CHAPTER 2
LITERATURE REVIEWS

Bird song is widely accepted for their complex vocalizations (Price *et al*., 2007; Catchpole and Slater, 2008), and songs differ greatly between species. In general, songs could be referred to the vocalizations that tend to be long, consist of a number of distinct sections which are spontaneously produced, and usually have a characteristic of diurnal rhythm. Songs are usually produced by males in the breeding season for most in temperate birds (Marler, 2004; Catchpole and Slater, 2008). In the tropics, it has been reported in several tropical birds that songs are common for females to sing as well as males (Mennill and Vehrecamp, 2005; Valderama *et al*., 2007), and both sexes may do so throughout the year even though breeding only occurs during a restricted period (Langmore, 1998).

Bird song is important in territory defense and mate attraction and, as consequence, it is important in speciation as a pre-mating isolation mechanism (Grant and Grant, 1996; Slabbekoorn and Smith, 2002; Catchpole and Slater, 2008). Differences in vocalizations can serve to distinguish between different individuals (e.g. Brooks and Falls, 1975), different populations (e.g. Koetz *et al*., 2007; Petrusková *et al*, 2010), or different species (e.g. Kirschel *et al*., 2009; Tobias and Seddon, 2009). These differences arise due to many factors; for example, vocal differentiation can result from differences in habitat (Slabbekoorn and Peet, 2003; Wood and Yezerinac, 2006), morphology (Podos, 2001), and through spontaneous changes during the process of learning or cultural drift (Grant and Grant, 1996).

The species recognition hypothesis proposes that species-specific features persist in a particular form because they function as isolation mechanisms (Dobzhansky, 1937; West-Eberhard, 1983). Species recognition provides mechanisms for production and reception of species-specific signals, acting as inter-specific barriers between members of different adapted populations. Species recognition demonstrates that these selections favor distinctive traits in two ways; 1) increased intra-specific compatibility by signal stereotypes (e.g. Seddon, 2005), 2) inter-specific interaction emphasizing reproductive isolation mechanisms (e.g. Sætre *et al*., 1997; Kirschel *et al*., 2009). Therefore, understanding species recognition of sympatric

populations is an important question, however few studies have tested this hypothesis, particularly for widespread sympatric species in the tropics.

Distinctive features of song enable birds to recognise each other as the same species and to make appropriate mate choice and territory defense decisions (Slabbekoorn and Smith, 2002; Grether *et al*., 2009). Several previous studies suggest that assortative mating based on song can help to maintain population boundaries and lead to further speciation by preventing interspecific hybridization (Patten *et al*., 2004; Ruegg, *et al*., 2006). Song may be influenced by interspecific competition between different species, particularly for species which live in sympatry and share the same habitat. Consequently, species recognition based on song structure could be important in enabling two species to coexist by minimizing interspecific conflict. Sympatric species may show acoustic convergence for some signals, and divergence in other signals (e.g. Tobias and Seddon, 2009). As a premating isolation mechanism, species-specific song should reinforce recognition between closely related species or, at a minimum, differentiate between similar species to limit hybridization; otherwise confusion in communication would reduce the fitness of both sender and receiver (Price, 1998; Beckers and Ten Cate, 2001; Slabbekoorn and Smith, 2002; Kirschel *et al*., 2009).

The *Pycnonotus* bulbuls (Aves, Pycnonotidae) are a biodiverse group of small passerines comprising 45 species, many of which live in areas of sympatry and share common food resources (Fishpool and Tobias, 2005; Woxvold *et al*., 2009). They are Asiatic birds, and they are understood to be distinct from their African counterparts based on molecular research (Pasquest *et al*., 2001; Moyle and Mark, 2006). Their distribution is widespread throughout Asia, especially in the tropical forests of South Asia and Southeast Asia where vegetation diversity is very high (Fishpool and Tobias 2005). They are nonmigratory arboreal frugivores and live in various types of habitat, including scrub, bamboo, deciduous, broadleaf evergreen, and coniferous forest. Bulbuls are a dominant frugivorous songbird in Southeast Asia, foraging mainly on a variety of plant foods (leaves, ripe or unripe fruit, and nectar; (Corlett, 1998; Kitamura *et al*., 2002; Wydhayagarn *et al*., 2009) and, very rarely, animal foods (insects and small lizards; Bhatt and Kumar, 2001). They play an important role as seed dispersers in both mature and secondary forest (Corlett 1998; Kitamura *et al*.

2002; Wydhayagarn *et al*. 2009). Bulbuls often assemble in mixed-species flocks and feed together on highly productive fruit plants, especially when fruits are abundant (Sanitjan and Chen, 2009; Wydhayagarn *et al*., 2009; Sreekar *et al*, 2010). Group size during the non-breeding season may contain as few as 10 individuals or as many as several hundred individuals. Smaller flocks, or pairs of birds, occur during the breeding season.

The genus *Pycnonotus* includes many highly vocal species. They are capable of producing a broad variety of sounds (Fishpool and Tobias, 2005), although most of their sounds have only been described anecdotally, without any quantitative bioacoustic detail. A few species have been studied in some detail. For example, Red-vented Bulbuls produce six types of vocalization based on variation in context (Kumar and Bhatt, 2000), and sing a stereotypic song (Kumar, 2004). Many birds in this genus produce melodious, complex vocalizations that are aesthetically appealing to humans; consequently, many species have become popular cage birds. For example, the wild population of Straw-headed Bulbuls (*P. zeylanicus*), which may have the most melodious song of the genus, is in extreme decline and may soon be extirpated from Thailand due to both the cage bird trade and habitat loss (Fishpool and Tobias, 2005). Similarly, the Red-whiskered bulbul (*P. jocosus*) is prized as a cage bird that competes in song contests, and, consequently, it has become one of the most threatened species in Thailand. Traded around the globe, Red-whiskered Bulbuls have established populations in non-native habitat after caged birds have escaped; self-sustaining populations are now found in California, Florida, Java and Sumatra, Malaya, Australia, Mauritius and Hawaii (reviewed in Amiot *et al*., 2007).

In this study the acoustic features of the songs of six sympatric *Pycnonotus* bulbul species are investigated. Detailed bioacoustic analyses of the songs of all six species are quantified to evaluate whether these species are distinguishable on the basis of song, particularly between pairs of species with similar plumage characters. These species provide an interesting system for evaluating acoustic divergence because they overlap in range and often associate in mixed-species flocks, yet they have not received detailed acoustic descriptions or systematic acoustic comparisons. All six species are closely related, based on molecular data (Pasquest *et al*., 2001; Moyle and Mark, 2006), and field observations confirm that all six species produce

songs while defending resources from both conspecific and heterospecific animals at flowering and fruiting trees. Based on the expectation that songs convey species-specific information, song differentiation should occur between sympatric species, and that the most closely-related species – where hybridization should be most likely – should be distinguished by the greatest differences in song structure. Further prediction is that vocal distinctiveness would be highest between species that are most often encountered in flocks together. To investigate whether song differences are predictable and influence species evolution; the most apparent sources of selection can be considered as morphological (Podos, 2001; Martin *et al*., 2011) and genetic divergences (Irwin, 2000; Price *et al*., 2007). Therefore, it is expected that *Pycnonotus* songs vary corresponding with morphology and/or genetics. The species songs descriptions may be valuable for Bulbul conservation and application for population estimates programs.