

COMPARATIVE PHYLOGEOGRAPHY OF
FOUR MONTANE BIRD SPECIES IN
SABAH, MALAYSIAN BORNEO

A Thesis

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ABSTRACT

Because of a dearth of modern quantitative studies of the ecology and evolution of birds, our understanding of the biogeography of the Bornean avifauna is rudimentary. Although paleogeographic evidence provides a well known mechanism for speciation in the lowlands of Borneo (i.e., repeated colonization and isolation of populations on Sunda islands caused by sea level changes), the process of speciation in montane areas is less easily explained. Knowledge about the processes responsible for montane speciation in Borneo is desirable because mountains clearly have played a key role in the evolution of the island's avifauna, as evidenced by the relatively large number of montane endemics (25 of Borneo's 39 endemic bird species are montane). To provide insight into the dynamics of montane speciation in Borneo, I examined the phylogeographic relationships of selected populations of four species across five sites in the mountains of Sabah, Malaysian Borneo. To determine the connectivity of bird populations among these sites, I compared DNA sequences of the second and third subunits of the mitochondrial nicotinamide adenine dinucleotide dehydrogenase gene of four species that have populations at all the sites: Streaky-breasted Spiderhunter (*Arachnothera affinis*), Temminck's Babbler (*Pellorneum pyrrogenys*), Grey-throated Babbler (*Stachyris nigriceps*), and Ochraceous Bulbul (*Alophoixus ochraceus*). Divergence among populations at the five sites was very low, but interesting genetic patterns were still evident. The spiderhunter, which is distributed in both lowland and highland areas, showed no phylogenetic structure among its populations, as would be expected of a vagile species that is not restricted montane areas. For *P. pyrrogenys* and *S. nigriceps*, the most geographically distant population was phylogenetically distinct from all others. This isolation-by-distance pattern is reasonable for these small babblers, which are restricted to high elevations and assumed to be poor dispersers. The bulbul displayed the most

interesting pattern. Its population in western Sabah near the Sarawak border was distinct from all others. Because this bulbul is presumed to be a good disperser and thus capable of moving among all the localities, this result suggests that the Lumaku birds represents a group with closer genetic ties to Sarawakian mountain populations than to Sabahan populations.

CHAPTER 1 INTRODUCTION

Background Information

Borneo is the third largest island in the world, covering some 743,330 km², an area slightly larger than Texas. It is the largest of the five main landmasses on the Sunda shelf of Southeast Asia, the others being the Malay Peninsula, Sumatra, Java and Palawan. Borneo is also the only island in the world divided among three different countries (Fig. 1.1): Negara Brunei Darussalam, commonly called Brunei, which occupies roughly 5,760 km²; Indonesia,



Fig. 1.1. The Malay Archipelago, with depictions of the Sunda Shelf and Wallace's Line. The map derives from data included with ArcView GIS 3.2 (©-Environmental Systems Research Institute, Inc. Redlands, CA).

occupying the largest portion of the island at 539,460 km²; and Malaysia, which occupies approximately 198,160 km². Indonesian Borneo, called Kalimantan, dominates the southern two-thirds of the island. Malaysian Borneo consists of two states, Sabah in the northeast and Sarawak in the northwest. Together these Malaysian states surround Brunei on the northwest coast.

Sabah, formerly known as British North Borneo, is 73,371 km² in area and represents about 10% of Borneo. It lies close to the equator, between about 4°10'N and 7°30'N and, thus, has a classic tropical climate. Although there are mild annual rainfall shifts caused by the Indo-Australian monsoon system, the state does not experience a dry season and accumulates from 200-400 cm in rainfall per year (Chatfield 1972, MacKinnon et al. 1996). Physiographically, Sabah consists mainly of low rolling hills and flat lowlands in its central and eastern parts (Fig. 2). Forest in these areas is dominated by trees in the family Dipterocarpaceae, but there are also extensive swamps and mangroves near the east coast, as well as smaller areas of forest growing on limestone, sand (kerangas forests) and ultrabasic (ultramafic forests) soils in the interior (Whitmore 1984, MacKinnon et al. 1996). In the western part of Sabah, the topography becomes more mountainous (Fig. 1.2). This area includes Mt. Kinabalu, a World Heritage Site and the

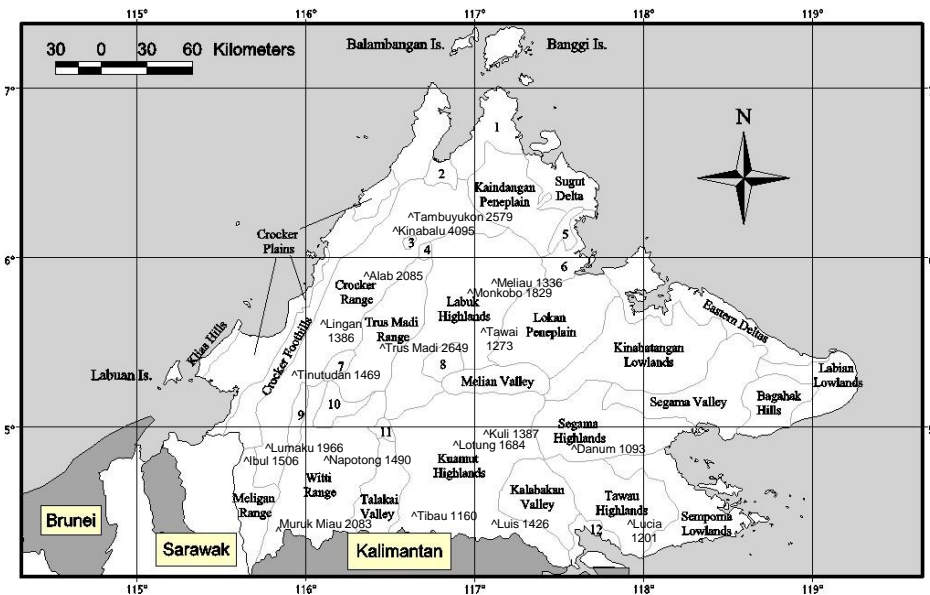


Fig. 1.2. Physiographic regions of Sabah from Collenette (1963). (1) Bengkoka Lowlands, (2) Bandau Plain, (3) Pinosuk Plain, (4) Ranau Plain, (5) Bongaya Hills, (6) Labuk Delta, (7) Keningau Plain (8), Mananam Plain, (9) Tenom Plain, (10) Sook-Dalit Plain, (11) Penawan Plain, (12) Cowie Delta. ^ Marks prominent peaks.

highest mountain in Southeast Asia at 4,095 m, as well as a series of mountain ranges with elevations from 500 to 2600 m. These mountains display a range of habitats, depending upon elevation, slope, aspect, and soil type.

Sabah has a relatively small human population of about 2.5-3.0 million (<http://www.ids.org.my/stats/Population/index.htm>). Most of these people live in or near the major towns of Kota Kinabalu, Sandakan, Lahad Datu, and Tawau (Fig. 1.3) and in more rural areas along the west coast and in the western mountain valleys. Relatively few people live in the interior lowland areas that comprise most of the central and eastern parts of the state. Despite this small population, the forests of Sabah have suffered severe degradation from logging and plantation development over the last 30 years. Although forest is reported to cover about 44,000 km², or approximately 60% of Sabah (Sabah Forestry Department 1999), this “forested” area

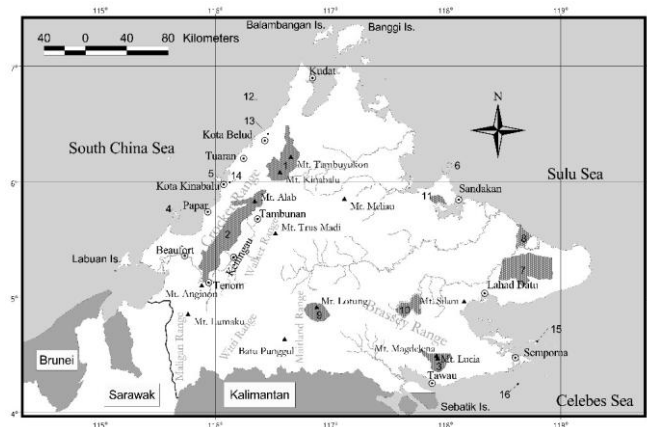


Fig. 1.3. The major cities, mountain ranges, peaks, and protected areas of Sabah. (1) Kinabalu Park, (2) Crocker Range, (3) Tawau Hills Park, (4) Pulau Tiga Park, (5) Tungku Abdul Rahman Park, (6) Turtle Islands Park, (7) Tabin Wildlife Reserve, (8) Kulamba Wildlife Reserve, (9) Maliau Basin Conservation Area, (10) Danum Valley Conservation Area, (11) Kabili-Sepilok Forest Reserve, (12) Mantanani Islands Bird Sanctuary, (13) Kota Belud Bird Sanctuary, (14) Kota Kinabalu Bird Sanctuary, (15) Bohey Dulang Island Bird Sanctuary, (16) Sipidan Island Bird Sanctuary.

includes potential as well as actual forest (McMorrow and Talip 2001). Most of the state's forests have been severely logged and many have been replaced with plantations (e.g., oil palm and *Acacia*), especially in the eastern lowlands. In addition, substantial areas have been converted permanently to grasslands by repeated burning of logged forests (Beaman et al. 1985, Walsh 1996). In fact, only about 13% (10,000 km²) of Sabah's primary forest remains, and it is distributed in small scattered patches (Marsh and Greer 1992, Sheldon et al. 2001). The only moderately large remnants of undisturbed low elevation forest are in Danum Valley Conservation Area (438 km²), Maliau Basin Conservation Area (390 km²), Tawau Hills Park (280 km²) and Imbak River Forest Reserve (181 km²). Fortunately, Sabah's montane forests are in better condition than its lowland areas because mountains are naturally protected from logging and development by their steep slopes. As a result, conservationists have been successful in preserving fairly large areas in mountains, including Kinabalu Park (766 km²) and the Crocker Range National Park (1,399 km²). The latter is the largest totally protected area in the state. Nevertheless, montane areas in Sabah are under constant assault from shifting cultivation and exurban development because of their attractive cooler climate, rich mineral deposits, and proximity to the populous coast (Sheldon 1986).

Borneo has approximately 622 species of birds, of which 434 are known or thought to breed and 39 are endemic (Smythies 1999). Of these, Sabah has about 526 species, of which 395 are resident, 35 are Bornean endemics, and 4 are state endemics (Sheldon et al. 2001). The distribution and general habitat requirements of Bornean birds are well understood because of the many ornithological expeditions and surveys of the island (Whitehead 1893, Smythies 1999, Sheldon et al. 2001). However, remarkably few modern studies have been conducted on Bornean bird ecology, behavior, and evolution. Most ecological work has focused on the effects

of forest disturbance on bird populations (e.g., Lambert 1992, Mitra and Sheldon 1993, Johns 1996, Zakaria and Nordin 1998, Sodhi 2002) or on species or groups of specific conservation concern: e.g., megapodes (Ahmad 1999), pheasants (Nijman 1998), edible-nest swiftlets (Francis 1987), and hornbills (Leighton 1982). Modern evolutionary studies are even fewer than ecological studies. Although the number of phylogenetic projects that include Bornean bird species is growing (e.g., Sibley and Ahlquist 1990; Cibois 2003; Gamauf and Haring 2004; Moyle et al. 2006a,b, in press), only one molecular population study of Bornean birds has been published to date (Moyle et al. 2005).

