Evolutionary Genetics of Kloss's Gibbons (*Hylobates klossii*):

Systematics, Phylogeography, and Conservation

by

Danielle June Whittaker

A dissertation submitted to the Graduate Faculty in Anthropology in partial fulfillment of the requirements for the degree of Doctor of Philosophy,
The City University of New York

2005

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This manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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ABSTRACT

Evolutionary Genetics of Kloss's Gibbons (*Hylobates klossii*):

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Advisor: John F. Oates

While the behavior and ecology of the Kloss's gibbon (*Hylobates klossii*), a species endemic to the Mentawai Islands of Indonesia, have been studied in some detail, its relationship to other gibbon species has remained poorly understood, as have any patterns of intraspecific variation. This dissertation presents a new molecular phylogeny of the gibbons, the first study of intraspecific genetic variation in the Kloss's gibbon, and an assessment of the species' conservation status.

Fecal samples were collected from unhabituated gibbon groups at 7 sites on all four Mentawai Islands in 2001 and 2003. A 500 base pair segment of the hypervariable region I of the mitochondrial control region, or D-loop, was amplified and sequenced. Samples were genotyped at six microsatellite loci. Additionally, population surveys were conducted throughout the Mentawais using a method based on gibbon loud calls.

The Kloss's gibbon appears to be a recently derived member of the lar group of gibbons, clustering with the geographically close *H. agilis* and *H. moloch*, rather than a basal taxon as previous morphological studies have suggested.

While the other endemic Mentawai primates (*Macaca pagensis*, *Presbytis potenziani*, and *Simias concolor*) have been categorized into two geographically separated subspecies based on variation in coat color, the Kloss's gibbon shows no obvious variation, as all

individuals are completely black. The Kloss's gibbon shows no genetic differentiation between islands in either the mitochondrial or nuclear data. Generation time for gibbons is twice as long as for the cercopithecoid species, and the islands may not have been separated long enough for lineage sorting to occur in gibbons.

The primates of the Mentawai Islands are threatened by logging and hunting, and the conservation status of the Kloss's gibbon has not been evaluated since 1980. Based on the surveys, there are 20,000-25,000 Kloss's gibbons remaining in the wild, with the largest proportion located on Siberut, representing a decline of up to 50% since 1980. An upgrade of the conservation status of *H. klossii* to “Endangered” is thus recommended. Conservation planning for the Mentawai primates should focus on enforcement of existing protected areas and conservation education to reduce hunting.

ACKNOWLEDGMENTS

This research was supported by a Doctoral Dissertation Improvement Grant from the National Science Foundation (BCS-0335949), grants from the Charles A. and Anne Morrow Lindbergh Foundation, Primate Conservation, Inc., and Conservation International, and by the City University of New York Graduate Center, the New York Consortium in Evolutionary Primatology (NYCEP) and the Center for Environmental Research and Conservation (CERC) at Columbia University.

I am grateful to the Indonesian Institute of Sciences (LIPI) and the government of the Republic of Indonesia for granting permission to conduct research in Indonesia.

Many people helped me not only with this project, but also throughout my seven years of graduate school and dissertation research. I express my sincere thanks to:

My advisor, the illustrious John F. Oates, who has become my mentor, ally, and friend;

My "unofficial" advisor, Juan Carlos Morales, for guiding me through the difficulties of genetics methods and analysis and for his enthusiastic support;

My committee members, Roberto Delgado and Rob DeSalle, for insightful comments and excellent suggestions;

Sara Stinson and Larissa Swedell for serving on my second exam committee and providing many helpful comments on my proposals;

Eric Delson, director of NYCEP, for always looking out for me;

Don Melnick and Todd Disotell for generously providing the use of their laboratory facilities;

Noviar Andayani (University of Indonesia) and Amsir Bakar (Andalas University) for acting as sponsors for my field research;

Prithiviraj Fernando, Zoltan Takacs, and Ben Evans, for assistance in the laboratory;

All of the faculty and students of NYCEP for contributing to a fun, friendly, collaborative, and intellectually stimulating and productive atmosphere (which I fear I will always look back on as "the good old days"), especially my friends Rich Bergl, Andy Burrell, Paul Buzzard, Michael Campbell, Siobhan Cooke, Kate Detwiler, Rachel Dvoskin, Katy Gonder, Rebecca Jabbour, Jenna Lawrence, Josh Linder, Rachel Nuger, Tara Peburn, Amy Schrier, Stephanie Spehar, Denise Su, Lissa Tallman, Nelson Ting, Tony Tosi, and Kim Williams-Guillen;

The students of CERC, especially Kate McFaddin and Rasit Bilgin, for their help (technical and otherwise) in the lab;

The gibbonologists who have supported and encouraged me throughout this work: David Chivers, Thomas Geissmann, Alan Mootnick, and especially my friend and collaborator Susan Lappan;

Sasimar Sangchantr, Agustin Fuentes, Lisa Paciulli, and Christophe Abegg, because I would not have had the courage to work in the Mentawais without the advice and support of those who had gone before me;

My field assistant Kathleen “Kaja” Donovan, and my many wonderful Mentawai field assistants: Albinus, Bisol, Rijal, Roimek, Omar, Iros, Markus, Natim, Karlo, Martinus, Mus, Eri, Ardon, Kristian, Elisa, and Al, for their hard work and much-needed assistance;

Rizaldi and Firman, for helping me in Padang and Jakarta;

Christina Fowler and Chris Scurrah, of the Hotel Batang Arau in Padang, for providing a home away from home;

The ladies of LUPEC, for taking my mind off it all;

Jessica Satkoski and Suzanne Hagell, for seeing me through the worst times and sharing the best times in graduate school, and for being my closest friends;

Misha Whittaker, for his patience;

My parents, John and Rose Whittaker, for always believing in me;

And finally, my husband, Nathan Burroughs for his endless love and support. I never expected him to accompany me to the Mentawais and work for me in the field, but he did. That’s love.

Dedication

To my husband, Nathan Burroughs

For his unwavering love and support

"The [Mentawai] islands are not very pleasant collecting-grounds…"

- Cecil Boden Kloss, 1927

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CHAPTER 1

Introduction

1.1 Introduction to the dissertation

This study addresses the interspecific relationships, intraspecific diversity, and conservation biology of the Kloss's gibbon (*Hylobates klossii*). This species is endemic to the Mentawai Islands, located off the west coast of Sumatra, Indonesia (Figure 1.1). While the behavior and ecology of the Kloss's gibbon have been studied in some detail (see below), its relationship to other gibbon species has remained poorly understood, as have any patterns of intraspecific variation. This dissertation presents a new molecular phylogeny of the gibbons, as well as the first study of intraspecific genetic variation in the Kloss's gibbon.

This dissertation consists of seven chapters: Introduction, Methods, Systematics, Phylogeography, Population Survey, Conservation Action Plan, and Summary and Conclusions. The introductory chapter will begin with a review of previous studies of the Kloss's gibbon and of the geology and biogeography of the Mentawai Islands, and conclude by presenting the research questions to be addressed in this dissertation. The Methods chapter presents a description of the field sites, field methods, and laboratory methods used in this study. Because of the disparate nature of the questions addressed, each subsequent chapter (Systematics, Phylogeography, and Population Survey) will consist of an introduction to the topic, a short review of the methods, and a detailed description of the analytical methods, results, and discussion of the results. Chapter 6 is a Conservation Action Plan for the Mentawai Primates, which reviews the conservation

status of all four primates, chronicles past conservation action, and presents a set of conservation recommendations for the future. The final chapter reviews the conclusions reached in this dissertation and suggests directions for future research.

1.2 Gibbon taxonomy, biology and behavior

Gibbons, or the small apes, belong to the family Hylobatidae, within the superfamily Hominoidea. The number of genera recognized in the family Hylobatidae has varied widely over the years. In the past, many researchers have recognized a single genus (*Hylobates*) with four subgenera: *Hylobates* (the lar group), *Symphalangus* (the siamang), *Bunopithecus* (the hoolock gibbon), and *Nomascus* (the crested gibbons), each with distinct chromosome numbers (Chiarelli 1972; Groves 1972). Recent molecular analyses (Melnick et al. 2000; Roos and Geissmann 2001) have recommended that these subgenera should be elevated to the level of genus, as genetic distances among them equal or exceed those observed between *Homo* and *Pan*. Groves (2001) has suggested that *Bunopithecus hoolock* may require a new genus name, as it does not appear congeneric with the fossil type *Bunopithecus sericus*. For this dissertation, the taxonomy of Brandon-Jones, et al. (2004) is used as the basis for analysis, as it represents a consensus of recent taxonomic evaluations (Table 1.1). In Brandon-Jones, et al. (2004), the genus *Hylobates* is equivalent to the previously recognized subgenus *Hylobates*.

Gibbons are found in the tropical forests of south and southeast Asia. They are completely arboreal, preferring the upper levels of the tropical forest canopy. All gibbons are specialized brachiators, with much longer forelimbs than hindlimbs, and spend longer periods of time in forelimb suspension than any other primate (Hollihn 1984). Gibbons are much smaller than other apes, with body weights ranging from 5.5-7.5 kg for the

genera *Hylobates*, *Bunopithecus*, and *Nomascus*, and about 12 kg for the siamang (*Symphalangus*) (Geissmann 1993). Most hylobatids are primarily frugivorous (with the exception of the larger siamang, which relies more on foliage).

Gibbons have been characterized as living in small, monogamous family units consisting of one adult male, one adult female, and their offspring (Preuschoft et al. 1984; Leighton 1987). Gibbon groups are territorial, and the mated pair typically sings a duet each morning; this duet has been hypothesized to function as a pair-bonding mechanism and as a means of resource defense (Mitani 1985; Cowlishaw 1992).

The typical model of the gibbon social group, consisting of a pair-bonded male and female and their offspring, has been challenged by recent research that has found significant departures from this model in many populations of gibbons, including extra-pair copulations and groups with more than two adults (Srikosamatara and Brockelman 1987; Bleisch and Chen 1991; Palombit 1994a, 1994b; Reichard 1995; Brockelman et al. 1998; Jiang et al. 1999; Lappan 2005). Recent genetic and behavioral analyses of hylobatids have shown that many social groups display extra-pair paternity (Palombit 1994a, 1994b; Reichard 1995) or immigration of additional adults or subadults (often siblings of the adult male or female) (Oka and Takenaka 2001; Lappan 2005).

1.3 Previous studies of the Kloss's gibbon

The Kloss's gibbon was discovered in 1902 during a collecting expedition to the Mentawai Islands (Miller 1903), when it was first described as a "dwarf siamang" due to its small size and completely black pelage. Subsequent morphological studies concluded that it was more closely related to other "lar group" gibbons (genus *Hylobates*) than to the siamang (Schultz 1932; Miller 1933; Schultz 1933), a classification which is still

generally accepted (Chivers 1977; Haimoff et al. 1982; Creel and Preuschoft 1984; Marshall and Sugardjito 1986; Geissmann 1993). Molecular and vocal studies have further elucidated the phylogenetic placement of this species as not basal to the lar radiation but as a derived taxon (Garza and Woodruff 1992; Geissmann 1993; Zehr 1999; Chatterjee 2001; Takacs et al. in press), though studies differ as to which gibbon species is most closely related to the Kloss's gibbon (see Chapter 3 for a detailed discussion). No subspecies have been proposed for the Kloss's gibbon.

Another collecting expedition was undertaken in 1924 (Chasen and Kloss 1927), but due to the inaccessibility of the Mentawai Islands and reports of difficult terrain, no further studies of Mentawai wildlife were undertaken until 1970, when Richard Tenaza made a one-week reconnaissance expedition to Siberut, the largest and northernmost of the Mentawai Islands (Tenaza and Hamilton 1971). Tenaza observed unhabituated Kloss's gibbons for a period of three months in 1972 at a site in Siberut known as "Tei-tei Peleigei" (1º24' S, 99º1'E). Kloss's gibbons were found to live in small groups reported to consist of one adult male, one adult female, and one to three offspring, and occupied territories averaging 6.7 ha (Tenaza 1974). Tenaza (1974, 1976) observed that, unlike most gibbon species, Kloss's gibbons do not sing duets; rather, the males sing in a chorus before dawn, while the females chorus after dawn.

Tenaza also suggested that Kloss's gibbons choose their sleeping trees as a response to human predation. Unlike groups of lar gibbons (*Hylobates lar*), the members of which sleep scattered in different trees, Kloss's gibbon groups all sleep together in the same emergent tree. Tenaza observed that local Mentawai people have traditionally hunted all

four Mentawai primates, and that the sleeping-tree choices of Kloss's gibbons may have evolved as an anti-predation strategy (Tenaza 1974).

Following Tenaza's pioneering study, Ronald Tilson studied four groups of partially habituated Kloss's gibbons at Tei-tei Peleigei, following and observing the gibbons from a distance for 21 months between 1973-1974. Tilson observed group membership changes in several social groups, and concluded that the adults exclude same-sex maturing offspring from their natal group through intrasexual aggression. In some cases, the dispersing offspring acquired a territory adjacent to the natal territory with the assistance of one or both parents (Tilson 1980, 1981).

Anthony Whitten was the first (and so far only) researcher to successfully habituate a group of Kloss's gibbons in his 2-year study of Kloss's gibbon ecology between 1976-1978 (Whitten 1982a, 1982b, 1982c, 1982d). Whitten's study site, "Paitan," was located at 1º21'S, 98º59'E, about 10 km NW of Tenaza and Tilson's site. Whitten found home ranges of 31-35 ha, substantially larger than those observed by Tenaza (1974) and Tilson (1980) but closer to the size observed for all other gibbon species (Whitten 1982d). Kloss's gibbon males and females were found to prefer emergent trees for singing, and singing in both sexes tends to be inhibited by rain (Whitten 1982a). Whitten described the Kloss's gibbon diet, which is mainly frugivorous (72%) but includes more arthropods (25%) and less leaves (2%) than other gibbon species (Whitten 1982b).

No further studies on wild Kloss's gibbons have been conducted since Whitten's research. Other recent Mentawai primate studies have focused on the Mentawai langur, *Presbytis potenziani* (Fuentes 1994, 1996; Sangchantr 2004) or on assessing the densities of all four primate species in the Pagai Islands (Paciulli 2004). Researchers are currently

studying the behavior and conservation of the Mentawai macaque (*Macaca pagensis*) in northern Siberut (Kobold et al. 2003; Roos et al. 2003).

1.4 Mentawai geology and biogeography

The Mentawai Islands are situated 85 to 135 km off the coast of West Sumatra, between 0°55' to 3°20' South and 98°31' to 100°40' East (Figure 1.1). There are four islands: Siberut, Sipora, North Pagai, and South Pagai. This island chain has been isolated from mainland Sumatra throughout most of its history, even when sea levels were low enough that the rest of Sundaland was connected.

The Sunda shelf comprises Sumatra, Borneo, Java, and mainland Malaysia, as well as the many smaller islands in this area. The Mentawai Islands, along with the Batu Islands and Nias Island, were uplifted during the Tertiary period by the subduction of the Indian tectonic plate under the Sunda plate. Deep basins, including the 1500-meter deep Mentawai Basin, were left separating these islands from mainland Sumatra (Karig et al. 1980; Moore et al. 1980; Whitten et al. 2000).

During middle Pleistocene glaciations, Sundaland was fully exposed several times as a connected continent by sea level drops of 230 meters below current levels (Batchelor 1979). Geological evidence indicates that the Mentawai Islands were never fully connected to Sundaland, but were joined to Sumatra by a land bridge north of Siberut, through the Batu Islands (Batchelor 1979; Dring et al. 1990) (Figure 1.2). Assessing the most recent connection of this tectonically unstable region to Sumatra is problematic, as these islands are continuing to be pushed upwards: initial reports suggest the earthquakes of 2004-2005 have lifted the Mentawais about 2-3 meters (USGS 2005). However, the available evidence suggests that the last time the Mentawais were connected to

Sundaland was between one million and 500,000 years ago, the last time sea levels were 200 meters below present levels (Batchelor 1979).

This long history of isolation from the mainland likely accounts for the high level of endemism in the Mentawai Islands: 65% of non-volant mammals in the Mentawai islands are endemic at the genus or species level (World Wildlife Fund 1980). The relationships of these species to other Sunda species are not well understood. The mammalian fauna of the Mentawai Islands is different enough from the Batu Islands to have led some authors to reject the possibility of this land bridge as a migration route for the Mentawai primates (Fuentes 1994). Instead, rafting across the Mentawai Strait has been suggested (Brandon-Jones 1998), despite extreme sea conditions that may make such an event very unlikely (Dring et al. 1990).

The Mentawai Islands have been suggested to have played a crucial role in the evolution of southeast Asian biota (Brandon-Jones 1998; Gathorne-Hardy et al. 2002). Brandon-Jones (1998) suggests that the gibbons, macaques, and colobines of the Mentawai Islands are basal to primates found throughout southeast Asia. In this scenario, the primates of Sumatra went extinct during Pleistocene glaciations, and the Mentawai Islands provided a reservoir from which primates recolonized Sumatra during interglacials. A study of termite diversity has also suggested that rainforest persisted in the Mentawai Islands throughout the Pleistocene glaciations, but does not propose that these insects subsequently recolonized Sumatra (Gathorne-Hardy et al. 2002). Based on the geological data discussed above, the restocking of the Sundaland fauna from the Mentawais seems unlikely. Furthermore, molecular studies including my analysis in Chapter 3 suggest that Kloss's gibbons are not basal to the genus *Hylobates* (Garza and

Woodruff 1992; Geissmann 1993; Zehr 1999; Chatterjee 2001; Takacs et al. in press), and studies of colobine genetic and morphological data indicate that the Mentawai primate *Simias concolor* (and its sister taxon, *Nasalis larvatus*) are not basal colobines (further discussed below) (Delson 1975; Ting et al. 2005).

1.5 The monkeys of the Mentawai Islands

In addition to the Kloss's gibbon, the Mentawai islands are home to three endemic monkey species, including two colobines and one cercopithecine.

1.5.1 The snub-nosed pig-tailed langur, or simakobu monkey, *Simias concolor* (Miller 1903)

This colobine is considered a member of the "odd-nosed" group of colobines, which includes the genera *Nasalis*, *Pygathrix*, and *Rhinopithecus*. Some morphological analyses have suggested that *Simias* has an affinity to the proboscis monkey *Nasalis larvatus* of Borneo, and may actually be a member of the genus *Nasalis*, or a subgenus within *Nasalis* (Groves 1970; Delson 1975). A recent analysis of mitochondrial DNA suggests that the level of genetic difference between *Nasalis* and *Simias* is comparable to that between other colobine congenerics, such as members of the genus *Trachypithecus* or of *Colobus*. Pairwise sequence differences in the cytochrome *b* gene within genera (and between *Simias* and *Nasalis*) are below 10%, while differences between genera are above 10%. Thus, *Simias* may belong within the genus *Nasalis* (Ting et al. 2005). However, current classification places the simakobu monkey in its own genus, thus making *Simias* a primate genus endemic to the Mentawai Islands (Brandon-Jones et al. 2004).

There are currently two subspecies of *S. concolor* recognized: *S. concolor concolor*, found on the islands of Sipora, North Pagai, and South Pagai; and *S. c. siberu*, found on the island of Siberut (Chasen and Kloss 1927; Brandon-Jones et al. 2004).

1.5.2 The Mentawai Island langur, *Presbytis potenziani* (Bonaparte 1856)

The Mentawai Island langur is currently classified in the genus *Presbytis* based on skeletal morphology (Brandon-Jones 1993), though earlier studies suggested an affinity with *Trachypithecus* (Washburn 1944), and the species was originally named *Semnopithecus potenziani* (Bonaparte 1856). Based on cranial, vocal, and pelage characteristics, the Mentawai langur is considered to be most closely related to *Presbytis hosei* in Borneo and *P. thomasi* in northern Sumatra (Wilson and Wilson 1976; Brandon-Jones 1993). No molecular analysis of *Presbytis potenziani* has yet been conducted.

Two subspecies of this langur are recognized: *P. potenziani siberu* in Siberut, and *P. p. potenziani* on the southern islands of Sipora, North Pagai, and South Pagai (Chasen and Kloss 1927; Brandon-Jones et al. 2004).

1.5.3 The Mentawai macaque, *Macaca pagensis* (Miller 1903)

The original description of the Mentawai macaque named it as a unique species (Miller 1903), though some later authors regarded it as a subspecies of the pig-tailed macaque, *Macaca nemestrina* (Chasen 1940; Fooden 1975). The Mentawai macaque was again granted specific status by Wilson and Wilson (1976), and it is currently recognized as such (Brandon-Jones et al. 2004).

Subspecies were never formally described for *M. pagensis*, though the distinctiveness of the Siberut form compared to that on the southern islands was suggested (Whitten and Whitten 1982). The subspecies *M. pagensis pagensis* on Sipora and the Pagais and *M. p.*

siberu on Siberut were inadvertently named without description by Fuentes and Olson (Fuentes and Olson 1995) and are still recognized (Brandon-Jones et al. 2004). A recent molecular analysis has suggested raising these subspecies to specific status based on the divergence between mitochondrial haplotypes (Roos et al. 2003); however, this suggestion requires further study and is not generally accepted.

