himachal respectively), so plausibly note (syllable) repetition is favored in the southeast so that the message is recognized. This may be in addition to song repetition, which is nearly similar both in the northwest and southeast. Birds use message repeat strategy to counteract noise to get the message across in noisy environments (Wiley and Richards 1982, Brumm and Slater 2006, Catchpole and Slater 2008, Wiley 2013). Besides southeast is more species rich and birds in species rich environments sing simpler songs (Wiley 2013).

Higher bandwidth in the west is mainly because the songs in the northwest has lower minimum frequency, which could possibly be because in the southeast lower frequency space is occupied by higher intensity ambient noise restricting lower frequency communication .

In a recent review Price (2013) based on predictions of signal detection theory argues that song repetition in birds could also be because the females are fastidious and have higher response threshold in species in which sexes associate only briefly during breeding such as migrants and polygynous species. This implies that *P. xanthoschitos* should have high female response threshold, meaning higher sexual selection by female choice compared to *P. reguloides* which do not repeat songs (see Chapter 4). But the idea is not supported by the fact that *P. reguloides* is apparently more seasonal migrant and as shown above rarely repeats song types in whole song.

Hence most of the hypotheses do not explain geographical pattern in P. xanthoschistos song. Most plausible explanation for geographical pattern of complex songs in the northwest and simpler songs in the southeast is that communication in noisy and species rich environment favours simpler and longer songs with high syllable repetition, and in the

northwest song complexity in partly achieved by running of introductory note into the song and by lowering of minimum frequency.

3.4.3 Song recognition

Despite conspicuous differences in the song features of the population from northwest to southeast and also among four recognized subspecies (see Table 3.11 and also Figure 3.10), there is not much difference in song recognition as shown by the playback experiments (see Figure 3.10). That is possibly because the change is gradual and more importantly not enough to significantly affect interpopulation recognition. Change in use of introductory notes could be drastic as some of the populations do not share introductory notes (see Table 3.5). But introductory notes may be serving just restricted function of alerting the receiver about the message to follow, rather than themselves being important cognition signal (Richards 1981).

Chapter 4

Geographical variation in the song of the Blyth's Leaf-Warbler *Phylloscopus reguloides*

4.1 Introduction

Blyth's leaf Warbler, *Phylloscopus reguloides* has a breeding range along the Himalayas from Pakistan eastwards to Arunachal Pradesh in India, the Northeast Hills of India, southeast Bangladesh, western Myanmar, northwest Thailand, northwest and south Vietnam, and in northwest Yunnan in China (Olsson et al. 2005, Rasmussen and Anderton 2005, Päckert et al. 2009, Martens 2010, Martens et al. 2011). Within the Indian subcontinent Ali and Ripley (1987) recognized three subspecies *kashmiriensis, reguloides* and *assamensis,* but more recently *kashmiriensis* and *reguloides* have been united and *assamensis* is only known definitely from western Myanmar (Olsson et al. 2005, Päckert et al. 2009, Martens 2010). Distribution limits of this species complex are imperfectly known and taxonomy is quite difficult and not yet final (Martens 2010). An important clue to systematics in birds in general and *Phylloscopus* warblers in particular is song (Alström and Ranft 2003).

In the Himalayas *P. reguloides* breeds between 2000 and 3600m but in the Khasi Hills in Northeast India it breeds as low as 1400m (Ali and Ripley 1987). A feature of the distribution of *P. reguloides* is that it is bounded altitudinally above and below and also geographically to the west, by closely related species with similar songs (see Figure 4.2). Throughout its Indian breeding distribution *P. xanthoschistos* lies below it, and in the altitudinal range of overlap the two species regularly encounter each other, and to the human ear sing very similar songs. Altitudinally above *P. reguloides* one encounters *P. trochiloides*, while to the west *P. reguloides* is replaced by a very similar species *P. occipitalis,* which is its closest relative in the Himalayas (Figure 4.2). The geographical zone of overlap between *P. occipitalis* and *P. reguloides* extends from the Nepal border to western Himachal Pradesh. In this zone *P. occipitalis* lies below *P. reguloides*, and

above *P. xanthoschistos*. One consequence is that *P. reguloides* does not encounter *P. xanthoschistos* in the western part of its range.

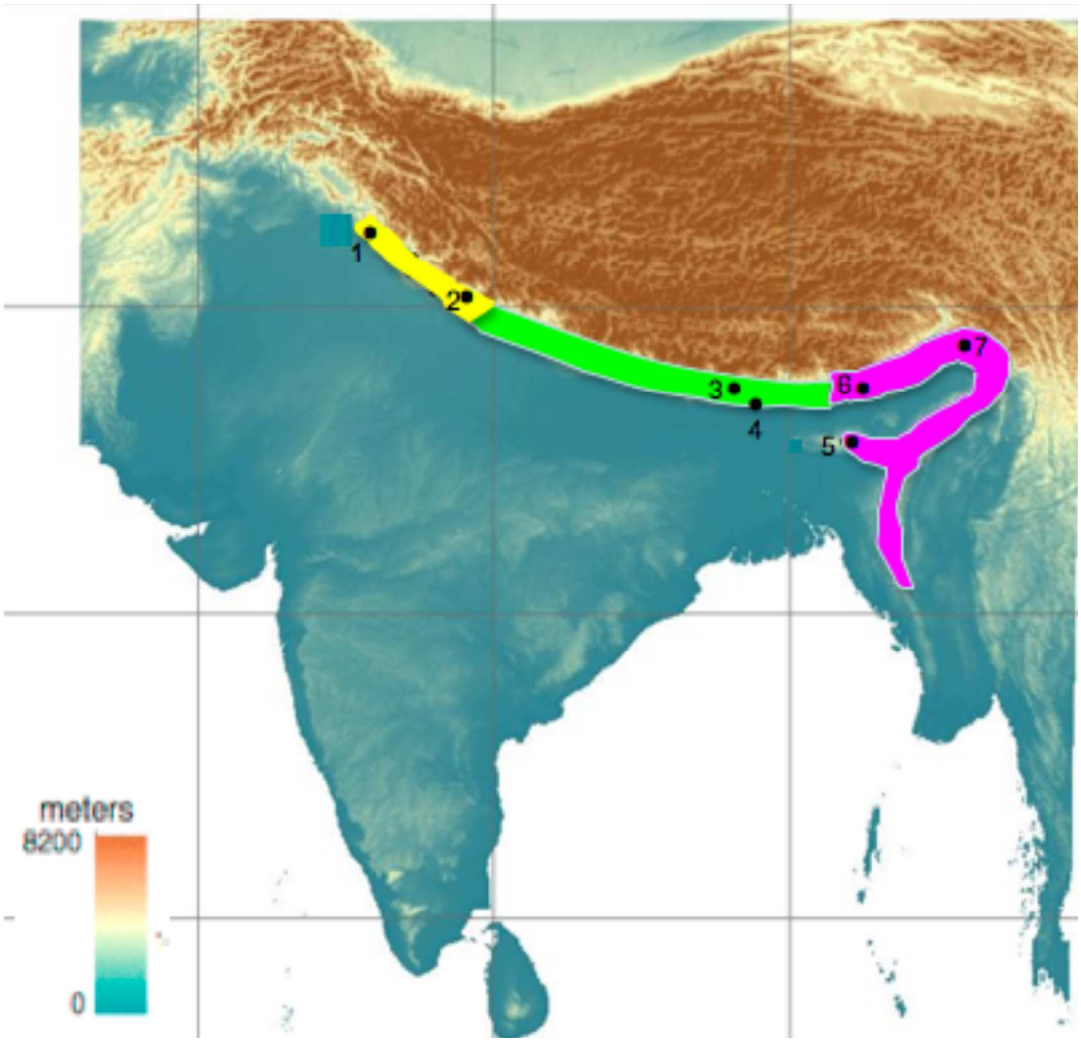

Figure 4.1 Topographical map of India indicating locations of study and approximate distributions of the 3 subspecies of *P. reguloides* (Ali and Ripley 1987, see Table 4.1). The locations are 1: Banjar-Jalori, Himachal Pradesh; 2: Kedarnath, Uttarakhand; 3: Yuksom-Tsoka, Sikkim; 4: Singalila-Senchal, North Bengal; 5: Shillong, Meghalaya; 6: Eaglenest, Arunachal Pradesh and 7: Mehao, Arunachal Pradesh. Yellow, green and pink colours represent distribution ranges of *kashmiriensis*, nominate-*reguloides* and *assamensis* subspecies respectively.

The present study investigates geographical and altitudinal variation of *P. reguloides* song, and also explores interspecific aggression of this species with closely related elevational replacements (see Figure 4.2).

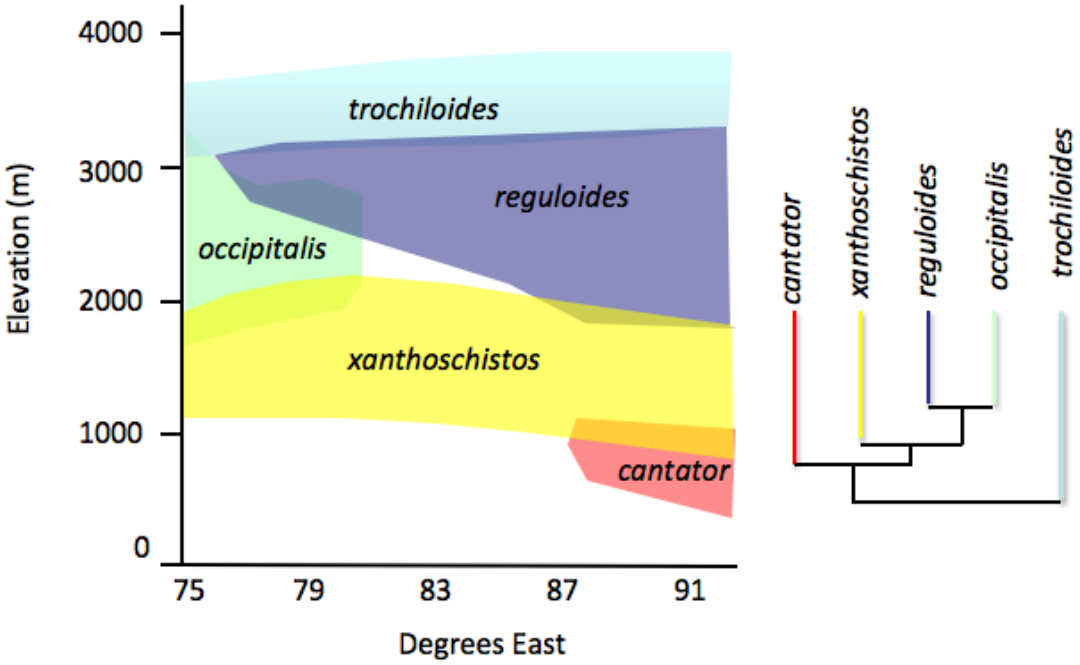

Figure 4.2 Geographical and elevational distribution of *P. xanthoschistos*, *P. reguloides* and their three closest relatives in the Himalayas (excluding *P. magnirostris* which is associated with streams) during breeding season, with their phylogenetic relationship illustrated (adapted from Price et al. 2011). *P. reguloides* has contiguous breeding distribution with *P. xanthoschistos* in the east, but not in the west where *P. occipitalis* breeds in between.

4.1.1 Systematics

Watson et al. (1986) allocated 7 taxa to *P. reguloides* namely *kashmiriensis, reguloides, assamensis, ticehursti, claudiae, goodsoni* and *fokiensis*. According to Ali and Ripley (1987) and Rasmussen and Anderton (2005) three subspecies, *kashmiriensis, reguloides* and *assamensis* breed in India, and one subspecies *claudiae* winters in eastern India. But recent studies based on molecular and vocalization analysis do not support the above species limits and distribution (Olsson et al. 2005; Päckert et al. 2009; Martens 2010; Martens et al. 2011). Olsson et al. (2005) divided all seven taxa allocated to *P. reguloides* into three main clades. One of the clades, the Himalayan-south-east Asian clade, comprises *kashmiriensis*, *reguloides*, *assamensis* and *ticehursti*; the other two clades are the central Chinese *claudiae* and south-east Chinese *goodsoni* and *fokiensis*. The latter two clades were later elevated to full species, i.e. *P. claudiae* and *P. goodsoni* respectively by Olsson et al. (2005) and supported by Päckert et al.

(2009). The *sensu stricto* clade within *P. reguloides* was further divided into the following three groups by Olsson et al. (2005).

(1) *kashmiriensis* and *reguloides* from the Himalayas, as *reguloides*

(2) *assamensis (sensu stricto)* from western Myanmar, and

(3) *assamensis* from north-western Thailand and Yunnan (south central China) (sensu Alström and Olsson, 1993), a previously unassigned population from north-western Vietnam, and *ticehursti* from southern Vietnam united into *ticehursti*.

Olsson et al. (2005) found the cytochrome b divergence between these three clades to be substantial implying a barrier to gene flow (Figure 4.3). Olsson et al. (2005) stated that *reguloides* and *kashmiriensis* were doubtfully separable morphologically, but Martens (2010) did not concur with this view, citing Ticehurst (1933) and Vaurie (1954). According to Päckert et al. (2009) the vocalizations of the three subspecies now considered to comprise *P. reguloides* are not distinctly different but instead show continuous differences in frequency characters. However, the species *claudiae*, goodsoni and *reguloides* sensu stricto, which together form the *reguloides* superspecies complex are thought to have quite distinctive vocalizations (Päckert et al. 2009).