Because of the dearth of modern quantitative studies, our understanding of the evolution of the Bornean avifauna is rudimentary. It has been pieced together mainly by examining bird distributions in Southeast Asia and drawing inferences about invasions and speciation events. All that we know for certain is that the Bornean avifauna most closely resembles that of mainland Asia and the islands of Sumatra and Java (Banks 1937, Smythies 1999). In general, explanations of Bornean biogeography emphasize the influence of eustatic sea level changes caused by Pleistocene glaciation, which allowed the movement of populations to and from islands and the mainland and, thus, acted as a speciation pump, increasing diversity by promoting colonization and isolation events (Whitmore 1981, 1987; Heaney 1986). Sea level changes are also thought to have played a particularly important role in the evolution of endemic species on Borneo and the other islands. Most endemic birds of Borneo, for example, have montane distributions (25 of Borneo's 39 endemic species; Smythies 1999). A common explanation for montane endemism is that, during periods of elevated sea level, mountains offered refuge for otherwise lowland populations. These populations diverged genetically while

isolated on peaks, and when seas subsided, were displaced from the lowlands by invading congeneric competitors (Sheldon et al. 2001, Han et al. 2000).

It cannot be over-emphasized, however, that we have no direct evidence of the causes of diversification in Bornean birds in either the mountains or the lowlands because we have almost no information on the genetic relationships among species or populations on the island. Without a phylogenetic perspective, the monophyly of groups is unknown, regardless of how similar or different its potential members may appear, and the sequence of events that led to their distributions cannot necessarily be inferred accurately (Moyle et al. 2005).

Because mountains have played an important role in the evolution of the Bornean avifauna, and understanding of the dynamics of montane bird populations is essential to understanding the evolution of Bornean birds as a whole, I investigate in this project the phylogeographic relationships of selected populations of montane species in Sabah. This is a preliminary step to reconstructing the role of mountains in the evolution of Bornean birds as a whole. Because Sabah contains Borneo's highest mountains, Kinabalu, Trus Madi, and Tambuyukon, and it features a wide variety of contiguous and isolated ranges and peaks, it is ideal for such a study (Sheldon et al. 2001; Moyle and Wong 2002, Moyle et al. 2005). I have selected five montane sites based on their inherent biological characteristics, degree of isolation from one another, and ease of access: Mt. Kinabalu, Crocker Range Park Headquarters, Mt. Trus Madi, Mt. Lumaku, and Mt. Lucia. To determine the connectivity of these sites, I compared the mitochondrial DNA of four common bird species that have populations at all the sites. These species are Streaky-breasted Spiderhunter (*Arachnothera affinis*), Temminck's Babbler (*Pellorneum pyrrogenys*), Grey-throated Babbler (*Stachyris nigriceps*), and Ochraceous Bulbul

(*Alophoixus ochraceus*). Each species differs in its dispersal ability, which may affect the levels of gene flow among its populations in mountain ranges. The primary objective of the study is to develop a basic understanding of the geographic, ecological, and historical factors that have influenced isolation and dispersal, and hence genetic continuity and differentiation, among bird populations in the mountains of Sabah. This study is the first comparative phylogeographic study of birds in Southeast Asia and will help provide direction for future systematic and biogeographic work in the region.

Bornean Biogeographic Terms and Issues

Borneo lies in Southeast Asia, a region consisting of Indochina and the Malay Peninsula (Malaya) on the mainland and the Indo-Malayan Archipelago extending south and east of the mainland (Fig. 1.1). Geologically, Malaya and much of the maritime portion of Southeast Asia lie on the Sunda Shelf, an extension of the continental shelf of Southeast Asia. The term “Sundaland” refers to land areas of the Sunda shelf, i.e., Malaya, Sumatra, Java, Bali, Borneo, Palawan, and smaller islands (Whitmore 1981, 1987). Sundaland is distinct from most of the Philippine islands, which are largely oceanic and of volcanic origin (Heaney 1986), and from the islands of Wallacea, i.e., Sulawesi, the Moluccas, and Lesser Sundas, which lie east of Wallace’s line on the Sahul (Australian) continental shelf (Darlington 1957, Whitmore 1981, White and Bruce 1986). The entire geographic province from Sumatra and Malaya in the west to the Bismarck Archipelago in the east is called “Malesia” (Whitmore 1981, 1987).

During glacial periods of the middle and late Pleistocene, eustatic sea level changes caused the Sunda islands to be connected to the Asian mainland and to one another by land bridges (Heaney 1986, Whitmore 1987, Voris 2000). These lowland connections allowed for

colonization of the islands from the mainland and movement of organisms among the islands and even back to the mainland. For Borneo, which lies on the eastern side of the Sunda shelf, the connections were extensive in the west and south, but not the north and east. Thus, during the three main glacial maxima, 250,000 bp, 150,000 bp, and 17,000 bp, the western and southern parts of the island were joined to Indochina, Malaya, Sumatra, and Java for relatively long periods of time (Figs. 1.4 and 1.5), and there were major opportunities for faunal exchanges, especially along now inundated river systems (Voris 2000, McConnell 2004). However, because northeastern Borneo was not directly connected to Indochina, Malaya or major Sunda islands during periods of low sea level, organisms colonizing Borneo would have had to filter slowly eastward through the island to reach the area of modern Sabah. The only major exception to this isolation of northeastern Borneo in the Pleistocene was a short-lived land bridge to Palawan about 160,000 bp (Heaney and Rickart 1990).

The Pleistocene geographic history of Borneo may explain, at least in part, some patterns of biogeographic subdivision within the island. For example, Sabah in the northeastern part of Borneo has several endemic species and subspecies of lowland birds which are distinct from their widespread, lowland sister taxa (Smythies 1999, Sheldon et al. 2001), e.g., White-fronted Falconet (*Microhierax latifrons*), Black-and-crimson Pitta (*Pitta ussheri*), and White-crowned Shama (*Copsychus stricklandi*). Moreover, evidence of a genetic distinction between Sabah and western Borneo (specifically Sarawak) has been discovered in several groups, including birds (Moyle et al. 2005), bats (Murray 2007), treeshrews (Han et al. submitted), and oaks (Cannon and Manos 2003). The relationships among montane regions of Borneo and other Sunda islands are more complex and difficult to understand. Nearly half the endemic mammals (Payne et al. 1985) and a majority of endemic birds (Smythies 1999) occur in montane areas. This pattern,

combined with what we know about opportunities for faunal movement in the lowlands during the Pleistocene, suggests that montane areas of Borneo have been isolated much longer than

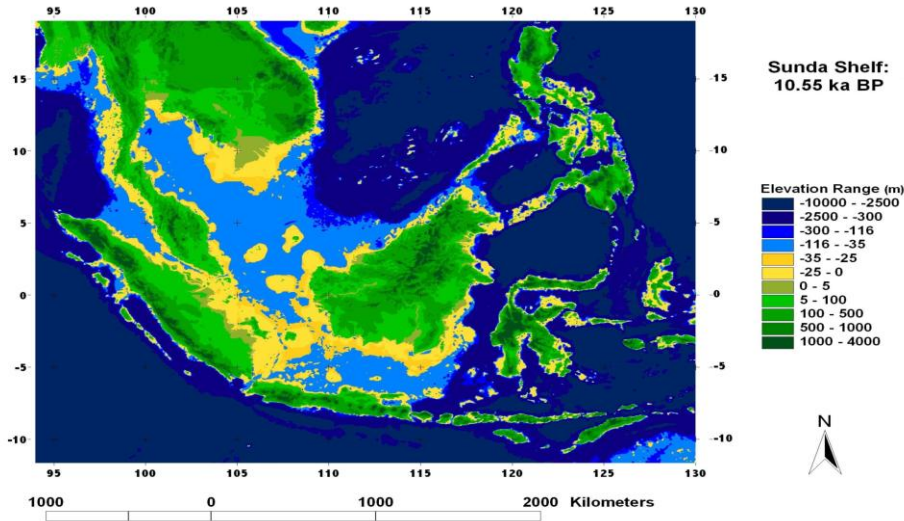


Fig. 1.4. Estimate of the areas of exposed land in the Indo-Australian region 10.55 ka years before present (YBP). The ancient shorelines are based on present day depth contours of 10, 20, 30, 40, 50, 75, 100, and 120 m. (© 2006 Field Museum of Natural History, Chicago, Illinois USA)

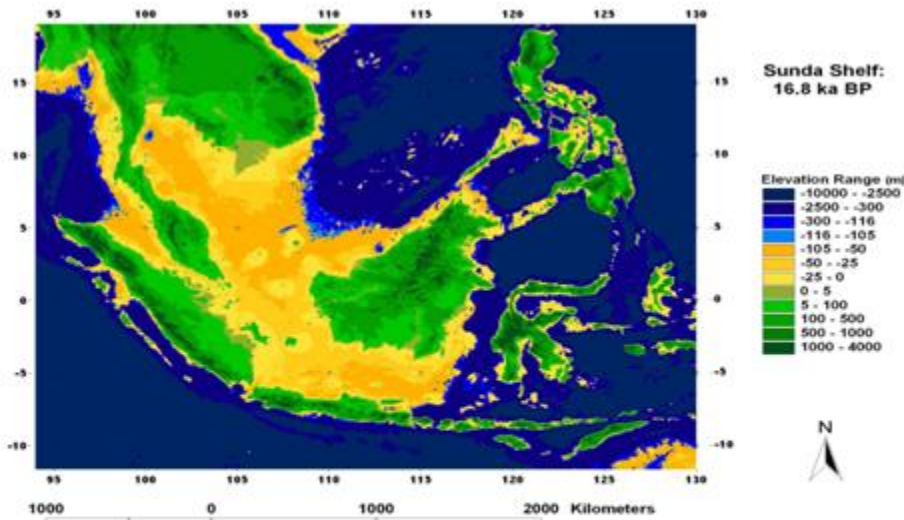


Fig. 1.5. Estimate of the areas of exposed land in the Indo-Australian region during 16.8 ka years before present (YBP). The ancient shorelines are based on present day depth contours of 10, 20, 30, 40, 50, 75, 100, and 120 m. (© 2006 Field Museum of Natural History, Chicago, Illinois USA)

lowland areas, or that montane populations evolve faster than those in the lowlands because of their smaller population sizes.