1.6 A cultural note on taxonomy

The local Mentawai names for the primates follow the same pattern as the taxonomic designations: the gibbons have the same name over all four islands (*bilou*), whereas the other three species have different names in Siberut than on the southern islands (Table 1.2).

Within the Mentawai language, there is great variation in local dialects. The greatest variation occurs within the island of Siberut, where dialects differ between the clans that inhabit different river basins (Whitten 1982e). While the Pagai peoples and dialects have their origin in Siberut, natives of the Pagai islands have difficulty understanding natives of Siberut. Why, then, does the gibbon have the same name across all dialects? Perhaps it is recognized as truly the same biological entity, whereas the differences between the other taxa are recognized linguistically. On the other hand, the importance of the Kloss's gibbon in local mythology may play a role in preserving its name in all dialects.

According to a Siberut creation myth, long ago there were no humans in the Mentawais, but there were many *bilou*. The treetops became overcrowded with *bilou*, and they had a meeting to decide what to do about it. After much discussion, it was decided that half of the *bilou* should move down to they ground. They did, and eventually changed into humans (Whitten 1982e). Traditional Mentawai religion honors the spirits

of all animals, but particular focus is placed on the Kloss's gibbon, with many songs and dances dedicated to this primate. Thus, hunting of gibbons has traditionally been taboo except in very specialized circumstances, such as a boy's first hunt in the coming-of-age ceremony. Although the traditional animist religion has all but disappeared due to the Christianization efforts of Protestant and Catholic missionaries beginning in the 1950s, as well as the insistence of the Indonesian government since the Sukarno administration that all citizens adhere to one of five approved religions (Catholicism, Protestantism, Buddhism, Hinduism, and Islam), memories of the myths persist. Gibbons are still rarely hunted in the southern islands, where conversion to modern religions is complete (although some local people suggest that this lack of hunting is due not to taboo but to the distastefulness of gibbon meat, as well as the difficulty of hunting an animal that moves quickly high in the canopy).

1.7 Research questions and hypotheses

The following questions are addressed in this study:

1. **How is the Kloss's gibbon related to other members of the genus *Hylobates*?** Past analyses have disagreed on the placement of the Kloss's gibbon within the genus *Hylobates*. This dissertation presents a phylogenetic analysis that attempts to overcome the flaws of past studies with increased sampling and sequence data from a rapidly mutating gene, the mitochondrial control region, which may be able to resolve the rapid radiation patterns of this genus. This question is addressed in chapter 3, Molecular Systematics of the Lar Group of Gibbons (Genus *Hylobates*).

2. **Are geographically separated populations of *H. klossii* differentiated genetically?** As noted above, subspecies have been named for different populations of

the other Mentawai primate species, but not for the Kloss's gibbon. Chapter 4, Phylogeography of Kloss's Gibbons, tests whether Kloss's gibbons have also differentiated, using mitochondrial control region sequence data and nuclear microsatellite genotypes.

3. **How many Kloss's gibbons remain?** Kloss's gibbons have never been censused on all four islands, and new population estimates have not been published since the World Wildlife Fund's (1980) publication. Chapter 5, Population Survey Results, addresses this question with a survey based on gibbon loud calls, and also assesses the extent of remaining forest in the Mentawais.

4. **How should conservation planning in the Mentawai Islands proceed?** New data on populations, as well as genetic analysis of intraspecific diversity, should inform conservation action. Chapter 6, Conservation Action Plan for the Mentawai Primates, reviews all available data on the status of the four Mentawai primate species and presents a conservation action plan for the future.

Genus	Chromosomes	Species	Subspecies
Hylobates	44	*H. agilis*	*agilis*, *albibarbus*, *unko*
		H. klossii	
		H. lar	*lar*, *carpenterii*, *entelloides*, *vestitus, yunnanensis*
		H. moloch	*moloch*, *pongoalsoni*
		H. muelleri	*muelleri*, *abbotti*, *funereus*
		H. pileatus	
Bunopithecus	38	*B. hoolock*	*hoolock*, *leuconedys*
Nomascus	52	*N. concolor*	*concolor*, *furvogaster*, *jingdongensis*, *lu*
		N. gabriellae	
		N. leucogenys	*leucogenys*, *siki*
		N. sp. cf. *nasutus*	*nasutus*, *hainanus*
Symphalangus	50	*S. syndactylus*	*syndactylus*, *continentis*

Table 1.1: Gibbon taxonomy used in this study (Brandon-Jones et al. 2004)

Taxon	Island(s)	Local Mentawai name
Hylobates klossii	Siberut, Sipora, N & S Pagai	*Bilou*
Macaca pagensis pagensis	Sipora, N & S Pagai	*Siteut*
Macaca pagensis siberu	Siberut	*Bokkoi*
Presbytis potenziani potenziani	Sipora, N & S Pagai	*Atapaipai*
Presbytis potenziani siberu	Siberut	*Joja*
Simias concolor concolor	Sipora, N & S Pagai	*Simasepsep*
Simias concolor siberu	Siberut	*Simakobu*

Table 1.2: Taxonomic and vernacular names for Mentawai primates

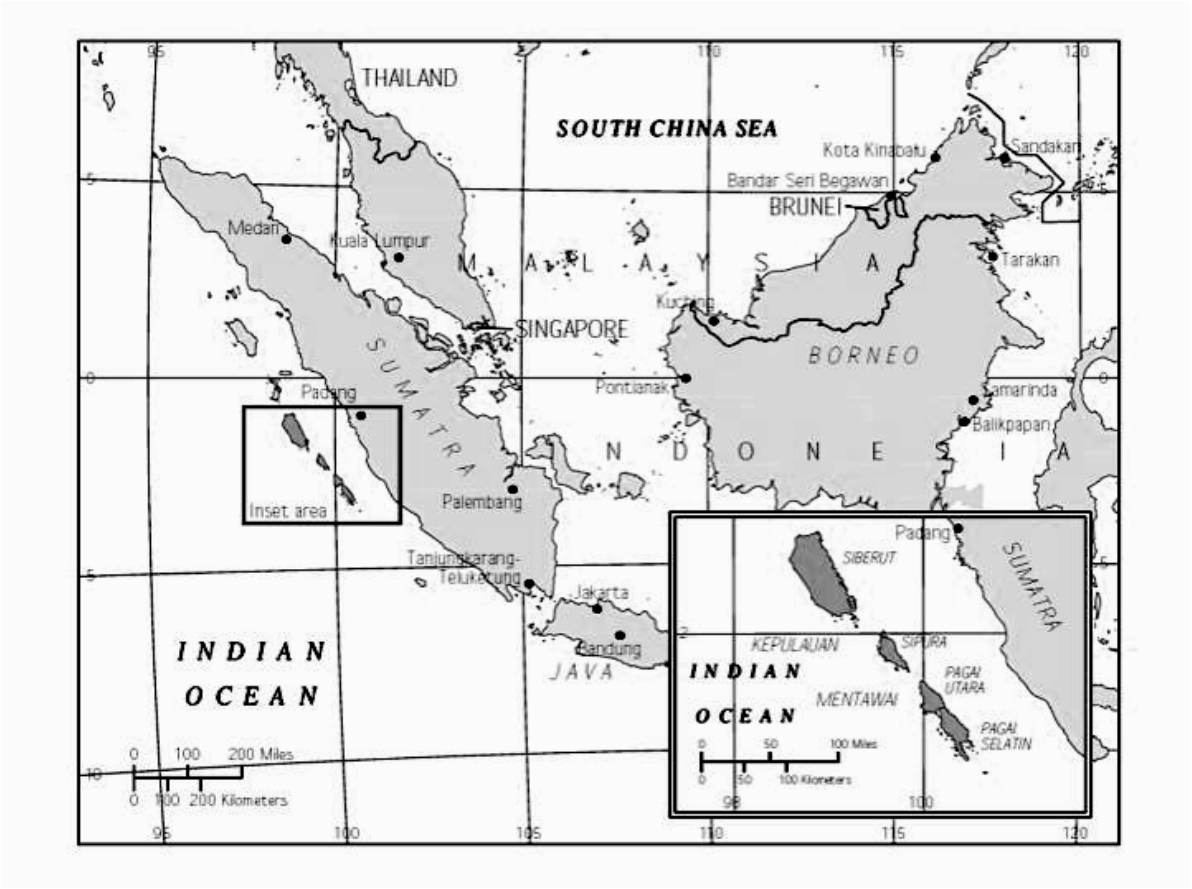

Figure 1.1: Map showing the location of the Mentawai Islands (Falk 2000)

Figure 1.2: Map of Sundaland showing shorelines when sea levels were at their lowest (Muir et al. 2000)

CHAPTER 2

Study Site and Methods

For this project, I visited the Mentawai Islands twice, from January through May 2001 and August through December 2003. In the 2001 pilot study, I tested sample collection and survey methods. In 2003, I collected more fecal samples and conducted population density surveys using gibbon loud calls. Lab work was conducted Fall 2002-Spring 2003 and throughout 2004 to sequence mitochondrial DNA and genotype nuclear microsatellites.

The aim of this chapter is to describe the Mentawai Islands and specifically the sites visited for the study, and to explain the field and laboratory methods used. Analytical methods will be described in detail in subsequent chapters.

2.1 Site descriptions

2.1.1 Mentawai environment

The Mentawai Islands are situated 85 to 135 km off the coast of West Sumatra, Indonesia (Figure 2.1). The four islands of the Mentawai archipelago (Siberut, Sipora, North and South Pagai) have a total area of about 7,000 km^2. Siberut is the northernmost and largest island with a total area of 4,030 km^2. North and South Pagai are separated by a narrow strait and together have an area of 1,675 km^2. Sipora is the smallest island, with an area of only 845 km^2.

The climate of the Mentawai Islands is consistently hot and humid. The mean minimum and maximum daily temperatures are 22ºC and 31ºC, while humidity levels range from 80-95% (World Wildlife Fund 1980; PHPA 1995). Rainfall records from

1918-1941 show average annual rainfall of 3,400 mm in Siberut and 4,200 mm in the Pagais (Tilson 1980), and records over a 12-year period (1974-1985) found an average rainfall of 4,420 mm per year (Tenaza and Fuentes 1995). Monthly rainfall is highly variable among sites and from year to year, but the heaviest rains (up to 480 mm/month, though Sangchantr (2004) records 690 mm in October 2000) are usually during the monsoon period (October-February), while the lowest rainfall occurs between April and June (Tilson 1980; Fuentes 1994; Sangchantr 2004). The Mentawais do not experience a dry season; during the driest months, rainfall averages 200-270 mm (Tilson 1980; Fuentes 1994). Whitten has described the Mentawais as having four indistinct seasons: two wet, one very wet, and one incredibly wet (Whitten 1982e).

Much of the Mentawai Islands are covered in tropical rain forest. The forest types present include primary Dipterocarp forest, primary mixed forest, and secondary regenerating logged Dipterocarp forest. Less common are freshwater swamp forest, mangrove forest, sago swamps, and west coast beach vegetation (PHPA 1995).

Primary Dipterocarp forest is dominated by trees from the family Dipterocarpaceae, most commonly genus *Dipterocarpus* followed by genus *Shorea*. Other common Dipterocarp genera are *Hydnocarpus* and *Palaquium*, the latter often emergent. This forest type is found mostly on high ridges and hills, and the average continuous canopy height is about 30-35 m, with emergents sometimes reaching 70 m. Ground vegetation tends to be sparse, and epiphytes and large woody lianas are not abundant, though rattans are quite common (World Wildlife Fund 1980; PHPA 1995).

On the slopes and low-lying areas below these ridges, primary mixed forest is more common. Many tree families are represented in this forest type, most commonly

Dipterocarpaceae, Euphorbiaceae, Myristicaceae, and Dilleniaceae; in most areas none of these tree families are dominant. Unlike mixed forests in Sumatra, legumes (family Fabaceae) are rare. The average canopy height in this forest type is lower than primary Dipterocarp forest at 25-30 m. Emergents in primary mixed forest are most commonly from the genera *Shorea*, *Dipterocarpus*, *Dialium*, *Pentace*, and *Durio*, and are less abundant than in primary Dipterocarp forest. Epiphytes, woody lianas, and rattan are abundant in primary mixed forest, and ground vegetation is dense (World Wildlife Fund 1980; PHPA 1995).

Secondary, regenerating logged forest is found in areas throughout the Mentawai Islands where logging companies failed to replant, despite their concession agreements. These forests vary greatly, depending on the original forest composition, degree of disturbance and length of time since they were logged. Some are dominated by fast-growing pioneer species, though the more heavily disturbed areas have abundant vines and lianas that hamper regeneration. Indonesian scientists have found that areas with light logging can regenerate well and show many dipterocarp saplings in the understory (PHPA 1995).

Much of the forest is highly disturbed, with many logging companies present on all four islands. One of the goals of this study was to estimate how much forest remains in the Mentawais (see below). Much of the area of North and South Pagai falls within the boundaries of PT Minas Pagai Lumber Company, and is selectively logged, regenerating forest. Many other areas throughout the Mentawai Islands have been divided into smaller logging concessions and have been clear-cut.

The only legally protected area in the Mentawai Islands is Siberut National Park (192,660 hectares), which covers nearly half of Siberut Island (Figure 2.2). The park is divided into three management zones: sanctuary, traditional use, and park village zones. Hunting is strictly prohibited within the sanctuary zones, and while limited traditional hunting is allowed by permit in the traditional-use zones, hunting of Kloss's gibbons and simakobu monkeys (*S. concolor*) is banned. Logging is not permitted in the sanctuary or traditional-use zones. The three park village zones are inhabited by native Mentawai people, and no restrictions are placed on their land-use (PHPA 1995).

2.1.2 Mentawai people

The island of Siberut has been inhabited for about 2,000-3,000 years, and Sipora and the Pagais were likely colonized more recently, within the last 200-400 years (Loeb 1929; Nooy-Palm 1968). Mentawai tradition states that the people migrated to Siberut from the island of Nias, located north of Siberut, and southwards through Sipora and the Pagais. The clan names found in Sipora and the Pagais are traceable to southern Siberut, supporting this dispersal (Nooy-Palm 1968). Traditionally, the Mentawai people have practiced sago and taro agriculture, as well as hunting with bow and arrow, and had a neolithic material culture lacking pottery or woven materials; in recent decades, the culture has become more modern due to trade with Sumatra, immigration from Sumatra and other areas, and religious conversion by Protestant and Catholic missionaries. Siberut remains more traditional than the southern islands (Nooy-Palm 1968).

Today, the Mentawai population is about 56,000 people, including indigenous people and migrants. There are 25,000 people in Siberut (6.2 people/km^2), 9,000 in Sipora (10.7 people/km^2), and 22,000 in the Pagais (13.1 people/km^2) (Fuentes 1996/1997).

2.1.3 Field sites

The sampling strategy for this project aimed to sample each of the islands and also to get a cross-section of existing forest types and levels of disturbance. At each of seven sites across the four Mentawai islands (Figure 2.1), I collected fecal samples for genetic analysis and conducted population density surveys (Table 2.1). When possible, I chose sites that were visited by previous researchers. In South Siberut and Sipora, no previous research had been conducted, and instead I located sites after speaking with local authorities and villagers about where I could find forest with gibbons.

2.2 Field methods

Population surveys and collection of genetic samples were conducted at each site. Research permits were obtained from the Indonesian Institute of Sciences (Lembaga Ilmu Pengetahuan Indonesia, or LIPI) for both field seasons (no. 329/II/KS/2001, and no. 4373/SU.3/KS/2003). Samples were exported from Indonesia under CITES export permits (permits 36499/VI/SATS-LN/2001 and Sk. 78/IV/Set-3/2004) and imported into the United States under CITES and US Department of Agriculture permits held by D. J. Melnick at Columbia University.

2.2.1 Population surveys

Because gibbon groups are difficult to detect by sight in tropical rain forests, survey methods using line transects tend to underestimate gibbon densities (Brockelman and Ali 1987). No gibbons were detected on line transects in a pilot study for this project (see below). Researchers have found surveys based on gibbon loud calls to be more accurate than transects (Brockelman and Srikosamatara 1993). The contagious nature of singing in

Kloss's gibbons, by which singing by one group stimulates nearby groups to sing, facilitated this type of survey (Tenaza 1976).

Transects vs. Vocalization surveys. During the pilot study phase of this project (2001), I conducted both vocalization and line transect surveys in the Peleonan forest of North Siberut to test which method was more reliable for estimating gibbon density. We cut two parallel transects, four kilometers long and 500 meters apart. We walked each transect slowly three times, pausing every 200 meters to listen for animals. If any of the four species of primate was seen or heard, we wrote down the time, location on transect, species of primate, direction and distance from the transect of the animals, and, if known, the number of individuals in the group.

An average of 5.5 primate groups were encountered per kilometer walked. For the species *S. concolor* alone, 1.9 groups were encountered per kilometer walked. We encountered an average of 1.7 groups of *M. pagensis* and 1.1 groups of *P. potenziani* per kilometer. As other researchers have noted, line transects are not an accurate way to estimate gibbon densities, as gibbons are difficult to detect visually (Brockelman and Ali 1987; Brockelman and Srikosamatara 1993). No gibbon groups were encountered during my transect surveys, but we heard the calls of an average of 0.59 *H. klossii* groups per kilometer. Transects did not seem to be the best way to estimate gibbon densities, as I never visually detected gibbons on the transects.

Loud-call survey methods. I used loud-call monitoring to census gibbon populations at sites throughout the Mentawai Islands. I sat from 6:00-10:00 am at a listening post (located on an elevated terrain feature where possible), and for each loud call heard I noted the time of commencement, and the direction and estimated distance of the calling

animal. I mapped out the calls to scale on graph paper, and I considered songs from gibbons that mapped more than 500m apart to be from separate groups (Brockelman and Ali 1987; O'Brien et al. 2004). I conducted surveys between 4-16 mornings from the same listening post at each site to increase accuracy. Kloss's gibbons, like other gibbons, maintain stable territorial boundaries, and thus repeated sampling in the same area likely represented the same social units over the sample period (Tenaza 1975; Tilson 1981; Whitten 1982a).

When the listener is located at the top of a hill and there are no large geographic barriers, Kloss's gibbon calls can be heard from distances up to approximately 1 km (L. Paciulli, pers. comm.). However, without a detailed survey of each site, I did not know whether the surrounding area was unobstructed by barriers in all directions. I was able to confirm the reliability of distance estimates up to 600m by going to the calling gibbon group and measuring the distance from the listening post using a GPS unit. Therefore, only calls within a 600m radius are included in the analysis, resulting in a sampling area (A) of 0.36 km^2 ($A=\pi r^2$) at each site.

From these data, I calculated minimum and maximum population densities, using the formula: **$D = n/p(m)A$**, where D = estimated density, n = the number of groups heard, p(m) = the probability of an individual calling during sample period m, and A = the size of the listening area. For this project, I set n equal to the highest number of groups heard on any one day (Brockelman and Ali 1987).

Due to time constraints, it was not possible to empirically estimate p(m) for *Hylobates klossii*, which would require 8-10 sample periods at each site (Brockelman and Ali 1987). For the minimum population estimate, I set the probability of calling to 1.0;

this value assumes that 100% of gibbon groups in the listening area call within the sample period. Since singing in Kloss's gibbons is highly contagious, this conservative estimate may be accurate (Tenaza 1976). In related gibbon species *H. lar* and *H. pileatus* in Thailand, p(m) has been estimated as about 85-90% in a sample period of 3 days (Brockelman and Ali 1987). To arrive at a maximum population estimate in the present study, I set p(m) to 0.85. These two figures provide a conservative estimate of the gibbon population. While underestimation is a possibility, sample periods ranged from 4-16 days in an effort to reduce this problem.

Kloss's gibbon pairs do not duet, a characteristic that is unusual among gibbon species (and shared only with *H. moloch*). Most male songs occur in the hour before dawn, while female Kloss's gibbons sing only after dawn, usually between 8:00-9:00 am, after the first feeding bout (Whitten 1982a). Unmated "floating" male Kloss's gibbons sing, perhaps even more frequently than mated males, indicating that male gibbon song may function for mate attraction (Tenaza 1976). Female gibbons, however, probably sing to defend a territory (Cowlishaw 1992). While data were collected and analyzed for both male and female calls, the final population estimates rely only on female calls as I considered female calls more likely to indicate the presence of a gibbon group.

Average group size was estimated during collection of fecal samples, and whenever groups were opportunistically encountered. When wild groups were encountered, my field assistants and I attempted to count the number of individuals present, and categorize them as adult, juvenile, or infant. Males and females could not be distinguished visually, however.

Surveys on male pre-dawn calls were conducted only from base camp. The Mentawai forests are home to many species of venomous snake, and venturing out before sunrise was considered unsafe. In South Pagai, base camp was the logging camp where the logging workers lived, located too far from the forest patches to hear gibbon calls. No male pre-dawn data are available for that site. Female and male post-dawn calls were surveyed from better listening sites.