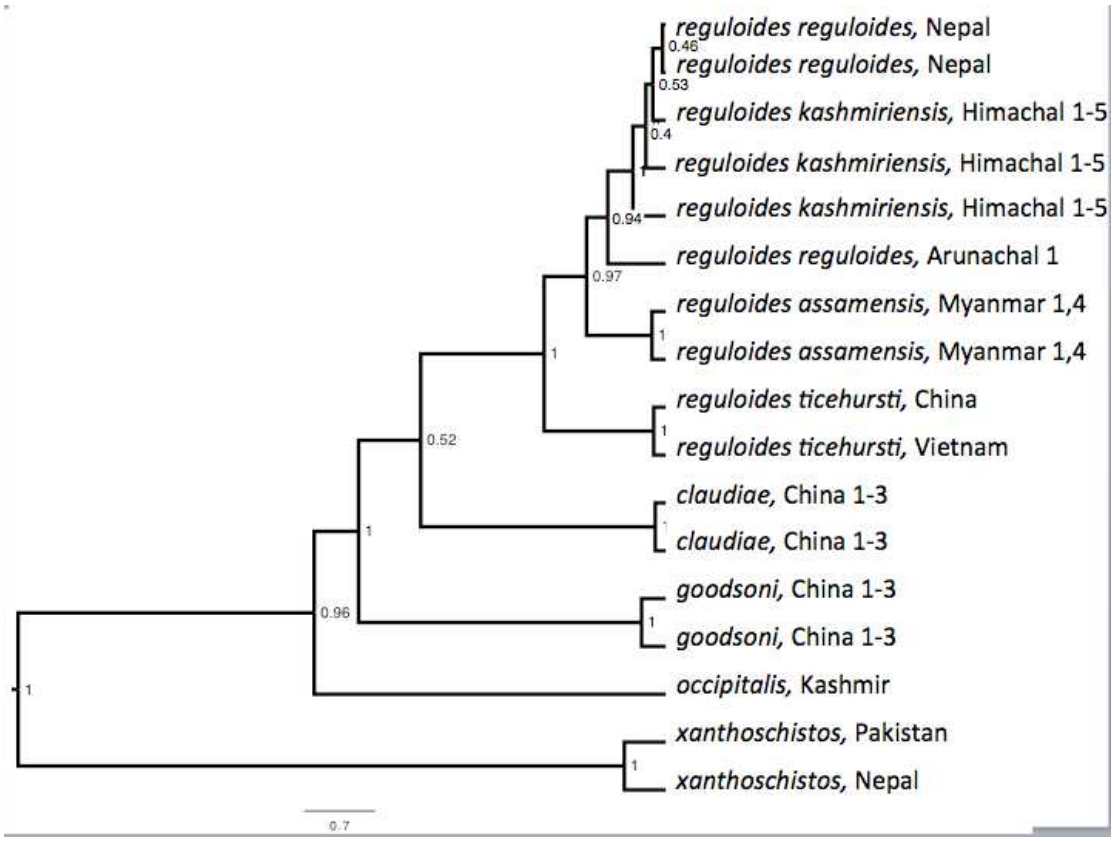

Figure 4.3 Phylogeny of *P. reguloides* and relatives, based on the mitochodrial cytochrome b gene (the species relationships are identical in phylogenies built from multiple markers, Price 2010). Computed in BEAST (Drummond and Rambaut 2007) following methods in Price (2010); numbers at nodes indicate posterior probabilities. Numbers adjacent to taxon names indicate presence of song types in 5 categories, as indicated in the results section of the chapter. Genbank numbers are (from top) EU771010, EU771011, Y10736, *, *, *, EU771021, EU851078, EU851079, AY652633, EU771027, EU771041, EU771049, EU771048, Y10735, *, EU771072. Four new sequences were collected for this wok, as indicated by* (genebank numbers pending); all other sequences are from, or referenced in, Päckert et al. (2009). Y10736 is from Manali, Himachal (32.24°N 77.16°E, cf. Päckert et al. 2009). * (*reguloides kashmiriensis*, 31.62°N, 77.35°E, 2nd June 2010) *(*reguloides kashmiriensis*, 31.62°N, 77.35°E, 2nd June 2010) *(*reguloides reguloides* from Arunachal 27.13°N, 92.6°E , 25th April 2010) **xanthoschistos* from Pakistan (34.60N 73.33E, U. Olson pers. comm.).

Table 4.1 Taxonomy and distribution of *Phylloscopus reguloides* superspecies complex. Distribution limits and status of *kashmiriensis*, *reguloide*s and *assamensis* subspecies are unresolved.

Taxonomy and distribution	
Watson et al. 1986, Ali and Ripley 1987, Rasmussen and Anderton 2005	**Olsson et al. 2005, Päckert et al. 2009, Martens 2010**
P. reguloides kashmiriensis; Distribution: Breeds in Western Himalayas from Murree and Kashmir east to Garhwal, between 2400 and 3300m	*P. reguloides reguloides;* Distribution: Breeds in Himalayas
P. reguloides reguloides; Distribution: Breeds in Himalayas from Kumaon to eastern Bhutan, between 2000 to 3500m	
P. reguloides assamensis; Distribution: Breeds in Arunachal Pradesh and the hills south of the Brahmaputra, Nagaland and Manipur, between 2400 and 3600m in Himalayas, above 1400m in Khasi Hills, and on Mt. Victoria between 2000 and 3000m.	*P. reguloides assamensis;* Distribution: Known definitely from Mt. Victoria in Myanmar, status of birds breeding in North-east hills of India unclear
P. reguloides ticehursti; Distribution: Breeds in Thailand, Vietnam and Yunnan, China.	*P. reguloides ticehursti;* Distribution: Breeds in Thailand and Vietnam and Yunnnan, China
P. reguloides claudiae; Distribution: Breeds in China	upgraded to species *P. claudiae;* Distribution: Breeds in China
P. reguloides goodsoni; Distribution: Breeds in China	upgraded to species *P. goodsoni;* Distribution: Breeds in China
P. reguloides fokiensis; Distribution: Breeds in China	

4.1.2 Songs of the *Phylloscopus reguloides* complex

Päckert et al. (2009) have described songs of the *Phylloscopus reguloides* superspecies comprising *P. reguloides, P. occipitalis, P. claudiae* and *P. goodsoni*. The song of all forms except *P. goodsoni*, begins with an introductory note separated from the rest of the song, which has a regular structure of repeated units, which may be single notes or syllables (group of notes) (Päckert et al. 2009, Figure 4; Martens 2010). One song pattern of repeated syllables of 2-4 notes is common to all four species (pattern 1 in Figure 4 of Päckert et al. 2009),

and it is the only pattern previously reported for *P. reguloides* species. *P. claudiae* has additional song that consists of trills of single repeated element combined with one or two introductory notes (pattern 2 in Figure 4 of Päckert et al. 2009). In one location, S. Shanxi (China) trills are replaced by verses of repeated syllables (Päckert et al. 2009, Martens 2010). The song of *P. goodsoni* consists of 2-3 highly modulated notes at the beginning followed by a long repetition of syllables (aabcdbcdbcd……), and the short narrow banded introductory note of other allospecies of the P. *reguloides* superspecies complex is missing (Päckert et al. 2009, see Figure 4; Martens 2010, see Figure 9). These additional song patterns found in *P. claudiae* and *P. goodsoni* have not been reported in any of the subspecies of *P. reguloides sensu stricto.* However, Päckert et al. (2009) noticed a *P. claudiae* trill song in the background of *Certhia familiaris* recording from Himachal Pradesh India I sent to Professor Jochen Martens, and the possibility that *P. reguloides* in this region sing such songs was further investigated as part of this thesis

In this chapter, I present a detailed analysis of the songs of *P. reguloides* within India. I consider how song varies locally (less than one kilometer), altitudinally, and geographically, and evaluate the significance of any variation using playbacks. I show substantial and apparently discrete geographical variation with the Himachal Pradesh population, which differs substantially from elsewhere in the Himalayas. Further, a remarkable feature of the Himachal populations is that they incorporate songs typical of the closely related, but geographically distant, species *P. claudiae* and *P. goodsoni*.

4.1.3 Study sites

I visited 7 sites, 6 across Indian part of the Himalayas and one in the North-east Hills of India (Table 4.2, Figure 4.1). Details of the study area are provided in Chapter 2 and Table 4.2 below. Some additional aspects of the study sites pertaining to *P. reguloides* are provided below.

***Banjar-Jalori*:** Recordings and playbacks at Banjar-Jalori site were carried out along Soja-Jalori Pass road up to the Pass and about 1 km beyond, along the track

to the lake and temple and on the ridge above the track. The road does not have much traffic, especially during early morning. Here *P. reguloides* occurred more in mixed conifer and *Quercus* forest areas whereas in pure conifer areas *P. occipitalis* was common.

***Kedarnath*:** Here the fieldwork was carried out along Kanchula Kharak-Chopta road and along Chopta-Tungnath track in Kedarnath wildlife sanctuary. *P. reguloides* occurred all along the Tungnath track except in highest part, and for about 2 kms along Chopta-Kanchula Kharak road. Lower adjacent areas had *P. occipitalis*.

***Yuksom-Tsoka*:** In Yuksom-Tsoka area of Khangchendzonga Biosphere Reserve the fieldwork was carried out along Yuksom-Dzongri track, especially at and near Yuksom, Sachin and Tsoka. *P. reguloides* was found from Yuksom to Tsoka and till about 2 kms beyound Tsoka on Dzongri track. Closely related *P. xanthoschistos* is distributed at Yuksom and in adjacent lower areas, whereas it's other close relative *P. trochiloides* occurs higher up near Dzongri. Just above Yuksom, on Yuksom-Tsoka track and on Yuksom Monastery track *P. xanthoschistos* meets *P. reguloides*.

***Singalila-Senchal*:** In Singalila National Park area the fieldwork was carried out along Sandakhpo track between Kalipokhari and Tumling, and at Senchal along a road passing by Forest Rest House in Senchal Wildlife Sanctuary. In Singalila National Park *P. reguloides* is replaced by its close relative *P. trochiloides* in the higher areas close to Sandakhpo, which is the highest area along the track.

***Shillong*:** At Shillong in Khasi Hills the fieldwork was carried out near Shillong peak where *P. reguloides* breeds, apparently unconnected with other breeding areas, as nearby areas are too low for breeding. *P. xanthoschistos* occurred in the same area adjacent to *P. reguloides,* and also exclusively in more open pine areas.

***Eaglenest and Mehao*:** The fieldwork was undertaken in Eaglenest Wildlife Sanctuary and in Mehao Wildlife Sanctuary in Arunachal Pradesh mainly along the roads passing through these sanctuaries. Both these areas have close

relatives, *P. xanthoschistos* and *P. cantator* distributed in the adjacent lower areas.

4.2 Methods

I carried out fieldwork from 2007 to 2010 during the breeding season (April-June) (Table 4.2). The fieldwork consisted of recording songs and carrying out playback experiments.

4.2.1 Song recording

Recording methodology has been described in Chapter 2.

Additional recordings

To make the study more comprehensive I also analysed a few songs from extralimital *P. reguloides ticehursti* and *P. reguloides assamensis*. In addition, I studied *P. claudiae* (indicated by Päckert et al. 2009 in Himachal Pradesh) and *P. goodsoni* songs, because as will show below, Himachal Pradesh populations of *P. reguloides* sing songs similar to these species. Per Alström kindly provided two recordings of *P. reguloides assamensis* from Myanmar and five recordings of *P. reguloides ticehursti* from Thailand and Vietnam. I used two recording of *P. reguloides ticehursti* from Xanto-canto.org (for checking song syntax including introductory note shape), one by Craig Robson (Craig Robson, XC19227, accessible at www.xeno-canto.org/19227) and another by David Edwards (David Edwards, XC27621, accessible at www.xeno-canto.org/27621). I also used two *P. goodsoni* and three (two more for playbacks) *P. claudiae* recordings kindly sent by Per Alström.

Table 4.2 Study sites coordinates, subspecies (Ali and Ripley 1987) distributed, fieldwork duration and songs analyzed.

Site	Lat.	Long.	Altitude	Subspecies	Duration of fieldwork	Songs analyzed	Whole songs analyzed
Banjar-Jalori, Himachal Pradesh	31.62	77.35	2770-3110	kashmiriensis	10-14 June 2009, 31 May-03 June 2010	21	22
Kedarnath Sanctuary, Uttarakhand	30.49	79.21	2650-3190	*reguloides*	23-26 May 2010	21	17
Yuksom-Tsoka, Sikkim	27.36	88.21	1770-3040	*reguloides*	3-28 May 2007	20	16
Singalila-Senchal, West Bengal	27.05	88.3	2280-2930	*reguloides*	8,10-13 May 2008	23	13
Shillong, Khasi Hills, Meghalaya	25.62	91.9	1735-1850	*assamensis*	22-23 April 2009	12	5
Eaglenest, Arunachal Pradesh	27.13	92.6	1800-2450	*assamensis*	3,5-6,13-18,23-30 April 2008	35	32
Mehao, Arunachal Pradesh	28.345	95.88	1430-2520	*assamensis*	27-28 April 2009	27	27

4.2.2 Playback Experiments

Playback experiments were carried out to test the significance of geographical variation in *P. reguloides* songs, and also to investigate responses of congeners (see Chapter 5). Playback protocol has been described in Chapter 2. I used several experiment and control tapes during playbacks to minimize the effect of pseudo-replication on the results (see Table 4.3).

Table 4.3 Summary of playback experiments done and recordings used.

A: Intraspecific playbacks				
Site	**Playback experiments**	**Experiment recordings**	**Control experiments**	**Control recordings**
Banjar-Jalori	15	14	13	4
Kedarnath	6	6	2	1
Eaglenest	10	10	10	7
Shillong	6	5	6	6
Mehao	7	7	6	4
Singalila-Senchal	2	2	2	2
Total	46	44	39	24
B: Inter-species playbacks				
Species pairs	**Playback experiments**	**Experiment recordings**	**Control experiments**	**Control recordings**
P. claudiae to P. reguloides	5	4	5	3
P. goodsoni to P. reguloides	5	1	4	4
P. reguloides to P. trochiloides	5	5	4	4
P. xanthoschistos to P. reguloides	12	8	11	6
P. trochiloides to P. reguloides	1	1	1	1
P. reguloides to P. xanthoschistos	6	6	6	6
P. reguloides to P. occipitalis	3	3	2	2
Total	37	28	33	26

4.2.3. Analysis

4.2.3.1 Definition of terms used: I used vocalization terminology defined in Chapter 2. However, to describe peculiar song features of *P. reguloides* I define following additional terms.

Immediate Variety: Songs sung in a sequence in which each song type has different song type before and after it in contrast to *eventual* variety in which a bird repeats a song type few times before switching over to another song type (Catchpole and Slater 2008). *P. reguloides* sings with style close to immediate variety in contrast to its close relative *P. xanthoschistos* that sings with eventual variety (Chapter 3). *P. reguloides* often does not render its whole song in a pure

immediate variety pattern, but in some songs it occasionally repeats a song once or twice before switching to different song. Song repetition rate is a summary measure of singing style, with a value equal to 1 implying perfect immediate variety, when no song type is repeated.

4.2.3.2 Selection of recordings for analysis: For song analysis, I selected recordings with minimal background noise. Some recordings included two males, as identified based on song intervals, and I did not use these for "whole song" analysis. I concentrated on long recordings to compare whole song variation (e.g. in number of song types sung) between populations, but used both long and short recordings to characterize song parameters such as frequency.

4.2.3.3 Identification of song types: Identification of song types was made, as in the case of *P. xanthoschistos* (Chapter 3, section 3.2.3.3)

4.2.3.4 Whole song parameter analysis: Repertoire size, song rate, and song sharing were estimated for selected populations.

Song Repertoire Estimation: As noted, *P. reguloides* generally sings its song types with immediate variety. In the whole song a bird usually switches from one song type to another without repeating the same song type in the pattern of abcd….acbd…..cycling through the whole repertoire. But this is not a rule. In some songs one song type may be repeated a few times, and hence patterns like aabccd…acbbdd..., etc are found. Thus to get a fair approximation to repertoire size, whole songs with many more songs than number of song types were included whole song analyses. A plot of song types versus number of songs is given in Figure 4.4. This plot indicates that even recording a moderate number of songs (< 20) should capture the entire repertoire. 132 whole songs (songs ranging from 6 to 107) across seven localities were analyzed for repertoire estimation.