The mountains of Borneo consist mainly of a backbone of highlands extending northeast to southwest across the island, from Mt. Kinabalu in Sabah, through the Kelabit Uplands of Sarawak, to the Madi Plateau and the Schwaner mountains of Kalimantan (Fig. 1.6). The tallest

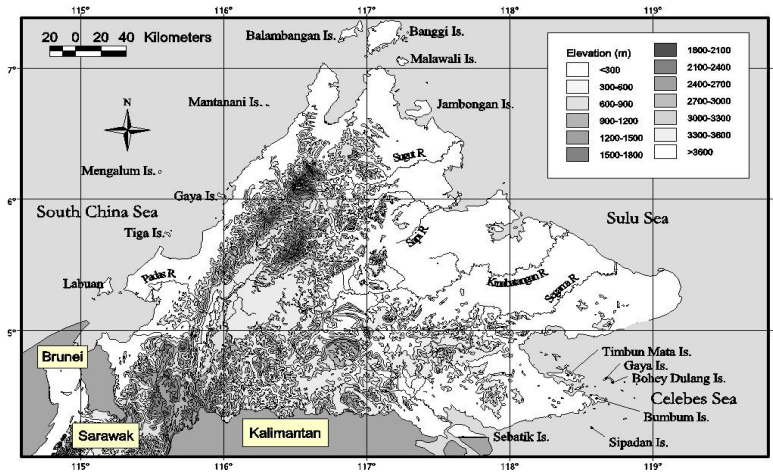


Fig. 1.6. Topography of Sabah. This map derived from data provided by Pennsylvania State University’s Digital Chart of the World Server.

mountains occur in Sabah: Mt. Kinabalu (4,095 m), Mt. Trus Madi (2,649 m), and Mt. Tambuyukon (2,579 m). These mountains also have the largest number of endemic species, and they feature several bird species with odd distributions. The best-known example is the Island Thrush (*Turdus poliocephalus*), widespread in Malesia but restricted in Sundaland to the three highest mountains in Sabah. Another species, the Friendly Bush Warbler (*Bradypterus accentor*), occurs only on the three high Sabah Mountains, whereas another, the mountain Blackeye (*Chlorocharis emiliae*), is restricted to the highest mountain peaks in Sabah, Sarawak,

and Kalimantan, and thus has a unique distribution among birds. On the other hand, many montane bird species are widespread, not only in Borneo but also across all of Sundaland. We have no knowledge of the evolutionary forces that have caused any montane bird distributions within and between Sunda islands. However, we are beginning to discern some genetic patterns. For example, recent molecular and morphological study has shown that the Bornean Swiftlet (*Collocalia dodgei*), an endemic of Mt. Kinabalu, is most closely related to Linch's Swiftlet (*Collocalia linchi*) in Java (Somadikarta 1986, Moyle et al. in press). Similarly, the Bornean White-crowned Forktail (*Enicurus borneensis*) and the Sunda Bush Warbler (*Cettia vulcania*) are also probably most closely related to Javan taxa (Wells 1982, Moyle et al. 2005).

Geography of Sabah

Sabah lies in the northeastern corner of Borneo. It covers 73,371 km² and, thus, comprises about 10% of the island. In 1970, about 80-85% of the state was covered with primary forest, but by the year 2000, only about 10% of the undisturbed forest remained. Of this remnant, 2,450 km² lies in parks, and most of this park property is montane (Kinabalu, Crocker Range, and Tawau Hill parks). The largest blocks of lower elevation forest are at Danum Valley (438 km²) and Maliau Basin (390 km²) conservation areas. In addition, a total of 2,295 km² is designated as permanent virgin forest reserve (Table 2 in Sheldon et al. 2001), but much of this VJR forest has been logged (CAIMS 2005).

About 15% - 20% of Sabah's landscape is mountainous (above 900 m). Most of this high area occurs in the Crocker, Trus Madi, Meligan, and Wittu mountain ranges (Figs. 1.2 and 1.6), which are part of the montane backbone of Borneo extending from Mt. Kinabalu southwestward through Sarawak into Kalimantan. The Crocker Range is the dominant range of Sabah. Its

highest peak is Mt. Kinabalu (4,095 m), which surpasses all other Bornean peaks by approximately 1,500 meters and is the highest point between the Himalayas and New Guinea. The nearest mountains over 2,900 meters in elevation are found on the islands of Java, Sulawesi, Sumatra and Mindanao. In the Crocker Range, the next highest peaks after Kinabalu are Tambuyukon (2,579 m) and Alab (2,085 m). The rest of the Crocker Range lies well below 2,000 m, e.g., Lingan 1,386 m, Rinangisan 1,326 m, Tinutudan 1,469 m, and Malutut 1,287. The Trus Madi Range consists mainly of the long ridge of Mt. Trus Madi, which is 2,649 m at its highest point. The Meligan Range in southwestern Sabah extends into Sarawak. Its most prominent peaks are Mt. Lumaku (1,966), Ibul (1,506 m), and Bisan Hill (1,571). The Wittit Range in southwestern Sabah covers a broad area. Its highest peaks are Muruk Miau (2,083 m) in the south and Mt. Napotong (1,490 m) and Pisagan (1,197 m) in the north. There are also some lower ranges in Sabah, most of which are essentially upland areas (300-600 m) with some highland hills (600-900 m) and emergent peaks over 1,000 m (Fig. 1.6): Kuamut Highlands, Luis (1,426 m), Mt. Lotung (1,684 m), and Mt. Kuli (1,387 m); Tawau Highlands, Mt. Lucia (1,201 m) and Mt. Magdalena (1,311 m); Segama Highlands, Mt. Danum (1,093 m); and Labuk Highlands, Tawai Hill (1,273 m), Monkobo Hill (1,829 m), Mentapok (1,528 m), Meliau (1,336 m), and Mt. Menapod (1,212 m).

Southeast Asian Phylogeography

Phylogeography is a relatively new field within biogeography, concerned specifically with the processes governing the geographical distributions of genealogical lineages, especially those within and among closely related species (Avice et al. 1987, Avice 2000). The advent of modern molecular genetic tools was instrumental to the development of phylogeography. In

most phylogeographic studies, the mtDNA genome is characterized for multiple individuals sampled from throughout the geographical range of a species. MtDNA was selected as the optimal gene for phylogeographic studies because of its rapid rate of evolution relative to the nuclear genome, as well as its simple genetic properties (no recombination or repetitive DNA) and ease of isolation (Avice 2000). It was originally characterized by use of restriction fragment analysis (e.g., Gill et al. 1993), but nowadays is examined by direct sequencing of genes or comparison of other markers such as microsatellites (e.g., Kirchman et al. 2000). In either case, the resulting haplotypes or alleles are used to infer a phylogenetic tree. This estimate of phylogeny reflects the evolutionary relationships of the individuals and populations sampled. This gene tree, when combined with the location from which each population is sampled, can be used to specify the geographical characteristics of major gene lineages that comprise the tree (Riddle et al. 2000, Arbogast and Kenagy 2001). Since its inception, phylogeography has become the most powerful tool for exploring geographical patterns and the evolutionary history of subdivision of species and species complexes. An approach to phylogeography that particularly enhances its power is “comparative phylogeography” (Zink 1996), in which geographic patterns of evolutionary subdivision across multiple co-distributed species or species complexes are compared, instead of simply reconstructing the relationships among populations of only a single species (Arbogast and Kenagy 2001).

Although the term phylogeography was first introduced by Avice et al. (1987), as a discipline the study of the processes influencing the geographic distribution of lineages has existed much longer. Phylogeography has its roots in attempts to resolve one of the major debates in historical biogeography: the role of dispersal versus vicariance in explaining the distributions of organisms. Historical biogeography focuses on past events in the geological and

ecological history of the earth (such as continental drift, mountain building, sea-level changes, river formation, climate changes, and habitat shifts) and uses these to explain patterns in the spatial and temporal distributions of organisms. The spread of cladistic methods of phylogenetic reconstruction and classification in the 1960s and 1970s (Hennig 1965), combined with ideas from historical biogeography and the theory of continental drift, led to the field of vicariance biogeography in the 1970s (Croizat et al. 1974). Vicariance biogeography assumes that the most common cause of geographic differentiation and speciation is the splitting of populations by geologic events rather than the isolation of populations by dispersal of individuals (Rosen 1978). The combined development of vicariance biogeography with the growth of cladistics led naturally to the analytical approach called “area cladistics” (Nelson and Platnick 1981). Area cladistics combines information about the phylogenetic relationships of groups and their geographic distributions and makes predictions, or tests hypotheses, regarding these data in light of vicariant events assumed responsible for geographic area differences. In principle, area cladistics looks for relationships between the phylogeny of organisms and the geological history of the areas they inhabit, based primarily on vicariant events (Wiley 1988). A classic example is the distribution of organisms, such as ratite birds, marsupial mammals, and *Nothofagus* beech trees, on the Gondwanan continents (Cracraft 2001). In practice, however, because the historical relationships and chronological order of vicariance events among geographic areas is generally unknown, area cladistics consists of phylogenetic comparisons of multiple sets of taxa co-distributed in the areas of interest. The extent of agreement among the separate phylogenies, and the commonality in their patterns of branching, determine the order of assumed vicariance events that caused the co-distribution of the taxa. Exceptions to the general phylogenetic pattern are attributed to (rare) dispersal events.

Phylogeography brings analytical power to historical biogeography that is unavailable to area cladistics. Although area cladistics can be useful in studies of biogeography (Cracraft and Plum 1988, Cracraft 1994), it is limited by the problems inherent in comparisons of higher-level taxa, especially those presented by the erosion of evolutionary evidence over time (e.g., the obfuscation of characters, extinction of taxa, and general difficulty of reconstructing phylogeny). Comparative phylogeography, on the other hand, has the great advantage over area cladistics in that it compares closely related taxa. Thus, it is inured against the erosion of evidence, and it can exploit greater analytical sophistication than higher-level phylogenetics by employing the full range of molecular population-genetic tools to its taxic samples and data analysis. The newly evolving field of “statistical phylogeography” (Knowles 2004) fully exploits these tools. It not only compares co-distributed populations, but also requires extensive sampling of each population to allow assessments of gene coalescence, flow and selection.

One of the major contributions of phylogeographic studies is the revelation of unrecognized genetic diversification not reflected in taxonomy (e.g., Moyle et al. 2005, Zou et al. 2007). Careful study of population genealogies has often shown that nominal species are more complex than previously realized, and that many species are substantially subdivided genetically or even poly- or paraphyletic (Avice 2000). Most of these discoveries have been made in studies of areas for which comparative phylogeographic studies are common, i.e., North America, Europe, and Australia (Riddle et al. 2000, Miura and Edwards 2001, Guillaumet et al. 2006, Soltis et al. 2006). Phylogeographic studies of taxa in tropical regions, however, are relatively scarce. Nevertheless, virtually all phylogeographic studies of tropical taxa have uncovered hidden diversity and complexity (e.g., Capparella 1988, Marks et al. 2002, Lovette 2004, Moyle

et al. 2005, Zou et al. 2007). As more such research is conducted our understanding of diversity in tropical regions is going to change dramatically.

In Southeast Asia, phylogeographic studies of animal groups have focused mainly on endangered, charismatic, high profile species, such as Asian Elephant (Fleischer et al. 2001), pigs (Larson et al. 2007), Orangutan (Steiper 2006), and other primates (Evans et al. 2003a,b). However, studies of less charismatic species are becoming more common. These include preliminary work on rats and bats in the Philippines (e.g., Heaney et al. 2005, Roberts 2006). In the Malaysian archipelago, however, remarkably little phylogenetic work has been done on non-charismatic animals. A handful of studies have compared on small mammals, but these have yet to be published, e.g., treeshrews (Han 1991) and bats (Murray 2007). Some studies also have compared marine taxa (Louire et al. 2005). For birds, few studies have examined phylogeographic relationships, mainly because it is so difficult to obtain specimen material for comparisons. Although several projects are underway, only four phylogeographic studies have been conducted on Southeast Asian birds: Little Spiderhunter (*Arachnothera longirostra*; Rahman 2000), scimitar babblers (*Pomatorhinus*; Reddy 2005), White-crowned Forktails (*Enicurus leschenaulti*; Moyle et al. 2005), and fulvettas (*Alcippe*; Zou et al. 2007). With the exception of the spiderhunter study, these have revealed remarkable genetic diversification and the existence of substantial genetic diversity and hitherto unrecognized species.