2.2.2 Assessment of remaining gibbon habitat

Information on the status of Mentawai forests was compiled from existing estimates of forest cover (Fuentes 1996/1997), SPOT-4 VEGETATION satellite imagery of southeast Asia (Stibig et al. 2002), and interviews with representatives of PT Minas Pagai Lumber Corporation, Siberut National Park, and UNESCO. These data indicate that nearly 3,000 km^2 of forest (including primary Dipterocarp forest, primary mixed forest, and secondary regenerating forest) remains across the Mentawais. Kloss's gibbons are found to maintain healthy populations in all three of these forest types. While the level of disturbance throughout these remaining forest areas is likely uneven, Kloss's gibbons appear to maintain similar population densities in unlogged forest, forests logged 10 years ago, and forests logged 20 years ago (Paciulli 2004), perhaps due to dietary flexibility (Whitten 1982b). Estimates of forest cover for each island are discussed in detail in chapter 5.

2.2.3 Collection of genetic samples

Fecal samples were non-invasively collected from unhabituated wild gibbons at each field site. When collecting samples for DNA analysis from endangered animals, non-invasive sampling is most desirable in order to avoid disturbing or potentially harming

the animals. Various kinds of detritus are available from wild animals, such as shed hairs, skin, saliva, urine, or feces (Taberlet and Luikart 1999). Shed hair and feces are the two most commonly used noninvasive sample types for primate studies, and one study has shown quantitatively that extracts from feces contain far more DNA than those from hairs (average DNA concentration of 192 pg/μl and 4.4 pg/μl, respectively) (Morin et al. 2001). Feces contain cells shed from the epithelial lining of the intestines (Kohn and Wayne 1997), and have been used for molecular studies of a wide range of mammal species, such as bears (Höss et al. 1992; Taberlet et al. 1996; Taberlet and Luikart 1999), seals (Reed et al. 1997), wolves (Lucchini et al. 2002), reindeer (Flagstad et al. 1999), elephants (Fernando et al. 2003), and many primate species, including baboons (Constable et al. 2001), gibbons (Lappan 2005), and chimpanzees (Gonder 2000; Morin et al. 2001).

To collect samples, gibbon groups were located every morning by following the sound of their morning calls. Unlike other gibbon species, Kloss's gibbons do not duet. Males give a pre-dawn call usually starting about 5:00 am (though sometimes as early as 1:00 am), which continues until sunrise between 6:00 and 6:30. The male pre-dawn calls indicated where groups (or, less frequently, solitary males) were located in relation to base camp every morning, and I would choose one group to approach based on these calls. The female's song typically begins between 7:00-8:30 am, after the first feeding bout, and is a long, loud, easily identifiable structured call. During this call, my assistants and I would approach the gibbon group stealthily, pausing during the pauses in the call so that we would not be detected. Usually, the call continued long enough for us to reach the group. Once the group was within sight, the reaction of Kloss's gibbons to humans

facilitated the collection of fecal samples. Upon detecting humans, Kloss's gibbons typically alarm call (Tenaza and Tilson 1977), defecate, and flee. Feces can then be found underneath the tree in which the gibbons first alarm-called. Despite the height of the animals in the canopy (up to 40 meters), I obtained samples from 72% of gibbon groups sighted during the pilot study. Failure to find feces was usually due to not knowing in which tree the gibbons were located when they alarm-called. Occasionally, males will give a post-dawn call after the female calls, either instead of or in addition to the pre-dawn call, and these calls could be used to locate and approach groups as well (Tenaza 1976; Whitten 1982a).

Samples were collected from 2-8 groups for each site (Table 2.1), for a total of 32 gibbon groups sampled (see Appendix I for full list of samples). The “critical sample size” necessary to reject the hypothesis that unsampled character states exist in a population in an analysis of conservation units has been calculated to be 59 individuals (Walsh 2000). Other researchers have suggested that a sample of 20-50 individuals will include 95% or more of existing haplotypes in a population (Crandall et al. 2000). The equation (n-1)/(n+1) calculates the probability of sampling the deepest genetic divergence in a randomly mating population (Saunders et al. 1984). With 32 samples, this probability is 94%.

While it is not possible to determine which individual gibbon contributed each sample, groups can be differentiated. I considered individuals that mapped over 500 meters apart as members of different groups (Brockelman and Srikosamatara 1993). Unless I was able to verify with genetic data that different samples within a group were

from different individuals, all samples from a group were considered to be from a single individual. In most cases, the sampling "unit" is considered to be the social group.

When feces were found, latex gloves were worn to collect fecal matter into 5 ml mailing tubes (VWR International). Multiple samples were collected from each group when possible. Each tube was labeled with a unique sample code, and when possible multiple tubes were used for fragments of a single fecal bolus. Storage buffer (see below) was added to the tubes upon return to base camp, and the tubes were sealed with Parafilm and stored in plastic Zip-Loc bags.

Samples collected in the 2001 sampling season were preserved at room temperature in a lysis buffer solution (100 mM NaCl, 10 mM Tris, 25 mM EDTA, 2% SDS, 200 mM guanidine thyocyanate). Those collected in 2003 were stored at room temperature in RNA*later*® RNA Stabilization Solution (Ambion, Inc.) at a 1:1 ratio of sample to solution. For each sample, I recorded date, time, group composition, and GPS location. Once samples were transported to the laboratory, they were stored at -20°C.

2.3 Lab methods

Genetic analysis was conducted at the Center for Environmental Research and Conservation genetic laboratory at Columbia University. Microsatellite genotypes were analyzed at the Molecular Anthropology laboratory at New York University.

While collection of fecal samples is ideal for the purpose of leaving the study species undisturbed, these samples require special treatment in the laboratory. DNA in feces tends to be degraded, and amplification of long nuclear DNA sequences is very difficult. Compared to blood or tissue, feces tend to yield low amounts of DNA, but using higher quantities of sample in the extract can overcome this problem (Taberlet et al. 1999;

Fernando et al. 2003). Feces usually contain bile acids that inhibit PCR (Deuter et al. 1995). Studies have found that adding Bovine Serum Albumin (BSA) to PCR reactions can overcome these agents (Höss et al. 1992; Kohn and Wayne 1997; Fernando et al. 2003). In addition, an extraction method that includes a step to remove PCR inhibitors from the extract was used in this project (see below). Finally, because of the small quantities of DNA present in the extract, sometimes allelic dropout, or the selective amplification of only one allele in a heterozygote, can occur. Multiple replications of extractions and PCR reactions were conducted to overcome this problem (Navidi et al. 1992; Fernando et al. 2003).

2.3.1 Choice of loci

Mitochondrial DNA has proven very useful in phylogenetic studies because it is haploid, uniparentally inherited, and rapidly evolving (Borst 1977; Wilson et al. 1985). When working with degraded samples such as feces, mitochondrial DNA is preferable to nuclear DNA because there are many copies of mtDNA per cell (Robin and Wong 1988). This project uses hypervariable region I (HV-I) of the displacement loop, or D-loop, a region that has been used extensively in human and ape molecular evolutionary studies (Vigilant et al. 1989; Stoneking et al. 1991; Saltonstall et al. 1998; Gonder 2000) and thus has a well-studied mutation rate (Tamura and Nei 1993; Parsons et al. 1997; Excoffier and Yang 1999). The D-loop, or control region, is non-coding (and therefore supposedly neutral) and is involved in the replication of the mitochondrial genome (Kasamatsu et al. 1971; Gillum and Clayton 1979; Anderson et al. 1981). There are two hypervariable regions in the D-loop, and the HV-I region evolves more quickly than any other part of the primate mitochondrial genome. Thus, this region is useful for examining intraspecific

relationships and evolutionary relationships between closely related species (Avise 2000) and may be more appropriate than slower-evolving genes for the phylogenetic analysis of gibbons, a group that radiated over a short time span (Chatterjee 2001; Roos and Geissmann 2001). This locus was used to attempt to resolve the previously unclear relationships between the four subgenera or genera of gibbons (*Hylobates*, *Bunopithecus*, *Nomascus*, and *Symphalangus*) (Roos and Geissmann 2001), as well as those between subspecies of *H. lar* (Woodruff 1993), and was chosen for this project to elucidate the relationships within the genus *Hylobates*.

Because mtDNA is maternally inherited, mitochondrial loci do not give a complete picture of intraspecific phylogeny, and many researchers have argued for the need to include nuclear DNA loci in such studies (Moritz 1994). To provide a nuclear marker applicable to studies of population substructuring, I also analyzed microsatellites, short repetitive sequences in the nuclear genome that consist of repeats that are 2-5 base pairs in length (Weber and May 1989). They are subject to replication slippage and a rapid rate of mutation (up to 10^{-2}/gamete/ generation) (Jeffreys et al. 1988). Because of these qualities, microsatellites are useful for inferring population structure and degree of intraspecific genetic diversity (Dowling et al. 1996). Eleven microsatellite loci were used in this project; however, only six yielded data (see Chapter 4).

2.3.2 DNA extraction

To isolate whole genomic and mitochondrial DNA from fecal samples stored in the lysis buffer, samples were first digested overnight in digestion buffer (100 mM NaCl, 10mM Tris, 25 mM EDTA, 2% SDS) in a shaker at 70˚C and 100 rpm. The digests were then centrifuged at 13,000 rpm, and 500µl of the supernatant was pipetted into a separate

tube (Fernando et al. 2003). Standard phenol chloroform extraction procedures were followed using this supernatant (Sambrook et al. 1989). The resulting extract was then purified using QIAQuick® cleanup kits with manufacturer supplied reagents and protocols. DNA was extracted from samples stored in RNA*later*™ using Qiagen Stool Kits ® and manufacturer protocols. Qiagen Stool Kits include InhibitEx tablets, which absorb PCR inhibitors.

2.3.3 Amplification of target regions

All loci were amplified using optimized Polymerase Chain Reaction (PCR) protocols (Palumbi 1996) in 50μL (HV-I) and 25μL (microsatellite) reactions and processed on Perkin-Elmer® thermocyclers. Because of low concentration of DNA in each extraction (Morin et al. 2001), large quantities of template DNA were used in each reaction. Bovine Serum Albumin was added to each reaction to overcome any remaining PCR inhibitors.

For mitochondrial DNA, each 50 μl PCR reaction consisted of: 10 μl PCR buffer (Invitrogen Optimization Kit Buffer K), 1 μl each primer, 5 μl dNTPs, 7.2 μl of Bovine Serum Albumin (added to absorb PCR inhibitors present in DNA from fecal samples), 0.25 AmpliTaq DNA Polymerase, and 8 μl of template DNA. While most PCR reactions of this size include 1-2 μl of template DNA, the DNA from these samples was very poor, a problem shared by other gibbon researchers relying on fecal samples (Lappan, Reichard, pers. comm.). The thermocycling conditions were: 30 seconds at 94ºC, followed by 45 cycles of a denaturing step (1 minute at 94ºC), an annealing step (2 minutes at 55ºC) and an extension step (3 minutes at 72ºC). A final extension step of 7 minutes at 72ºC was included after the 45 cycles were completed.

2.3.4 DNA sequencing

The HV-I region of the D-loop was amplified and sequenced using the following gibbon-specific primers: GIBDLF3 (5' CTT CAC CCT CAG CAC CCA AAG C 3') and GIBDLR4 (5' GGG TGA TAG GCC TGT GAT C 3') (Andayani et al. 2001) which correspond to the human primers L15996 (Vigilant et al. 1989) and H16498 (Kocher et al. 1989). These primers amplify a fragment of 512 base pairs.

PCR products were purified with Qiagen PCR purification kits and cycle-sequenced using Perkin-Elmer's ABI Prism™ BigDye™ Terminator Cycle Sequencing Ready Reaction Kits. The ABI Prism™ 377 Automated Sequencer and ABI 3730 XL 96-well Capillary Sequencer were used for sequencing. Consensus sequences for each individual were generated using the ABI software package AutoAssembler© as well as the Sequencher 3.1 program.

2.3.5 Microsatellite genotyping

Microsatellite loci were amplified with Research Genetics Multi-Colored Fluorescent Human MapPairs® markers. Qiagen Multiplexing Kits were used to multiplex up to 4 loci in a single 25 µl PCR reaction following manufacturer protocols. These kits remove the necessity of optimizing PCR conditions. Allele sizes were ascertained using the ABI 3730 48-well Capillary Sequencer and the GeneMapper® software.

The most common problem when amplifying nuclear DNA, particularly from low concentration DNA extracted from detritus such as hair or feces, is allelic dropout, or the stochastic amplification of only one allele resulting in a "false homozygote" (Gagneux et al. 1997; Morin et al. 2001; Vigilant et al. 2001). Two to seven extractions and PCR reactions were necessary to confirm a homozygote, fewer (only 2) to confirm a

heterozygous genotype with a confidence level of 99% (Navidi et al. 1992; Taberlet et al. 1996). A more recent analysis determined that only 2 extractions and 2 replications were necessary for reliable genotyping (Fernando et al. 2003).

Site #	Site Name	Abbr.	Description	Other Researchers	Gibbon groups sampled	
					2001	2003
1	Peleonan forest	PL, CA	Regenerating mixed forest logged 15 years ago, hunting rare	Abegg (ongoing)	3	5
2	Simabuggai Biodiversity Research Station	SB	Inside Siberut National Park (traditional use zone), unlogged forest but hunting is common	Sangchantr (2004)	5	0
3	Taileleu	TL	Inhabited, heavily used, recently logged, logging company nearby		0	0
4	Saureinu	SR	Traditional use, logged about 20 years ago		0	3
5	Betumonga Research Station	NP	Primary forest, traditional use; site has since been logged	(Fuentes, Paciulli)	5	0
6	Muntei Research Area	NP	Secondary forest, heavily used area	Sangchantr (2004)	3	0
7	PT Minas Pagai Lumber Co. Base camp	SP	Regenerating patches of selectively logged forest, traditional use, heavy hunting	Paciulli (2004)	4	4

Table 2.1: List of sites sampled for this project

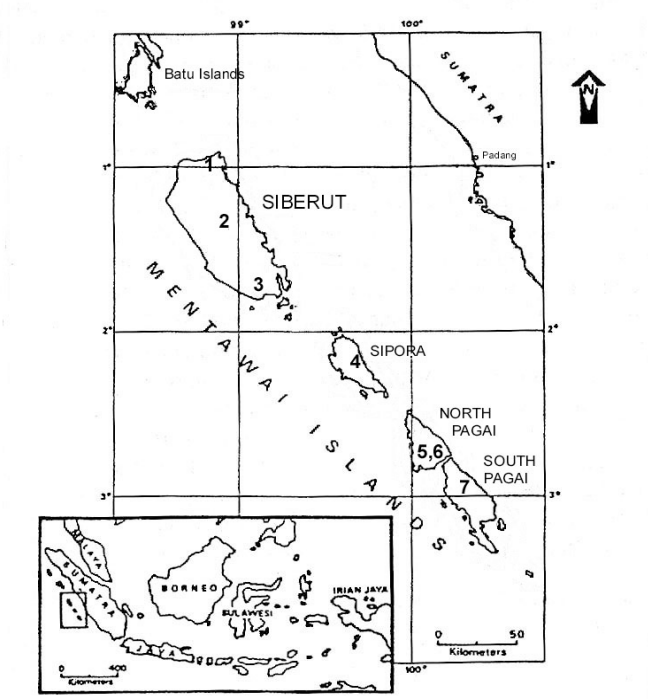

Figure 2.1: Map of sample sites in the Mentawai Islands

Numbers indicate sites described in text and in Table 2.1.

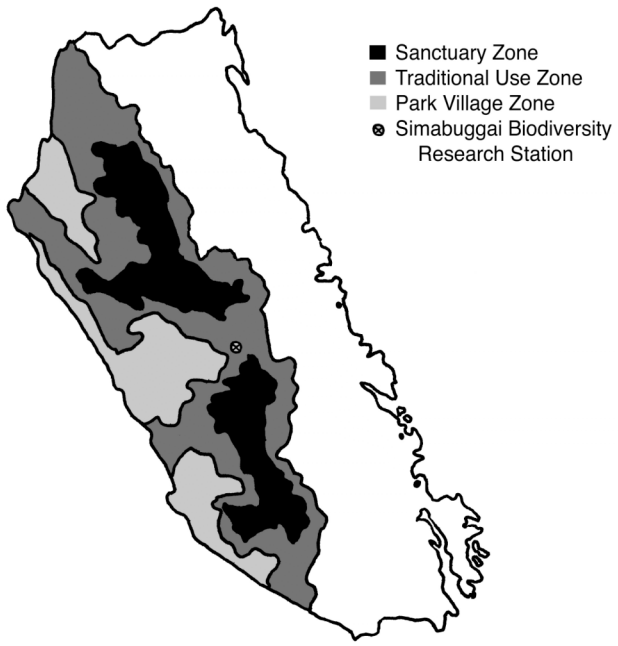

Figure 2.2: Map of Siberut National Park showing management zones

CHAPTER 3

Molecular systematics of the lar group of gibbons (Genus *Hylobates*)

3.1 Introduction

This chapter aims to elucidate the position of the Kloss's gibbon within the lar group, genus *Hylobates*, using phylogenetic analysis of mitochondrial D-loop sequences.

The Kloss's gibbon (*Hylobates klossii*) was first described as a "dwarf siamang" due to its black pelage and small size (relative to the siamang), and was placed in the genus *Symphalangus* (Miller 1903) and later in the subgenus *Symphalangus* within the genus *Hylobates* (Groves 1968). Later observations and morphological studies led to the conclusion that the Kloss's gibbon is neither a dwarf nor a siamang (Tenaza and Hamilton 1971; Groves 1972). Based on a variety of shared characters, including cranial shape, intermembral index, genital features, and especially chromosome number ($2n$=44), Kloss's gibbons are currently placed in the same genus (*Hylobates*) as the gibbons of the lar group (*H. lar*, *H. agilis*, *H. muelleri*, *H. moloch*, and *H. pileatus*) (Chiarelli 1972; Groves 1972). However, past phylogenetic analyses have disagreed on the relationship of the Kloss's gibbon to the members of the lar group.

Most morphological analyses have identified *H. klossii*'s characteristics as primitive, and suggested that it was the first to speciate from the ancestral stock (Groves 1972; Haimoff et al. 1982; Groves 1984; Brandon-Jones 1998). Molecular studies have suggested that the Kloss's gibbon is a derived member of the lar group, yet have disagreed its position within the radiation (Garza and Woodruff 1992; Geissmann 1993; Geissmann 1995; Hayashi et al. 1995; Zehr 1999; Melnick et al. 2000). The variety of

phylogenetic conclusions from different gibbon phylogenies have led to a confused picture of southeast Asian biogeography, with some authors positing the Mentawai Islands as a Pleistocene refuge that later gave rise to all Asian primates that subsequently migrated eastward (Brandon-Jones 1998) and other suggesting a complex series of dispersal and speciation events to explain their results (Groves 1972; Chivers 1977; Chatterjee 2001).

3.1.1 History of the Kloss's gibbon in gibbon systematics

Morphological studies. Early studies placed the Kloss's gibbon as a sister taxon to the siamang (*Symphalangus syndactylus*) based primarily on pelage, as both species are completely black, unlike any other gibbons (Miller 1903; Groves 1968). Schultz (1933) places the Kloss's gibbon in its own subgenus, *Brachitanytes*, separating it from the lar group (subgenus *Hylobates*), and suggests that many of its characters indicated that the Kloss's gibbon was primitive (Schultz 1933). These characters include reduced hair density, webbing between the second and third toes, comparatively long thumbs and great toes, higher average number of vertebrae, proportionally longer radius and tibia resulting in much longer limbs than other gibbons, and reduced cranial capacity and cranial dimensions.

Groves (1972) examines the evolutionary systematics of the Hylobatidae with an analysis of characters including pelage coloration and hair patterns, cranial and postcranial anatomy, dentition, reproductive system, and soft tissue anatomy (Groves 1972). In this analysis, Groves considers *lar*, *agilis*, *moloch*, *muelleri*, and *pileatus* as subspecies of *H. lar*. Groves notes several similarities between *H. klossii* and *S. syndactylus* when compared to the lar group: reduced number of hairs/cm^2 (429-462,

compared to 1,226-2,030 in the lar group); and the frequency of multiple infraorbital foramina (63-75%, compared to 0-50% in the lar group) and persistent cranio-pharyngeal canal in adults (93-100%, compared 22-73% in the lar group). In all of these characteristics, Groves finds that *Bunopithecus hoolock* (which he refers to as *Hylobates hoolock*) falls closer to the range of measurements found in the lar group than *H. klossii* does. Groves also suggests that a high number of coccygeal vertebrae, shared by *B. hoolock* and *H. klossii*, is a primitive characteristic. The siamang has a laryngeal sac, which the Kloss's gibbon lacks, and this throat area is completely bare of hair. Thus Groves does not consider the siamang and the Kloss's gibbon to be sister taxa, although he notes that *H. klossii* has a nearly bare area where the laryngeal sac would be located. Groves concludes that the lar group is a sister taxon to the hoolock gibbon, and he places *H. klossii* as the basal taxon in this clade (Figure 3.1). *H. klossii* and *B. hoolock* are referred to as "intermediate" between the lar group and the siamang (Groves 1972).