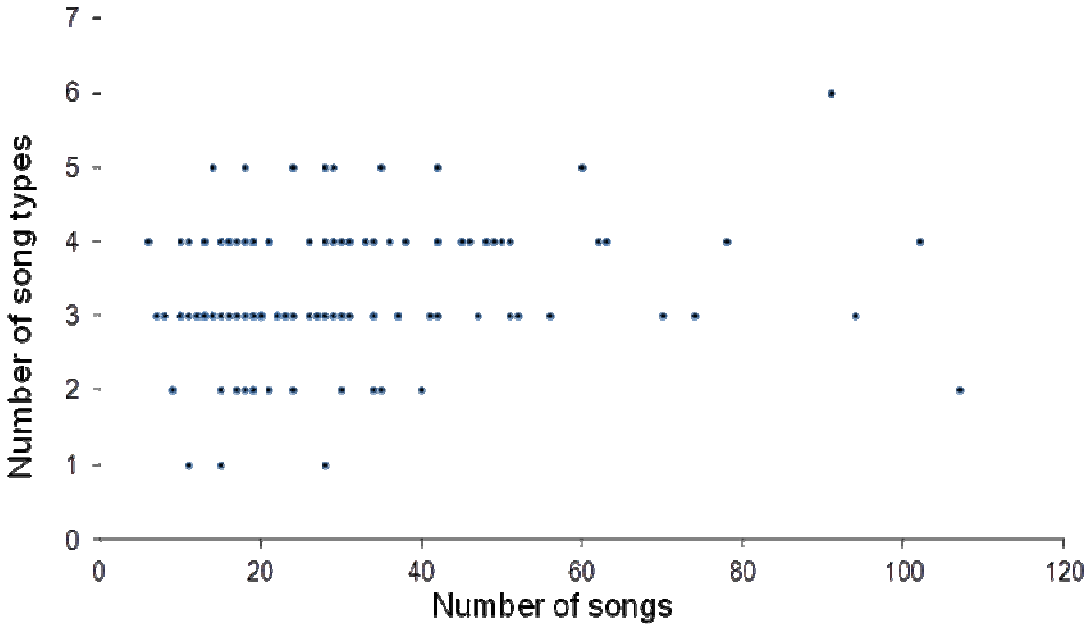

Figure 4.4 Accumulation of song types with songs recorded for individual recordings. The number of whole songs I analysed for all 7 sites was 132, ranging from 5 to 32 per site. The number of songs in individual birds varied from 6 to 107, having only 5 whole songs containing less than 10 songs.

Song repetition rate estimation: As defined in Chapter 2 song repetition rate is a good measure of singing style i.e. eventual or immediate variety. Song repetition rate for a whole song was calculated by dividing number of songs by number of sequences (unlike in *P. xanthoschistos* where because of high repetition only five sequences were chosen for calculation of repetition rate), leaving first and last sequences. For example the whole song abbcdefgh, where a,b,c,d,e,f,g, and h are song types, has a song repetition rate i.e. 7/6 = 1.11. A whole song with repetition rate close to 1 has singing style approaching immediate variety. 100 whole songs with 16 or more songs were analyzed for song repetition rate estimation (Table 4.4)

*Song rate estimation***:** As described in Chapter 3 song rate = n/dt, where dt is time measured from beginning of 1st song to the beginning of n+1th song. Song rate was calculated from long whole songs, including whole song sections not having more than 10 second inter-song intervals. 118 whole songs, across the sites, having more than or equal to 8 songs (n = 7) in such sections were analyzed.

4.2.3.5 Song type parameter measurements: Following the same method as in the case of *P. xanthoschistos* (Chapter 3, section 3.2.3.5) I measured the following song parameters from the spectrograms: (1) minimum frequency, (2) maximum frequency, (3) central frequency, (4) song length, (5) number of total notes in a song and (6) number of distinct notes in a song.

I measured at least 20 song types (but only one song per song type) from each of the sites except Shillong, where 12 song types were measured (see Table 4.2). Only one song type, the first clean song type in the whole song, was selected from one individual. I measured frequency-time parameters using Raven Pro 1.3, and counted visually syntax parameters, i.e. number of total and distinct notes.

4.2.3.6 Statistical Analysis: The software used and tests performed are the same as used in case of *P. xanthoschistos* (Chapter 3).

4.3 Results

I first describe aspects of the whole song and geographical variation of its parameters. Next I consider the classification of song types and how they vary with latitude, longitude and altitude. Introductory notes are described in a final section.

4.3.1 Whole song

4.3.1.1 Singing variety: *P. reguloides* songs approximate immediate variety. Some songs do repeat but only once and rarely twice or more. The song repetition rates for different locations as given in the Table 4.4 below are quite close to 1. Site mean of repetition rate does not show significant latitudinal (R = 0.28, P = 0.22, N = 7) and longitudinal (R= 0.47, P = 0.09, N = 7) trend.

Table 4.4 Song repetition rates (see definitions) for study populations of *P. reguloides.* Values close to 1 indicate that the birds sing with nearly immediate variety.

Site	**N* (Whole songs)**	**Song repetition rate (Ratio ± s.e.)**
Banjar-Jalori	19	1.27 ± 0.07
Kedarnath	10	1.52 ± 0.20
Singalila	9	1.14 ± 0.05
Yuksom-Tsoka	13	1.13 ± 0.04
Shillong	4	1.25 ± 0.18
Eaglenest	24	1.22 ± 0.05
Mehao	21	1.11 ± 0.02
Kruskal Wallis Test N =100, d.f. = 6		$\chi^2 = 8.00$, P = 0.24

*Number of whole songs, each with 16 or more songs

4.3.1.2 Song rate: Mean song rate varies from 6.39 songs per minute for Kedarnath to 7.81 songs per minute for Shillong. Mean song rate for the combined data is 7.11 (s.d. = 1.66, N = 118). Song rate differences between sites were close to statistically significant (P = 0.06, see Table 4.5 below). However, these small differences may be because of differences in breeding stages of birds in the sites surveyed.

There was no geographical trend detected when song rate site means were regressed with latitude ($R^2 = 0.05$, P = 0.65) and longitude ($R^2 = 0.01$, P = 0.84).

Table 4.5 Repertoire size and song rate for study sites (Mean values and standard error shown). F statistics and Kruskal-Wallis test values do not show significant variation among sites for repertoire size, although song rate differences are close to significant.

	Repertoire size		**Song rate**	
Sites	**Mean ± s.e.**	**N**	**Mean ± s.e.**	**N**
Banjar-Jalori	3.36 ± 0.19	22	7.80 ± 0.41	22
Kedarnath	3.06 ± 0.28	17	6.39 ± 0.37	15
Yuksom-Tsoka	3.31 ± 0.15	16	7.54 ± 0.49	15
Singalila-Senchal	3.38 ± 0.21	13	7.54 ± 0.42	12
Shillong	3.40 ± 0.24	5	7.81 ± 0.86	4
Eaglenest	3.41 ± 0.16	32	6.69 ± 0.27	26
Mehao	3.48 ± 0.16	27	6.77 ± 0.30	24
		Total = 132		Total = 118
F test	$F_{6,125}$ = 0.51, P = 0.80		$F_{6,111}$ = 2.08, P = 0.06	
Kruskal-Wallis Test	χ^2(d.f. = 6, N = 132) = 1.61, P = 0.95		χ^2 (d.f. = 6, N = 118) = 11.54, P = 0.07	

4.3.1.3 Song repertoire: The mean number of songs I studied was 29.10 per individual bird (N = 132 individuals, range 6-107) and only 5 contained less than 10 songs. Across the 132 whole songs the number of song types per individual varied from 2 to 5, with four exceptions: three with only one song type and one with 6 song types (mean = 3.36, s.d. = 0.87, N = 132).

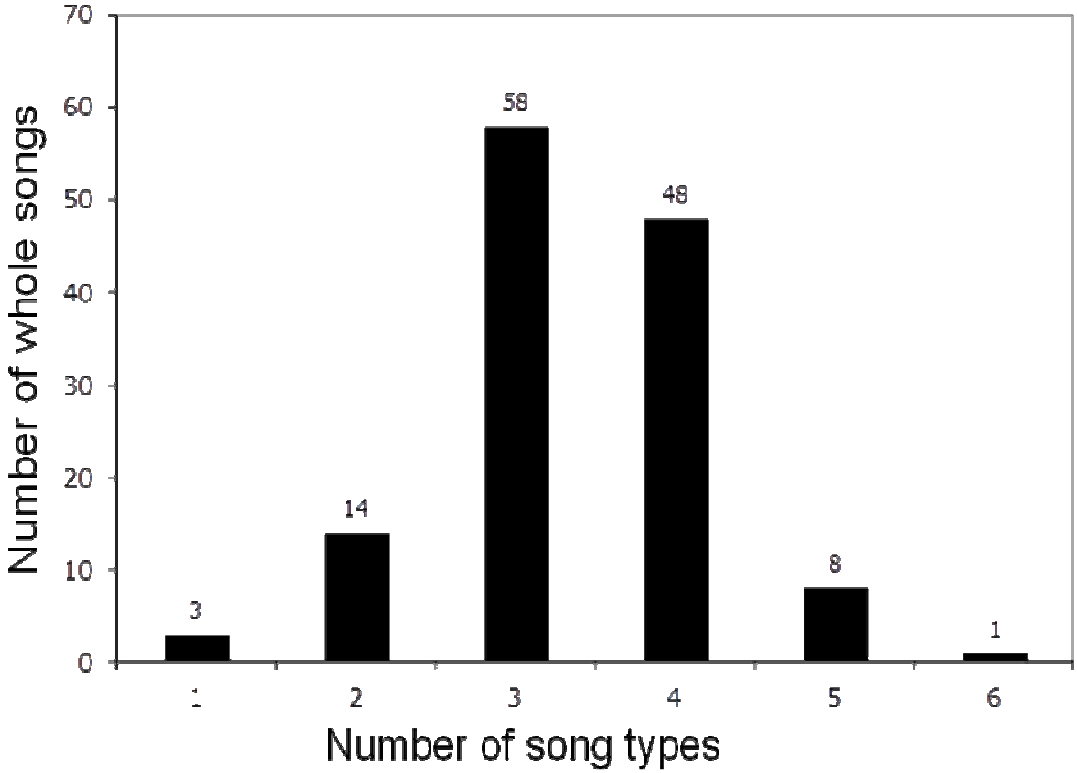

Figure 4.5 Distribution of song repertoire size among individuals of all the populations analyzed (N = 132). As evident from the figure the majority of the individuals sing with repertoires of three and four song types.

The most common repertoire size was three followed by four (Figure 4.5). Across sites the number of song types per individual did not vary significantly ($F_{6, 125} = 0.45$, P = 0.85). However, mean song repertoire for sites shows a positive trend with longitude and is close to significant ($R^2 = 0.48$, P = 0.09, N = 7) but no trend with latitude ($R^2 = 0.22$, P = 0.29, N = 7).

4.3.1.4 Song type sharing: Some songs are shared among neighbours but the pattern of sharing is not very clear. However, one out of three sites shows significant decrease in sharing with distance (see Figure 4.6 below).

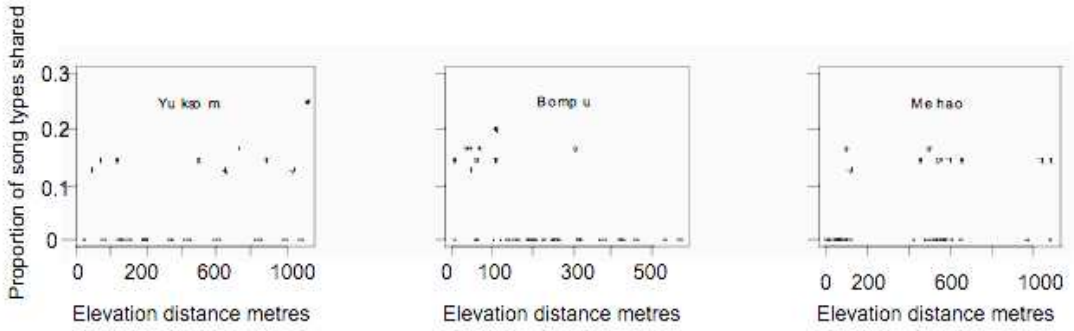

Figure 4.6 Proportion of song types shared as a function of altitudinal separation; note the different scales on the x-axis. Yuksom (Sikkim), R = 0.4, N = 8, P = 0.48; Bompu in Eaglenest (west, Arunachal), R = -0.47, N = 9, P = 0.003. Mehao (east Arunachal), R = 0.22, N = 9, P = 0.2.

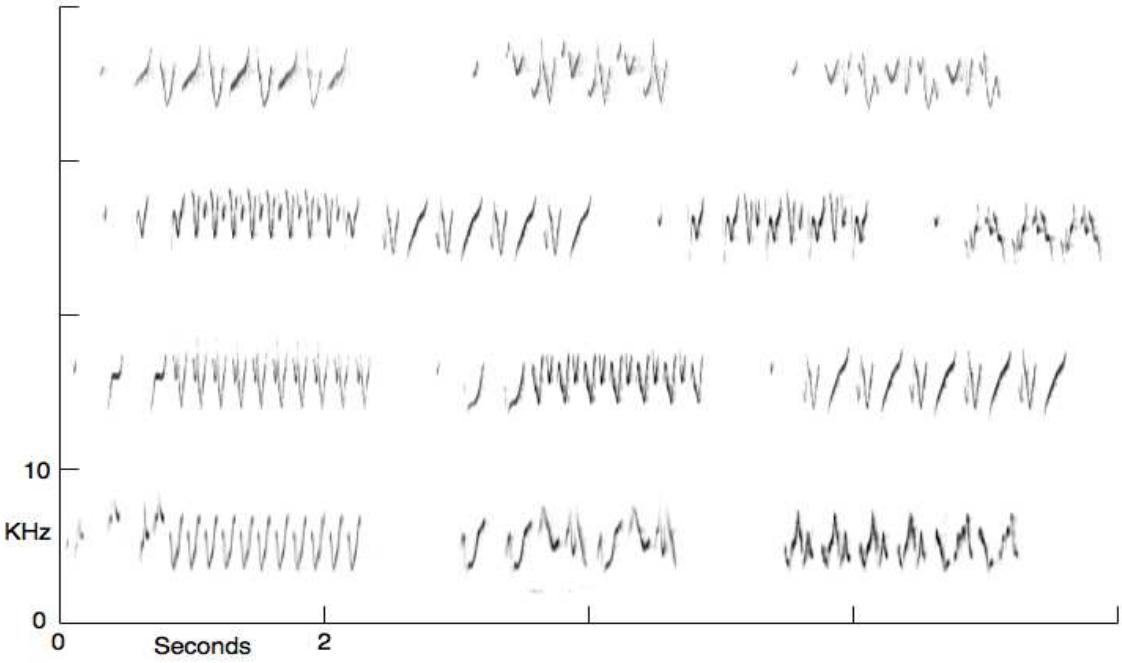

Figure 4.7 Spectrograms from *Phylloscopus reguloides* and closely related forms indicating the range of variation. Top row: 3 songs from north Bengal. Center rows: 6 songs from Himachal. Bottom row, from left: (i) *P. claudiae* song (from Hebei Province, China) to illustrate a trill (same note repetition, compare with song directly above). (ii) *P. goodsoni* song (from Fujian Province, China) to illustrate syntax similarity with song above. (iii) *P. trochiloides* from Singalila (West Bengal) song to illustrate a two-note combination the first of which is trilled. For additional illustrations of the other species see Päckert et al. (2009) and Irwin (2000).