CHAPTER 2 MATERIALS AND METHODS

The taxa and collection localities examined in this study are listed in Table 1, and described in detail below. The species are Gray-throated Babbler (*Stachyris nigriceps*), Temminck's Babbler (*Pellorneum pyrrogenys*), Streaky-breasted Spiderhunter (*Arachnothera affinis*), and Ochraceous Bulbul (*Alophoixus ochraceus*). They were selected because they are common at each site and thus easily sampled, and also because they exhibit different ecological characteristics and thus presumed dispersal capabilities. I attempted to compare two individuals of each species from each site. As outgroups, I selected closely related species collected in Sabah or populations of the same species from the mainland. The outgroups for *S. nigriceps* were 2 individuals from China; for *P. pyrrogenys*, one individual of *P. tickelli*, one *P. abliventer*, and one *P. capistratum*; for *A. affinis*, one *A. longirostra* from Sabah; and for *A. ochraceus*, one *A. bres*. Because of uncertainty about the species status of *A. affinis* in lowland versus highland areas (Davison 1999), I compared four individuals of *A. affinis* from lowland sites to those from montane populations.

Species Studied

Gray-throated Babbler (*Stachyris nigriceps*)

Stachyris nigriceps in Sabah is a common, small babbler (ca. 16 g), found most often between 750-2200m in primary and secondary lower to upper montane forest. It generally occurs in single- species and mixed flocks, foraging near the ground for insects (Smythies 1999, Sheldon et al. 2001). This species is presumed to be a poor disperser because it moves slowly through the understory and rarely flies long distances.

Table 2.1. List of taxa and collecting localities

Taxon	Sample No.	Source	Collection Locality	Elevation (m)
<i>Pellorneum pyrrogenys</i> (Temminck's Babbler)	B36316	LSUMNS	Crocker Range HQ	1000
<i>P. pyrrogenys</i>	B36335	LSUMNS	Crocker Range HQ	1000
<i>P. pyrrogenys</i>	B52544	LSUMNS	Mount Trus Madi	1500
<i>P. pyrrogenys</i>	B52568	LSUMNS	Mount Trus Madi	1500
<i>P. pyrrogenys</i>	B38635	LSUMNS	Mount Kinabalu	1600
<i>P. pyrrogenys</i>	B38639	LSUMNS	Mount Kinabalu	1600
<i>P. pyrrogenys</i>	B51195	LSUMNS	Mount Lucia	1000
<i>P. pyrrogenys</i>	B51010	LSUMNS	Mount Lumaku	1100
<i>P. pyrrogenys</i>	B51015	LSUMNS	Mount Lumaku	1100
<i>Alophoixus ochraceus</i> (Ochraceous Bulbul)	B36311	LSUMNS	Crocker Range HQ	1000
<i>A. ochraceus</i>	B36336	LSUMNS	Crocker Range HQ	1000
<i>A. ochraceus</i>	B36453	LSUMNS	Mount Trus Madi	1500
<i>A. ochraceus</i>	B36463	LSUMNS	Mount Trus Madi	1500
<i>A. ochraceus</i>	B38614	LSUMNS	Mount Kinabalu	1600
<i>A. ochraceus</i>	B38620	LSUMNS	Mount Kinabalu	1600
<i>A. ochraceus</i>	B51168	LSUMNS	Mount Lucia	1000
<i>A. ochraceus</i>	B51176	LSUMNS	Mount Lucia	1000
<i>A. ochraceus</i>	B51005	LSUMNS	Mount Lumaku	1100
<i>A. ochraceus</i>	B51006	LSUMNS	Mount Lumaku	1100
<i>Stachyris nigriceps</i> (Grey-throated Babbler)	B36321	LSUMNS	Crocker Range	1000
<i>S. nigriceps</i>	B36328	LSUMNS	Crocker Range	1000
<i>S. nigriceps</i>	B36435	LSUMNS	Mount Trus Madi	1500
<i>S. nigriceps</i>	B36438	LSUMNS	Mount Trus Madi	1500
<i>S. nigriceps</i>	B38615	LSUMNS	Mount Kinabalu	1600
<i>S. nigriceps</i>	B38623	LSUMNS	Mount Kinabalu	1600
<i>S. nigriceps</i>	B51158	LSUMNS	Mount Lucia	1000
<i>S. nigriceps</i>	B51163	LSUMNS	Mount Lucia	1000
<i>S. nigriceps</i>	B51000	LSUMNS	Mount Lumaku	1100
<i>S. nigriceps</i>	B51013	LSUMNS	Mount Lumaku	1100
<i>Arachnothera affinis</i> (Streaky-breasted Spiderhunter)	B36309	LSUMNS	Crocker Range	1000
<i>A. affinis</i>	B36310	LSUMNS	Crocker Range	1000
<i>A. affinis</i>	B52653	LSUMNS	Mount Trus Madi	1500
<i>A. affinis</i>	B52661	LSUMNS	Mount Trus Madi	1500
<i>A. affinis</i>	B38631	LSUMNS	Mount Kinabalu	1600
<i>A. affinis</i>	B38634	LSUMNS	Mount Kinabalu	1600
<i>A. affinis</i>	B51142	LSUMNS	Mount Lucia	1000
<i>A. affinis</i>	B51193	LSUMNS	Mount Lucia	1000

Table 2.1 cont.

<i>A. affinis</i>	B50996	LSUMNS	Mount Lumaku	1100
<i>A. affinis</i>	B51037	LSUMNS	Mount Lumaku	1100
<i>A. affinis</i>	B36402	LSUMNS	Tawau Hills Park	250
<i>A. affinis</i>	B36416	LSUMNS	Tawau Hills Park	250
<i>A. affinis</i>	B47062	LSUMNS	Serinsim, Kinabalu Park	200
<i>A. affinis</i>	B47093	LSUMNS	Serinsim, Kinabalu Park	200
Outgroups				
<i>Pellorneum capistratum</i> (Black-capped Babbler)	B36430	LSUMNS	Tawau Hills Park	250
<i>Pellorneum albiventer</i> (Spot-throated Babbler)	KU10145	KUMNH	Guangxi province, China	1000
<i>Pellorneum tickelli</i> (Buff-breasted Babbler)	KU10186	KUMNH	Guangxi province, China	1000
<i>Alophoixus bres</i> (Grey-cheeked Bulbul)	B38567	LSUMNS	Tawau Hills Park	250
<i>Stachyris nigriceps</i> (Grey-throated Babbler)	KU10091	KUMNH	Guangxi province, China	1000
<i>S. nigriceps</i>	KU10124	KUMNH	Guangxi province, China	1000
<i>Arachnothera longirostra</i> (Little Spiderhunter)	B36306	LSUMNS	Crocker Range HQ	1000

Stachyris nigriceps is a member of the family Timaliidae and is monophyletic with some, but not all, other species of *Stachyris*, as well as the scimitar babblers, *Pomatorhinus* and *Xiphirhynchus* (Cibois 2003). It occurs in mountains from Nepal through northeast India, Indochina, and the Malay Peninsula to Sumatra and Borneo (Robson 2000). Currently, *S. nigriceps* is divided into 11 subspecies (Dickinson 2003), two of which are found on Borneo: *borneensis*, described originally as a separate species from Mt. Kinabalu by Sharpe (1887), and *hartleyi*, described from a few specimens collected on Mt. Penrissen and Mt. Poeh near Kuching, Sarawak, in southwestern Borneo (Chasen 1935). In general, *hartleyi* is assumed to occur throughout Borneo and *borneensis* to be restricted to the region of Mt. Kinabalu (Smythies 1999). This assumption is based on Thompson's (1966) identification of specimens from Crocker Range near Tenom, Sabah, as *hartleyi*. Such a distribution implies that the sampling in my study encompasses both subspecies, because Thompson's collecting site in Tenom lies closer

to Mt. Kinabalu than to either Mt. Lumaku or Mt. Lucia. However, inspection of specimens in the LSU collection, including nine individuals from Kinabalu, eight from Trus Madi, two from the Crocker Range Park Headquarters, five from Lumaku, and four from Lucia, disclosed no consistent differences in plumage. All appear to be members of subspecies *borneensis*.

Temminck's Babbler (*Pellorneum pyrrogenys*)

In Sabah, *Pellorneum pyrrogenys* is a fairly common, small babbler (ca. 15 g), found most often between 700-1500m in mature secondary forest and tall primary montane forest. It usually occurs in mixed-species flocks with other babblers and understorey species, where it forages mainly near the ground for ants and other large insects (Smythies 1999, Sheldon et al. 2001). Like *S. nigriceps*, this species is presumed to be a poor disperser because of its foraging habits.

Pellorneum pyrrogenys is also in the Timaliidae, but its position within the family is uncertain because it has not been compared in recent phylogenetic studies. It occurs in mountains on the islands of Sumatra, Java, and Borneo (Smythies 1999), and is currently divided into four subspecies (Dickinson 2003), three of which are found on Borneo: *erythrote* (Sharpe 1887) of the Poeh mountain range in southwestern Sarawak, *longstaffi* (Harrisson & Hartley 1934) in the mountains of Northeast Sarawak, and *canicapillum*, described as a separate species from Mt. Kinabalu by Sharpe (1887). In general, *erythrote* and *longstaffi* are thought to occur throughout western Borneo, and *canicapillum* is thought to be restricted to the region of Mt. Kinabalu (Smythies 1999). This distribution suggests that the sampling in my study could include both *longstaffi* and *canicapillum*, because *longstaffi* occurs in northeast Sarawak and may extend to Mt. Lumaku. However, inspection of specimens in the LSU collection (five

individuals from Mt. Kinabalu and one each from Mt. Lucia, Mt. Lumaku, and the Crocker Range) indicates all are members of the subspecies *canicapillum*.

Ochraceous Bulbul (*Alophoixus ochraceus*)

Alophoixus ochraceus in Sabah is a common, large bulbul (ca. 45 g), found most often in the interior and on the edge of mature lower montane forest, between 600-1700m. It occurs most often in pairs or small flocks, feeding almost exclusively on berries in fruiting trees or bushes (Smythies 1999, Sheldon et al. 2001). This species flies relatively long distances in search of food sources and is presumed to be a relatively good disperser.

Alophoixus ochraceus is a member of the family Pycnonotidae and is closely related to the other *Alophoixus* bulbuls in Southeast Asia (Moyle and Marks 2006). It is widespread throughout the mountains in the region, occurring from Myanmar through parts of Thailand and Indochina, the Malay Peninsula, Sumatra, and Borneo (Smythies 1999). Presently, *C. ochraceus* is divided into eight subspecies (Dickinson, 2003), two of which occur on Borneo: *ruficrissus*, described by Sharpe (1879), found only on Mt. Kinabalu, and *fowleri*, described from several specimens collected in the Kelabit Uplands in north-central Sarawak (Amadon and Harrison 1956). In general, *ruficrissus* is thought to be restricted to Mt. Kinabalu and *fowleri* is assumed to occur throughout the rest of Borneo. Such a distribution implies that the sampling in my study includes both subspecies. However, inspection of specimens in the LSU collection, including four from Mt. Kinabalu, five from Mt. Trus Madi, and one each from Mts. Lumaku and Lucia, reveals no consistent differences in plumage. All appear to be members of the subspecies *ruficrissus*.

Streaky-breasted Spiderhunter (*Arachnothera affinis*)

In Sabah, *Arachnothera affinis* is a common resident spiderhunter, found in secondary, primary and logged forest, where it occurs from sea level to 1500m. It tends to be solitary, flying low through the forest, probably trap-lining nectar sources such as banana flowers (Smythies 1999). It also eats insects, spiders, and small fruits (Sheldon et al. 2001). Like *Alophoixus ochraceus*, this species is highly mobile and presumed to be a good disperser.