Later morphological analyses raised the members of the lar group to species status and recognized the Kloss's gibbon's affinity to the lar group (Chivers 1977; Haimoff et al. 1982; Creel and Preuschoft 1984; Marshall and Sugardjito 1986). For instance, in a multiple discriminant analysis of 90 cranial and dental variables by Creel and Preuschoft (1984), *H. klossii* clusters with the lar group, far from the siamang, the hoolock, or the crested (*Nomascus*) gibbons. However, these later studies note the special features of the Kloss's gibbon identified in earlier studies and still place this species as basal to the rest of the lar group (Figure 3.1). The other gibbons of the lar group are indistinguishable on the basis of cranial characters (Marshall and Sugardjito 1986), and the cranium of the Kloss's gibbon stands out mostly because it is smaller, which could be the result of island

dwarfism. The phenomenon of species isolated on islands becoming either larger (gigantism) or smaller (dwarfism) than their mainland counterparts has been observed in many mammals (Foster 1964). However, while the Kloss's gibbon does exhibit smaller cranial measurements, the average body size of *H. klossii* is not outside the range seen in other lar group species (Table 3.2).

Although Groves (1972) states that characteristics such as hair density "are of considerable taxonomic importance, " the characteristics described above may not be robust indicators of phylogenetic relationships. Hair density, limb proportions, and number of vertebrae are all characters that could have adaptive significance, and may or may not be useful characters for phylogenetic analysis.

Karyology. Chromosome analysis revealed that *H. klossii* shares the same chromosome number (2*n*=44) with the other members of the lar group (Chiarelli 1972). *Bunopithecus hoolock* has a diploid chromosome number of 38; the *Nomascus* species have 52 chromosomes; and the siamang (*Symphalangus*) has a diploid number of 50. These differences in karyology form the basis for later arguments that these groups should be raised to generic status, and were among the first reasons for including the Kloss's gibbon in the lar group (Prouty et al. 1983).

Vocalization studies. Vocalizations have been considered reliable taxonomic identifiers of closely related species, including African colobines (Struhsaker 1981; Oates and Trocco 1983; Oates et al. 2000), Asian colobines (Wilson and Wilson 1975), guenons (Gautier 1988), lion tamarins (Snowdon et al. 1986), howler monkeys (Whitehead 1995), galagos (Zimmermann 1990), tarsiers (Shekelle 2003), and gibbons (Marshall and Marshall 1976; Marshall et al. 1984; Marshall and Sugardjito 1986). While vocal

characteristics are useful for delineating species and identifying possible sister taxa, determining the polarity of characters and differentiating between homology and homoplasy can be problematic for phylogenetic analysis (Creel and Preuschoft 1984).

Geissmann (1993, 2002) has analyzed gibbon phylogenetic relationships using vocal characters (Figure 3.1). Based on these characters, *H. klossii* is considered the sister taxon of the Javan silvery gibbon (*H. moloch*) because these two species, unlike all other gibbon taxa, do not sing duets; the males and females have separate songs (Geissmann 1993, 2002). While the basis for the determination of "ancestral" versus "derived" states is unclear for some characteristics, Geissmann suggests that duet-splitting (partners singing at different times of the day) is a derived characteristic, evolving after song-splitting (partners singing different parts of a duet).

Molecular studies. Most molecular phylogenies of the gibbons have been based on mitochondrial DNA (Garza and Woodruff 1992; Hayashi et al. 1995; Hall et al. 1998; Zehr 1999; Melnick et al. 2000; Chatterjee 2001; Roos and Geissmann 2001), though at least one has assessed nuclear DNA relationships as well (Zehr 1999).

The cytochrome *b* gene of the mitochondrial genome is commonly found useful in phylogenetic studies, as it mutates at a relatively slow rate. Garza and Woodruff (1992) sequenced a short region of the cyt *b* gene (252 bp), and their analysis shows *H. klossii* as an integrated member of the lar group, clustering with *H. pileatus* and *H. muelleri*. Hall *et al* (1998) sequenced the complete cyt *b* gene (1140 bp), but unfortunately did not include *H. klossii* in the analysis. Because the topologies of the trees produced by these two studies disagreed, Chatterjee (2001) re-analyzed the cyt *b* gene for all hylobatids. These results place *H. klossii* within the lar group, as a sister taxon to *H. pileatus*.

The NADH dehydrogenase regions of the mitochondrial genome have also been used to attempt to resolve hylobatid relationships. In analyses of the ND4-5 region, the Kloss's gibbon appears most closely related to *H. lar* (Figure 3.1) (Hayashi et al. 1995; Zehr 1999). However, a more recent analysis of the ND3-4 locus places *H. klossii* as the sister taxon to *H. moloch*, but does not show any further resolution in the genus *Hylobates* (Takacs et al. in press).

Zehr (1999) also sequenced the cytochrome c oxidase subunit II gene. In this analysis, *H. klossii* clusters with some of the *H. agilis* samples, with the rest of the *H. agilis* samples forming a sister clade with *H. muelleri* and *H. lar*.

One gibbon phylogeny has been produced with a nuclear locus, the X-linked G6PD gene, that includes *H. klossii* (Zehr 1999). The trees have low resolution and low bootstrap support values, but Zehr concludes that in this analysis, *H. klossii* appears as the sister to *H. moloch*, with *H. lar* as the next most closely related taxon.

While all of the molecular studies show the Kloss's gibbon as a recently derived taxon within the lar group, rather than a basal taxon, there is no resolution concerning its place within the group. *H. klossii* has been shown as a sister taxon to every species in the lar group. The conflicting results of these studies have led some authors to conclude that the gibbon group most likely radiated very rapidly, and in order to resolve the relationships among the species a more quickly mutating locus is necessary to distinguish speciation events (Garza and Woodruff 1992; Chatterjee 2001; Roos and Geissmann 2001).

3.1.2 Goals of the present study

The control region, or D-loop, is the most rapidly evolving region of the mitochondrial genome. There are two hypervariable regions in the D-loop, which mutate more quickly than the rest of the control region. The hypervariable region I (HV-I) has been used to attempt to elucidate relationships among gibbon genera (Chatterjee 2001; Roos and Geissmann 2001); however, the species *H. klossii* has not been included in these analyses. This chapter will address the phylogenetic position of the Kloss's gibbon within the genus *Hylobates*, using the HV-I region of the mitochondrial D-loop.

3.2 Methods

Samples. Fecal samples were collected from wild Kloss's gibbon populations at seven sites on four islands, as described in Chapter 2 and detailed in Appendix I. Samples were stored in RNA*later*® at room temperature, and total genomic DNA was extracted using QIAGEN QIAamp Stool Mini Kits and manufacturer supplied protocols. The hypervariable region I of the mitochondrial control region, or D-loop, was amplified and sequenced as described in Chapter 2.

Sequences from other gibbon species were obtained from GenBank (*H. agilis*: 2; *H. lar*: 2; *H. moloch moloch*: 5; *H. moloch pongoalsoni*: 8; *B. hoolock*: 1; *N. gabriellae*: 1; *S. syndactylus*: 1); Table 3.1 presents the GenBank acquisition number and the source for each sequence. Sequences for *H. muelleri* and *H. pileatus* were not available on GenBank. DNA extracted from blood samples from zoo specimens (*H. muelleri*: JP92, JP93; *H. pileatus*: JP99; and *H. agilis albibarbus*: JP90) was sequenced following the same protocols as for the fecal samples.

Sequences were aligned using the CLUSTAL X Multiple Sequence Alignment Program, version 1.81 (Jeanmougin et al. 1998); Appendix 2 shows the complete alignment. Three types of phylogenetic inference analyses were performed using PAUP*4.0b10 (Swofford 2002): neighbor-joining, maximum parsimony, and maximum likelihood. One sequence from each of the other three genera (*Bunopithecus*, *Nomascus*, and *Symphalangus*) were used as outgroups for the analyses.

Neighbor-joining is an algorithm that successively groups the least different pairs of taxa based on a distance matrix (Saitou and Nei 1987). This distance-based method finds the minimum evolution tree by evaluating overall sequence differences, not individual nucleotide substitutions, and applies a correction for multiple substitutions (Van de Peer 2003). Because the control region evolves very quickly, a large number of homoplasious substitutions are expected. For example: In Taxon 1, A mutates to G. In Taxon 2, A mutates to T and later to G. Because the "T" existed in the past, we only see the "G", and these mutations could suggest a false relationship between Taxa 1 and 2. The neighbor-joining method has been suggested as a good way to minimize the effect of these substitutions on the cladogram (Roos and Geissmann 2001).

Maximum parsimony methods select trees that minimize the total tree length, or number of evolutionary steps (via nucleotide substitutions) required to explain the data (Swofford et al. 1996). These methods rely on the concept that the simplest explanation is likely closest to the truth. Both unweighted (no restraints on permissible character-state changes) and weighted (based on observed transition/transversion ratios in the data) algorithms were employed in the present study. Weighted parsimony methods reflect the

idea that transitions are more common than transversions, and thus the influence of observed transversions on the final tree should be greater.

Maximum likelihood procedures evaluate possible trees according to a model of evolutionary change that calculates the probabilities of specific nucleotide substitutions and then picks the tree with highest probability, or likelihood. These models can incorporate a number of different parameters, including the probability of transitions versus transversions, the equilibrium frequency of each nucleotide, and the rate of site substitution (Jukes and Cantor 1969; Kimura 1980; Felsenstein 1984). Because each locus evolves at different rates and with different restrictions, a model should be chosen that best fits the observed data. To determine which model of evolutionary change best fit the data, the program MODELTEST 3.6 was employed (Posada and Crandall 1998), using the hierarchical likelihood ratio test (hLRT) to choose which of 56 models best fit the data. The hLRT tests goodness of fit with the traditional statistic δ.

Bootstrapping, a nonparametric resampling technique, was used to provide a measure of statistical confidence for internal branches of the trees through an estimate of sampling variance (Felsenstein 1985; Swofford et al. 1996). In this method, the sequence data are randomly resampled by selecting columns from the original data until a new dataset is created (a bootstrap replicate) which will not include some of the original characters while possibly including other characters more than once. From this replicate, a tree is constructed. This process is repeated, usually 1,000 times, to produce an estimate of statistical confidence (a bootstrap support value) for clades indicating the percentage of replicates that support that grouping (Van de Peer 2003).

3.3 Results

In all of the trees generated by all analyses, *Hylobates klossii* clusters with *H. moloch* and *H. agilis*, inside the lar group, and not basal to the lar group. The lar group is monophyletic in all analyses.

3.3.1 Neighbor-joining

The neighbor-joining phylogram was created, as well as a bootstrap neighbor-joining tree based on the same distance criteria, with 1,000 replications (Figure 3.2). In these analyses, *H. klossii* is shown as a sister taxon to *H. agilis*; however, bootstrap support for this clade is fairly low (58%). *H. klossii*, *H. agilis*, and *H. moloch* form a clade with a stronger bootstrap support value of 87%. *H. lar* and *H. pileatus* are possible sister taxa (with a bootstrap value of 57%) placed in a basal position of the lar group. This analysis shows *Bunopithecus* as the basal taxon for the hylobatid radiation.

3.3.2 Maximum parsimony

Unweighted parsimony. Heuristic searches (with 1,000 bootstrap replications) were first run with transitions and transversions weighted equally (unweighted). Gaps were treated as "missing" (a) and then as "fifth character state" (b), which produced identical topologies with nearly identical bootstrap values (Figure 3.3). *H. klossii*, *H. agilis*, and *H. moloch* again form a clade, though with a low support value of 45%. In this analysis, *H. moloch* is the sister taxon to *H. klossii*, again with low bootstrap support (36%). The other three *Hylobates* species form a clade with equally low support (33%). *Bunopithecus* appears basal to the hylobatid radiation, with *Nomascus* and *Symphalangus* together forming a sister clade to *Hylobates*.

Weighted parsimony. The average transition/transversion ratio was 4.36, as calculated by MODELTEST. A heuristic maximum parsimony search (1,000 bootstrap replications) was carried out with a user-defined step-matrix assigning a weight of 1 for transitional changes and a weight of 4 for transversions. Gaps were treated as "missing." Figure 3.4 shows the bootstrap consensus tree. Branches with bootstrap support of less than 50% were collapsed, resulting in an unresolved polytomy of the members of the genus *Hylobates*. *H. lar* and *H. pileatus* form a clade within this polytomy. Conspecifics are monophyletic with high bootstrap support, but no further resolution is found in the *Hylobates* clade. As in the unweighted trees, *Bunopithecus* appears as basal to all hylobatids.

3.3.3 Maximum likelihood

Using the hLRT, the best fitting nucleotide substitution model was HKY+G (Hasegawa et al. 1985). This model assumes that transitions are more likely than transversions, that purine and pyrimidine transitions are equally likely, and that the substitution rate follows a gamma distribution. Using a heuristic search in PAUP*, three equally likely trees were produced. I also conducted a heuristic maximum likelihood search with 100 bootstrap replications of "fast" stepwise addition in PAUP*. The strict consensus of the three most likely trees is shown in Figure 3.5, with bootstrap values indicated for branches with high support. *H. klossii* and *H. agilis* are shown as sister taxa, with *H. moloch* as the next most closely related, followed by *H. muelleri*, *H. lar*, and finally with *H. pileatus* as the basal taxon. However, these groupings have very low bootstrap support, with values of 27% for the *klossii-agilis* clade, and 23% for the *klossii-*

agilis-moloch clade. *Bunopithecus* is basal to the tree, with *Symphalangus* and *Nomascus* together forming a sister clade to *Hylobates*.

3.4 Discussion

3.4.1 Phylogenetic placement of *H. klossii*

The data do not support the hypothesis that *H. klossii* is basal to the lar radiation, as has been suggested by several morphological analyses. Rather, the Kloss's gibbon is an integral member of the lar group. In fact, in all cladograms, *H. klossii* appears to be one of the most recently derived taxa.

While all genetic analyses, regardless of locus, have found *H. klossii* to cluster inside the *Hylobates* genus, there has been no agreement on the most closely related taxon. The Kloss's gibbon has been linked to every species of the lar group. The data presented here show the Kloss's gibbon to be most closely related to the agile gibbon (*H. agilis*) and the Javan silvery gibbon (*H. moloch*), though the trees disagree as to which of those two is the sister taxon. Bootstrap support values in all analyses presented here are very low, suggesting that these results are not certain. However, the agreement of all three analyses lends some support to the existence of a *klossii-agilis-moloch* clade. Geographically, the Kloss's gibbon is located nearest the Sumatran agile gibbon, with the Javan gibbon the next nearest neighbor (Figure 3.6). These species thus make intuitive sense as the sister taxa for *H. klossii*.

H. lar and *H. pileatus* are sister taxa, and are placed basally in the *Hylobates* radiation. The position of *H. muelleri* is unclear: the unweighted parsimony analysis shows a *muelleri-lar-pileatus* clade, while the neighbor-joining, weighted parsimony and maximum likelihood trees place it with the *klossii-agilis-moloch* clade.

3.4.2 Monophyly of taxa and DNA barcoding

Recognized species were monophyletic in all analyses, with very high bootstrap support (values ranging from 78 to 100), despite suggestions to raise *H. agilis albibarbus* to a full species (Groves 2001; Hirai et al. 2004; Tanaka et al. 2004). The genus *Hylobates* is generally supposed to have speciated over a short period of time, as evidenced by overall phenotypic similarity, comparatively low levels of genetic sequence divergence, and difficulty of resolving phylogenetic relationships (Garza and Woodruff 1992; Roos and Geissmann 2001). These six species also hybridize easily: three hybrid zones exist where the ranges of different species meet (*H. lar* and *H. pileatus* in Thailand, *H. lar* and *H. agilis* in Malaysia, and *H. agilis* and *H. muelleri* in Borneo) (Marshall and Sugardjito 1986). The data presented here suggest that, although hybridization is observed in wild populations, gene flow among species has been minimal.

The genus *Hylobates* is also monophyletic with 96-100% bootstrap support in all analyses, suggesting a long separation of the gibbon genera with no gene flow among them. This suggestion is supported by the different chromosome numbers of the four genera, which may act as a postzygotic reproductive isolating mechanism (King 1993), as well as the lack of intergeneric hybrids observed. The genetic distances among the genera further support their classification as full genera (see Appendix III).

The ability of the HV-I region to separate species suggests that it may be useful as a "DNA barcode." The mitochondrial COI locus has been presented as such a barcode, as conspecifics show a consistent level of sequence variation that is much lower than that found among species (Hebert et al. 2003; Hebert et al. 2004). Critics have commented that closely related sister taxa have not been adequately sampled to show whether this

locus can be used to differentiate species that may have diverged recently or very quickly (Moritz and Cicero 2004). While the COI gene has not yet been sequenced for all gibbon species, the HV-I region presented here clearly separates species into monophyletic groups. This locus could thus be useful for identifying zoo animals or even bushmeat specimens, and could prove to be a powerful tool for gibbon conservation.

3.4.3 Reliability of these results

Nuclear insertions of the mitochondrial genome (numts). Researchers have recently discovered that portions of the mitochondrial genome are often copied into the nuclear genome, where they then accumulate mutations at a different rate than their mitochondrial counterparts (Zischler et al. 1998; Bensasson et al. 2001; Thalmann et al. 2004). PCR can accidentally amplify these nuclear insertions, or numts, rather than the true mitochondrial sequence. One study found that numts were preferentially amplified from orangutan samples, although the same primers preferentially amplified the mitochondrial sequence in other hominoids (Collura and Stewart 1995). The difference was caused by evolutionary divergence in the flanking regions of the orangutan sequence, so that the primers would not amplify it. Amplification of the numt rather than the mitochondrial sequence can cause spurious results in a phylogenetic analysis.

The source of *H. klossii* DNA in this study was fecal samples. These samples, having fallen from 30-40 meter high tree crowns and splattering on vegetation on the way down, were so degraded that amplification of any DNA was very difficult (as evidenced by the low success rate: out of 87 fecal samples, only 27 samples (31%) were successfully sequenced). Each cell has multiple mitochondria, and thus multiple copies of the mitochondrial genome, and only a single copy of the nuclear genome. Mammalian cells

have been found to have 220-1,720 mitochondrial DNA molecules per cell (Robin and Wong 1988). Preferential amplification of nuclear DNA over mitochondrial DNA from these degraded samples seems unlikely. Furthermore, use of a numt in a phylogeny often produces surprising results; sometimes the numt sequence of a hominoid may show closer resemblance to a human nuclear sequence than to the mitochondrial sequence of the same taxon, or may be extremely difficult to align (Thalmann et al. 2004). No such surprises are seen in this study; all conspecifics are monophyletic, as are congenerics, with bootstrap values of or near 100 in all analyses.

3.4.4 Comparison with previous studies

Although previous molecular studies have produced a variety of conclusions concerning the placement of *H. klossii*, some agreement can be found with the present study. Zehr (1999) analyzed several loci for her study; the trees produced by the mitochondrial COII show *H. klossii* as a sister taxon to *H. agilis*, while the nuclear G6PD gene trees show *H. klossii* as a sister taxon to *H. moloch*. Takacs et al. (in press) have found *H. klossii* and *H. moloch* to cluster in their analysis of the ND3-4 region. Finally, the grouping of *H. klossii* with *H. agilis* and *H. moloch* in the present study agrees with Geissmann's (1993) "non-communicatory" dataset, in which *H. klossii* clusters with *H. agilis* (based on a strong reduction of the upper third molar), and his vocal dataset, which groups *H. klossii* and *H. moloch.*

Past studies have produced different topologies that disagree with each other and with the current study. Most of these studies have used the same set of samples, all of which are hairs or blood from the same zoo specimens (Garza and Woodruff 1992; Hayashi et al. 1995; Hall et al. 1998; Zehr 1999; Chatterjee 2001). In previous studies using more

than one sample from each species, paraphyly was often a problem, which could have been caused by species misidentification. Though a detailed system has been derived for identifying gibbon species based on coloration and vocalizations (Geissmann 1995), such errors do occur, and many specimens identified as *H. klossii* may have been *H. agilis* (Takacs et al. in press). Other zoo animals are of unknown geographic origin and may even be hybrids. Most of the samples (including *H. klossii*, *H. moloch*, and *H. agilis*) in the current study are from wild gibbons with documented geographic locations, and phylogenetic results from such a dataset may be more reliable than results based only on zoo samples.

Only a few studies have used the D-loop for gibbon systematics. Andayani et al. (2001) used the entire control region to assess differentiation within the Javan silvery gibbon (*H. moloch*). The present study reconstructs that grouping of the western and central subspecies (except the weighted parsimony tree, which moves the western NAN12 to the central clade) although with much lower bootstrap support values than presented by that study (Andayani et al. 2001).

While reconstructing the phylogeny of the four genera was not a goal of this study, two other studies have attempted such a reconstruction with the control region (Chatterjee 2001; Roos and Geissmann 2001). In Chatterjee's (2001) analysis, the genus *Hylobates* appeared to be paraphyletic; she thus rejected the control region as too divergent to be useful for phylogenetic studies. However, in the present study the genus *Hylobates* is monophyletic with 100% bootstrap support, which suggests that Chatterjee may have isolated some nuclear insertions.

In all analyses presented here, one representative of each of the other three genera was used as an outgroup (*N. gabriellae*, *B. hoolock*, and *S. symphalangus*). Contrary to the results of Roos and Geissmann (2001), this study consistently places *Bunopithecus* as the most basal member of the hylobatids, rather than *Nomascus*. More recently, Geissmann (2002) has commented that *Bunopithecus* appears to be more basal than previously thought, based on primitive vocal characters such as a lack of sexual dimorphism in calls (Geissmann 1993) and a few other molecular and morphological analyses (e.g., Zehr 1999; Creel and Preuschoft 1984).