4.3.2. Song syntax and song parameters

4.3.2.1 Syntax of P. reguloides *song and its geographical variation*: All the studied populations of *P. reguloides* start their song with an introductory note that is hook (√) shaped, except in Meghalaya songs where it is v shaped. Note repetition in songs is another aspect that varies among populations (see also next section). Notes are repeated in groups (syllables) of two to four notes in all populations, but at Banjar-Jalori in Himachal Pradesh birds have additional patterns too. Three-note repetition is the most common pattern, except at Shillong in Meghalaya, where the two-note pattern dominates. Three-note repetition pattern is highly dominant in Arunachal populations (see Figure 4.8). Four-note repetition pattern is a rare occurrence in all the populations. But exception is Himachal population song syntax (where syntax is much variable and matches Chinese taxa *P. claudiae* and *P. goodsoni*), which is described next.

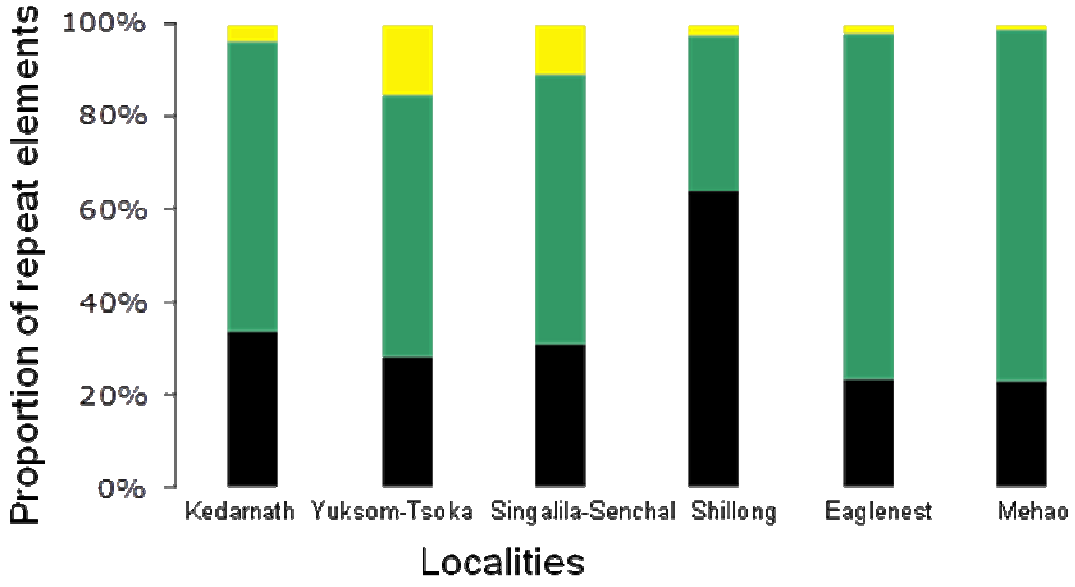

Figure 4.8 Distribution of note-repeat pattern in *P. reguloides* populations from northwest to southeast, excluding Himachal population which has much more complex syntax. Black, green and yellow colours represent two, three and four note repetition. The Shillong population, with a dominant pattern of two-note repetition, on an average uses the least number of notes in its song.

Syntax of Himachal birds: In the northwest of the Himalayas, only some of *P. reguloides* songs match the general description above. Himachal birds have the following five patterns of song syntax (see Figure 4.7).

Pattern 1: Typical *P. reguloides* songs, introductory note followed by repetition of 2-4 notes as described above (see top row of Figure 4.7).

Pattern 2: 2-3 highly modulated notes, rarely one note, followed by two-note repetition (see 2nd panel of 3rd row in Figure 4.7), and often ending with the same highly modulated notes. This pattern is characteristic of *P. goodsoni* song (Packert et al. 2009), although *goodsoni* has no introductory note.

Pattern 3: 2-3, rarely one, highly modulated notes followed by a trill (see 1st panel of 3rd row in Figure 4.7). In a few songs trill is not preceded by above highly modulated notes. The former pattern is similar to that recorded for *P. claudiae* from China by Päckert et al. (2009).

Pttern 4: Mix of pattern 2 and 1, mix of pattern 2 and 3, repetition of pattern 2 and two typical *P. reguloides* patterns combined (see 1st panel of 2nd row in Figure 4.7).

Pattern 5: One highly modulated note followed by repetition of three to four note complex, having the first note the same highly modulated note (see 2nd panel of 2nd row in Figure 4.7).

Patterns "4" and "5" are not reported in *P. reguloides* or in *P. claudiae* or *P. goodsoni*. In 22 whole songs analyzed in Himachal 14 had two patterns, 6 had three, 1 had four and 1 had only one. Pattern "1" and "2" are almost equally common being present in 19 and 18 birds respectively, pattern "3" was in 9

birds, and patterns “4” and “5” were less common being present in 3 and 4 birds respectively. Pattern “4” was also observed in *P. reguloides assamensis* from Myanmar (2 recordings of different birds analyzed) in which out of 28 song types 5 had pattern “4” in a bird (see discussion).

Grouping of populations based on song syntax: Based on the above description *P. reguloides* in Himachal has different syntax than any other population in India, besides Meghalaya population, which has the distinct v shaped song introductory note. Hence Himachal, Meghalaya and the rest of Himalayan populations have broadly distinct syntax features.

4.3.2.2 Frequency-time parameters and song notes: *P. reguloides* sings across sites with minimum frequency ranging (mean ± s.e.) from 3327 ± 88 to 3489 ± 109 Hz, combined mean, maximum frequencies ranging from 8316 ± 121 to 8535 ± 212 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 seconds (see Table 4.6). Central frequency ranges from 5599 ± 94 to 5916 ± 42 Hz across sites.

There was no significant difference in song frequency-time parameters of the seven populations studied, except for song length and central frequency (Table 4.6). If Himachal population, which has different syntax from the rest, is excluded, the difference in song length become less significant ($F_{5,132}$ = 2.1974, P = 0.06). Central frequency difference is mainly due to Kedarnath and Shillong birds, which sing at lower mean frequencies.

Table 4.6 Frequency-time parameters and song-notes of *P. reguloides song* for study sites.

Site, N (Songs analyzed)	**Min. freq.**	**Max. freq.**	**Cent. Freq.**	**Band-width**	**Song-length**	**Total notes**	**Dist. notes**
Banjar-Jalori, 21	3263±105	8316±121	5726±59	5053±152	1.82±0.05	11.90±0.63	3.48±0.15
Kedarnath, 21	3249±120	8506±135	5599±94	5257±140	1.71±0.06	11.14±0.54	3.86±0.20
Sikkim, 20	3489±109	8510±115	5896±64	5021±158	1.68±0.05	10.90±0.45	3.75±0.14
SingalilaSenchal, 23	3453±93	8327±96	5850±57	4874±115	1.79±0.05	11.57±0.46	4.13±0.14
Shillong , 21	3229±154	8535±212	5649±122	5306±234	1.67±0.06	10.00±0.52	3.50±0.19
Eaglenest, 35	3437±57	8489±85	5916±42	5052±97	1.61±0.03	10.11±0.26	3.86±0.08
Mehao, 27	3327±88	8507±96	5787±49	5180±106	1.68±0.04	10.30±0.29	3.89±0.06
F-test, degrees of freedom = (6,152)	F = 1.13, P = 0.35	F = 0.62, P = 0.71	F = 3.48, P < 0.01	F = 1.10, P = 0.37	F = 3.12, P < 0.01	F = 2.8, P = .012	F = 2.62, P = 0. 02
Kruskal -Wallis Test, DF = 6, N =159	χ^2 =10.32, P = 0.11	χ^2 = 3.73, P = 0.71	χ^2 =17.63, P = 0.007	χ^2 = 6.16, P = 0.41	χ^2= 16.30, P = 0.01	χ^2 = 11.60, P = 0.07	χ^2 =16.69, P = 0.01
[c]Mean, N = 159	3364±36	8454±43	5795±25	5091±50	1.70±0.02	10.82± 0.17	3.81±0.05

[c]Mean: Combined population mean, when all site data is combined.

There is a highly significant difference in frequency time parameters of initial note of the song. Meghalaya birds have song introductory note significantly lower in frequency than at other places (see Table 4.10) followed by Kedarnath birds. This difference is reflected in lower minimum frequency, lower maximum frequency and lower central frequency of introductory note.

4.3.2.3 Geographical variation in frequency–time parameters and notes: Variation in the above seven frequency-time parameters and song notes was analysed using Principal Component Analysis. The first four principal components (named as PC1, PC2, PC3 and PC4) explain 87% of total variation (see Table 4.7). Low values of the variance in the first components indicate that the original parameters are not highly correlated with each other. Though, number of total notes and song length are directly related, and bandwidth is difference in maximum and minimum frequency.

PC1 has high negative correlation with bandwidth, and the effect is mainly due to decrease in maximum frequency with increase in PC1. PC2 is highly correlated with minimum frequency and central frequency; the latter could be largely as an effect of the first. PC3 has high correlation with total notes (and song length), which implies PC3 increases with song length. PC4 is negatively correlated with distinct notes, implying songs with high PC4 sing with fewer notes, e.g. birds in Shillong.

Table 4.7 PC correlations with original song parameters of *P. reguloides*. Correlation values >0.7 are bold faced.

	PC1	**PC2**	**PC3**	**PC4**
Minimum frequency	0.35	**0.78**	-0.18	0.31
Maximum frequency	-0.69	0.45	0.43	0.18
Central frequency	-0.11	**0.73**	0.14	0.11
Bandwidth	**-0.84**	-0.18	0.50	-0.07
Song length	0.46	-0.35	0.62	0.45
Total notes	0.60	0.08	**0.73**	-0.04
Distinct notes	0.26	0.31	0.29	**-0.84**
% Variance explained	28	23	21	15

Site means of PC scores and individual parameters- minimum frequency, maximum frequency, bandwidth, central frequency, song length and number of distinct notes were regressed with latitude and longitude separately. As shown in Table 4.8 below there was no geographical trend detected except longitudinal trend with PC3 i.e. number of notes or song length. However this effect does not translate to significant effect on mean song length (see Table 4.8 below), and also one significant result in the table is not significant once we do the bonferonni correction.

Table 4.8 Regression of *P. reguloides* site mean song parameters and mean principal component scores with latitude and longitude. F1: Minimum frequency, F2: Maximum frequency, DF: Bandwidth, DT: Song length, CF = Central frequency, N-dist: Distinct notes and PC: Prinicipal component.

		F1	**F2**	**DF**	**DT**	**CF**	**N-dist**	**PC1**	**PC2**	**PC3**	**PC4**
Latitude	R^2	0.16	0.17	0.00	0.30	0.14	0.04	0.13	0.23	0.46	0.07
	P	0.37	0.35	0.95	0.21	0.41	0.67	0.42	0.27	0.09	0.57
Longitude	R^2	0.13	0.24	0.00	0.44	0.22	0.08	0.22	0.30	0.58	0.17
	P	0.43	0.27	0.93	0.11	0.29	0.53	0.29	0.20	<0.05	0.36

For the combined data positive effect of altitude on song length was detected (R = 0.20, P = 0.012) but low value of R suggests that altitude explains very small part of variation in song length. The effect of altitude was further explored for individual sites, which is elaborated below.

Altitudinal variation in song parameters at site level: Song frequency time parameters, when taken together for all sites, do not show altitudinal variation except that song length increases with altitude (0.00010 ± 0.00004 second per meter, P = 0.01, N = 159). When analyzed for individual sites the following patterns were found (also see Table 4.9).

a) Minimum frequency increases with altitude (2.061 ± 0.958 Hz per metre, P = 0.04, N = 21) in Banjar-Jalori, Himachal Pradesh. Central frequency also increases with altitude (1.342 ± 0.513, P = 0.02, N = 21) in Banjar-Jalori and these effects are related as increase in minimum frequency is likely to result in increase in central frequency.
b) Number of distinct notes in song increases with altitude in Yuksom-Tsoka (0.0010 ± 0.0004 notes per meter, P < 0.01, N = 20).
c) Song length increases with altitude in Kedarnath (0.000746 ± 0.000335 second per metre, P = 0.04, N = 21) and decreases with altitude in Singalila-Senchal (_0.000393 ± 0.000171 second per metre, P = 0.03, N = 23).

Table 4.9 Altitudinal variation of song parameters for study sites, P values shown.

	Banjar-Jalori	**Kedarnath**	**Sikkim**	**Singalila Senchal**	**Shillong**	**Eaglenest**	**Mehao**
Dist. notes	0.45	0.66	**0.01**	0.19	0.95	0.07	0.18
Song length	0.93	**0.04**	0.58	**0.03**	0.58	0.30	0.28
Central freq	**0.02**	0.26	0.41	0.13	0.79	0.08	0.59
Min. freq	**0.05**	0.14	0.17	0.93	0.63	0.82	0.15
Max. freq	0.62	0.76	0.21	0.06	0.66	0.11	0.58
Bandwidth	0.35	0.11	0.05	0.10	0.94	0.12	0.50

The above patterns are suggestive but not highly significant, especially when we apply Bonferroni correction to significance levels, but need further testing with more data.

Introductory note parameters: Like song I also analyzed introductory note frequency-time parameters and temporal separation of introductory note from the song. All the frequency time parameters show highly significant difference across sites, but the time-interval between introductory note and rest of the song does not vary across sites (see Table 4.10 below).

Table 4.10 Introductory note parameter means for study sites (with standard errors).

Site	**N**	**I-note gap (sec)**	**Min.Freq. (Hz)**	**Max.freq. (Hz)**	**Bandwidth (Hz)**	**Cent.freq. (Hz)**	**Length (sec)**
Banjar-Jalori	21	0.21±0.02	5973±138	7070±254	1097±231	6288±163	0.030±0.004
Kedarnath	21	0.22±0.03	5564±108	6553±125	989±167	5857±112	0.034±0.005
Sikkim	20	0.21±0.03	5714±133	6998±179	1284±171	6240±199	0.041±0.006
Singalila	23	0.23±0.03	5755±118	6789±199	1035±204	6119±169	0.039±0.006
Shillong	12	0.22±0.03	5450±128	6356±194	906±193	5692±140	0.035±0.005
Eaglenest	35	0.21±0.03	5804±133	6971±236	1166±245	6167±158	0.038±0.005
Mehao	27	0.22±0.03	5867±139	6976±162	1109±167	6227±154	0.041±0.006
F Statistics (6, 152)		F=2.00, P=.0687	F=33.29, P=.0001	F=30.18, P=.0001	F=6.64, P=.0001	F=32.37, P=.0001	F=11.36, P=.0001
Kruskal-Wallis Test, DF=6, N=159		χ^2 = 9.44, P=0.15	χ^2 = 87.41, P< 0.0001	χ^2 = 81.76, P< 0.0001	χ^2 = 32.15, P< 0.0001	χ^2 = 81.68, P< 0.0001	χ^2 = 51.33, P< 0.0001

To study any geographical trend in introductory note song parameters I performed principal component analysis of introductory note parameters (see Table 4.11 for principal component (PC) correlations and variation explained by first three components).