Arachnothera affinis is a member of the sunbird family, Nectariniidae. It occurs in Borneo, Java, and Bali. Across most of Borneo, it is thought to be a montane species, replaced in the lowlands by the Gray-breasted Spiderhunter, *A. modesta* (Davison 1999, Smythies 1999). However, in Sabah, *A. modesta* is absent, and *A. affinis* occurs in both the mountains and the lowlands (Sheldon et al. 2001). Inspection of specimens of *A. affinis* in the LSU collection, including two individuals from Trus Madi, eight from Mt. Kinabalu, two from Mt. Lumaku, and one each from Mt. Lucia, Crocker Range and Tawau Hills, no consistent differences in plumage or size were evident. All appear to be members of the sole Bornean subspecies *everetti*. Nevertheless, I compared four individuals from the lowlands to assess genetic differentiation between upland and lowland populations.

Study Sites

The sites examined in this study were as follows (Fig. 2.1). In the Crocker Range: Mt. Kinabalu (6°00'N 116°32'E; 1,600 m) and the Crocker Range Park Headquarters (5°23'N 116°06'E; 900 m); in the Trus Madi Range: Mt. Trus Madi (5°35'N 116°29'E; 1,500 m); in the

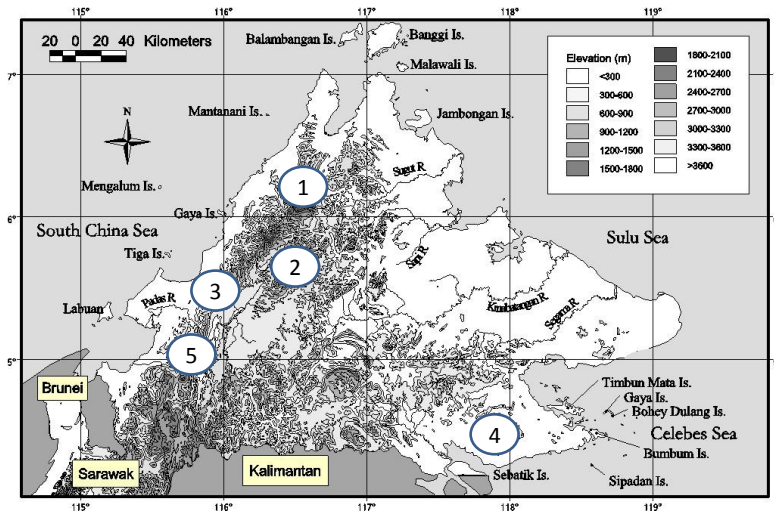


Fig. 2.1. Study Sites. (1) Mount Kinabalu, (2) Mount Trus Madi, (3) Crocker Range, (4) Mount Lucia, and (5) Mount Lumaku. This map derived from data provided by Pennsylvania State University’s Digital Chart of the World Server.

Meligan Range: Mt. Lumaku ($4^{\circ}51'N$ $115^{\circ}42'E$; 1,100 m); and in the Tawau Highlands: Mt. Lucia ($4^{\circ}28'N$ $117^{\circ}56'E$; 1,000 m).

Geologically, these are distinct sites, although Mt. Kinabalu and the Crocker Range Headquarters are connected via the Crocker Range and are relatively close to one another (ca. 75 km) and to Trus Madi (ca. 55 km from each). As indicated by Collenette (1958) and Hutchinson (2005), the Crocker mountains probably uplifted in the Early Miocene, some 18-24 million years ago. However, Mt. Kinabalu was formed by the intrusion and uplift of a granitic batholith that comprises its core. This intrusion is believed to have begun within the last nine million years, and the uplift resulting in its current height is thought to have occurred only within the last 1.5 million years. Geologically, Trus Madi is much older than Kinabalu, having uplifted during the Lower to Middle Miocene, roughly 13 to 24 million years ago. Mt. Lumaku, which lies at the northern end of the Meligan Range and southern end of the Crocker Range is a bit of a geologic

mystery. Wilson and Wong (1964) described it as part of the Meligan Range, uplifted during the Upper Miocene, roughly 5 to 10 million years ago. Hutchinson (2005), however, described it (only briefly) as part of the Crocker Range. In any event, it well isolated from the other Crocker Range sites by both low intervening hills and distance (75 km). Mt. Lucia is the most isolated of the sites, lying about 200 km from the Kinabalu, Crocker Range, and Trus Madi sites. Not only are there no highland connections between Lucia and the other sites, but it also lies in a park that is surrounded on oil palm on the west, south and east sides and by heavily logged forest to the north. Mt. Lucia is an extinct volcano of Pleistocene age (Kirk 1962) and thus about as old as Mt. Kinabalu.

Laboratory Methods

For this study, I sequenced the entire second and third subunits of the mitochondrial nicotinamide adenine dinucleotide dehydrogenase gene (ND2 and ND3). DNA from all species was extracted from pectoral muscle from tissue preserved for molecular study. Genomic DNA was extracted using proteinase K digestion following the manufacturer's protocol (Dneasy tissue kit, Qiagen). Primers for the ND3 gene were L10755 and H11151 (Chesser 1999). Primers for the ND2 gene were L5215 (Hackett 1996), and H6313, L5758, and H5766 (Johnson and Sorenson 1998). I purified PCR products with Perfectprep PCR cleanup kits (Eppendorf). Sequencing of purified PCR products was performed with BigDye Terminator Cycle Sequencing Kits (Applied Biosystems). Primers used for PCR were also used for cycle sequencing reactions, resulting in bi-directional sequence for all taxa. Cycle sequencing products were run on an ABI Prism 3100 automated DNA sequencer (Perkin-Elmer Applied Biosystems). The computer

program Sequencher 4.1 (Genecodes) was used to reconcile chromatograms of complementary fragments and align sequences across taxa.

Data Analysis

Base frequencies and sequence variation and divergence values were determined using MEGA 4.0 (Tamura et al. 2007). Trees were visualized using TreeView (Page 1996) and MacClade 4.06 (Maddison and Maddison 2003). Maximum parsimony (MP) and maximum likelihood (ML) analyses were performed using PAUP* 4.0b10 (Swofford 2002). Because few sites differed among sequences compared among populations, corrections for back mutations were assumed to be minimal. Thus, MP analyses used unweighted data. For ML, the model of evolution was determined by hierarchical likelihood ratio tests and the Akaike information criterion in Modeltest 3.06 (Posada and Crandall 1998). In the bootstrap analyses, we employed 10 heuristic searches with random addition of taxa and TBR branch swapping and reanalysis of the data 100 times.

CHAPTER 3 RESULTS

Entire sequences of ND2 and ND3 genes (1041 and 351 nucleotides, respectively) were obtained from the four target species as follows: nine individuals of *Pellorneum pyrrogenys*, 10 individuals each of *Alophoixus ochraceus* and *Stachyris nigriceps*, and 14 individuals of *Arachnothera affinis* (including both highland and lowland populations). Entire ND2 and ND3 genes were also sequenced in outgroups of the target species: two individuals of *S. nigriceps* (China), and one individual each of *A. longirostra*, *P. capistratum*, *P. tickelli*, and *P. albiventer*. *Alophoixus bres* was sequenced by Moyle and Marks (2006). All sequences appear to be genuine mitochondrial DNA, rather than nuclear copies. The sequences contain no stop codons, insertions or deletions, and they exhibit nucleotide frequencies and codon site variation typical of mitochondrial DNA (see below; Edwards et al. 1991, Nunn and Cracraft 1996, Sheldon et al. 2005).

Pellorneum pyrrogenys nucleotide base frequencies are as follows: A = 30.4%, C = 33.9%, G = 12.0%, and T = 23.8%. Of the total 1392 total nucleotide sites, 31 are variable (2.2%), three (0.2%) are potentially parsimony informative, and 28 are autapomorphic. Of the 464 amino acid sites, six are variable (1.3%), and one (0.2%) is potentially parsimony informative. Of the variable sites, four occur at the first codon position, two at the second position, and 25 at the third position.

Alophoixus ochraceus nucleotide base frequencies are as follows: A = 30.6%, C = 33.2%, G = 11.6%, and T = 24.6%. Of the 1392 total nucleotide sites, 20 are variable (1.4%), 10 (0.7%) are potentially parsimony informative and 10 (0.7%) are autapomorphic. Of the 464

amino acids sites, none is variable. Of the variable nucleotide sites, all 20 occur at the third codon position.

Stachyris nigriceps nucleotide base frequencies are as follows: A = 30.4%, C = 35.7%, G = 10.8%, and T = 23.1%. Of the 1392 total nucleotide sites, 22 are variable (1.6%), 14 (1.0%) are potentially parsimony informative and 8 (0.5%) are autapomorphic. Of the 464 amino acid sites, eight are variable (1.7%), and three (0.7%) are potentially parsimony informative. Of the variable sites, nine occur at the first codon position, two at the second position, and 11 at the third position.

Lowland and montane *Arachnothera affinis* have combined nucleotide base frequencies as follows: A = 29.5%, C = 35.2%, G = 11.5%, and T = 23.8%. Of the total 1392 total nucleotide sites, 32 are variable (2.3%), seven (0.5%) are potentially parsimony informative and 25 (1.8%) are autapomorphic. Of the 464 amino acids, four (0.9%) are variable, and none is potentially parsimony informative. Of the variable sites, five occur at the first codon position, none at the second position, and 27 at the third position.

Uncorrected proportional ND2 and ND3 distances (p-distances) are shown in Table 3.1. Distances from *Pellorneum pyrrogenys* in the Crocker Range to all sites average 0.6% (range: 0.3% to 1.4%), from Mt. Trus Madi to all sites average 0.6% (range: 0.2% to 1.4%), from Mt. Kinabalu to all sites average 0.6% (range: 0.2% to 1.4%), from Mt. Lucia to all sites average 1.4% (range was 1.4% across all sites), and from Mt. Lumaku to all sites average 0.7% (range: 0.4% to 1.4%). The average distance from *P. pyrrogenys* to outgroup *P. albiventer* is 18.6% (range: 18.1% to 18.9%), to *P. capistratum* is 23.5% (range: 23.2% to 23.8%), and to *P. tickelli* is 13.9% (range: 13.5% to 14.2%).

Table 3.1. Genetic distances across all sites.

<i>Pellorneum pyrrogenys</i>					
	Crocker Range	Mount Trus Madi	Mount Kinabalu	Mount Lucia	Mount Lumaku
Crocker Range	0.00300				
Mount Trus Madi	0.00300	0.00100			
Mount Kinabalu	0.00275	0.00150	0.00100		
Mount Lucia	0.01400	0.01400	0.01400	0.00000	
Mount Lumaku	0.00450	0.00400	0.00425	0.01400	0.00400
<i>Alophoxius ochraceus</i>					
	Crocker Range	Mount Trus Madi	Mount Kinabalu	Mount Lucia	Mount Lumaku
Crocker Range	0.00100				
Mount Trus Madi	0.00100	0.00100			
Mount Kinabalu	0.00150	0.00100	0.00000		
Mount Lucia	0.00150	0.00100	0.00100	0.00100	
Mount Lumaku	0.00900	0.00875	0.00900	0.00900	0.00400
<i>Stachyris nigriceps</i>					
	Crocker Range	Mount Trus Madi	Mount Kinabalu	Mount Lucia	Mount Lumaku
Crocker Range	0.00400				
Mount Trus Madi	0.00550	0.00100			
Mount Kinabalu	0.00675	0.00150	0.00300		
Mount Lucia	0.00750	0.00650	0.00800	0.00000	
Mount Lumaku	0.00700	0.00150	0.00300	0.00800	0.00000
<i>Arachonthera affinis</i>					
	Crocker Range	Mount Trus Madi	Mount Kinabalu	Mount Lucia	Mount Lumaku
Crocker Range	0.00200				
Mount Trus Madi	0.00500	0.00500			
Mount Kinabalu	0.00425	0.00500	0.00500		
Mount Lucia	0.00300	0.00450	0.00400	0.00300	
Mount Lumaku	0.00200	0.00400	0.00350	0.00250	0.00200

Distances from *Alophoxius ochraceus* in the Crocker Range to all sites average 0.3% (range: 0.1% to 0.9%), from Mt. Trus Madi to all sites average 0.3% (range: 0.1% to 0.9%), from Mt. Kinabalu to all sites average 0.3% (range: 0.1% to 0.9%), from Mt. Lucia to all sites

average 0.3% (range: 0.1% to 0.9%), and from Mt. Lumaku to all sites average 0.9% (range: 0.9% to 0.9%). The average distance from all *A. ochraceus* to outgroup *A. bres* is 14.4% (range: 14.3% to 14.5%).