3.4.5 A biogeographic scenario

In the analyses presented here, the most basal members of the radiation are *H. lar* and *H. pileatus*, which have the northernmost distribution. The southernmost species, *H. agilis*, *H. klossii*, and *H. moloch* are the most derived, suggesting that the ancestral stock followed a single north-to-south dispersal (Figure 3.6). During Pleistocene glacial maxima, populations were likely isolated in retracted forest patches and subsequently differentiated; when the forest expanded, the populations expanded until they met barriers, such as the Sunda river systems (Marshall and Sugardjito 1986). Later, rising sea levels contributed to the present species distribution.

The low bootstrap values in this study, and the difficulty of resolving the gibbon radiation in general, suggest that gibbons may not have speciated in a strict bifurcating or branching pattern, as assumed in phylogenetic methods. Instead, gibbon phylogenetic relationships may in fact represent a “hard” polytomy, or a simultaneous or nearly simultaneous multiple speciation event. It seems possible that populations of a single ancestral species were simultaneously isolated by rising sea levels and then differentiated.

Marshall and Sugardjito (1986) have observed that with the exception of the siamang, all gibbons are ecologically and behaviorally similar, and because of their non-overlapping distributions have not needed to adapt to different niches. Thus, the primary differences between the gibbon species are characters that aid in species identification, including coloration and vocalizations.

3.5 Conclusion

Based on the data presented here and a consideration of previous studies, the Kloss's gibbon is not basal to the lar group. The Kloss's gibbon forms a clade with the agile gibbon and the Javan silvery gibbon, which show morphological (*H. agilis*) and vocal (*H. moloch*) similarities to the Kloss's gibbon, and are geographically close. *H. lar* and *H. pileatus* appear as basal to *Hylobates*. In the analyses presented here, *Bunopithecus* is basal to all hylobatids.

While a "soft" polytomy in a phylogenetic analysis is often considered to be an indication that the data are insufficient to resolve the phylogeny, hylobatid relationships may actually be a "hard," or real, polytomy. Congruence testing between the results presented here and results from other studies, as well as the inclusion of other types of data (such as morphological or vocal) may improve the reliability of this phylogeny.

Taxon	Sample ID	GenBank Acquisition Number	Reference
H. agilis	NAN04, NAN39	AF338876, AF338905	Andayani et al. 2001
H. lar	lar2, lar3	AF311724, AF311723	Roos & Geissmann 2001
H. moloch moloch	NAN08, NAN12, NAN14, NAN26, NAN41	AF338880, AF338884, AF338886, AF338897, AF338906	Andayani et al. 2001
H. moloch pongoalsoni	NAN06, NAN07, NAN10, NAN13, NAN28, NAN30, NAN33, NAN35	AF338878, AF338879, AF338882, AF338885, AF338899, AF338900, AF338902, AF338904	Andayani et al. 2001
B. hoolock	Bunopithecus	AF311725	Roos & Geissmann 2001
S. syndactylus	Symphalangus	AF311722	Roos & Geissmann 2001
N. gabriellae	Nomascus	AF193804	Roos & Geissmann 2001

Table 3.1: List of sequences retrieved from GenBank.

	Mean length (mm)		Mean body weight (kg)	
Species	**Braincase**	**Skull**	**Males (*n*)**	**Females (*n*)**
H. klossii	75.1	96.1	5.67 (2)	5.89 (4)
H. agilis	81.3	104.1	5.88 (19)	5.82 (10)
H. lar	80.4	103.0	5.90 (84)	5.34 (66)
H. moloch	79.2	100.2	6.58 (1)	6.25 (1)
H. muelleri	77.9	99.9	5.71 (20)	5.35 (19)
H. pileatus	81.4	101.0	5.50 (1)	5.44 (1)
N. concolor	87.1	110.9	7.77 (7)	7.62 (13)
N. leucogenys	86.6	110.1	7.41 (8)	7.32 (4)
S. syndactylus	91.4	122.7	11.88 (7)	10.71 (10)
B. hoolock	85.0	111.5	6.87 (13)	6.88 (5)

Table 3.2: Selected gibbon cranial measurements and body weights

Cranial measurements from Groves (1972), body weights from Geissmann (1993)

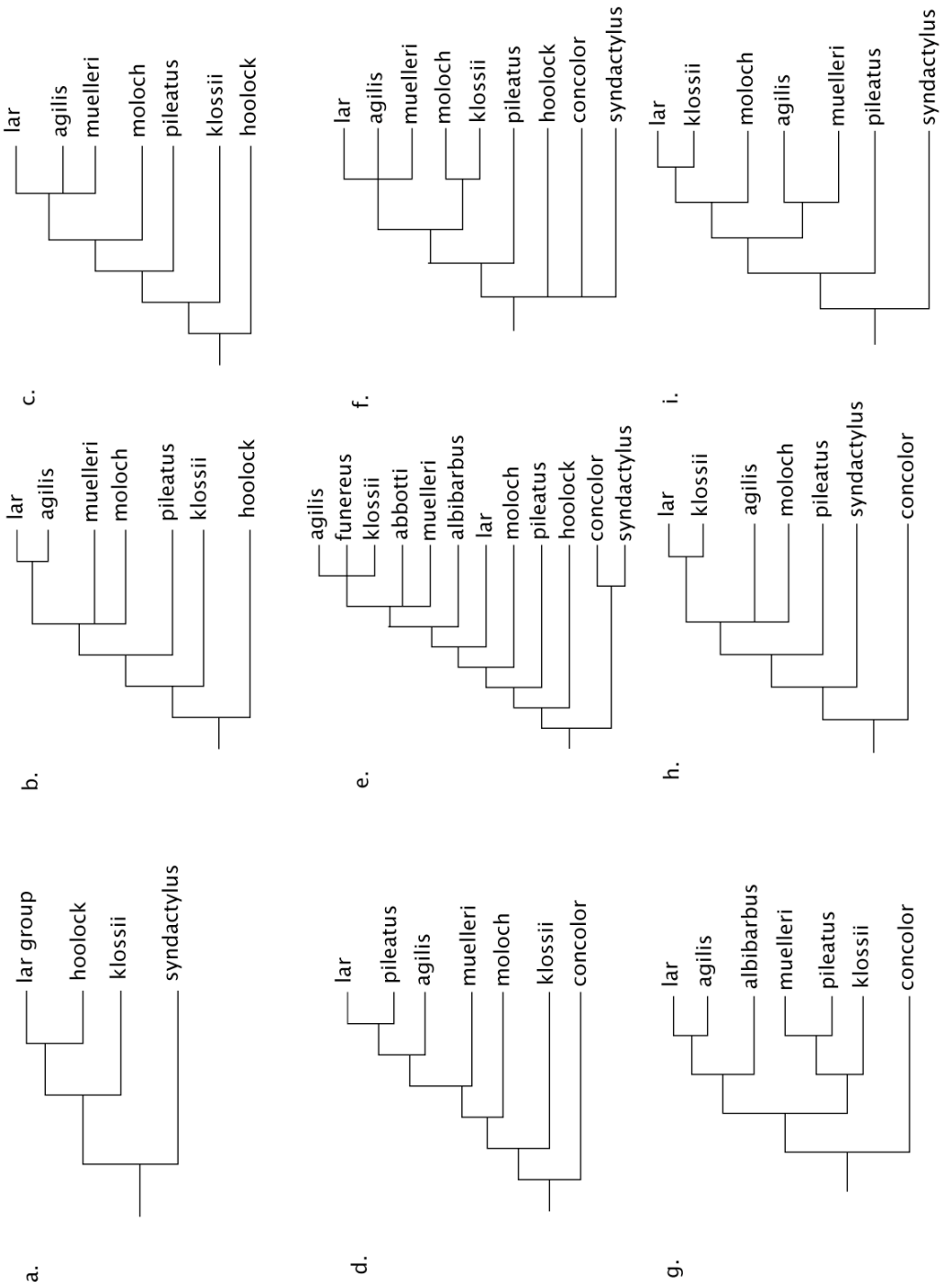

Figure 3.1: Phylogenetic trees produced by: a. Groves 1972; b. Chivers 1977; c. Haimoff et al. 1982; d. Creel and Preuschoft 1984; e. Geissmann 1993, “non-communicatory” data; f. Geissmann 1993, vocal data; g. Garza and Woodruff 1992; h. Hayashi et al. 1995; i. Zehr 1999, combined dataset

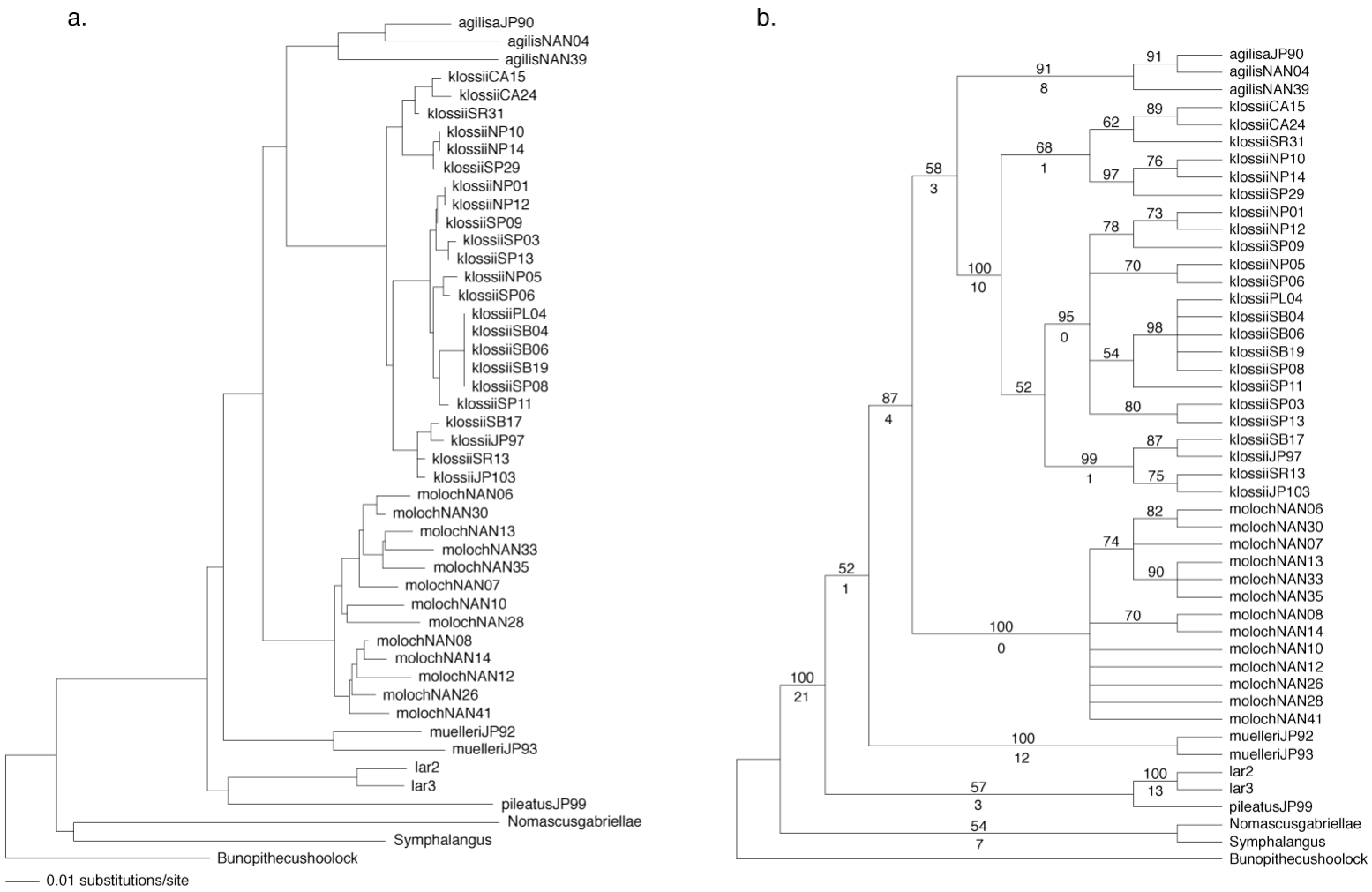

Figure 3.2: Gene trees produced by neighbor-joining. a. NJ phylogram; b. NJ bootstrap cladogram, 1000 replications. Bootstrap support values appear above the branches; number of unambiguous changes appear below the branches.

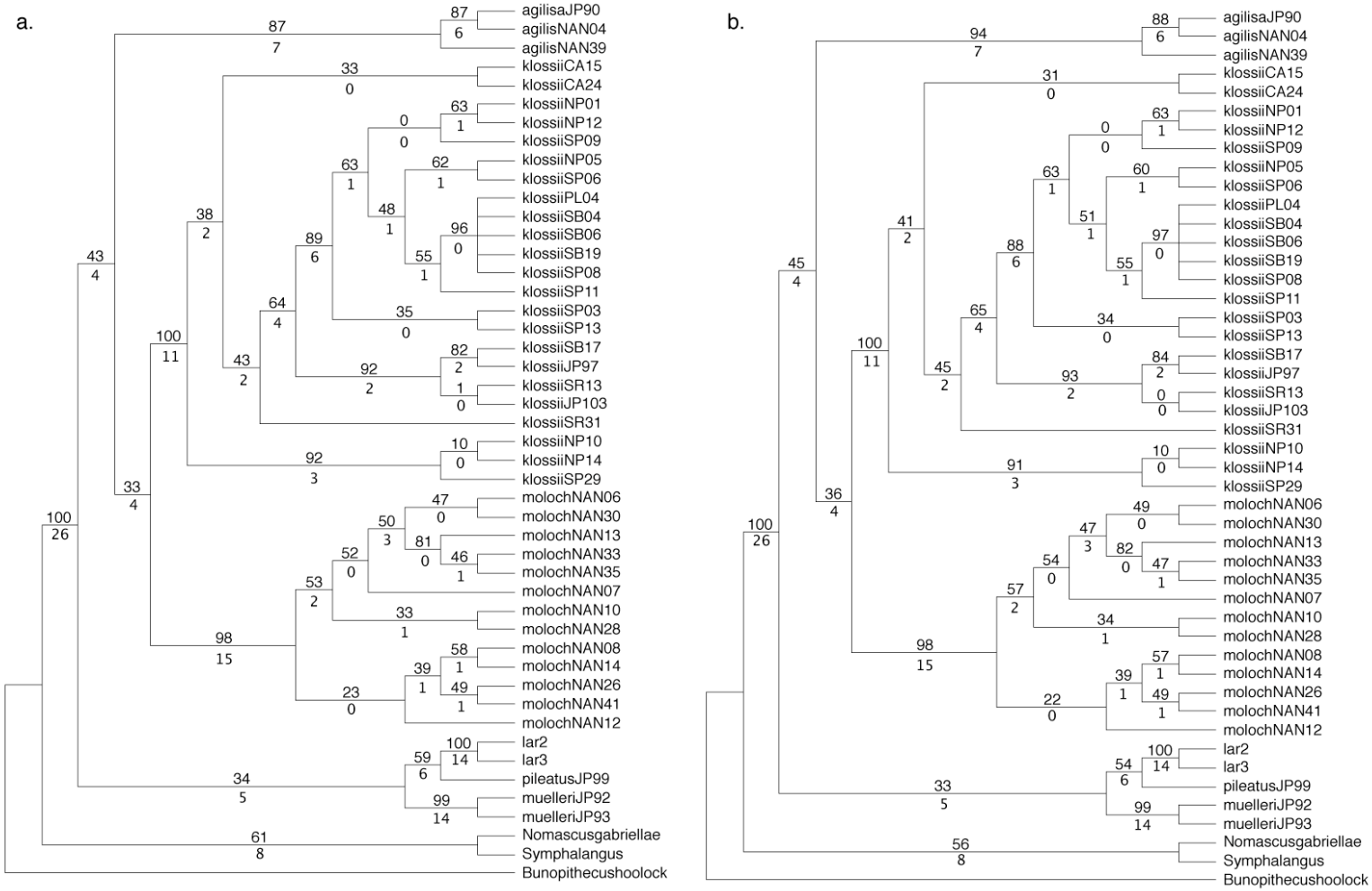

Figure 3.3: 50% majority rule bootstrap unweighted maximum parsimony trees. a. Gaps treated as "missing", b. Gaps treated as "fifth character state". Bootstrap values appear above the branches, number of unambiguous changes below.

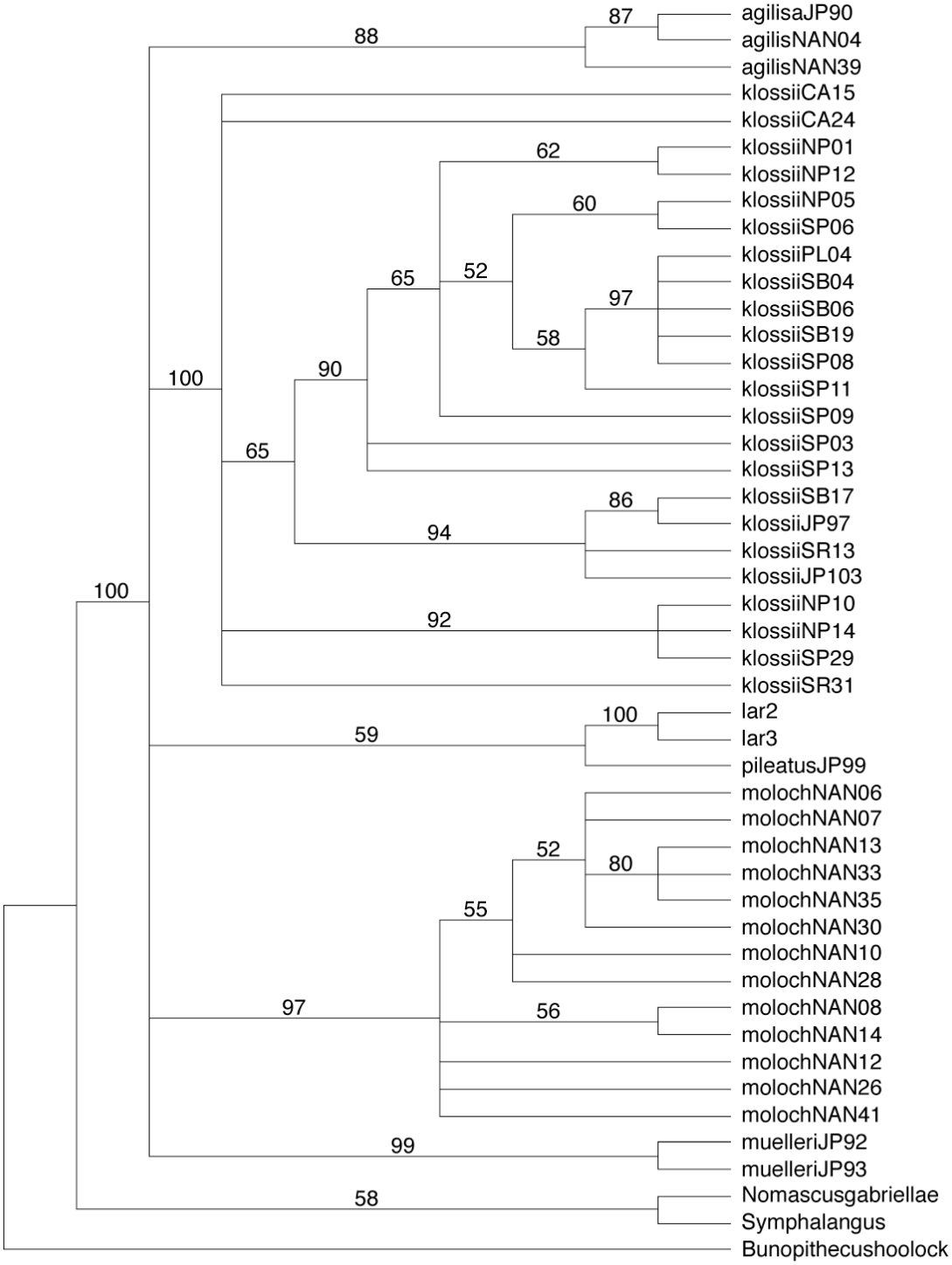

Figure 3.4: Weighted maximum parsimony tree, 1000 bootstrap replications. Branches with bootstrap values of less than 50% are collapsed.