Table 4.11 Correlations of introductory note principal components with original parameters

	PC1	**PC2**	**PC3**
Minimum frequency	**0.79**	-0.55	0.14
Maximum frequency	**0.95**	0.20	-0.21
Bandwidth	0.55	**0.74**	-0.39
Central frequency	0.12	**0.60**	**0.78**
Length	**0.87**	-0.27	0.25
% variance explained	52	27	18

I regressed site means of PC scores and means of original parameters with latitude and longitude. Mean PC scores do not show significant geographical variation (see Table 4.12 below), but PC3 which is highly correlated with central frequency shows a nearly significant trend (Table 4.12). Among the original measurements, the length of introductory note was associated with longitude ($R = 0.75$, $P = 0.05$).

Table 4.12 Regression of site means of introductory note parameters and principal component scores with latitude and longitude. R^2 and P values upto two decimal places shown. See Table 4.8 for abbreviations. R^2 values more than 0.5 are boldfaced.

		Mean F1	**Mean F2**	**Mean DF**	**Mean DT**	**Mean CF**	**Mean PC1**	**Mean PC2**	**Mean PC3**
	R^2	0.24	0.12	0.00	0.32	0.11	0.12	0.44	0.25
Latitude	P	0.27	0.44	0.90	0.18	0.46	0.46	0.10	0.25
	R^2	0.01	0.00	0.01	**0.57**	0.00	0.00	0.31	**0.57**
Longitude	P	0.82	0.97	0.80	0.05	0.97	0.99	0.19	0.05

Summary of geographical variation of frequency-time parameters of *P. reguloides* song: As shown above there is not strong evidence for geographical variation of frequency-time parameters of song. Introductory note does show variation in length with longitude, although that is borderline significant.

4.3.2.4 Song variation among subspecies and population groups: I considered four different groups of taxa within the Himalayan and North-east Indian reguloides, based on past classifications (C1, C2 and C3), and new insights based on the results from this study (C4), and compared how these classifications separate subspecies/populations compared to grouping based on biogeographic classification (C5) in selected frequency-time parameters of song and number of notes. The summary of the geographical distributions of the population groups compared is in fig. 4.9. Only song length, distinct notes in song and central frequency were selected as they show more significant inter-population variation compared to rest of the studied parameters (Table 4.6). The P values of F static and Kruskal Wallis test are given in Table 4.13 and mean values of parameters for first four groupings are given in Table 4.14. As given in Table 4.13 most of the introductory note frequency-time parameters, including central frequency, which is a robust measurement, are significantly different among all groupings, indicating that introductory note is not a good vocalization feature to seaparate different classifications. Hence the song features- length, central frequency and notes of songs separating subspecies/groups have been highlighted below.

1. **Old classification (C1):** According to former classifications (Watson et al. 1986, Ali and Ripley 1987, Rasmussen and Anderton 2005; see Table 4.1 for distribution) three subspecies were recognized to have breeding distribution in India. The subspecies *kashmiriensi*s is thought to be distributed up to Garhwal Himalayas, and subspecies *reguloides* from Kumaon eastwards. My study site Kedarnath is in eastern Garhwal, very close to Kumaon, and based on song syntax, I have treated the taxon here as nominate *reguloides*. The three subspecies differ significantly in song length ($F_{2,156} = 6.71$, $P < 0.01$)). Song is longest in *kashmiriensis* and shortest in *assamensis*.

2. **Recent classification (C2):** Following recent classification (Olsson et al. 2005, Päckert et al 2009) and assuming Meghalaya population to be *assamensis*, there are no significant differences in subspecies in song frequency-time parameters but introductory note parameters differ. Meghalaya birds sing with significantly lower minimum and maximum frequency introductory note than nominate subspecies, which is reflected also in lower central frequency (central freq means 5692 ± 130 and 6154.52 ± 206 respectively, the difference being highly significant: $F_{1,157} = 0.95$, $P < 0.0001$). The bandwidth of introductory notes is also significantly low in Meghalaya birds (see Table 4.10).

3. **Old classification, with ranges modified to incorporate song syntax differences (C3):** If we follow the song syntax differences to differentiate populations, bird songs from Banjar-Jalori, Himachal Pradesh, subspecies *kashmiriensis*, which have five song syntax patterns are different from rest of the populations, which generally have only one. Meghalaya population (possibly *assamensis*) is different in introductory note shape from rest of the Himalayan populations with typical syntax. Rest of the Himalayan populations, have typical syntax. The above three groups also differ in song length ($F_{2,156} = 3.86$, $P = 0.02$ and number of distinct notes in songs ($F_{2,156} = 5.60$, $P < 0.01$) (see Tables 4.10 and 4.13). In this grouping the subspecies are the same as in old classification but distribution ranges of subspecies change, *kashmiriensis* and *assamensis* get restricted to Himachal and Meghalaya respectively and the nominate *reguloides* ranges from Garhwal to Arunachal. Accordingly it has been named as old classification-range modified.

4. **Himachal and rest of the populations (C4)**: This comparison differs drastically in song syntax features, and hence if we ignore song introductory note variations and consider only song syntax, *P. reguloides* can be classified into two groups. These groups are separated by song length which is more in Himachal Pradesh and number of notes which are more in the rest of the populations (see Table 4.13 and Table 4.14).

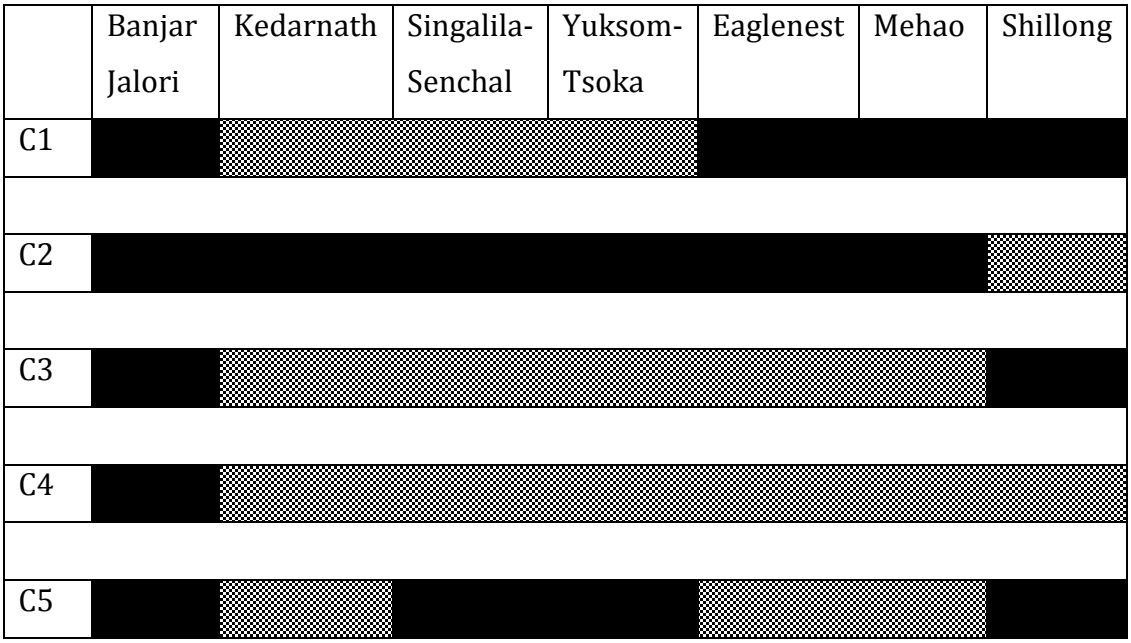

Figure 4.9 Distribution of subspecies and populations grouped in five different ways- C1, C2, C3, C4 and C5 (see text).

5. **Populations grouped according to biogeographic distribution (C5):** If we group populations falling in 5 different biogeographic provinces i.e. Banjar-Jalori in Northwestern Himalayas, Kedarnath in Western Himalayas, Yuksom-Tsoka and Singalila - Senchal in Central Himalayas, Eaglenest and Mehao in Eastern Himalayas, and Shillong in Assam Hills biogeographic provinces, the first, last and the rest have distinct song or introductory note syntax. These populations are separated by significant differences in song length, central frequency and number of notes in song.

   More than one of above classifications yield similar results, and hence syntax is the only criteria which uniquely separates the populations.

Table 4.13 P-values of F statistics and Kruskal-Wallis test for *P. reguloides* subspecies/population groups song and introductory note parameters. The first row pertains to the three subspecies as defined by Ali and Ripley (1987), second row is for two subspecies defined by Olsson et al. (2005), the third row is for Himachal, Meghalaya and combined populations of rest of India separated by song and introductory note syntax differences (see text) and the fourth is for Himachal and the combined rest of India populations differentiated by highly distinct song syntax of Himachal birds. The last row is for populations falling in 5 different biogeographic provinces (Rodgers and Panwar 1987; see Chapter 2).

		Song			**Introductory note**				
		Length	**Cent. freq.**	**distinct notes**	**Min. freq.**	**Max. freq.**	**Band-width**	**Length**	**Central freq.**
C1	F-test	**<0.01**	0.41	0.02	**<0.0001**	**<0.001**	0.99	**<0.0001**	**<0.001**
	χ^2(Kruskal-Wallis)	**<0.01**	0.32	0.04	**<0.0001**	**<0.0001**	0.97	**<0.0001**	**<0.001**
C2	F-test	0.66	0.10	0.08	**<0.0001**	**<0.0001**	**<0.01**	0.16	**<0.0001**
	χ^2(Kruskal-Wallis)	0.77	0.19	0.05	**<0.0001**	**<0.0001**	**<0.01**	0.11	**<0.0001**
C3	F-test	0.02	0.12	**< 0.01**	**<0.0001**	**<0.0001**	**<0.01**	**<0.0001**	**<0.0001**
	χ^2(Kruskal-Wallis)	0.04	0.15	**< 0.01**	**<0.0001**	**<0.0001**	0.02	**<0.0001**	**<0.0001**
C4	F-test	**<0.01**	0.29	**0.01**	**<0.0001**	**<0.001**	0.94	**<0.0001**	**<0.001**
	χ^2(Kruskal-Wallis)	**0.01**	0.19	**0.01**	**<0.0001**	**<0.001**	0.84	**<0.0001**	**<0.001**
C5	F-test	**<0.01**	**<0.01**	**0.02**	**<0.0001**	**<0.0001**	**<0.001**	**<0.0001**	**<0.0001**
	χ^2(Kruskal-Wallis)	0.02	0.01	**0.01**	**<0.0001**	**<0.0001**	**<0.01**	**<0.0001**	**<0.0001**

Table 4.14 Mean values (± s.e.) of frequency-time parameters of subspecies and population groups. C_1a: Banjar-Jalori population (N=21), C_1b: Kedarnath, Singalila-Senchal and Sikkim populations (N=64), C_1c: Arunachal and Meghalaya populations (N=74); C_2a: Himachal population (N=21), C_2b: Kedarnath, North Bengal, Sikkim and Arunachal populations (N=126), C_2c: Meghalaya populations (N=12); C_3a: Himachal to Arunachal populations excluding Meghalaya population (N=147), C_3b: Meghalaya population (N=12); C_4a: Himachal Population (N=21), C_4b: all populations excluding Himachal population (N=138).

West ->east		**Subspecies (Ali and Ripley 1987)**		**Populations with distinct syntax**		**Subspecies recent**		**Himachal and the rest**	
Song	Min frq	C_1a	3263±105	C_2a	3263±105	C_3a	3374±37	C_4a	3263±105
		C_1b	3397±62	C_2b	3393±40	C_3b	3229±154	C_4b	3379±39
		C_1c	3363±49	C_2c	3229±154				
	Max frq	C_1a	8316±121	C_2a	8316±121	C_3a	8447±43	C_4a	8316±121
		C_1b	8443±66	C_2b	8469±46	C_3b	8535±212	C_4b	8475±45
		C_1c	8503±62	C_2c	8535±212				
	Bandwidth	C_1a	5053±152	C_2a	5053±152	C_3a	5073±51	C_4a	5053±152
		C_1b	5046±80	C_2b	5076±54	C_3b	5306±234	C_4b	5096±53
		C_1c	5140±71	C_2c	5306±234				
	Cent. frq	C_1a	5726±59	C_2a	5726±59	C_3a	5807±25	C_4a	5726±59
		C_1b	5782±45	C_2b	5820±28	C_3b	5649±122	C_4b	5805±28
		C_1c	5826±35	C_2c	5649±122				
	Dist notes	C_1a	3.48±0.15	C_2a	3.48±0.15	C_3a	3.8±0.05	C_4a	3.5±0.1
		C_1b	3.92±0.10	C_2b	3.90±0.06	C_3b	3.50±0.19	C_4b	3.9±0.1
		C_1c	3.81±0.06	C_2c	3.50±0.19				
	Song length	C_1a	1.82±0.05	C_2a	1.82±0.05	C_3a	1.70±0.02	C_4a	1.82±0.05
		C_1b	1.73±0.03	C_2b	1.68±0.02	C_3b	1.67±0.06	C_4b	1.68±0.02
		C_1c	1.64±0.02	C_2c	1.67±0.06				
Introductory note	Min freq	C_1a	5973±30	C_2a	5973±30	C_3a	5785±14	C_4a	5973±30
		C_1b	5679±18	C_2b	5754±14	C_3b	5450±37	C_4b	5728±15
		C_1c	5770±23	C_2c	5450±37				
	Max frq	C_1a	7070±56	C_2a	7070±56	C_3a	6901±21	C_4a	7070±56
		C_1b	6777±31	C_2b	6873±22	C_3b	6356±56	C_4b	6828±24
		C_1c	6873±36	C_2c	6356±56				
	Bandwidth	C_1a	1097±50	C_2a	1097±50	C_3a	1116±18	C_4a	1097±50
		C_1b	1098±28	C_2b	1119±19	C_3b	906±56	C_4b	1101±19
		C_1c	1103±26	C_2c	906±56				
	Cent. frq	C_1a	6288±36	C_2a	6288±36	C_3a	6154±17	C_4a	6288±36
		C_1b	6071±28	C_2b	6131±18	C_3b	5692±40	C_4b	6093±20
		C_1c	6112±28	C_2c	5692±40				
	length	C_1a	0.030±0.001	C_2a	0.030±0.001	C_3a	0.038±0.001	C_4a	0.030±0.001
		C_1b	0.038±0.001	C_2b	0.039±0.001	C_3b	0.035±0.001	C_4b	0.038±0.001
		C_1c	0.039±0.001	C_2c	0.035±0.001				

4.3.3 Song recognition

Figure 4.10 shows difference in playback response to control and experiment, lower value indicates greater response. Results show that response to intraspecific playbacks is significantly stronger ($F_{1,82}$ = 8.12, P < 0.0001) than to inter-specific playbacks. Compared to mean intra playback response (1.34 ± 0.17, N = 46) inter-specific responses to *P. xanthoschistos* (1.78 ± 0.31, N = 18), Chinese taxa (*P. claudiae* and P. *goodsoni*) (1.80 ± 0.25, N = 10, response combined because of low sample size) are weak but the weakest response is to *P. trochiloides* (2.83 ± 0.17, N = 6) and *P. occipitalis* (3.00 ± 0, N = 3).