Distances from *Stachyris nigriceps* in the Crocker Range to all sites average 0.7% (range: 0.6% to 0.8%), from Mt. Trus Madi to all sites average 0.4% (range: 0.2% to 0.7%), from Mt. Kinabalu to all sites average 0.5% (range: 0.2% to 0.8%), from Mt. Lucia to all sites average 0.8% (range: 0.7% to 0.8%), and from Mt. Lumaku to all sites average 0.5% (range: 0.2% to 0.8%). The average distance from *S. nigriceps* to outgroup *S. nigriceps* from China is 4.0% (range 3.9% to 4.2%).

Distances from *Arachnothera affinis* in the Crocker Range to all sites average 0.4% (range: 0.2% to 0.5%), from Mt. Trus Madi to all sites average 0.5% (range: 0.4% to 0.5%), from Mt. Kinabalu to all sites average 0.4% (range: 0.4% to 0.4%), from Mt. Lucia to all sites average 0.4% (range: 0.3% to 0.5%), and from Mt. Lumaku to all sites average 0.3% (range: 0.2% to 0.4%). Distances from lowland *A. affinis* to montane *A. affinis* average 0.4% (range: 0.3% to 0.5%). The average distance from *A. affinis* to outgroup *A. longirostra* is 23.2% (range: 23.0% to 23.5%).

Phylogenetic relationships among populations of *Pellorneum pyrrogenys* were estimated by MP and ML (Figs. 3.1 and 3.2). MP analysis produced two most parsimonious trees, 212 steps in length (CI 0.80, RI 0.81, and RC 0.65). The Lucia population appeared basal to all other populations. MP bootstrapping indicated only one branch as well-supported, which is the one distinguishing the Lucia population from all others. Only three sites were parsimony informative for the ingroup, and two of these grouped Lumaku and Lucia together. Unfortunately, I only had

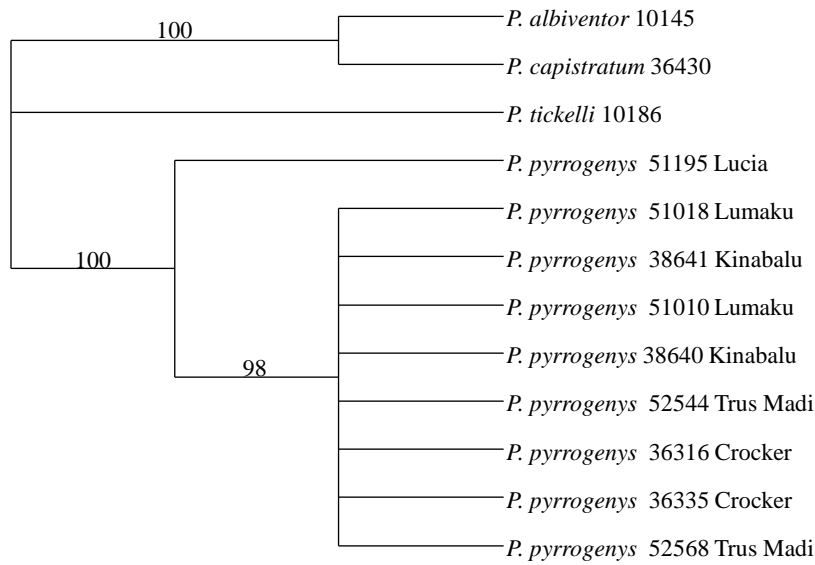


Fig. 3.1. Parsimony bootstrap tree of *Pellorneum pyrrogenys* populations. Numbers indicate bootstrap support.

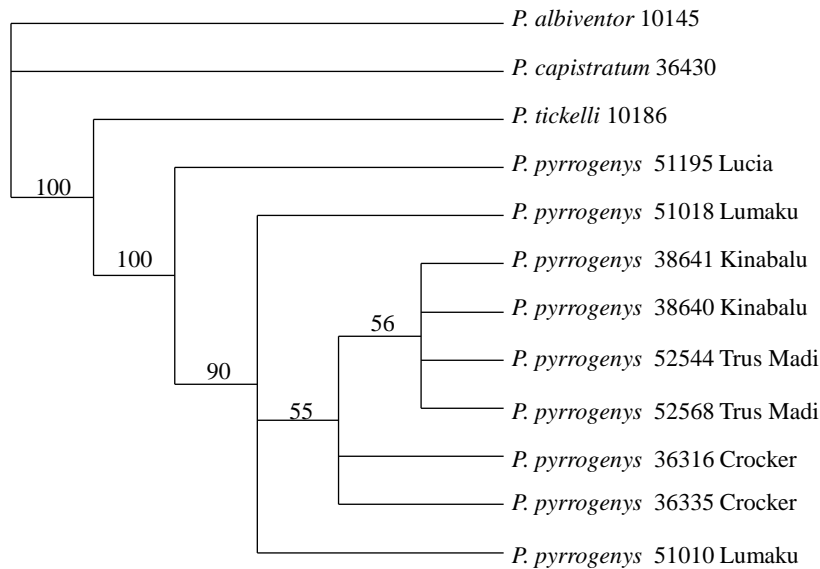


Fig. 3.2. Maximum likelihood bootstrap tree for *Pellorneum pyrrogenys* populations. The tree was bootstrapped 1000 times using an HKY model with the following parameters: A = 0.305, C = 0.338, G = 0.120, T = 0.237; ti/tv = 5.6248; invariable sites = 0; equal rates for all sites. Numbers indicated bootstrap support.

one individual from Mt. Lucia, so I could identify no synapomorphies for that population. ML bootstrapping yielded the same tree as MP, with Lucia strongly supported as basal to the other populations, and Lumaku and the Crocker Range populations marginally differentiated from the Kinabalu and Trus Madi populations.

Phylogenetic relationships among populations of *Stachyris nigriceps* were estimated by MP and ML (Figs. 3.3 and 3.4). MP analysis produced two most-parsimonious trees of 72 steps

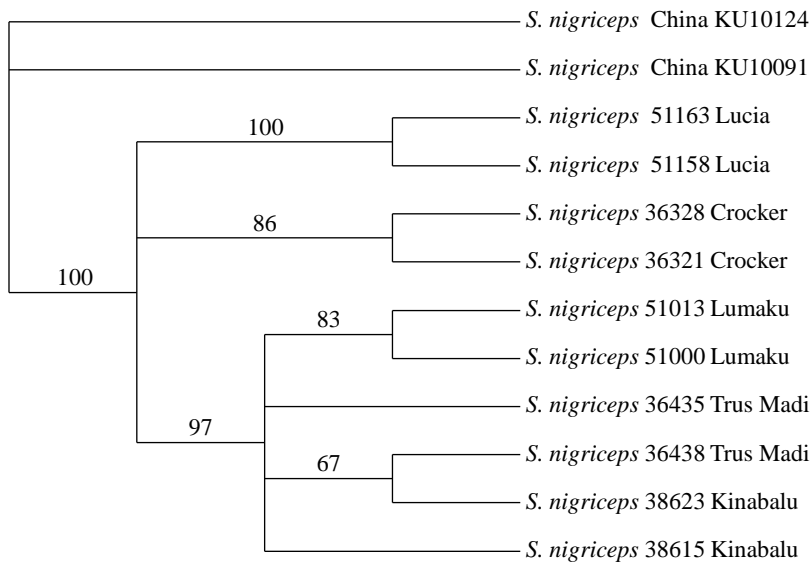


Fig. 3.3. Parsimony bootstrap tree of *Stachyris nigriceps* populations. Numbers indicate bootstrap support.

in length (CI 1.0, RI 1.0, and RC 1.0). These trees both placed Lucia and Crocker Range populations basal to a well supported Lumaku, Trus Madi, and Kinabalu clade. The Lucia population exhibited the largest number of synapomorphic changes (5), as opposed to the Crocker Range and Lumaku populations (2 each). As with *P. pyrrogenys*, the Lucia population is the most distinct. However, Lucia and Crocker Range populations were united by three

synapomorphies in their ND3 sequences, which counteracted Lucia's apparent distance from the western populations. ML produced much the same topology as MP, in which the Lumaku, Trus

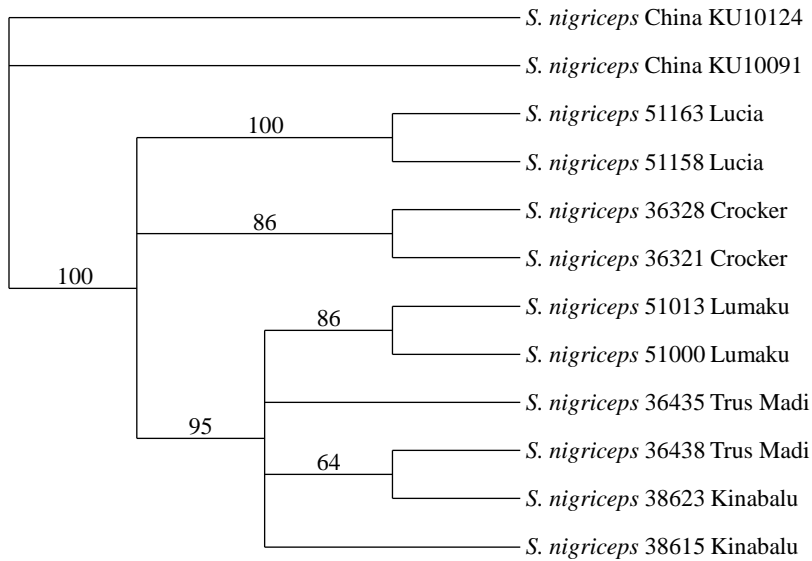


Fig. 3.4. Maximum likelihood bootstrap tree for *Stachyris nigriceps* populations. The tree was bootstrapped 1000 times using an TVM model with the following parameters: A = 0.306, C = 0.356, G = 0.108, T = 0.231; rates AC = 1450009728.0, AG = 10988273664.0, AT = 0.0, CG = 82322268616.0, CT = 10988273664.0, GT = 1.0; invariable sites = 0; equal rates for all sites. Numbers indicate bootstrap support.

Madi, and Kinabalu populations form a strongly supported group distal to the Lucia and Crocker Range populations.

Phylogenetic relationships among populations of *Alophoixus ochraceus* were estimated by MP and ML (Figs. 3.5 and 3.6). MP analysis produced two most-parsimonious trees of 17 steps in length (CI 0.82, RI 0.81, RC 0.67). These trees both place Mt. Lumaku populations basal to all other populations. MP bootstrapping indicated only one branch as well-supported, again the one distinguishing the Mt. Lumaku population from all others. Ten sites were parsimony informative for the ingroup, and nine of these sites separated the Lumaku populations from the rest of the sites. In contrast to *S. nigriceps* and *P. pyrrogenys*, the Mt. Lumaku

population is the most distinct. ML bootstrapping yielded the same tree as MP, with strong support for the Mt. Lumaku population basal to all other populations.