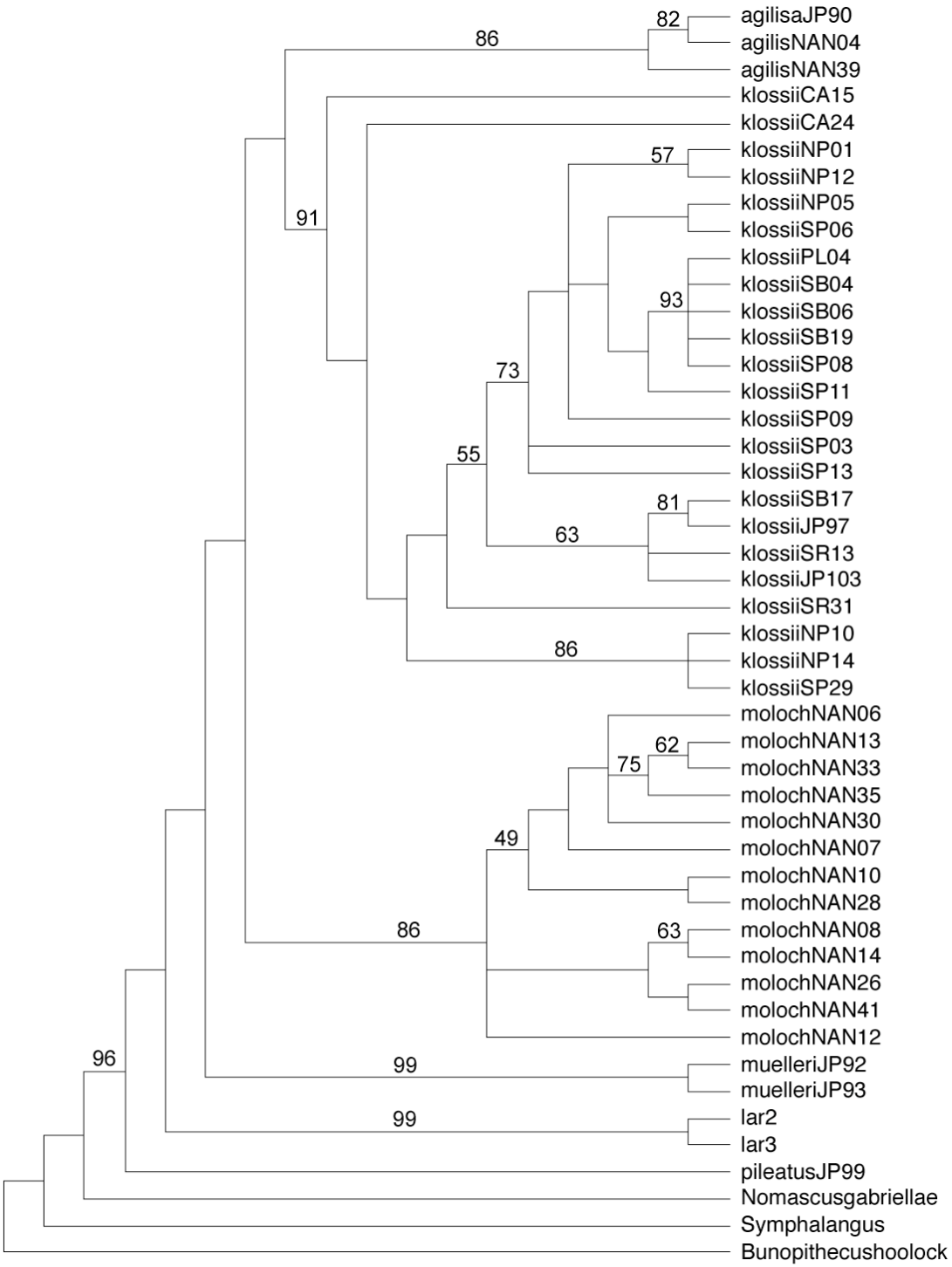

Figure 3.5: Maximum likelihood, strict consensus of three trees. Bootstrap values (100 replications) are indicated for clades with high support (over 50%).

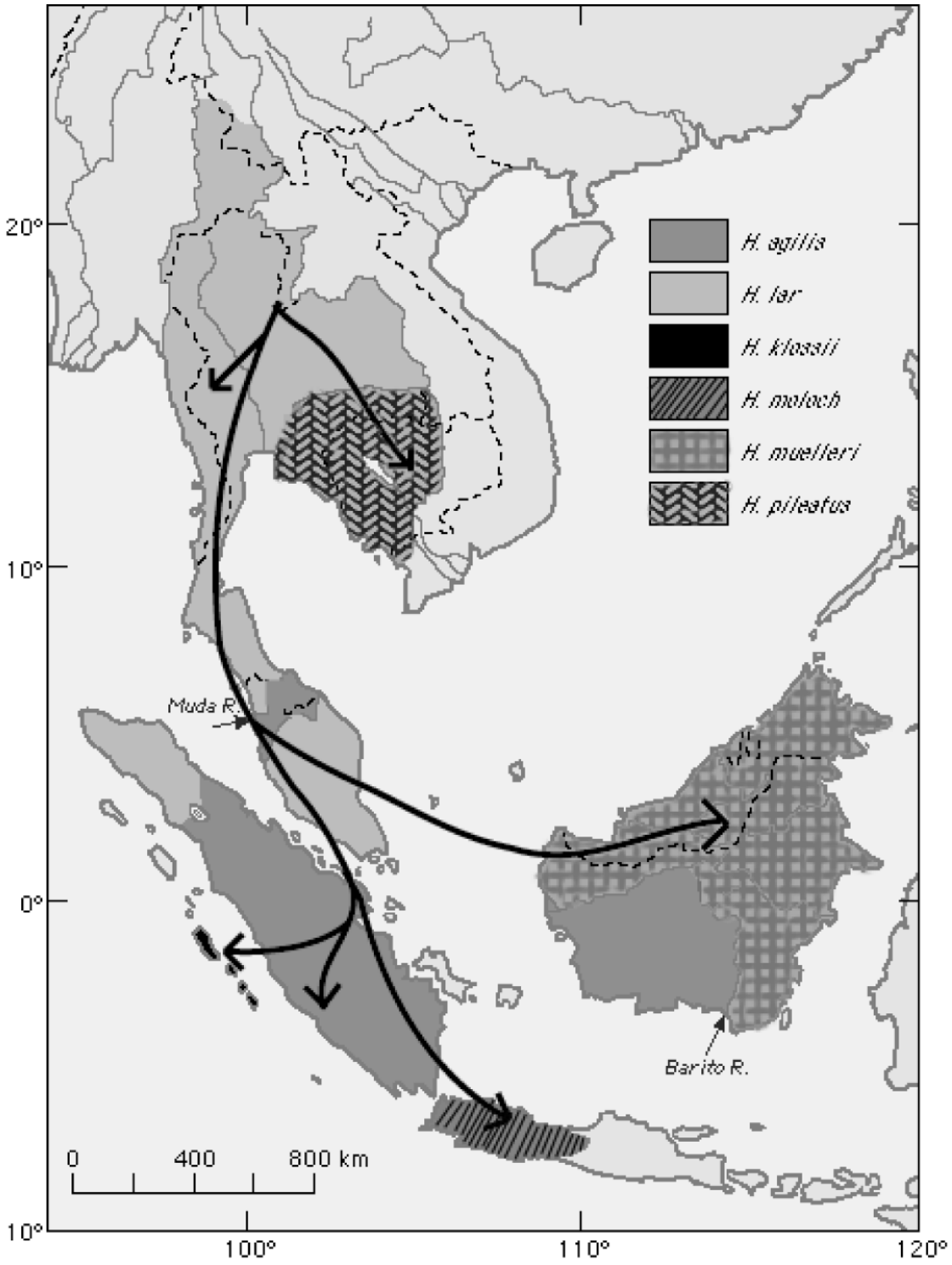

Figure 3.6: Hypothetical path of ancestral migration in biogeographic scenario.

Adaptation of map by Thomas Geissmann (www.gibbons.de).

CHAPTER 4

Phylogeography of Kloss's Gibbons

4.1 Introduction

The Mentawai Islands primates are geographically separated across the four islands, and the other three primate species have been divided into different subspecies (one on Siberut, one on the southern islands) on the basis of phenotypic variation (see below). The Kloss's gibbon, however, shows no obvious intraspecific variation in external appearance: the pelage of Kloss's gibbons is uniformly black, with no markings. Behavioral studies of *H. klossii* have only been conducted on the island of Siberut, so any behavioral variation is unknown. However, since the four Mentawai primate species all share the same biogeographic history, it might be expected that the Kloss's gibbon should have differentiated as well. On the other hand, if no genetic differentiation is found in the gibbons, the accepted subspecific status of the other Mentawai primates may need to be re-examined. The aim of this chapter is to examine intraspecific genetic variation in the Kloss's gibbon using phylogeographic and population genetic methods to determine whether there are geographically separated, genetically distinct lineages within the Mentawai Islands.

Phylogeography is a relatively new field concerned with the geographic distribution of genetic lineages within species. Phylogenetic methods, designed to examine relationships among species, can also identify lineages within a species that have been separated physically and thus historically have experienced little gene flow among them. Mitochondrial DNA is preferable for phylogeographic analysis, as it is uniparentally

inherited, without recombination. Patterns of mtDNA inheritance thus represent a genealogy, comparable to patterns of paternal last names in studies of human genealogical studies. Phylogeographic methods aim to identify geographically separated lineages and explain their spatial distribution (Avise 1995, 1998, 2000). In this chapter, I use phylogeographic analyses to address the following research question by testing two hypotheses:

Are there historically genetically differentiated lineages within the species *H. klossii* that correspond with geographic discontinuities?

Hypothesis 1: There are no diagnosable units within the species *Hylobates klossii*. Kloss's gibbons display no morphological variation across the Mentawai Islands, and may exhibit little genetic variation as well. Populations on different islands should display the same genetic lineages.

Hypothesis 2: There is a division between the Siberut populations and those on the southern islands. Despite morphological appearances, all of the Siberut primates share a history of isolation from the other Mentawai Islands, and although no pelage differences have evolved in the Kloss's gibbon, genetic variation will reflect this vicariance. Distinct lineages should be found on Siberut and on the southern islands.

Population genetics methods, on the other hand, are designed to examine current and recent population processes affecting the distribution of genetic variation, such as gene flow, natural selection, genetic drift, and mating patterns (Hartl and Clark 1997). Typically, such questions are addressed using allele frequencies of rapidly mutating

nuclear loci, such as microsatellites. I test three hypotheses using population genetics analyses to address the research question:

Is there a relationship between geography and current patterns of gene flow among populations of Kloss's gibbons? Factors known to influence population substructuring include physical barriers to dispersal, isolation by distance, and mating systems and social structure.

Hypothesis 3: There is no significant population substructuring. Under this null hypothesis, geography should not play a role in the genetic structure of populations.

Hypothesis 4: Patterns of gene flow display concordance with geographic barriers. The geographic barriers expected to play the most significant role in Kloss's gibbon dispersal are the straits between the islands. These channels are very rough due to currents from the Indian Ocean, and any rafting across them is unlikely (Dring et al. 1990). Under this hypothesis, gene flow should not be occurring between each of the four islands.

Hypothesis 5: Gene flow displays a pattern consistent with isolation by distance models. Long distances restrict gene flow in many species, so that neighboring populations exchange more migrants than those that are distant (Wright 1943). Not only should more gene flow occur within an island, but neighboring populations within an island should exhibit more gene flow than more distant populations on the same island.

These two research questions approach the same problem, differentiation within Kloss's gibbons, in different ways: the first using phylogeographic methods to examine

the species' history, the second using population genetics methods to address current population processes. Potentially, two different patterns could be found with these different methods, and conflicting hypotheses could be supported. For example, there may not be historically differentiated lineages observed in the mtDNA data, yet the current gene flow among populations may be restricted by geography.

4.1.1 The Mentawai colobines

No study of intraspecific genetic differentiation has ever been conducted for *Presbytis potenziani* or *Simias concolor*. The subspecies *P. potenziani siberu*, *P. p. potenziani*, *S. concolor siberu*, and *S. c. concolor* were named by Chasen and Kloss (1927) based on coat color differences. The *P. potenziani* subspecies are described as differing in the extent of the red coloration on the underparts, with *P. p. siberu* having hair tipped with black on the underside. *S. concolor siberu* is described as differing from *S. c. concolor* in the same way, with the Siberut subspecies showing a darker coat overall and hairs tipped with black on the underside (Chasen and Kloss 1927). These observations are based, however, on very few specimens (10 *P. potenziani*, 7 *S. concolor*). The variation observed may not be geographically patterned, and the suggested differentiation may simply be an artifact of small sample size. The authors admit that the adult female *S. concolor* from Siberut cannot be differentiated from the three Sipora specimens (Chasen and Kloss 1927). More in-depth study of morphological and genetic variation is necessary to determine whether these taxonomic designations represent biological differentiation, though pelage coloration has been recognized as an indicator of subspecific status (see below).

4.1.2 The Mentawai macaques

Differences between the Siberut form of the Mentawai macaque and those on the southern islands follow the same pattern. The Siberut macaques, like the Siberut colobines, are darker in coloration than those in Sipora and the Pagais (Whitten and Whitten 1982). One genetic study has recently been conducted of *Macaca pagensis* which proposes dividing the Mentawai macaques into two species, *Macaca siberu* in Siberut and *M. pagensis* on the southern islands (Roos et al. 2003). This proposal is based on evidence from a single mitochondrial locus, cytochrome *b*, and a sample of only 28 Mentawai macaques. The sample includes 12 individuals identified as Siberut macaques. Of these 12, only 5 were sampled on Siberut itself. Two individuals are from the Bukittinggi zoo, and are of ambiguous origin. The origin of the remaining five is identified as Padang, Sumatra. These animals are probably pets, since there are no free-ranging Mentawai macaques in Padang. Pet owners often do not know the origin of their Mentawai primates, and there is a substantial pet trade coming out of the Pagais. It is possible, then, that individuals identified as Siberut macaques may actually be from other islands.

Macaques exhibit very strong female philopatry, and thus show very different genetic population structures when comparing mitochondrial and nuclear loci. Since females always stay in the natal group, and mitochondrial DNA is maternally inherited, macaque groups tend to show low intra-group diversity and very high inter-population diversity. The average difference between macaques from Siberut and Sumatra and those from Sipora and South Pagai found in the Roos *et al* study was 5.9%, not dramatically different from the range of estimated mtDNA sequence divergence found between rhesus

macaque populations (0.2% - 4.5%), even without physical isolation (Melnick and Hoelzer 1992). The differentiation observed in *M. pagensis* could be a result of female philopatry, and not indicative of a species-level distinction. Analysis of nuclear DNA for other macaque species shows much broader genetic homogeneity, since males disperse from their natal groups and nDNA is inherited from both parents. For this reason, genes on the Y-chromosome have recently been included in the analysis of macaque evolutionary patterns (Tosi 2000). A much broader study of genetic variation, in both nuclear and mitochondrial DNA, in Mentawai macaques is necessary before such conclusions can be drawn.

4.1.3 The Kloss's gibbon

As mentioned above, no phenotypic variation is observed in the Kloss's gibbon. All Kloss's gibbons have completely black pelage with no markings. However, in the small sample (8 individuals from Siberut and 2 from Sipora) examined by Chasen and Kloss (1927), some variation in the direction of the hair of the forearm was observed. In the Sipora specimens, the hair pointed towards the elbow, while in the Siberut specimens the hair pointed towards the wrist (Chasen and Kloss 1927). This dissertation is the first study to examine genetic variation in this species.

4.1.4 Species concepts, subspecies, and ESUs

Scientists have long debated how to define a species, arguing over both what a species is and how to identify it. Two species concepts that are commonly invoked are the Biological Species Concept (BSC) (Mayr 1942) and the Phylogenetic Species Concept (PSC) (Cracraft 1983). The BSC states that "species are groups of actually or potentially interbreeding populations that are reproductively isolated from other such

groups" (Mayr 1942). This definition is often accepted as a working concept, yet it can be problematic to operationalize. If populations are isolated geographically, they may be considered "potentially" interbreeding populations, but this hypothesis is not testable in nature. The PSC focuses instead on how to recognize a species, and defines a species as the smallest diagnosable unit on the basis of fixed, or reciprocally monophyletic, character states (Platnick 1979; Cracraft 1983; Nixon and Wheeler 1990).

Under the BSC, geographically isolated populations that display phenotypic differentiation are often considered subspecies. No criteria are established that specify what level of differentiation is sufficient to designate populations as subspecies, and some systematists have argued that this largely subjective system should either be abandoned entirely or replaced with a more careful system of defining "evolutionarily significant units" (ESUs), particularly for the purpose of making conservation decisions (Ryder 1986; Vogler and Desalle 1994). In practice, ESUs are defined as genetically, ecologically, and/or morphologically distinct lineages; this definition also meets the requirements for the PSC, and the PSC can be used to identify populations for conservation. In the present study, I focus on identifying whether populations are genetically distinct under the PSC.

4.2 Methods

Fecal samples were collected from wild Kloss's gibbon populations at seven sites on four islands (Figure 2.1), as described in Chapter 2 and detailed in Appendix I. Samples were stored in lysis buffer (samples collected in 2001) or RNA*later*® (2003) at room temperature, and total genomic DNA was extracted using QIAGEN QIAamp DNA Stool Mini Kits and manufacturer supplied protocols. The hypervariable region I of the

mitochondrial control region, or D-loop, was amplified and sequenced as described in Chapter 2. Additionally, samples were genotyped at several microsatellite loci. Eleven loci that were found to work in other gibbon species were screened (Oka and Takenaka 2001; Chambers et al. 2004; Lappan 2005). Only six loci produced sufficient results and were polymorphic in *Hylobates klossii* (Table 4.2). Laboratory protocols for amplification, replication, and genotyping are described in detail in Chapter 2.

To address the question of genetically differentiated lineages, three types of analyses were conducted: 1) Phylogenetic inference was conducted using MODELTEST 3.6 (Posada and Crandall 1998) and PAUP* 4.0 (Swofford 2002). 2) A median-joining network was constructed using Network 4.1.0.7 (Bandelt et al. 1999)(www.fluxus-engineering.com). 3) Population Aggregation Analysis (PAA) was conducted using MacClade 4.0 (Maddison and Maddison 2000).

To identify breaks in current gene flow and determine whether they correspond with geography, both the mitochondrial D-loop sequence data and the nuclear microsatellite genotype data were examined. With the mtDNA sequence data, I used Arlequin 2.0 (Schneider et al. 2000) to conduct an analysis of molecular variance and to estimate F_{ST} and nucleotide diversity and divergence. I calculated F_{ST} and R_{ST} statistics with the microsatellite data using Arlequin 2.0 and RSTCALC (Goodman 1997).

4.2.1 Phylogenetic inference

Although phylogenetic analysis is typically used to examine relationships among species, gene trees constructed with phylogenetic algorithms should also identify distinct lineages within a species (Avise 2000). This method has identified geographically separated lineages, some of which have been proposed as different subspecies, in Javan

silvery gibbons (*H. moloch*) (Andayani et al. 2001), chimpanzees (*Pan troglodytes*) (Gonder et al. 1997; Gonder 2000), and orangutans (*Pongo pygmaeus*, *P. abelli*) (Zhi et al. 1996), to name a few.

I used three different algorithms: neighbor-joining, which can tolerate high levels of saturation as might be expected in a quickly mutating locus (Roos and Geissmann 2001); maximum parsimony, which finds the tree that describes the fewest number of evolutionary changes needed to explain the data (Swofford et al. 1996); and maximum likelihood, which finds the tree that is explained by an evolutionary model of nucleotide substitution, defined *a priori* based on goodness-of-fit with the data (Posada and Crandall 1998). These methods are described in greater detail in Chapter 3.

The dataset used for this analysis was compiled to assess the phylogenetic relationships within the genus *Hylobates*, and includes *H. agilis* (n=3), *H. lar* (n=2), *H. moloch* (n=13), *H. muelleri* (n=2), and *H. pileatus* (n=1). One sample from each of the other three gibbon genera (*Bunopithecus*, *Nomascus*, and *Symphalangus*) was included as outgroups. These sequences were either downloaded from GenBank or sequenced from blood samples of captive individuals, as described in Chapter 3.

4.2.2 Median-joining network

Because intraspecific genealogies are not hierarchically arranged, some researchers argue that a bifurcating tree such as those produced by the above analyses cannot accurately represent the relationships within a species. The ancestral states of the terminal nodes are usually still extant, and divergence within a species is usually too recent to be detected by phylogenetic analysis (Bandelt et al. 1999; Posada and Crandall 2001). To solve these and other problems, a variety of network methods have been devised to

represent multifurcations, reticulations, and extant ancestral nodes. The median-joining network, designed for non-recombining genes such as mtDNA, joins individuals with the fewest number of changes into clusters, which are then joined to other clusters to create a whole network (Bandelt et al. 1999). This method is based on the distance between sequences, but instead of generating many unresolved equally parsimonious trees, it produces a single network that shows many alternative evolutionary paths between individuals, and can thus tolerate homoplasy better than the usual phylogenetic methods (Disotell 1999).

4.2.3 Population aggregation analysis

Population aggregation analysis (PAA) is a character-based method that identifies genetically distinct lineages by analyzing patterns of distribution of genetic variation. Under this method, a profile is created for each population describing the presence or absence of each attribute in each individual. Only attributes that are fixed in populations are informative for this analysis. Populations are grouped together based on these attributes. After successive rounds of grouping local populations together, the result is either one group with no diagnosable units, or two or more distinct populations that under the phylogenetic species concept (PSC) could be considered species (Davis and Nixon 1992).

Scientists have argued that this character-based approach is necessary because it identifies the smallest units for which phylogenetic analysis is legitimate (Goldstein et al. 2000). Above this level, units are organized as nested hierarchies; while below this level, relationships between members of a sexually reproducing species cannot be depicted accurately in this manner. The units identified by PAA are presumed to have been

isolated long enough that different characters have become fixed in each population. Thus, the identification of these units suggest an historical absence of gene flow between the populations (Davis and Nixon 1992; Goldstein et al. 2000).