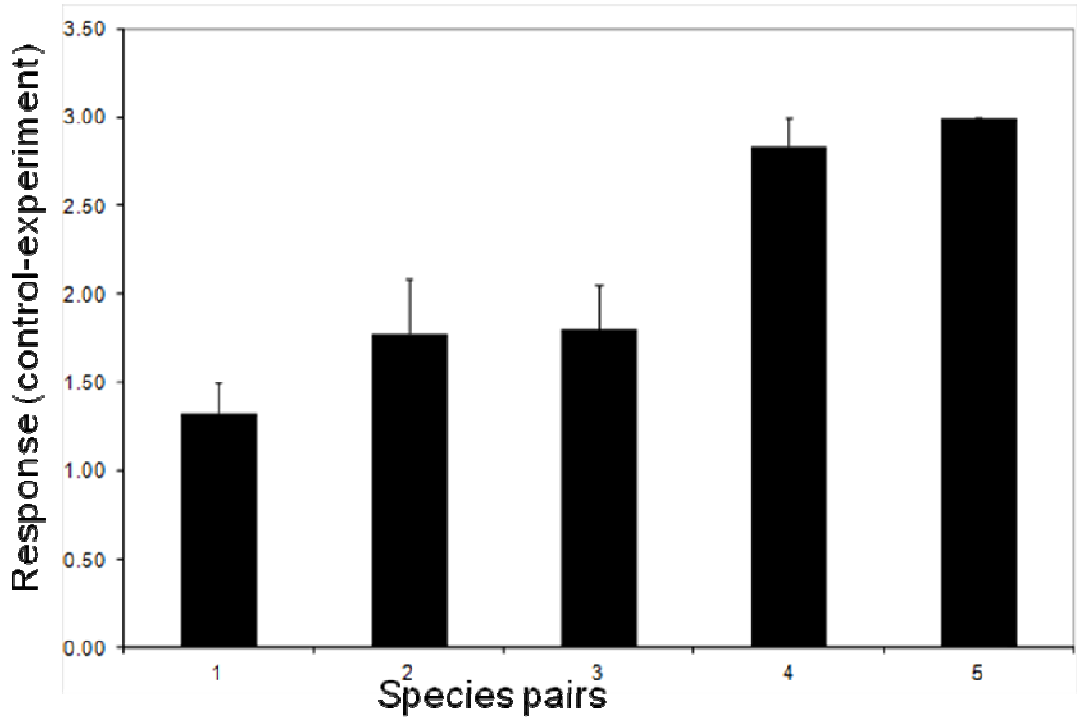

Figure 4.10 Playback responses for intra and inter specific playbacks with standard error bars. "1" on X-axis is for playbacks involving *P.reguloides* species populations (N = 46) ,"2" playbacks involving *P. reguloides* and *P. xanthoschistos* (N=18), "3" is for playbacks involving *P. reguloides* and *P. claudiae* and *P. goodsoni* combined (N = 10), "4" playbacks involving *P. reguloides* and *P. trochiloides* (N = 6) and and "5" is for playbacks involving *P. occipitalis* (N = 3).

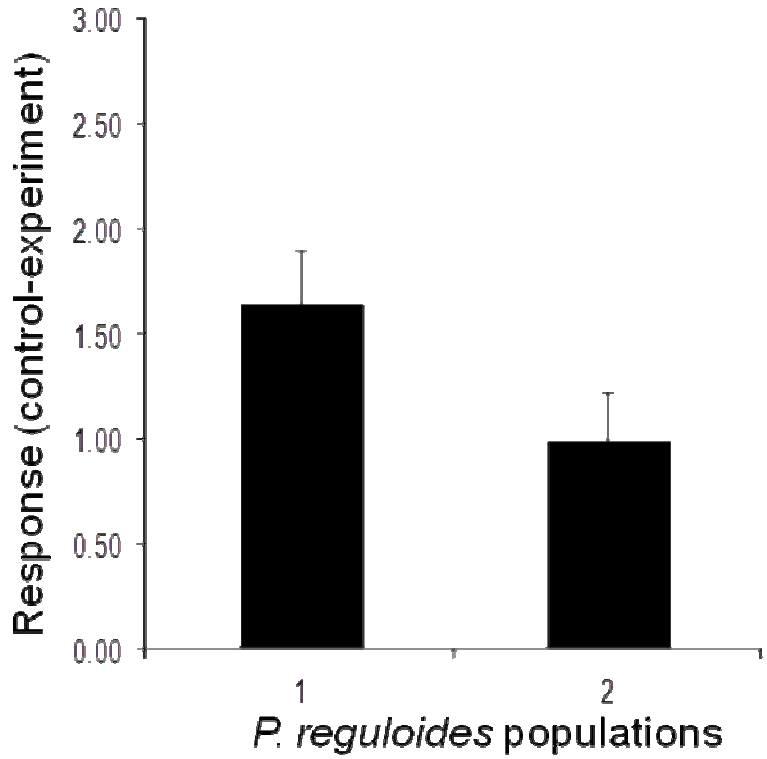

Figure 4.11 *P. reguloides* inter-population song playback responses involving Himachal birds as playback site or song site (left, N = 23) and the rest (right, N = 23) with standard error. Inter-population song recognition is lower in playbacks involving Himachal birds. See Table 2.3 for playback response scoring.

4.4 Discussion

In the above detailed analysis of *P. reguloides* vocalizations I have for first time described the song in detail. *P. reguloides* sings in singing style approximating immediate variety with on average 7.11 songs rendered per minute and 3.36 song types (range 1-6) per bird for combined data. Repertoire size does not vary significantly across sites and geographically. A typical *P. reguloides* song consists of an introductory note followed by repetition of groups of 2 to 4 notes, the most common songs being with three-note repetitions (see Figure 4.8), except in Himachal where birds have different and much complex song syntax.

4.4.1 Song Syntax

As stated above typically a *P. reguloids* sings with an introductory note followed by repetition of note groups (syllables) comprising 2-4 notes. But, the song

syntax of Himachal birds is highly varied and includes song syntax features of other two species of *P. reguloides* superspecies complex i.e. *P. claudiae* and *P. goodsoni*, except an introductory note is added to *goodsoni* like songs. These latter species are distributed in China, geographically closer to other Himalayan populations, e.g. Arunachal birds, which sing only the typical songs. mtDNA sequencing results place the Himachal population close to other Himalayan populations rather than to Chinese taxa (see Figure 4.3). I propose the following possible explanations for atypical *P. reguloides* songs in Himachal Pradesh.

(i) Himachal birds with distinct songs are genetically distinct from rest of the *P. reguloides* populations and the cytochrome b gene is possibly not truly reflecting genetic distance with Chinese taxa (Figure 4.3) (and therefore with other Indian populations). As observed by Martens (2010) that molecular genetic distance values based on just one or two genes among many thousand others, both mitochondrial and nuclear, do not supply the ultimate evidence, or necessarily even the most important evidence, for a relationship at the level of species or below.

(ii) Wintering Himachal birds and Chinese taxa meet somewhere and Himachal birds learn Chinese bird songs. *P.claudiae* is supposed to winter in North-east India (Ali and Ripley 1987, Rasmussen and Anderton 2005) and hence there is possibility of meeting of Himachal *P. reguloides kashmiriensis* with wintering *P. claudiae* somewhere in North-east India.

(iii) Himachal taxa may have had history of variable and unpredictable environment, which according to Botero et al. (2009) may result in selection for higher cognition in birds. Enhanced cognition, in turn, according to Botero et al. (2009) may lead to development of elaborate songs, for example *P. reguloides* may develop complex songs by copying song syntax of closely related adjacently occuring congener *P. trochiloides*. In respect of occurrence of trill and mixing of two song types *P. trochiloides* shares syntax with Himachal *P. reguloides* but differ in other features like lack of introductory notes and highly modulated notes preceding rest of the song (Figure 4.7).

(iv) Himachal population of *P. reguloides* migrates to greater distances compared to other populations, which may be local migrants and the Meghalaya population may even be resident. Greater migratory population may have evolved greater song complexity due to sexual selection by female choice (Collins et al. 2009).

(v) Character displacement in song (Brown and Lemon 1979, Wallin 1986, Mahler and Gil 2009) in areas where *P. occipitalis* and *P. reguloides* share habitat, which happens in Himachal where there is considerable altitudinal overlap in the distribution of both the species. In Himachal Pradesh I found birds of both species occurring adjacent to each other, compared to Kedarnath where there was considerably less overlap in distribution, and the study sites further east do not have *P. occipitalis. P. reguloides* and *P. occipitalis* have similar sounding typical songs, and hence in the areas where there is considerable sharing of habitat with *P. occipitali*s, *P. reguloides* might have evolved songs with different syntax for better species cognition.

(vi) If we look at the three species within the *P. reguloides* superspecies, the northerly *P. claudiae* have complex song syntax. Hence *P. reguloides kashmiriensis* which is the northwestern most population of *P. reguloides* might have retained complex songs from common ancestor whereas populations in the east might have lost those, may be because of more male-male competition there due to higher density (Ghosh 2013), and consequently selection for shorter and simpler song. The phylogeny actually does indicate this scenario, i.e. that reguloides has lost its songs in the south, rather than the northern ones gained them (Figure 4.3). Himachal population has the longest songs, but not too longer than Singalila - Senchal songs from the east.

4.4.2 Introductory Note

All the songs of *P. reguloides* begin with a characteristic hook shaped note. But in Meghalaya birds the left arm of the note is much longer, sometimes longer than right arm, making them v shaped. Such v-shaped notes are rare in Himalayan populations. They are not present in the Myanmar population of *P. reguloides*

assamensis (songs of two birds examined). Nor are they present in Thailand populations of *P. reguloides ticehursti*, but *P. reguloides ticehursti* from Vietnam do have them. These findings indicate that v shape is not a phylogenetic signal but possibly habitat-selected feature or a random variation due to cultural drift.

4.4.3 Geographical Variation in frequency-time parameters

There is no significant geographical variation in frequency-time parameters and number of notes (a measure of song complexity) of *P. reguloides* songs (see Table 4.6) unlike in *P. xanthoschistos,* which has latitudinal pattern of increase in both of these parameters (Chapter 3). In Himachal, song complexity instead increases in terms of song syntax features. Southeast and northwest differences in climatic conditions in Himalayas e.g. in precipitation and temperature variation become less as we go higher in the Himalayas, and climate at higher altitudes (>2500) becomes similar, for example precipitation becomes similar, though there is more snow and less rain in the northwest (Price et al. 2011). Hence, southeast-northwest habitat dissimilarity in *P. xanthoschistos* is expected to be higher than in *P. reguloides*, which occurs higher. For example, leaf densities (based on total leaf intersections of an imaginary pole stretching to the sky) in southeast and northwest were substantially different (189 and 130±15) in *P. xanthoschistos* habitats, but were comparable (173±19 and 166) in *P. reguloides* habitats (Singh and Price, in prep). This could possibly explain absence of geographical variation in *P. reguloides* song parameters.

There is no general altitudinal trend in song parameters except song length increases with altitude, which is apparently because in the west birds occur at higher altitude, as the trend is not supported at individual sites. Only two sites show any altitudinal trend i.e. song length increases with altitude in Uttarakhand but decreases with altitude in North Bengal. Similarly central frequency increases with altitude in Himachal Pradesh, and number of distinct notes in song increases with altitude in Sikkim, but there is no pattern across sites for these parameters. Further detailed studies are needed to see if these site specific effects are real, and if so, what the underlying causes are.

4.4.4 Song recognition

As expected, response to intra-specific playbacks is stronger than response to inter-specific playbacks. Within intraspecific playbacks, the response is poorer where Himachal birds are involved in playbacks, implying that the different song syntax of Himachal birds has a bearing on song recognition.

Among inter-specific playbacks the response was more between *P. reguloides* and Chinese taxa *P. claudiae* and *P. goodsoni* and between *P. reguloides and P. xanthoschistos* playbacks than between other species playbacks. The former is expected, in fact response should have been comparable to intra specific response as *P. claudiae* and *P. goodsoni* share part of song syntax with *P. reguloides*, and they are part of same super species complex. In the latter case high response may be because many of the songs of *P. xanthoschistos,* mostly in the east, resemble those of *P. reguloides*, except they have different introductory notes. In fact in the east, in the area of overlap, *P. xanthoschistos and P. reguloides* are often identified most easily by their different singing styles, eventual versus immediate, rather than by listening to individual song types (pers. observations).

There is no response to playbacks of *P. reguloides* to *P. occipitalis* in the areas of their co-occurance, though the songs of both sound similar (but differ in song syntax features: *P. occipitalis* has 2-3 introductory notes followed by two-note syllable repetition in song, one of the two notes being same as the introductory note) but the sample size is too low.

4.4.5 Song and taxonomy

Among frequency time parameters of song, song length, central frequency and distinct notes separate different population groups. The best separation is achieved in grouping C4 (Himachal and the rest) and C5 (Biogeographical groupings) (Figure 4.9), which are quite different from each other in distribution, except that both treat Banjar-Jalori populations distinct. Hence it seems that frequency time parameters are not good for separating populations in the species. Introductory note parameters separate almost all populations groupings, and hence they too are not good at finding which grouping separates

the subspecies/ populations best. Hence apparently the better song criteria for population groupings is song syntax, and I propose two groups*, kashmiriensis* at Bamjar-Jalori with multiple syntax types, and *reguloides* in the rest of the populations with typical song syntax.

Chapter 5
Inter-specific interactions

5.1 Background

Species are distributed in space within limits, generated by various biotic and abiotic factors (Holt and Keitt 2005). There has been lot of work on range limits of species since Macarthur and Wilson (1967) predicted that future theory would concentrate on boundaries of species distributions (Holt and Keitt 2005). Parapatric distributions, and particularly abutting distributions of species along elevation gradients, have interested researchers for a long time (Cadena 2007). There have been studies of bird distributions along the Andean mountain elevation gradient, which have found a role of interspecific aggression in defining species altitudinal limits of distribution (Terborgh 1971, Terborgh and Weske 1975, Jankowski et al. 2010). In studies on Andean birds Terborgh (1971) and Terborgh and Weske (1975) attributed interspecific competition as a mechanism restricting elevation ranges of large number of birds. Terborgh and Weske (1975) showed that the Andean birds have a minimum of two thirds of species that had their distributional limits attributable to direct or diffuse competitive exclusion. Using hetero-specific playbacks Jankowski et al. (2010) in their study of five species belonging to two genera experimentally showed that interspecific aggression is a mechanism for spacing in tropical mountain birds in Costa Rica. In the Himalayas many congeneric species, during the breeding season, occur at varying altitudes replacing each other e.g. species belonging to *Alcippe*, *Stachyris*, *Phylloscopus* and *Aethopyga gener*a (Price et al. 2011). For example in the eastern Himalaya *Phylloscopus cantator*, *P. xanthoschistos*, *P. reguloides* and *P. trochiloides* occur sequentially along rising elevation gradient occupying abutting (or nearly so) ranges i.e. *P. cantator* occurring at the lowest range is replaced by *P. xanthoschistos* which is replaced by *P. reguloides* in higher areas, which is in turn replaced by *P. trochiloides* (Price et al. 2011). Similarly in the west *P. xanthoschistos*, *P. occipitalis, P. reguloides* and *P. trochiloides* replace sequentially

one another with rise in elevation (Figure 4.2, Chapter 4). One of the mechanisms for altitudinal replacement could be competitive exclusion as reported by Terborgh and Weske (1975) in case of Andean birds.