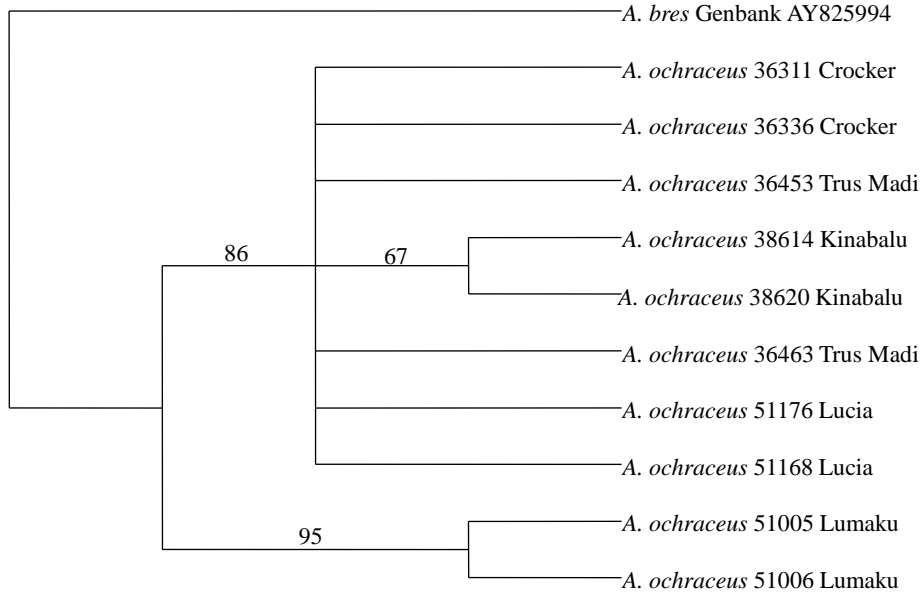


Fig. 3.5. Parsimony bootstrap tree of *Alophoixus ochraceus* populations. Numbers indicate bootstrap support.

Phylogenetic relationships among montane populations of *A. affinis* were estimated by MP and ML (Figs. 3.7 and 3.8). MP analysis produced four most-parsimonious trees of 269 steps (CI 0.98, RI 0.58, RC 0.57). ML bootstrapping yielded much the same tree as MP, largely unresolved. Phylogenetic relationships among montane and lowland populations of *A. affinis* were also estimated by MP and ML (Figs 3.9 and 3.10). MP analysis produced 20 most parsimonious trees of 279 steps (CI 0.97, RI 0.53, RC 0.51). These trees mostly disagreed with one another, except for a branch joining two lowland individuals from Tawau Hills Park. In this analysis, seven sites were parsimony informative, and the two lowland individuals from Tawau Hills shared two synapomorphies. ML bootstrapping yielded an unresolved tree in which the two lowland individuals again grouped together at 85%.

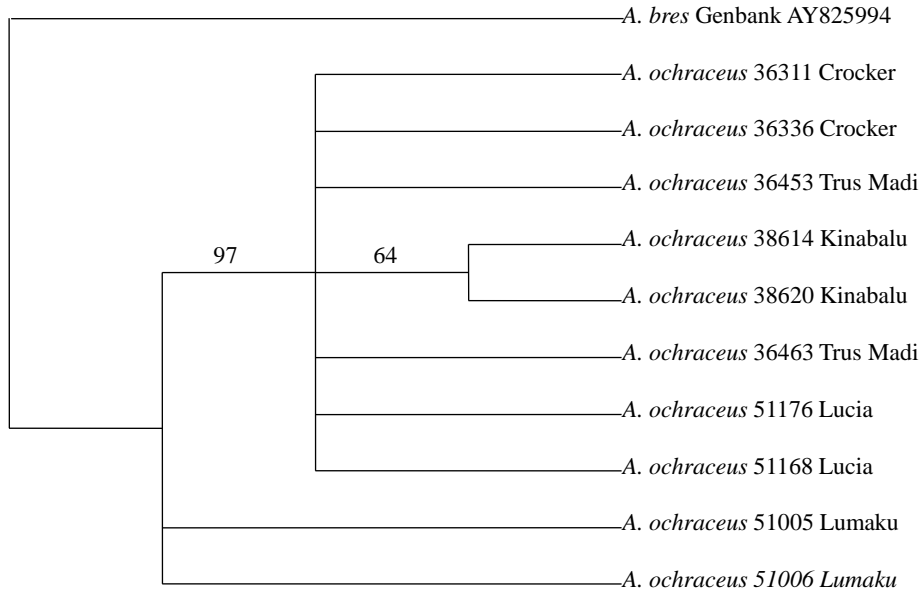


Fig. 3.6. Maximum likelihood bootstrap tree for *Alophoixus ochraceus* populations. The tree was bootstrapped 1000 times using an TrN model with the following parameters: A = 0.3065, C = 0.3335, G = 0.1156, T = 0.2445; rates AC = 1.0, AG = 69.4095, AT = 1.0, CG = 1.0, CT = 27.0325, GT = 1.000; invariable sites = 0; equal rates for all sites. Numbers indicated bootstrap support.

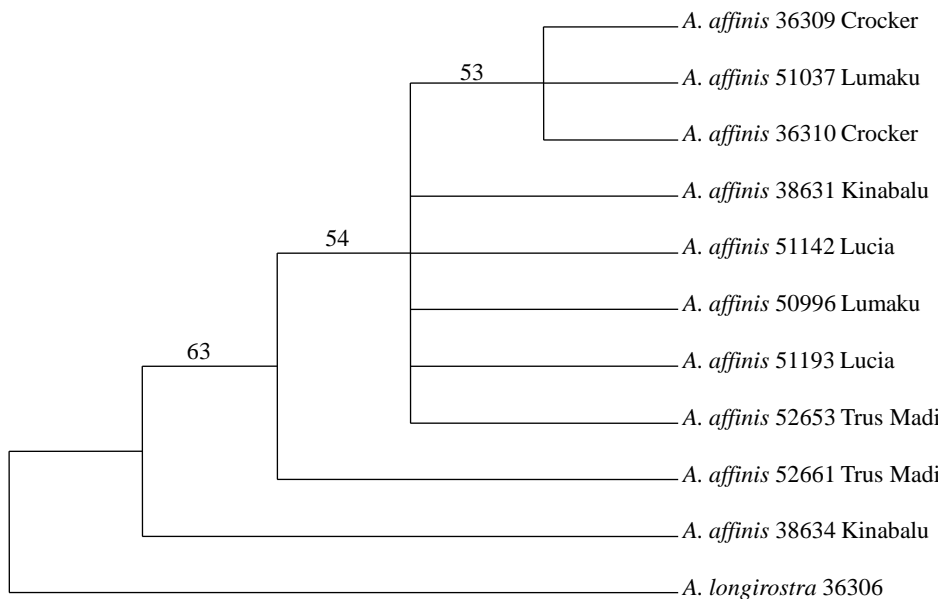


Fig. 3.7. Parsimony bootstrap tree of montane *Arachnothera affinis* populations. Numbers indicate bootstrap support.

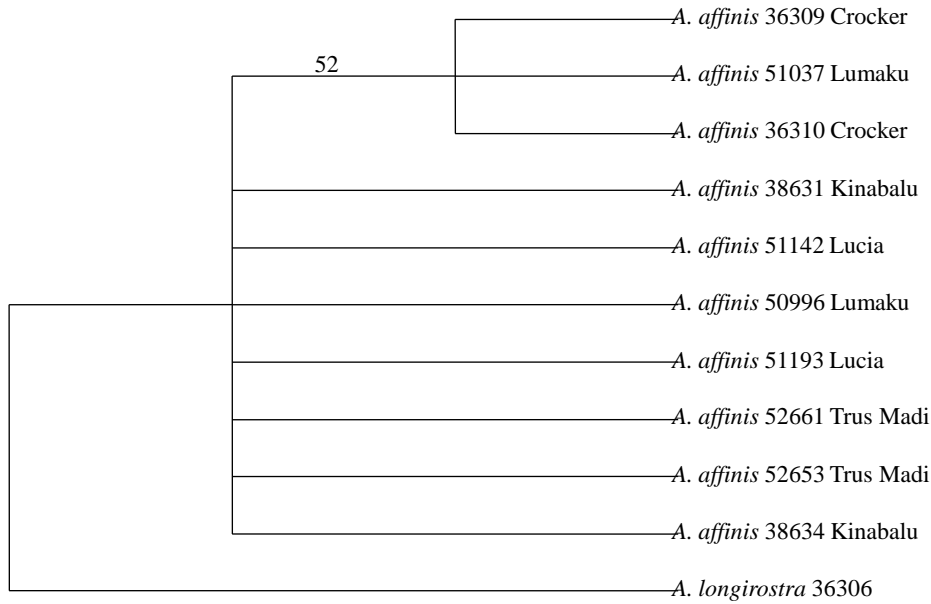


Fig. 3.8. Maximum likelihood bootstrap tree for montane *Arachnothera affinis* populations. The tree was bootstrapped 1000 times using a K81uf+G model with the following parameters: A = 0.3112, C = 0.3348, G = 0.1088, T = 0.2452; rates AC = 1.0, AG = 3.3965, AT = .1404, CG = .1404, CT = 3.3965, GT = 1.000; invariable sites = 0; Gamma distribution = .3296. Numbers indicated bootstrap support.

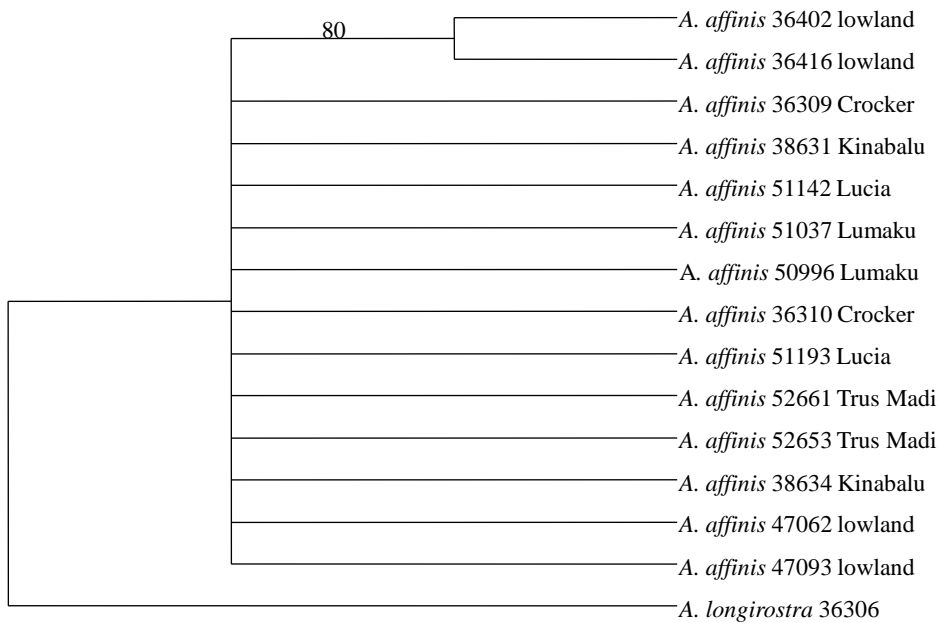


Fig. 3.9. Parsimony bootstrap tree of montane and lowland *Arachnothera affinis* populations. Numbers indicate bootstrap support.