4.2.4 Mitochondrial diversity, divergence, and AMOVA

Nucleotide diversity (π) is a measure of DNA sequence polymorphism within a population, and is defined as the average number of nucleotide differences per site between two sequences (Nei 1987). Nucleotide divergence (p) is a distance measure between individuals based on nucleotide substitutions. I used Arlequin 2.0 (Schneider et al. 2000) to calculate nucleotide diversity and divergence, and then compared nucleotide divergence within and between populations.

Hierarchical or nested analysis of variance techniques partition genetic variation into hierarchical levels of within and among populations using allele frequency data (Zar 1999). The analysis of molecular variance (AMOVA) uses molecular sequence data rather than haplotype frequency data, and thus incorporates all of the information available in the different sequences. Pairwise distance measures are calculated based on the number of mutations between sequences. This method tests hypotheses using permutational methods, making the usual ANOVA assumption of normal distribution unnecessary (Excoffier et al. 1992). I analyzed molecular variance at three levels using D-loop sequence data: within local populations, among local populations within island groups, and among island groups of populations. Arlequin 2.0 was used to perform AMOVA, and also to calculate the fixation indices (F-statistics) with these data (see below for a detailed description of F-statistics.) The number of migrants per generation (*Nm*) was then calculated by hand based on F_{ST}.

4.2.5 Microsatellite analysis and F-statistics

Many population genetics statistics, including F-statistics, assume that the loci under study are in Hardy-Weinberg equilibrium, meaning that they are not undergoing evolution. Thus, data must first be tested for equilibrium to avoid violating the assumptions of population genetics analyses. I tested microsatellite data for Hardy-Weinberg equilibrium using the program Arlequin 2.0 (Schneider et al. 2000). A locus is assumed to be undergoing no forces of evolution (natural selection, genetic drift, gene flow, or non-random mating) when the genotype frequencies are not significantly different from those expected under perfect conditions (large population, no mutation, no migration, no selection, random mating). Hardy-Weinberg equilibrium is tested on a two-allele system using the equation:

$$p^2 + 2pq + q^2 = 1$$

where p is the frequency of allele one, and q is the frequency of allele two, so that p^2 gives the expected frequency of genotypes homozygous for allele one, $2pq$ gives the expected frequency of heterozygous genotypes, and q^2 gives the expected frequency of homozygotes for allele two (Hartl 2000). The equation can be expanded for additional alleles. These expected genotype frequencies are then compared to the actual frequencies, and the differences are tested for significance.

Wright's F-statistics compare heterozygosity at *a priori* defined levels of population substructure to evaluate which level is the breeding population – *i.e.*, at which level heterozygosity equals that expected under a random mating model (Wright 1965; Weir and Cockerham 1984; Hartl and Clark 1997). The fixation index F_{ST} describes the

proportion of total genetic variance accounted for by variation among populations. F_{ST} is calculated with the following formula:

$$F_{ST} = \frac{H_T - H_S}{H_T}$$

where H_T is the heterozygosity of the total population and H_S is the average heterozygosity among subpopulations.

Using F_{ST}, the number of migrants per generation between populations (*Nm*) can also be calculated:

$$F_{ST} = \frac{1}{4Nm + 1}$$

Because of the stepwise nature of microsatellite mutation, R_{ST}, an analog of F_{ST}, has been developed for use with microsatellite data (Slatkin 1995). The mutation model used by F_{ST} assumes that an allele is equally likely to mutate to any one of *k* states, regardless of the previous state; it also assumes low mutation rates. Because of slippage during replication, microsatellites are more likely to mutate to an allele that differs from the original allele by a single repeat length (*e.g.*, in a tetra-repeat locus, an allele of 200 basepairs is most likely to mutate to 196 or 204 basepairs).

While F_{ST} is based on haplotype frequencies, R_{ST} is calculated using variance in allele size:

$$R_{ST} = \frac{\overline{S} - S_W}{\overline{S}}$$

where $\overline{S}$ represents twice the estimated variance in allele size across populations, and S_W is twice the estimated variance in allele size within each population (Slatkin 1995; Goodman 1997).

However, when sample sizes are small or when the number of loci used is less than 20, F_{ST}-based estimates may be more accurate than R_{ST} (Gaggiotti et al. 1999). In particular, R_{ST} may produce an overestimate of *Nm*. Thus, I calculated both F_{ST} and R_{ST}, and calculated *Nm* based on each of these statistics.

4.3 Results

A total of 31 gibbon groups were sampled, and 21 Kloss's gibbon individuals (each from separate groups) were sequenced (see Table 4.1). Only 17 of these individuals could be at least partially genotyped at six microsatellite loci (see discussion of low success rate below in section on microsatellite analysis). Additionally, blood samples from two zoo specimens were included (JP97 and JP103).

A 479 base-pair region of the mitochondrial D-loop was sequenced for 23 individuals. 15 haplotypes were found in this sample, with 37 polymorphic sites. Of these, 35 were transitions, one a transversion (site 213), and one an insertion/deletion (site 303). Appendix II shows the complete sequence alignment for the full hylobatid dataset.

4.3.1 Phylogenetic inference

Resulting trees from the phylogenetic analyses are shown in Figures 4.1-4.3. None of the three analyses (neighbor-joining, maximum parsimony, and maximum likelihood) separated the Siberut samples from the others.

Figure 4.1 shows the phylogram and the bootstrap consensus tree using the neighbor-joining algorithm. This tree identifies two lineages with moderate bootstrap support values (52 and 68), but individuals from Siberut and the Pagais are found in each lineage.

The weighted maximum parsimony tree (1,000 bootstrap replicates) is shown in figure 4.2. This tree has less resolution than the neighbor-joining tree, though many of the same clusters are identified.

Three trees were found by the heuristic maximum likelihood search. Figure 4.3 shows the strict consensus tree, with bootstrap values indicated for branches with high support. In this cladogram, unlike the neighbor-joining and maximum parsimony analyses, all of the Kloss's gibbon sequences appear to belong to a single lineage.

4.3.2 Median-joining network

The median-joining network (Figure 4.4) similarly finds no geographic structure in the sample. Siberut haplotypes occur throughout the network, and while most of the Pagai haplotypes cluster together, others are on the opposite end of the network.

4.3.3 Population aggregation analysis

Table 4.3 shows the 37 polymorphic sites in the DNA sequences. Nucleotide differences that are fixed in each population are called "characters"; those that are not fixed are called "traits". In this dataset, every site is a trait, not a fixed character, and no population has any fixed nucleotide differences. Therefore, under this criterion, *Hylobates klossii* is a single phylogenetic species.

4.3.4 Mitochondrial diversity and AMOVA

For the AMOVA, the data were partitioned into 3 island groups: Siberut, including the two local populations of North Siberut and Siberut National Park; Sipora; and the Pagais, including two local populations from North Pagai and South Pagai. The detailed results of the AMOVA are given in Table 4.4. Eight percent of diversity is partitioned

among islands, and 7.5% among populations within islands. The majority of the variation (84%) is due to variation within populations.

F_{ST} based on the sequence data is 0.157 ($p=0.07$), which falls within the range considered to indicate *great* genetic differentiation (Wright 1978). However, this result is not significant at the $p<0.05$ level, which suggests that despite the high F_{ST} value, it is not significantly different from zero. Thus, the difference between populations is not significantly different from none at all, and differentiation between populations cannot be inferred. Calculating *Nm* from an F_{ST} of 0.157 results in *Nm*=1.3. Population pairwise F_{ST} values are presented in Table 4.6. Two of the values (North Siberut x Sipora; North Pagai x South Pagai) are negative, which indicates that the populations are more alike than they are different. Two values are significant only at the $p<0.1$ level (North Siberut x South Pagai; Sipora x South Pagai); none are significant at the $p<0.05$ level.

Table 4.7 presents the nucleotide diversity (π) measures for each population. The highest diversity is found in North Siberut (π =0.31), while South Pagai and Siberut National Park display the lowest diversity (π =0.18).

Nucleotide divergence estimates are presented in Table 4.8. Within population divergences range from 0.2-4.3%, while between population divergences range from 0.2-4.5%. The greatest between-population divergence was between North Siberut and Siberut National Park (3.3-4.3%), which did not fall outside the range of within-population divergence in North Siberut (0.8-4.3%).

Appendix II presents nucleotide divergence estimates for the entire hylobatid dataset. The ranges for within-species sequence divergence are as follows: *H. agilis*, 5.3-8.9%; *H. lar*, 2.9%; *H. muelleri*, 5.9%; *H. moloch*, 1.2-5.7%; and *H. klossii*, 0.2-4.5%.

4.3.5 Microsatellite analysis

Characteristics of the six loci used for analysis are summarized in Table 4.8. In addition to genotyping *H. klossii* individuals, I also genotyped myself in order to find errors caused by contamination of the gibbon samples.

Sample size for the microsatellite analysis (n=17) was smaller than that for the mitochondrial sequence analysis (n=21) due to very low amplification of nuclear DNA from gibbon feces. The success rate for each locus ranged from 9-21%. Of the six loci that produced usable results, an average of 12 (range: 3-36) reactions were performed for each individual. An average of 3.5 reactions showed amplification, and of those, an average of 1.8 appeared to be reliable genotypes. A "reliable" genotype is one that is not my own genotype, falls within the range of allele sizes specified for that locus, and shows only one or two identifiable alleles. Allelic dropout occurred in an average 27% of replications (ranging from 10% for D3S1766 to 43% for D12S321).

Because of these low success rates I was unable to confirm all genotypes with the recommended number of replications. Because this failure reduces the sample size to a very low number, I have analyzed the data two ways: once with only the genotypes confirmed by at least 2 (for heterozygotes) or 3 (for homozygotes) replications, and once including all data. Genotypes are presented in Appendix IV.

Hardy-Weinberg Equilibrium. Tables 4.9 (all genotypes) and 4.10 (confirmed genotypes only) summarize the observed and expected heterozygosity for each locus in each population. Only one locus in one population was not in Hardy-Weinberg equilibrium (D3S1766 in South Pagai) due to a heterozygote deficiency. This locus is in

equilibrium when only confirmed genotypes are analyzed, suggesting that allelic dropout may have caused the observed heterozygote deficiency.

F_{ST}. Population pairwise F_{ST} statistics based on the microsatellite are summarized in Table 4.11. All values are non-significant, suggesting that none of the five populations are differentiated from each other. However, the overall F_{ST} averaged over all loci is 0.103 when all genotypes are included. This value is significant (p=0.002) and suggests that moderate differentiation has occurred (Wright 1978).The number of migrants per generation (*Nm*) based on this value is 2.18. When only confirmed genotypes are analyzed, F_{ST} averaged across all loci is = 0.09; this value also falls within the "moderate differentiation" range but is only significant at the $p<0.10$ value (p=0.08). *Nm* based on this value is 2.53 migrants per generation.

R_{ST}. I was unable to divide the samples into five populations for the RSTCALC analysis, as the program will not run with too many missing data. Instead, I divided the samples into three populations: Siberut (including the North Siberut and Siberut National Park samples), Sipora, and Pagais (including North and South Pagai). When all genotypes were included, overall R_{ST}=0.09 (p=.09), and *Nm* (as calculated by RSTCALC) is 2.65. If a significance level of $p<0.10$ is accepted, then these results indicate that the populations have undergone moderate divergence (Wright 1965).

When only the confirmed genotypes were included, R_{ST} = -0.047 (p=0.48), and *Nm*=-5.56. A negative R_{ST} value (and the corresponding *Nm*) indicates that the within-population variance is larger than the among-population variance in allele size, suggesting that there is no differentiation between the populations.

Population pairwise R_{ST} values are presented in Table 4.12. None are significant, and several are negative, suggesting again no differentiation.

4.4 Discussion

The mitochondrial data suggest that there is no significant differentiation among *Hylobates klossii* populations. The phylogenetic and phylogeographic analyses failed to find diagnosable units within the species. Thus, the hypothesis that *H. klossii* has genetically differentiated lineages is not supported; rather, it is a single phylogenetic species (as defined by the PSC, described above) as predicted by Hypothesis One.

Comparing within-population and between-population mitochondrial sequence divergence shows that between-population divergence does not fall outside the range seen within populations. In other gibbon species for which divergent populations have been identified, the observed sequence divergence is higher between populations than within populations. For example, the reported average within-population divergence for the western clade of *H. moloch* was 1.3%, and for the central clade was 3.1%; while the average divergence between these populations was 3.5% (Andayani et al. 2001). For different subspecies of *H. agilis* included here, divergence was as high as 8.9%.

The AMOVA and F_{ST} analyses also do not find significant population substructuring within the species. Table 4.12 summarizes the different F_{ST} and R_{ST} values produced by the different analyses. While the overall F_{ST} values based on both mitochondrial and microsatellite data suggest great or moderate differentiation, the only analysis with a significant result is based on all microsatellite genotypes produced, many of which could not be confirmed with replications. The R_{ST} analysis produced conflicting results depending on which genotypes were included; suggesting that either 1) the dataset is too

small when only including genotypes confirmed by replication, or 2) the inclusion of unconfirmed genotypes, which may be erroneous, causes unreliable results. No pairwise F_{ST} or R_{ST} analyses identified any populations as significantly different from each other at the $p<0.05$ level; however, pairwise F_{ST} comparisons using mitochondrial sequences found the South Pagai population to differ from North Siberut and Sipora ($p<0.1$), though not from Siberut National Park. Shared haplotypes were found between Siberut and South Pagai; thus, any inferred differentiation is problematic. Hypothesis three, that there is no significant population substructuring, is thus supported.

Possible explanations for a lack of differentiation within a species include: 1) recent gene flow, either natural or human-mediated; 2) historical gene flow; 3) incomplete lineage sorting; or 4) factors related to social organization.

4.4.1 Recent gene flow

Current or recent gene flow among the Mentawai Islands is nearly impossible. Gibbons are rarely observed to come to the ground, and they have never been seen to cross water. Furthermore, the water channels separating each of the islands are very dangerous, as the Indian Ocean has virtually no breaks between Madagascar and the Mentawai Islands. The resulting large waves make the Mentawais one of the most popular surfing spots in the world. Humans rarely cross the water within the Mentawai archipelago, preferring the safer route of traveling across the Strait to mainland Sumatra and then back out to another island.

While gibbons are popular pets in the Mentawais, the possibility that pet gibbons have been reintroduced into the wild across islands is very low. Pet gibbons rarely survive to adulthood (pers. observation), and reintroduction of any pet primate is

difficult. Primates that have been reared by humans have never learned how to interact with conspecifics, avoid predators, and rear young. Even with an extensive rehabilitation and reintroduction program, these abilities usually cannot be acquired later in life, and rehabilitated adults often are unable to raise offspring successfully (Yeager and Silver 1999). Furthermore, few Mentawai people travel between Siberut and the southern islands. The inhabitants of the Pagais and Sipora characterize the Siberut peoples as "primitive," and warn researchers against traveling there for fear of getting shot at with bows and arrows. Most Siberut peoples, on the other hand, are cash-poor and have few opportunities to travel outside of Siberut, or even outside of their own region within Siberut.

4.4.2 Historical gene flow

The Mentawai Islands have been separated from Sumatra for 500,000 to one million years by the 1500-meter deep Mentawai Strait (Whitten et al. 2000). However, sea levels between the individual Mentawai Islands are currently only 10-25 meters deep, as shown in nautical maps (London Admiralty 1993). Eustatic sea levels were about 25 meters lower than current levels approximately 7,000 years ago (Milliman and Emery 1968), which would have been low enough to connect all four Mentawai Islands into a single landmass. Gene flow could thus have occurred among the Mentawai primate populations as recently as 7,000 years ago, resulting in the genetic pattern seen here.

4.4.3 Incomplete lineage sorting

Genetic differentiation of mtDNA between populations occurs when ancestral lineages are pruned so that each group consists of descendants of different lineages, resulting in reciprocal monophyly (Avise 2000). Such pruning occurs much later than the

physical separation of the populations. Thus, despite a geographic separation, the Kloss's gibbons of Siberut and of the southern islands may have retained ancestral mtDNA haplotypes. Since the Mentawais may have been a single landmass as recently as 7,000 years ago, enough time may not have passed to allow lineage sorting.

4.4.4 Kloss's gibbon social organization

Within a population, substructuring is largely determined by social structure (Storz 1999). All gibbon species have been characterized as living in pair-bonded, one-male/one-female groups with their offspring, and both sexes disperse from the natal territory (Preuschoft et al. 1984; Leighton 1987). More recently, long-term studies have discovered that mating patterns and group structure in gibbons often deviate from this model, including multiple adults of either sex who may reproduce in the same group (Srikosamatara and Brockelman 1987; Bleisch and Chen 1991; Palombit 1994a, 1994b; Reichard 1995; Brockelman et al. 1998; Lappan 2002; Lappan 2005).

Group sizes observed in this study, particularly in North Siberut, were much larger than what has been described as "normal" for gibbons (see Chapter 5). Group sizes ranged from 4-15 individuals throughout the Mentawais, and average observed group size in North Siberut was 10. Several groups were observed with more than one infant.

Many questions arise from these observations. No behavioral study has been conducted on gibbon groups this large, so it is not known how cohesive these groups are, or how permanent or fluid the group membership. In most gibbon species, the male and female sing duets, complex calls consisting of alternating contributions from the male and the female. This is a trait also seen in the monogamous titi monkeys (*Callicebus*) and indri (*Indri*), and is believed to function in mate defense, resource defense, and pair-

bonding (Cowlishaw 1992; Muller and Anzenberger 2002; Powzyk and Mowry 2003). Kloss's gibbons do not duet (Tenaza 1976), which may suggest a weaker pair-bond. A social organization consisting of groups that are not very cohesive, with members of both sexes that transfer between groups or migrate further than previously supposed, could result in alleles moving faster throughout the population and thus less genetic substructuring would be seen. Low variation should be observed among groups, while variation within groups should be high. Further research, with more intensive sampling, is needed to address these questions before any conclusions can be made.

4.4.5 Implications for the other Mentawai primates

If Kloss's gibbons show no significant genetic differentiation, the subspecific taxonomy of the Mentawai colobines and macaque should also be questioned. As discussed in the Introduction, these designations rely on small differences in coat color and, for the macaques, differentiation in the mitochondrial genome that is not much greater than that seen between populations of other macaque species, due to the extreme female philopatry of macaques.

However, due to different generation times, it is possible that the other Mentawai species may display genetic differentiation while the gibbons do not. Gibbons have longer life histories and longer generation times than macaques and colobines. Generation time is equal to the length of time from the birth of a female to her age at first birth. While life history data are not available for all species, members of the same genus or family tend to have similar characteristics. Average generation time has been estimated at 54 months (range 46-65) for macaque species (Harvey et al. 1987); and 51 months (range 48-55) for Asian colobines (including *Nasalis larvatus*, the closest relative

of *Simias concolor*) (Harvey et al. 1987; Ross 1992). The generation time for hylobatids is twice as long, at 110 months (range 108-112) (Harvey et al. 1987). For every 1,000 years of separation, 222 generations would have passed for the macaques and leaf monkeys, and only 110 for the gibbons. In this way, it would be possible for the different Mentawai primates to have the same biogeographic history but different levels of genetic differentiation, due to lineage sorting occurring in the colobines and macaques but not in the gibbons.

On the other hand, there is little evidence for the taxonomic designations for the other primates, as no genetic studies have been conducted for *Simias* and *Presbytis potenziani*, and the only *Macaca pagensis* genetic study used only mtDNA, which is known to be highly structured within all macaque species. Therefore, no robust conclusions can be made about the Mentawai colobines or macaques based on the data from this study.

4.5 Conclusion

Based on the mitochondrial data, there are no diagnosable units within the species *Hylobates klossii*. The mitochondrial and nuclear data both show no significant differentiation between populations. Thus, the gibbons of Siberut, Sipora, and the Pagais are a single phylogenetic species, with no evidence for subspecific designations. The implications of this conclusion for conservation management are discussed in Chapter 6.

The results of the microsatellite analysis are more problematic; current gene flow between isolated populations is not possible, but the data do not rule out the effects of past gene flow or dispersal and social structure. Because of extremely low success rates and my inability to fully genotype most individuals, better sampling and more genotyping is probably needed to determine current patterns of population structure in Kloss's

gibbons. Some analyses produced significant or “near-significant” estimates of population substructuring, suggesting that 1) the microsatellite data are inadequate, and/or 2) populations are currently undergoing differentiation.

While the same mitochondrial lineages are observed throughout the Mentawai Islands, it seems highly unlikely that the species is a single panmictic population. Instead, geologic evidence suggests that the islands have not been separated long enough for lineage sorting to occur. The data presented here do identify divergent mitochondrial lineages that occur in all populations; a prediction may be made that in future generations, these lineages will be stochastically “pruned”, so that different lineages survive in different populations, and replicating this study would result in the identification of divergent populations. The failure of the microsatellite data to identify breaks in gene flow is more likely due to an inadequate dataset rather than panmixia.