Study of factors responsible for distribution of birds along mountain gradients have been mostly based on observing distribution patterns e.g. densities, distribution limits and correlating them with environmental variables, ecotones and replacement species (Terborgh 1971, Terborgh and Weske 1975, Price et al. 2011). Robinson and Terborgh (1995) used playbacks to show interspecific territorialty as spacing mechanism among congeneric Amazonian birds distributed along primary succession gradient. Jankowski et al. (2010) for the first time provided direct evidence of interspecific aggression as mechanism for spacing of closely related species along elevation gradient employing inter-specific playbacks. I used the interspecific playback approach to test the role of direct competition in limiting altitudinal distributional ranges in the selected *Phylloscopus* species.

5.2 Method used to study interspecific interactions

I used playbacks of heterospecific song to assess the inter-specific response between selected species that have adjacent altitudinal distributions. A similar protocol (described briefly below), as used for testing inter-population responses of geographically distant populations, was used for this purpose. Heterospecific songs were played using Apple Ipod Nano player and Saul Mineroff Speaker. Responses were noted for 5 minutes. Each test playback was followed by playback of a control. As far as possible different recordings, for the test as well as the control, were used for each playback experiment. Responses were categorized as strong, moderate, weak and no response, and were scored as 3, 2, 1 and 0 respectively (refer to Table 2.2 of Chapter 2). Test responses were deducted from control responses and the differences were averaged for different pairs of species to get response values; higher values, therefore, mean lesser response.

Table 5.1 Details of playback experiments, including responses and number of recordings used. Intraspecific playback experiments are included for comparing with inter-specific playback responses. Abbreviations: N: number of experiments, Pc: *Phylloscopus cantator*, Po: *Phylloscopus occipitalis*, Pr: *Phylloscopus reguloides*, Pt: *Phylloscopus trochiloides* and Px: *Phylloscopus xanthoschistos*.

S. N.	Category	N	Response*	Site	Recordings used			
			Mean ±s.e.		Experiment		Control	
					Numb.	Rec.	Numb.	Rec.
1	Pc-Pc	7	0.43±0.30	Mehao	5	5	0	0
				Namdapha Park	2	1	2	1
2	Pc-Px	5	2.75±0.25	Eaglenest	4	2	4	3
				Samsing	1	1	1	1
3	Px-Pc	5	2.40±0.60	Eaglenest	5	5	5	4
4	Px-Px	45	0.86±0.16	Patnitop-Ramban	7	7	3	2
				Banjar-Jalori	6	5	1	1
				Chakrata	7	7	6	3
				Dhanaulti-Mussoorie	7	6	4	4
				Nainital	6	6	3	3
				Nokrek	9	9	9	5
				Shillong	1	1	1	1
				Eaglenest	2	2	0	0
5	Px-Pr	12	1.83±0.41	Singalila-Senchal	3	2	2	2
				Eaglenest	9	7	8	4
6	Pr-Px	6	1.67±0.49	Samsing	1	1	1	1
				Nokrek	4	4	4	4
				Eaglenest	1	1	1	1
7	Pr-Pr	46	1.33±0.17	Banjar-Jalori	15	15	14	4
				Kedarnath	6	6	2	1
				Singalila-Senchal	2	2	2	2
				Eaglenest	10	9	10	6
				Mehao	7	7	6	4
				Shillong	6	5	6	6
8	Pr-Pt	5	2.80±0.20	Singalila-Senchal	5	5	5	4
9	Pt-Pr	1	3.00	Singalila-Senchal	1	1	1	1
10	Po-Px	4	3.00±0.00	Dhanaulati-Mussoorie	4	2	4	3
11	Pr-Po	3	3.00 ±0.00	Banjar-Jalori	3	3	3	2

5.3 Results

The results of all playback experiments are shown in Figure 5.1 and Table 5.1. As evident from the figure there is response to inter-specific playbacks between *P. xanthoschistos* and *P. reguloides*, though not strong. In other cases the response is weak or none.

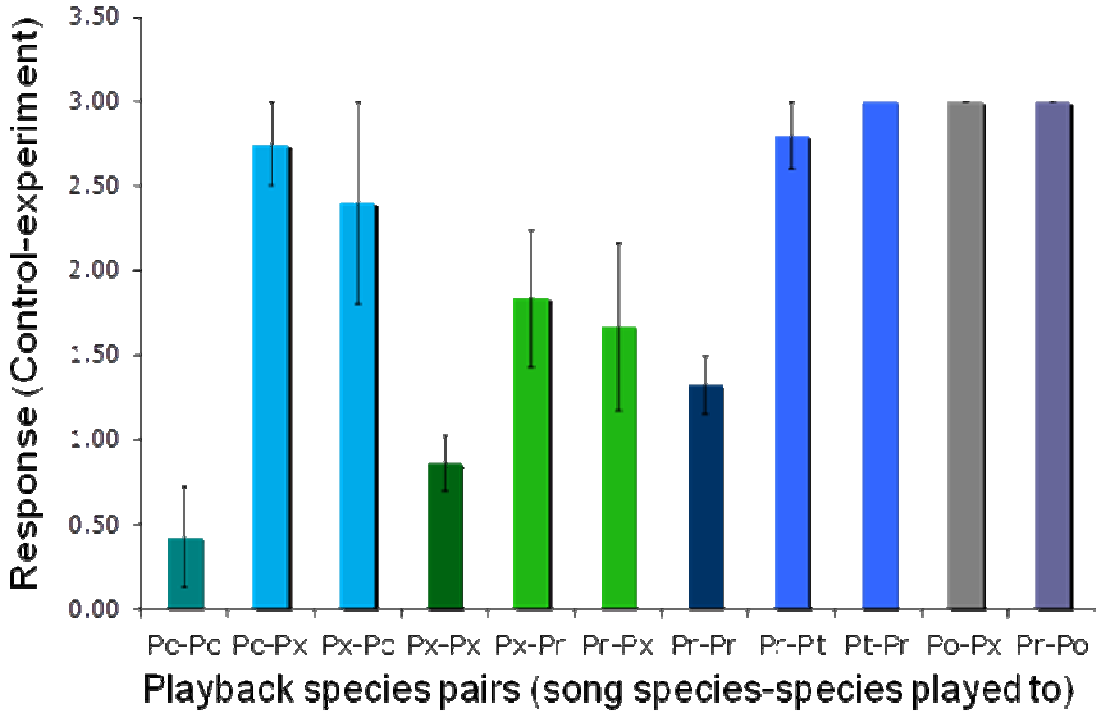

Figure 5.1 Mean values of playback responses (control-experimental) for species pairs and among populations. Pc, Px, Po, Pr and Pt stand for *P. cantator, P. xanthoschistos, P. occipitalis, P. reguloides* and *P. trochiloides* respectively, and recording of the first species in the pair was played to the second species, for example Px-Pr means recordings of *P. xanthoschistos* were played to *P. reguloides*. For sample sizes see Table 5.1 and for scoring see Table 3.2 of Chapter 3.

5.4 Discussion

The results do not support the idea that interspecific aggression based on song recognition is involved in spacing closely related congeners along altitude (Terborgh 1971, Jankowki et al. 2010) for all species pairs except the one i.e. *P. xanthoschistos* and *P. reguloides,* which do respond to each other's playbacks (see Table 5.1 and Figure 5.1 above). The following observations support a role for competitive exclusion in the altitudinal distribution of *P. xanthoschistos*.

(i) Altitudinal distributions in the southeast and northwest

P. xanthoschistos distribution in the northwest extends to higher altitude in Western Himalayas compared to the southeast. In the northwest *P. xanthoschistos*, where it does not encounter *P. reguloides* at its upper distributional limit, goes upto about 2400 m, whereas in the southeast it restricts to about 1600 m in wetter areas, and upto about 2100m in opener, drier areas (Price et al. 2011; Pers. Observations). In the southeast *P. xanthoschistos* stops as low as at 1500 m and *P. reguloides* begins as low as at 1600m in wetter areas (personal observation in Eaglenest Wildlife Sanctuary), but in the drier slopes of the same area *P. xanthoschistos* reaches upto about 2100 m where it is replaced by *P. reguloides*. So it is apparent that in the areas where *P. reguloides* is not present *P. xanthoschistos* goes up substantially.

(ii) Range overlap and interspecific aggression

In their study on Amazonian birds Robinson and Terborgh (1995) found that asymmetrical interspecific aggression is a common spacing mechanism among the congeneric birds having non-overlapping territories. Altitudinal replacements have three types of relative distributions: large overlap of few hundred meters e.g. between *P. cantator* and *P. xanthoschistos*, no or very little overlap as in case of *P. trochiloides* and *P. reguloides* and abutting distribution with very little overlap e.g. between *P. xanthoschistos* and *P. reguloides* in the southeast. In Eaglenest sanctuary I actually found gap in distribution of *P. xanthoschistos* and P. *reguloide*s between 1300-1500 m where none of these species were present, and in the adjacent area outside the sanctuary where opener habitat was available alongside dense forest both existed in a narrow belt of about 100m. It is likely that direct competition is an important mechanism in the last distribution (or abutting distribution is indicator of direct competitive exclusion), for other distributions environmental factors, ecotones or diffuse competition (Terborgh 1971) could be important.

For the results obtained I propose the following explanations.

5.4.1 Role of factors other than interspecific aggression

Terborgh (1971) recognized four types of distribution limits in birds along an elevation gradient in Andes, namely (1) those coincided with natural terminus to elevational gradient, (2) those determined by factors in biological and physical environment varying continuously and in parallel with the gradient, (3) those established by competitive interactions between congeners and (4) those coinciding with vegetational ecotones. In another study Terborgh and Weske (1975) attributed one third of all distributional limits to direct competition between congeners and another one third to diffuse competition. However Romdal and Rahbek (2009) in Tanzania found that elevational limits are poorly correlated with inter-specific competition and vegetational ecotones, and they suggested that interplay among species distribution, species richness and environmental factors needs more consideration. But Jankowski et al. (2010) experimentally demonstrated that song is involved in mediating interspecific competition in the elevational ranges of Neotropical birds. The present study did not find inter-specific aggression (direct competition) based on song as mechanism for deciding distributional limit among selected *Phylloscopus* species, except in *P. reguloides* and *P. xanthoschistos* pair. Hence there could be other mechanisms deciding distributional limits in other *Phylloscopus* warblers e.g. involving competition mediated by resource distribution. These could be (1) vegetation ecotones (2) continuously varying factors in physical and biological environment, or (3) a combination of both decides the distributional limits.

5.4.2 Seasonality and migrations in Himalayas

Himalayas differ from other mountain systems in the tropics, e.g. tropical Andes and Central American mountains, in terms of strong seasonality and consequently Himalayan avifauna shows strong elevational migratory movement. In winter most of the species move to south in the lower altitudes or adjoining plains, and some of them go as far as south India and Sri Lanka, and therefore altitudinal replacements, in breeding season, are not in constant contact throughout the year which could be a factor in interspecific aggression during breeding season. But this may not be the case in respect of *P. reguloides*

and *P. xanthoschistos* in the east where both the species winter in the foothills, and possibly remain in contact of each other, that will also hold true for *P. cantator* which could be in touch with *P. xanthoschistos* in winter, though shows very poor response to inter-specific playbacks. This could be because *P. cantator* and *P. xanthoschistos* are less similar in size than *P. reguloides* and *P. xanthoschistos*, and *P. cantator and P. xanthoschisto*s songs are much less similar in *song* than *P. reguloides* and *P. xanthoschisto*s (see Table 5.2 below). But other species like *P. trochiloides* and *P. occipitalis* migrate to southern areas in the winter, and western *P. reguloides* to the southeast.

Table 5.2 Summary statistics (mean ± s.e.) on songs of 5 *Phylloscopu*s species with their body masses and whole song features.

	@P. trochiloides N=11	*P. reguloides* N=159, 132*	*@P. occipitalis* N=10, 10*	*P. xanthoschistos* N=521,68*	@P. cantator, N=62, 20*
Number of introductory notes	0	1	[1]1(3)	1	[2]1
Presence of repeated Syllables	Yes	Yes	Yes	More in the east, rare in the west	Yes
[3]Sequence repeated syllables	Frequent	Rare	Absent	Absent	Absent
Singing variety	Immediate	Immediate	Eventual	Eventual	Immediate
Mass[$] (gm)	8.1	7.8	9.0	7.03	6
Repertoire	21.8[@]	3.3±0.1	2.2±0.2	9.8±0.3	2.7±0.4
Minimum frequency (Hz)	2937±70	3364±36	3420±153	3040±27	3351±41
Maximum Frequency (Hz)	7755±140	8454±43	8769±247	8957±20	8072±62
Central Frequency (Hz)	5023±82	5795±25	5177±168	5858±14	5935±46
Bandwidth (Hz)	4818±147	5091±50	5348±233	5917±34	4721±69
Song length (Seconds)	1.35±0.05	1.70±0.02	1.94±0.09	1.35±0.01	1.28±0.02
Distinct Note	2.18±0.16	3.81±0.05	2.00±0.00	5.59±0.05	4.90±0.12

" * " indicates sample size for repertoire calculation,@ source: Irwin (2000), $ Mass information kindly provided by T. Price.

[1] *P. occipitalis* repeats introductory note 2-3 times and song itself has introductory note in its repeating syllable,

[2] In *P. cantator*, introductory note often appears 3 times in the rest of the song.

[3] If one syllable contains 3 notes *(abc)* and another 3 notes *(def)* a song may be *abc abc abc def def def*

@ Liz Scordato kindly provided recordings of *P. trochiloides* from Himachal Pradesh, India. I used my own recordings of *P. cantator* from Samsing in North Bengal and Eaglenest in Arunachal Pradesh, and of *P. occipitalis* from Patnitop in Jammu and Jalori Pass in Himachal Pradesh.

5.4.3 Song similarity

Song similarity is apparently greater between *P. reguloides* and *P. xanthoschistos* as they have more over all similarity in song syntax and frequency-time parameters of song (see Table 5.2), and this could account for their greater responses.

In the conclusion it is likely that many factors are acting in spacing the closely related *Phylloscopu*s species along elevational gradient, and the present study detected interspecific agression mediated by song only in *P. xanthoschistos* and *P. reguloides* pair.