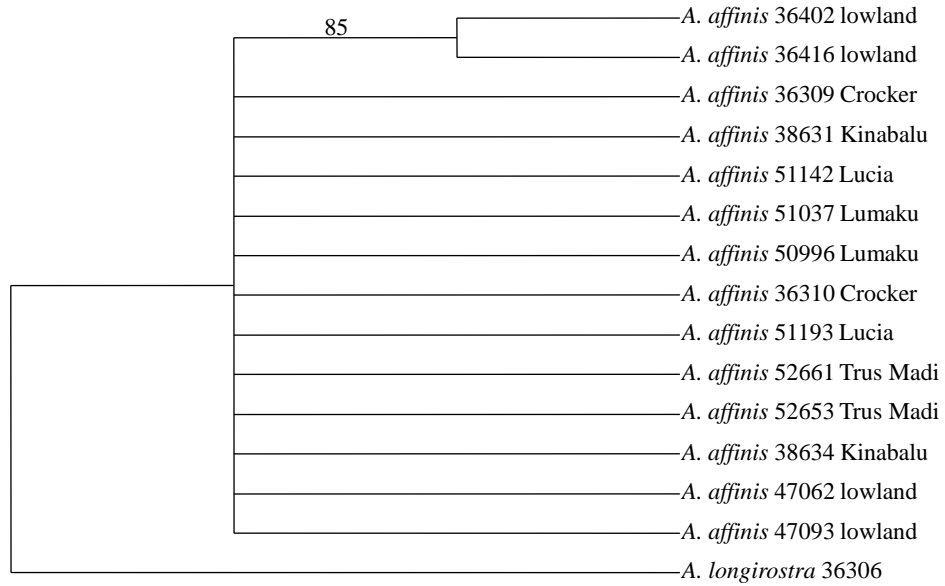


Fig. 3.10. Maximum likelihood bootstrap tree for montane and lowland *Arachnothera affinis* populations. The tree was bootstrapped 1000 times using a K81uf+G model with the following parameters: A = 0.3112, C = 0.3348, G = 0.1088, T = 0.2452; rates AC = 1.0, AG = 3.3965, AT = .1404, CG = .1404, CT = 3.3965, GT = 1.000; invariable sites = 0; Gamma distribution = .3296. Numbers indicated bootstrap support.

CHAPTER 4 DISCUSSION

Implications of Population Structuring

This study examined the phylogenetic relationships of populations of four species of passerines distributed in five montane localities in Sabah. The genes used for these comparisons, ND2 and ND3, have excellent evolutionary properties for the comparison of closely related taxa, including a relatively fast rate of evolution and relatively even distribution of nucleotide position changes across the genes (Hackett 1996, Sheldon et al. 2005). However, in spite of these good properties, the ND2 and ND3 comparisons had difficulty distinguishing relationships among the Sabah populations because of the close affinity of these populations for one another. This affinity was reflected in remarkably short genetic distances, infrequent apomorphies, and even more infrequent synapomorphies. Lack of differentiation was especially true for the three closest populations, Kinabalu, Crocker Range, and Trus Madi (Fig. 2.1). These sites lie within 55 - 75 km of one another. Kinabalu and Crocker Range are part of a contiguous, relatively high mountain chain, and only a narrow valley separates these two sites from Trus Madi. A longer distance and more profound landscape differences separate these three sites from Lumaku and Lucia. At least 75 km separates them from Lumaku, and although Lumaku appears to be connected to the Crocker Range by low hills (600 – 900 m), except where the Padas River gorge cuts the Crocker Range near Tenom, it is in fact more closely and directly connected by higher lands (900 – 1200 m) to the Meligan Range and mountains of Sarawak and Kalimantan. Lucia is even more remote. It lies at least 200 km from the other sites and is not connected by intervening mountains or even contiguous forested habitat, and several major rivers including the

Kinabatangan and Segama lie between it and the other sites. As a result, Lumaku and, especially, Lucia exhibit more differentiation in their populations than the three northwestern sites.

As expected, the amount of genetic differentiation among sites is not only a reflection of their geographic distance and isolation, but also of the characteristics of the birds. Specifically, the foraging habits and elevational range of the species play an important role in population connectivity. The species with the least geographic structure among its populations is the spiderhunter, *Arachnothera affinis* (Figs. 3.7-3.10). This species is highly vagile, often moving rapidly through the forest in search of flowers and possibly even trap-lining its feeding sources. It also occurs in a wide variety of disturbed and natural forest types from the lowlands up to 1500 m. Conversely, the species with the greatest geographic structure are the babblers, *Pellorneum pyrrogenys* and *Stachyris nigriceps*. Although there is not much genetic divergence among the populations in western Sabah, the Lucia populations of both these species are distinct, as reflected in phylogenies (Figs. 3.1, 3.2 and 3.3, 3.4) and genetic distances (1.4% and 0.8% respectively). These species are restricted to high elevations, neither having been recorded below 500 m, and both are largely interior forest dwellers. *P. pyrrogenys* is a strong-legged species that spends most of its time on or near the ground, and *S. nigriceps* is a highly social, flocking species that stays largely in the lower or middle part of the forest. Of the two, *S. nigriceps* is probably the better disperser, because its flock are more widely ranging.

Yet another factor at play in shaping the structure of Sabah's montane populations, apart from geographic distance and ecological characteristics, appears to be biogeographic history. The bulbul, *Alophoixus ochraceus*, exhibits an alternative population division-pattern that

suggests this possibility. In contrast to *P. pyrrogenys* and *S. nigriceps*, phylogenetic analyses of populations of *A. ochraceus* indicate that the Mt. Lumaku population is genetically distinct from the others (Figs. 3.5 and 3.6). The greater geographic proximity of Lumaku to the mountains of Sarawak and Kalimantan than to those of Sabah may explain this anomalous structure. A faunal divide in the vicinity of the border between Sabah and Sarawak has long been recognized. Several, apparently closely related, species pairs occur on either side of the border, e.g., the falconets, *Microhierax latifrons* and *M. fringillarius*; the pittas, *Pitta granatina* and *P. ussheri*, and the shama-thrushes, *Copsychus malabaricus* and *C. stricklandii*. In fact, both of the *C. malabaricus* and *C. stricklandii* morphotypes occur in the vicinity of Mt. Lumaku (Sabah Parks specimens). Evidence of genetic differentiation across the faunal divide is just coming to light in several groups of species that exhibit no obvious morphological differences between Sarawak and Sabah. Such cryptic differentiation has been observed in birds (Moyle et al. 2005), bats (Murray 2007), and tree shrews (Han et al. submitted). Why this faunal divide exists is unknown, but one possible explanation is that some of the vertebrate populations in Sarawak are recent Pleistocene invaders from the mainland or Sumatra, whereas the populations in Sabah represent older Bornean occupants. The likelihood that an historical, geographic component is responsible for the geographic structuring in *A. ochraceus* is supported by the fact that this bulbul is a very good disperser, in the habit of flying long distances in search of fruit sources (Smythies 1999, Sheldon et al. 2001). The geographically remote Lucia population shows little genetic differentiation from the Kinabalu, Crocker Range, and Trus Madi populations, whereas the geographically closer Lumaku population does.

Taxonomic observations

This study provides perspective on the designation of subspecies in the four species examined. No morphological difference was apparent for any of the populations examined, and genetic differentiation was generally small. Thus, only one subspecies of each species appears to exist in Sabah. *Stachyris nigriceps borneensis* is the appropriate designation for all populations in Sabah, even though Thompson (1966) identified specimens taken near Tenom in the Crocker Range as *hartleyi*. *Pellorneum pyrrogenys canicapillum* is the appropriate name for all populations in Sabah. If a different subspecies were to occur, it would most likely be found on Mt. Lucia, whose population is most diverged genetically from the rest. All of the *A. ochraceus* specimens appear to be *ruficrissus*. However, Borneo's other subspecies of *A. ochraceus*, *A. o. fowleri*, occurs in the Kelabit highlands, which are contiguous with the highlands surrounding Mt. Lumaku and the Meligan Range. Given the genetic distinction of the Lumaku population, it might be expected to represent *fowleri*. However, I could not distinguish any morphological difference between Lumaku birds and those from other Sabah populations. (I did not examine examples of *fowleri*.)

A particularly interesting controversy concerns the species status of *Arachnothera affinis*. In Borneo, it is thought to be a montane species, replaced in the lowlands by *A. modesta* (Davison 1999, Smythies 1999). Birdwatchers frequently identify both species at Poring Hot Springs, part of Kinabalu Park, where birding trails run from ca. 500 to 1000 m. In this study, I examined specimens collected at both lowland and highland locations, and Rob Moyle (pers. comm.) performed a morphometric study on approximately 92 Sabah specimens from both low

and highland locations. There is no evidence of consistent morphological or molecular differences between montane and lowland individuals. The upshot of these comparisons is that in Sabah there is only a single species. Whether this is true in other parts of Sabah is not clear.

Outgroup comparisons and genetic distances determined between ingroup and outgroup taxa in this project should be of interest to researchers working on higher-level phylogenetic relationships of bulbul, babblers, and spiderhunters. Among the three *Pellorneum* outgroups (*P. tickelli*, *P. albiventer*, and *P. capistratum*), *P. tickelli* was most similar to *P. pyrrogenys* (p-distance 14%) than to either *P. albiventer* (19%) or *P. capistratum* (24%). Such large distances are extremely unusual for congeners (Johns and Avise 1998, Sheldon et al. 2005), suggesting that further study may show *Pellorneum* to be an unnatural group. The distance from *Alophoixus ochraceus* to its apparent sister taxon, *A. bres* (Moyle and Marks 2006), is also unusually large for congeners (14%). These two taxa are parapatric lowland-upland taxa. *A. ochraceus* is widespread in SE Asia, but *A. bres* is Sundaic in distribution. That they are so diverged from one another suggests that they speciated allopatrically (probably on different islands) and then came back into proximity, rather than having speciated parapatrically. The distance from *Arachnothera affinis* to outgroup *A. longirostra* again is large, 23%. As of yet, no studies have examined higher-level relationships of spiderhunters, but they are such a uniform group morphologically that it is unlikely to be polyphyletic (as is probably the case with *Pellorneum*). It may be that spiderhunters are simply an old or fast-evolving group. Finally, the genetic distance from *Stachyris nigriceps* individuals from Borneo to outgroups of the same species in China are about 4%, an unusually large (but not unknown) distance for conspecific taxa. This probably reflects simply a long period of isolation between the two groups.

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VITA

A bright sunny day in early March 1980 goes down as the day Cheryl Leigh Haines entered the world, as the middle child of Don and Phyllis Haines, in Lake Charles, Louisiana. For the next eighteen years, Cheryl dreamed of leaving Lake Charles, longing to live with her grandparents in rural Arkansas. It was there where her life-long lust of the outdoors began. Grandmother encouraged Cheryl to catch crickets and grasshoppers in the corn fields to use as bait in the lake that was just steps outside the back door, or to climb the rolling hills, or to swim in the snow-fed streams. After graduating from Sam Houston High School in 1998, Cheryl enrolled in LSU, majoring in Zoology. During the last semester of her senior year, Cheryl took an ornithology course taught by Dr. J.V. Remsen, which derailed her plan to attend veterinary school. She graduated in May 2002, and in the fall of 2003, returned to LSU and enrolled in the Graduate Program of the Department of Biological Sciences, where she conducted research in the Museum of Natural Science. She has twice traveled to Southeast Asia for research, and these experiences started her on a likely lifelong search for a good piece of fruit, a deep appreciation for that region and its people, and an incurable wanderlust. Upon completion of her master's work, Cheryl will start a teaching position at the American School of Kuwait, in Kuwait City, Kuwait.