Chapter 6
Synthesis and Conclusions

In this study I have described the songs of *Phylloscopus xanthoschistos* and *Phylloscopus reguloides* in detail including their geographical variation within Indian limits. *P. xanthoschistos* sings with songs of 1.35 second mean length, between the mean maximum and minimum frequencies of 8957 and 3040 Hz and with 5917 Hz mean bandwidth, whereas *P. reguloides* sings with 1.70 second mean song length, with 5091 Hz mean bandwidth between the mean frequencies of 8454 and 3464 Hz (also see Table 5.2 of Chapter 5). Both the species sing with an introductory note, which is quite variable in *P. xathoschistos,* but stereotyped hook or v shaped in *P. reguloides*. The birds differ in whole song features as well, *P. xanthoschistos* sings with eventual variety with mean repertoire size of 9.81 song types and *P. reguloides* sings with approximately immediate variety with mean repertoire size of 3.34 song types. The above mean values are for the combined data of all study sites.

The patterns of geographical variation in the songs of the two *Phylloscopus* species do not match and therefore do not easily yield to northwest-southeast generalizations except that they both have the most complex songs in the northwest. *P. xanthoschistos* shows variation in song syntax and frequency-time parameters of song. Northwestern birds have more complex songs with wider bandwidth and more note types, whereas southeastern birds have simpler but longer songs with narrower bandwidth and fewer note types, which they often repeat in song. No such geographical pattern was detected in *P. reguloides* songs, but the northwestern most birds increase their complexity by singing songs with 5 different syntax types, in comparison to just one typical song syntax type in rest of the populations. The salient features of the findings are described and discussed below, alongwith suggestions for further research.

6.1 Song features, their geographical variation, and comparison of *P. xanthoschistos* and *P. reguloides*

6.1.1 Song Syntax

Both the species have songs that begin with an introductory note. Both the introductory note and rest of the song syntax features, including their geographical pattern differ in these species, which is described below.

6.1.1a Introductory Notes

Song of *P. reguloides* begins with an introductory note, which is generally hook shaped except in Meghalaya population where it changes to v shaped. The study shows that *P. xanthoschistos* sings with introductory notes, which unlike introductory note in *P. reguloides* are quite variable. An individual usually has a few different introductory notes in its repertoire of song types and a population of more than 20 individuals has about 10 different introductory notes. Unlike *P. xanthoschistos* songs, which are not shared among individuals separated by a few kilometers, introductory notes are less variable and populations separated by 100 km or more have some of the introductory notes in common. It has also been found that introductory notes in southeastern populations of *P. xanthoschistos* run into songs of northwestern populations making northwestern songs more complex. The following questions emerge from the above findings.

1. Why *P. xanthoschistos* has set of many introductory notes as compared to P. *reguloides,* which generally has a hook shaped introductory note?
2. Why introductory notes in southeastern populations run into the songs of northwestern populations? Is this a mechanism of increasing song complexity in other species too?

6.1.1b Song structure

P. xanthoschistos has variable song structure and the main variation is in the repetition of notes/set of notes in the song. There is geographical pattern associated with this song structure. *P. xanthoschistos* songs in the southeast have considerable note-group (syllable) repetition whereas birds in the northwest

have hardly any syllable repetition. The song of *P. reguloides* has repetition of set of notes for most part of its distributional range, the exception being Himachal populations where songs with trills and with some complex notes are added to the repertoire while also retaining the typical songs. The later song syntax features in in *P. reguloides* are similar to songs of Chinese taxa *P. goodsoni* and *P. claudiae*, and, somewhat, also to *P. trochiloides*. The above song structure variations patterns can be attributed to the following (see also chapters 3 and 4).

(i) *P. xanthoschistos* experiences noisy environment in the southeast and to communicate effectively birds repeat set of notes, and also sing with eventual variety. For *P. reguloides* there are not as much east-west differences in the environment as for *P. xanthoschistos,* which occurs at lower elevation, possibly resulting in less selection for within song variation in *P. reguloides*.

(ii) *P. reguloides* from Himachal is genetically different from *P. reguloides* in rest of Himalayas, and phylogeny based on the mtDNA cytochrome b gene does not capture this difference (see Figure 4.3 in Chapter 4).

(iii) There is character displacement in *P. reguloides* song in the areas where it has overlapping distribution with its close relative *P. occipitalis. P. reguloides* has complex syntax songs for better recognition in the western most areas where it has overlapping distribution with *P. occipitalis*, which has similar sounding songs as typical *P. reguloides*, to avoid hybridization with *P. occipitalis*.

(iv) The northwestern most population of *P. reguloides* might have retained complex songs from common ancestor whereas populations in the east might have lost those, the phylogeny also does indicate that reguloides has lost its songs in the south, rather than the northern ones gained them.

6.1.2 Frequency-time parameters of song

Mean value of frequency-time parameters of selected *Phylloscopus* species are given in Table 5.2. As listed in the table *P. xanthoschistos* sings with higher bandwidth, lower minimum and higher maximum frequencies but with similar central frequency as *P. reguloides*. Frequency and time parameters show following geographical variation.

a) P. xanthoschistos has higher bandwidth in the west (north) than in the east (south).

b) *P. xanthoschistos* has longer songs in the east than in the west.

Higher bandwidth in *P. xanthoschistos* in the west is accompanied by use of more notes. Both are indicative of high song complexity. Longer songs in the east can be attributed to the noisier environment in the east (see Chapter 3).

These differences are not significant in case of *P. reguloides*.

6.1.3 Whole song

The following are the salient differences in the whole songs of *P. reguloides* and *P. xanthoschistos* (see Table 5.2 in Chapter 5 and refer to whole song sections in Chapters 3 and 4).

(a*) P. xanthoschistos* has much higher repertoire than *P. reguloides*.

(b*) P. xanthoschistos* generally sings with eventual variety (serial redundancy) and *P. reguloides* sings with immediate variety.

Eventual variety of whole song in *P. xanthoschistos* is discussed below in the light of current hypotheses.

Serial redundancy in *Phylloscopus xanthoschistos*: Redundant serial signals are common and continued repetition of the same signal is employed to increase the likelihood of detection and correct identification of the signal (Bradbury and Vehrencamp 2011). It is common for birds with small repertoire to sing with eventual variety (Catchpole and Slater 2008), but this has not been observed in case of two study species. *P. xanthoschistos* sings with eventual variety but has larger song repertoire (mean = 9.81, s.d. = 2.66, N = 68) than *P. reguloides* (mean = 3.34, s.d. = 0.84, N = 132) which sings with approximately immediate variety. Anti-exhaustion hypothesis (Lambrechts and Dhondt 1988) argues that singing of the same song type leads to neuro - muscular fatigue and hence production of long singing bouts becomes difficult and switching to different song type with different muscular contraction allows maintaining high singing rate. Brumm and

Slater (2006) showed that redundancy in Chaffinch song increases with increase in environmental noise, and they questioned the validity of anti-exhaustion hypothesis.

In a recent review of repetition in bird song Price (2013) explains signal redundancy as a consequence of inter-sexual selection. According to this view males increase their detectability of the signal, which elicit favourable female response, by increasing song redundancy as well as intensity and distinctiveness. Female's response should select for song redundancy feature where females have high response thresholds to male song. Female response threshold can be influenced by many factors including environment noise as well as mating system, e.g. monogamy and polygyny. Environment noise is likely to be more in *P. xanthoschistos,* which occurs lower and in more species rich environment leading possibly to high song redundancy. Within a species signal redundancy at the level of syllable (group of notes in a song) has been found to be common in *P. xanthoschistos* in the noisy east and almost absent in the far west (see Chapter 3).

Non-repetition (or very rare repetition) of song types in *P. reguloides* could be because it breeds in less noisy environment, where species number and densities are lower. Among the five closely related *Phylloscopus* species distributed along elevational gradient two species, *P. xanthoschistos* and *P. occipitalis*, sing with eventual variety (Table 5.2). These are the species that occupy the breeding elevational zones with highest species richness in the Himalayas (Price et al. 2011).

6.1.4 Song Complexity

Song complexity as measured by bandwidth and number of distinct notes in song increases to the northwest in *P. xanthoschistos*. *P. reguloides* does not show such pattern, but it shows songs with five distinct song syntax types in the extreme northwest of its distribution, instead of just one in the rest of the sites (see section 4.3.2.1 in Chapter 4). So the complexity in the vocalization of the two species in the northwest is achieved in two different ways.

6.1.5 Song recognition among populations

There was inter population song recognition in both *P. reguloides* and *P. xanthoschistos* as shown by playback responses, though responses to songs of local and neighbouring populations were stronger (see Figure 3.10 in Chapter 3 and Figures 4.10 and 4.11 in Chapter 4). This corroborates the fact that these Himalayan populations have not diverged much as they have not been separated for a sufficiently long time (see Figure 4.3 in Chapter 4 for *P. reguloides* phylogeny). In *P. reguloides* there is a tendency for a stronger response to within region playbacks than between region playbacks (Mean ± s.e. values 1.14 ± 0.26, N = 22 and 1.48 ± 0.23, N = 26 respectively, lower value means stronger response, see Chapter 3 and 4) but the difference is not significant ($F_{1,49} = 0.94$, P = 0.34). In *P. xanthoschistos* there is also a tendency for a stronger response to within region playbacks than between region playbacks (Mean values 0.71 ± 0.26, N = 7 and 0.89 ± 0.23, N = 38 respectively) but again the difference is not significant ($F_{1,42} = 0.15$, P = 0.697).

6.2 Interspecifc competition

There was very poor response to interspecific playbacks among closely related altitudinally replacing *Phylloscopus* warblers, except moderate response between *P. reguloides* and *P. xanthoschistos* pair. Elevational distribution ranges of *P. xanthoschistos* in the southeast and northwest indicate support for competitive exclusion of *P. xanthoschistos* by *P. reguloides* in the southeast. The results indicate that other mechanisms in addition to interspecific aggression in some species could be important in altitudinal spacing of closely related species. Interspecific playbacks for other closely related species distributed along elevational gradient can provide general picture of role played by interspecific aggression as shown in tropical mountains of Costa Rica by Jankowski et al. (2010). Though Himalayan mountain system is quite different from tropical Andes and Central American mountains, say in terms of seasonality of climate, which influences migratory behaviour and may also have bearing on species interactions during breeding. Altitudinally replacing groups differ in many respects e.g. migratory behaviour, biogeographic history, ecological

requirements, and hence its likely that other mechanisms like environmental factors, ecotones and diffuse competition (Terborgh 1971, Terborgh and Weske 1975) may also be playing an important role in limiting distribution of species in the Himalayas.

6.3 Song diversity in related *Phylloscopus* species

Phylloscopus species though look quite similar in appearance but vary markedly in song features. As shown above two closely related species differ in many aspects of song. On comparison song features of five closely related, altitudinally replacing species i.e. *P. trochiloides*, *P. reguloides*, *P. occipitalis*, *P. xanthoschistos* and *P. cantator*, show large differences in both whole song and song type features (see Table 5.2). For example in song type parameters, *P. occipitalis* has the simple song with only 2 notes, whereas *P. xanthoschistos* has 5.59 mean number of notes; *P. occipitalis* has the longest song with 1.94 second mean length whereas *P. cantator* has the shortest song with1.28 mean song length, Bandwith ranges from 4721 Hz (*P. cantator*) to 5917 *(P. xanthoschistos*), and central frequency shows increase from 5023 Hz in *P. trochiloides* to 5935 Hz in *P. cantator*. Similarly, repertoire size varies from 2.2 song types in *P. occipitalis* to 21.8 song types in *P. trochiloides*, and singing variety from eventual in two to immediate in three. The present study can provide some help in understanding the great song diversity that exists in *Phylloscopus* species.

6.4 Conclusions

The study has analyzed songs of *P. reguloides* and *P. xanthoschistos* and their geographical variation covering varied aspects like whole song, repertoire, singing variety, number of notes in song, introductory note, frequency-time parameters, song syntax.and intraspecific and interspecific song recognition. It is the first study of song variation along Himalayas covering wide geographical range and song features stated above.

Podos and Warren (2007) have outlined five scenerios for geographical variation of song namely cultural drift, genetic drift, cultural selection, natural selection, and sexual selection. Mahler and Gil (2009) found that similarity due to common ancestry, acoustic adaptation to the habitat, sexual selection, and morphological constraints play a role in shaping different aspects of the song of *Phylloscopus* warblers like in other groups of birds. Biogeographic histories of the taxa may also be crucial in shaping the songs we hear today.

The study attempts to explain geographical variation but bird song is remarkably difficult phenomenon to capture in quantitative measurements (Kroodsma, 1977). So the study raises many questions, some of which I have attempted to answer, but still many remain unanswered.

6.5 Suggestions for further research

The present study has brought out song variation patterns in two in-depth study species, and I have attempted to explain these patterns based on the current hypotheses. These explanations need verification by further comparative and experimental studies, so that we can have better understanding of complex phenomenon of song development. In particular I propose following studies.

(i) Noisy environment and signal redundancy

Song repetition is attributed to singing in noisy environment and inter-sexual sexual selection. But it has not been tested in many species and it is not clear, for example, why P. *xanthoschisto*s and *P. occipitalis* sing with eventual variety whereas *P. cantator* and P. *reguloides* do not. A comparative study of the *Phylloscopus* genus with respect to song repetition pattern, noise level in habitat and some measure of sexual selection intensity e.g. extra pair paternity, will help in better understanding of significance of singing patterns. Manipulative playback experiments with changing song repetition patterns can experimentally test the role of song repetition patterns in communication in breeding

birds. Similarly repetition of syllable within song can be studied in a group of species, along with suitably designed playback experiments.

(ii) Himachal population of *P. reguloides*

An important finding of the study is atypical songs of *P. reguloides* in Himachal Pradesh (Banjar-Jalori site) resembling Chinese taxa. I have attempted to explain this finding based on some selected hypotheses. It would be worthwhile to devise study to investigate alternate explanations, so that we can have a better understanding of the phenomenon of song development in *P. reguloides* in particular, and songbirds in general.

(iii) Introductory notes in *P. xanthoschistos* song

Many species have introductory notes, but to my knowledge *P. xanthoschistos* is the only example of a species having multiple introductory notes, associated with different song types. Species differ in occurrence pattern of introductory note, e.g. in *P. occipitalis* occurs two to three times in the beginning of song and it makes one note of the two-note song syllable, in *P. reguloides* it is typical hook or v shaped and never occurs in the song, in *P. cantator* it can sometimes run up to three times in the song, in *P. xanthoschistos* introductory note is variable and an eastern population introductory note is often found in the beginning of rest of the song in the west, and *P. trochiloides* does not have an introductory note. I suggest a comparative study of presence and pattern of occurrence of introductory notes in a group of species, e.g. *Phylloscopus* species, mapped onto their habitat features and phylogeny, along with study to check their function using playbacks with manipulated songs with different introductory notes and without them.

(iv) Study of competitive exclusive in other altitudinal replacements

Most of the Phylloscopus species are long distance or altitudinal migrants. There are many group in the Himalayas which are not long distance migrants, and may be year round in contact with closely related

congeners distributed adjacently along altitudinal gradient e.g. *Alcippe* spp*, Pnopyga* spp*, Yuhina* spp, *Spelaeornis* spp. Study of such groups may provide better understanding of distribution of Himalayan avifauna.

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