Site	Sample code	Groups sampled	Individuals sequenced	Individuals genotyped
Peleonan forest, North Siberut	PL, CA	8	3	4
Simabuggai, Siberut National Park	SB	5	4	3
Taileleu, South Siberut	TL	0	0	0
Saureinu, Sipora	SR	2	2	2
Betumonga and Muntei, North Pagai	NP	8	5	2
South Pagai	SP	8	7	6
TOTAL		**31**	**21**	**17**

Table 4.1: List of samples collected, sequenced, and genotyped

Locus	Result	Reported use in gibbons
D1S548	Poor amplification	*H. lar* (Chambers et al 2004), *S. syndactylus* (Lappan, pers. comm.)
D3S1766	Polymorphic	*H. lar* (Chambers et al 2004)
D5S1457	Polymorphic	*H. lar* (Chambers et al 2004), *S. syndactylus* (Lappan, pers. comm.)
D10S1432	Poor amplification	*H. lar* (Chambers et al 2004)
D11S1366	Polymorphic	*S. syndactylus* (Lappan, pers. comm.)
D12S391	Polymorphic	*H. moloch* (Whittaker, unpublished)
D13S321	Poor amplification	*H. lar* (Chambers et al 2004)
D14S306	Polymorphic	*H. muelleri* (Oka and Takenaka 2001), *H. lar* (Chambers et al 2004), *S. syndactylus* (Lappan, pers. comm.)
D17S1290	Monomorphic	*H. moloch* (Whittaker, unpublished)
D19S714	Polymorphic	*S. syndactylus* (Lappan, pers. comm.)
D20S206	Poor amplification	*H. muelleri* (Oka and Takenaka 2001), *H. lar* (Chambers et al 2004)

Table 4.2: Microsatellite loci screened in *Hylobates klossii* samples.

	16	17	25	96	113	122	133	140	142	144	145	153	159	161	166	167	170	185	213	221	222	226	253	287	303	304	306	311	329	340	341	357	360	361	366	436	449
PL04	G	G	G	A	T	A	A	A	C	G	C	A	G	G	T	T	A	A	C	C	C	T	A	C	-	C	A	T	A	T	A	A	C	C	T	T	C
CA15	A	G	G	G	C	A	A	A	T	A	C	G	A	A	C	C	A	A	A	C	T	T	A	T	-	C	A	C	A	T	A	G	T	T	C	T	T
CA24	A	G	G	G	C	A	A	A	T	A	C	G	A	A	C	C	A	A	A	T	T	T	A	T	-	C	A	C	A	C	A	G	T	T	C	T	C
SB04	G	G	G	A	T	A	A	A	C	G	C	A	G	G	T	T	A	A	C	C	C	T	A	C	-	C	A	T	A	T	A	A	C	C	T	T	C
SB06	G	G	G	A	T	A	A	A	C	G	C	A	G	G	T	T	A	A	C	C	C	T	A	C	-	C	A	T	A	T	A	A	C	C	T	T	C
SB17	A	G	A	G	C	A	A	G	C	A	T	A	A	A	C	T	A	A	A	C	C	T	A	C	-	C	A	T	G	C	G	G	C	C	C	C	C
SB19	G	G	G	A	T	A	A	A	C	G	C	A	G	G	T	T	A	A	C	C	C	T	A	C	-	C	A	T	A	T	A	A	C	C	T	T	C
SR13	A	G	G	G	C	G	A	A	C	A	T	A	A	A	C	T	A	A	A	C	C	T	A	C	-	C	A	T	G	C	A	G	C	C	C	C	C
SR31	A	G	G	G	C	A	A	A	T	A	C	G	A	A	C	T	A	A	A	C	C	T	A	T	-	C	A	C	A	T	A	G	T	C	C	T	C
NP01	G	G	G	G	T	A	A	A	C	G	T	A	G	A	C	T	G	A	A	C	C	T	G	C	-	C	A	T	A	T	A	A	C	C	T	T	C
NP05	G	G	G	A	T	A	A	A	C	G	T	A	G	A	C	C	A	A	A	C	C	C	G	C	-	C	G	T	A	T	A	A	C	C	T	T	C
NP10	G	A	G	A	C	A	A	A	C	A	C	G	A	A	C	C	A	G	A	C	C	T	A	T	-	C	A	C	A	C	A	G	T	T	C	C	C
NP12	G	G	G	G	T	A	A	A	C	G	T	A	G	A	C	T	G	A	A	C	C	T	G	C	-	C	A	T	A	T	A	A	C	C	T	T	C
NP14	G	A	G	A	C	A	A	A	C	A	C	G	A	A	C	C	A	G	A	C	C	T	A	T	-	C	A	C	A	C	A	G	T	T	C	C	C
SP03	G	G	G	G	T	A	A	A	C	G	T	A	G	A	C	T	A	A	A	C	C	T	G	C	-	C	A	C	A	T	A	A	T	C	C	T	C
SP06	G	G	G	A	T	A	A	A	C	G	T	A	G	A	C	T	A	A	A	C	T	T	G	C	-	C	G	T	A	T	A	A	C	C	T	T	C
SP08	G	G	G	A	T	A	A	A	C	G	C	A	G	G	T	T	A	A	C	C	C	T	A	C	-	C	A	T	A	T	A	A	C	C	T	T	C
SP09	G	G	G	G	T	A	A	A	C	G	T	A	G	A	C	T	A	A	A	C	C	T	G	C	-	C	A	T	A	T	A	A	C	C	T	T	C
SP11	G	G	G	A	T	A	A	A	C	G	T	A	G	A	T	T	A	A	A	C	C	T	G	C	T	T	A	T	A	T	A	A	C	C	T	T	C
SP13	G	G	G	G	T	A	A	A	C	G	T	A	G	A	C	T	A	A	A	C	C	T	G	C	-	C	A	T	A	T	A	A	T	C	C	T	C
SP29	G	A	G	A	C	A	A	A	C	A	C	G	A	A	C	C	A	G	A	C	C	T	A	C	-	C	A	C	A	C	A	G	T	T	C	C	C
JP97	A	G	G	G	C	A	G	G	C	A	T	A	A	A	C	T	A	A	A	C	T	T	A	C	-	C	A	T	G	C	G	G	C	C	C	C	C
JP103	A	G	G	G	C	A	A	A	C	A	T	A	A	A	C	T	A	A	A	C	C	T	A	C	-	C	A	T	G	C	A	G	C	C	C	C	C

Siberut	A/G	G	A/G	A/G	C/T	A	A	A/G	C/T	A/G	C/T	A/G	A/G	A/G	C/T	C/T	A	A	A/C	C/T	C/T	T	A	C/T	-	C	A	C/T	A/G	C/T	A/G	A/G	C/T	C/T	C/T	C/T	C/T
Others	A/G	A/G	G	A/G	C/T	A/G	A	A	C/T	A/G	C/T	A/G	A/G	A/G	C/T	C/T	A/G	A/G	A/C	C	C/T	C/T	A/G	C/T	-/T	C/T	A/G	C/T	A/G	C/T	A	A/G	C/T	C/T	C/T	C/T	C
PAA	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T

Table 4.3: Population Aggregation Analysis of *H. klossii* D-loop sequences, showing only variable sites.

Source of Variation	d.f.	Sum of squares	Variance components	Percentage of variation
Among groups	2	19.714	0.51157 Va	8.17
Among populations within groups	2	14.910	0.46909 Vb	7.49
Within populations	16	84.519	5.28244 Vc	84.34
Total	20	119.143	6.26310	

Table 4.4: Results of AMOVA.

Population	n	Haplotypes	Nucleotide diversity (π)
North Siberut	3	3	0.0314 (+/- 0.0242)
Siberut National Park	4	2	0.0184 (+/- 0.0129)
Sipora	2	2	0.0205 (+/- 0.0214)
North Pagai	5	4	0.0249 (+/- 0.0159)
South Pagai	7	7	0.0179 (+/- 0.011)

Table 4.5: Diversity in mitochondrial D-loop haplotypes for each population

	N. Siberut	SNP	Sipora	N. Pagai	S. Pagai
N. Siberut	0.030	0.196	-0.133	0.058	0.223*
SNP	0.038	0.035	0.335	0.188	0.120
Sipora	0.023	0.024	0.020	0.100	0.310*
N. Pagai	0.030	0.026	0.027	0.031	-0.026
S. Pagai	0.030	0.023	0.026	0.017	0.016

Table 4.6: Population pairwise F_{ST} values and nucleotide divergences from mitochondrial sequence data

Figures above the diagonal are F_{ST} values (*$p<0.1$); figures on the diagonal are mean within-population divergence estimates; numbers below the diagonal are mean between-population divergence.

	CA15	CA24	PL04	SB04	SB06	SB17	SB19	SR13	SR31	NP01	NP05	NP10	NP12	NP14	SP03	SP06	SP08	SP09	SP11	SP13
CA15																				
CA24	0.0082																			
PL04	0.0389	0.0429																		
SB04	0.0389	0.0429	0.0000																	
SB06	0.0389	0.0429	0.0000	0.0000																
SB17	0.0327	0.0327	0.0348	0.0348	0.0348															
SB19	0.0389	0.0429	0.0000	0.0000	0.0000	0.0348														
SR13	0.0286	0.0286	0.0307	0.0307	0.0307	0.0082	0.0307													
SR31	0.0082	0.0123	0.0307	0.0307	0.0307	0.0245	0.0307	0.0204												
NP01	0.0368	0.0409	0.0143	0.0143	0.0143	0.0286	0.0143	0.0245	0.0286											
NP05	0.0389	0.0429	0.0164	0.0164	0.0164	0.0348	0.0164	0.0307	0.0348	0.0102										
NP10	0.0184	0.0184	0.0368	0.0368	0.0368	0.0307	0.0368	0.0266	0.0184	0.0389	0.0368									
NP12	0.0368	0.0409	0.0143	0.0143	0.0143	0.0286	0.0143	0.0245	0.0286	0.0000	0.0102	0.0389								
NP14	0.0184	0.0184	0.0368	0.0368	0.0368	0.0307	0.0368	0.0266	0.0184	0.0389	0.0368	0.0000	0.0389							
SP03	0.0286	0.0327	0.0184	0.0184	0.0184	0.0286	0.0184	0.0245	0.0204	0.0082	0.0143	0.0307	0.0082	0.0307						
SP06	0.0368	0.0409	0.0143	0.0143	0.0143	0.0327	0.0143	0.0286	0.0327	0.0082	0.0061	0.0389	0.0082	0.0389	0.0123					
SP08	0.0389	0.0429	0.0000	0.0000	0.0000	0.0348	0.0000	0.0307	0.0307	0.0143	0.0164	0.0368	0.0143	0.0368	0.0184	0.0143				
SP09	0.0348	0.0389	0.0123	0.0123	0.0123	0.0266	0.0123	0.0225	0.0266	0.0020	0.0082	0.0368	0.0020	0.0368	0.0061	0.0061	0.0123			
SP11	0.0409	0.0450	0.0102	0.0102	0.0102	0.0328	0.0102	0.0287	0.0328	0.0082	0.0103	0.0389	0.0082	0.0389	0.0123	0.0082	0.0102	0.0062		
SP13	0.0307	0.0348	0.0164	0.0164	0.0164	0.0266	0.0164	0.0225	0.0225	0.0061	0.0123	0.0327	0.0061	0.0327	0.0020	0.0102	0.0164	0.0041	0.0103	
SP29	0.0204	0.0204	0.0348	0.0348	0.0348	0.0286	0.0348	0.0245	0.0204	0.0368	0.0348	0.0020	0.0368	0.0020	0.0286	0.0368	0.0348	0.0348	0.0369	0.0307

Table 4.7: Nucleotide divergences estimates

Within-population divergences are highlighted for the five populations (from left to right: North Siberut, Siberut National Park, Sipora, North Pagai, and South Pagai).

Locus	Size Range (base pairs)	Total alleles observed	Heterozygosity (total population)
D3S1766	256-296	7	0.556
D5S1457	108-152	7	0.667
D11S1366	206-246	6	0.846
D12S321	208-244	7	0.727
D14S306	200-228	7	0.800
D19S714	236-292	8	0.667

Table 4.8: Characteristics of microsatellite loci amplified in *H. klossii*, for the population as a whole

	Sample	N. Siberut	SNP	Sipora	N Pagai	S Pagai	N alleles
Locus	***n***	**4**	**3**	**2**	**2**	**6**	
D3S1766	H_O	1.0	NA	1.0	NA	0.2	4
	H_E	1.0	NA	0.83	NA	0.87	
	p	1.0	NA	1.0	NA	0.02	
D5S1457	H_O	0.5	NA	0.5	1.0	1.0	3
	H_E	0.89	NA	1.0	1.0	0.83	
	p	0.33	NA	0.33	1.0	1.0	
D11S1366	H_O	0.67	1.0	1.0	NA	1.0	3
	H_E	0.60	0.8	0.67	NA	0.86	
	p	1.00	1.0	1.0	NA	0.67	
D12S391	H_O	1.00	1.0	1.0	1.0	1.0	3
	H_E	1.00	0.73	0.83	1.0	0.8	
	p	1.00	1.0	1.0	1.0	0.20	
D14S306	H_O	1.00	1.0	1.0	NA	0.67	3
	H_E	0.73	0.93	0.83	NA	0.79	
	p	1.00	1.0	1.0	NA	0.81	
D19S714	H_O	1.00	NA	1.0	NA	0.6	3
	H_E	0.87	NA	1.0	NA	0.91	
	p	0.46	NA	1.0	NA	0.14	
TOTAL	H_O	0.86	1.0	0.92	1.0	0.75	
	H_E	0.85	0.82	0.86	1.0	0.84	
	MNA	3.67	3.25	3.0	1.17	4.0	

Table 4.9: Observed and expected heterozygosities (and p values) for each locus by population (when all genotypes are included)

N alleles is the average number of alleles per population; MNA is mean number of alleles per locus. The only significant deviation from Hardy-Weinberg equilibrium is highlighted in gray ($p<0.05$). NA (not available) indicates that calculation of HWE was not conducted because only one allele appeared in the population.

	Sample	N. Siberut	SNP	Sipora	N Pagai	S Pagai	N alleles
Locus	***n***	**4**	**3**	**2**	**1**	**5**	
D3S1766	H_O	1.0	NA	1.0	NA	0.0	3
	H_E	1.0	NA	0.83	NA	1.0	
	p	1.0	NA	1.0	NA	0.33	
D5S1457	H_O	1.0	NA	1.0	NA	1.0	3
	H_E	0.83	NA	1.0	NA	1.0	
	p	1.0	NA	1.0	NA	1.0	
D11S1366	H_O	1.0	1.0	1.0	NA	1.0	2
	H_E	0.83	0.83	1.0	NA	0.67	
	p	1.0	1.0	1.0	NA	1.0	
D12S391	H_O	1.0	1.0	1.0	1.0	NA	5
	H_E	1.0	0.73	0.83	1.0	NA	
	p	1.0	1.0	1.0	1.0	NA	
D14S306	H_O	1.0	NA	1.0	NA	1.0	3
	H_E	0.73	NA	0.83	NA	0.83	
	p	1.0	NA	1.0	NA	1.0	
D19S714	H_O	1.0	NA	1.0	NA	0.5	2
	H_E	1.0	NA	1.0	NA	1.0	
	p	1.0	NA	1.0	NA	0.34	
TOTAL	H_O	1.0	1.0	1.0	1.0	0.7	
	H_E	0.90	0.78	0.92	1.0	0.9	
	MNA	3.17	2.33	2.50	1.33	2.17	

Table 4.10: Observed and expected heterozygosities (and p values) for each locus by population (when only genotypes confirmed by replications are included)

N alleles is the average number of alleles per population; MNA is mean number of alleles per locus. There are no significant deviations from Hardy-Weinberg equilibrium. NA (not available) indicates that calculation of HWE was not conducted because only one allele appeared in the population.

	N. Siberut	Siberut NP	Sipora	North Pagai	South Pagai
N. Siberut	2.35714	-0.24442	0.05706	0.04274	0.05651
Siberut NP	-0.57737	2.46667	-0.27626	-0.29032	-0.10284
Sipora	-0.08504	-0.49887	5.00000	-0.37634	-0.06695
North Pagai	0.03473	0.16176	-0.32174	0.33333	-0.11835
South Pagai	0.11784	-0.61446	-0.57706	0.06504	2.37879

Table 4.11: Population pairwise F_{ST} values based on microsatellite genotypes

Figures above the diagonal are based on all genotypes; figures below the diagonal are based on confirmed genotypes only. None of these values are significant.

	Siberut	Sipora	Pagais
Siberut		0.12791	0.12466
Sipora	0.04814		-0.02537
Pagais	0.01972	-0.31876	

Table 4.12: Population pairwise R_{ST} values

Figures above the diagonal are based on all genotypes; figures below the diagonal are based on confirmed genotypes only.

Analysis	F_{ST} (or R_{ST})	*Nm*	*p* value
mtDNA F_{ST}	0.157	1.3	0.07
Microsatellite F_{ST} (all)	0.103	2.18	0.002
Microsatellite F_{ST} (confirmed)	0.09	2.53	0.08
Microsatellite R_{ST} (all)	0.09	2.65	0.09
Microsatellite R_{ST} (confirmed)	-0.047	-5.56	0.48

Table 4.13: Summary of population substructuring estimates from different analyses

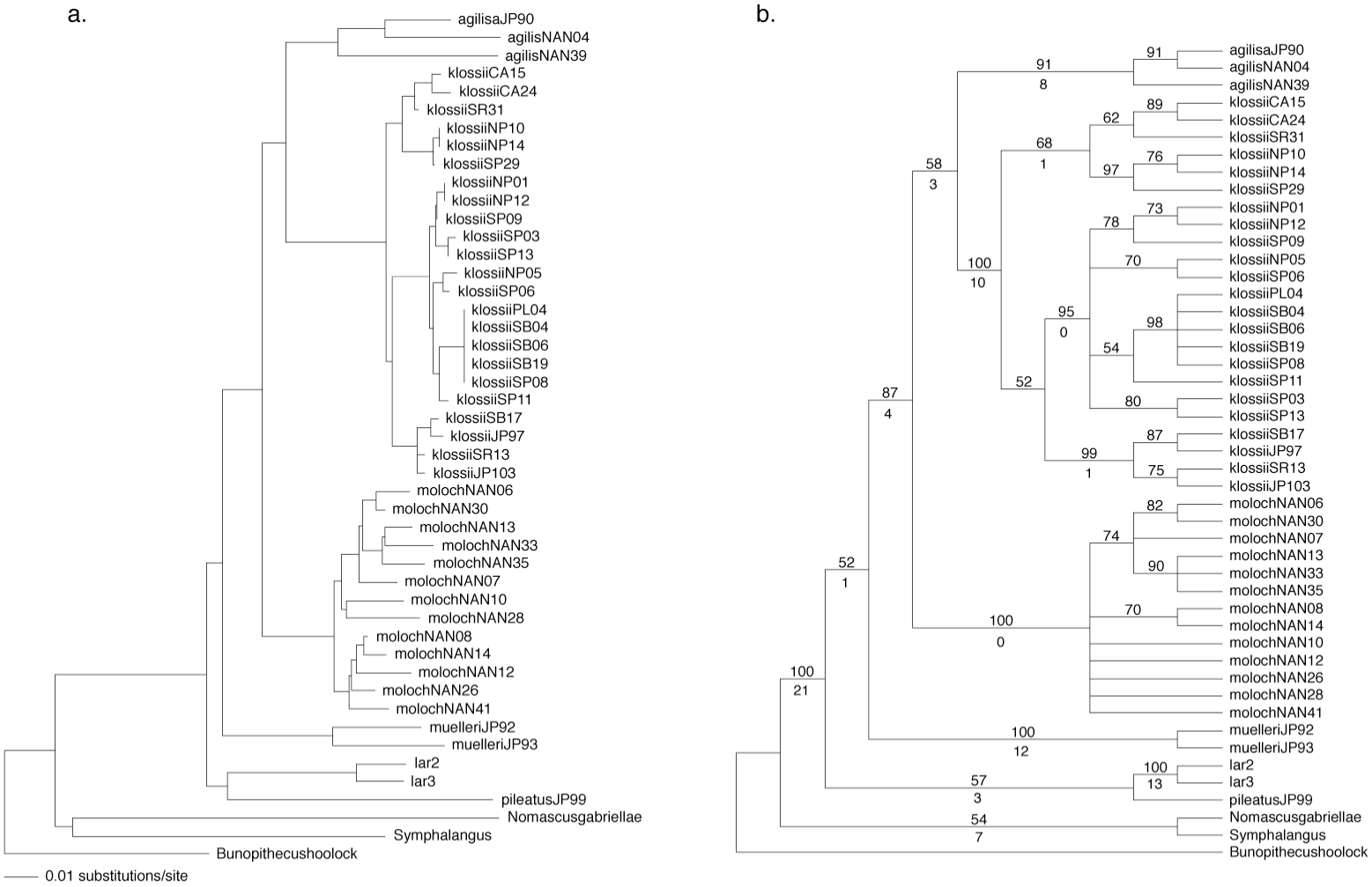

Figure 4.1: Gene trees produced by neighbor-joining. a. NJ phylogram; b. NJ bootstrap cladogram, 1000 replications. Bootstrap support values appear above the branches; number of unambiguous changes appear below the branches.

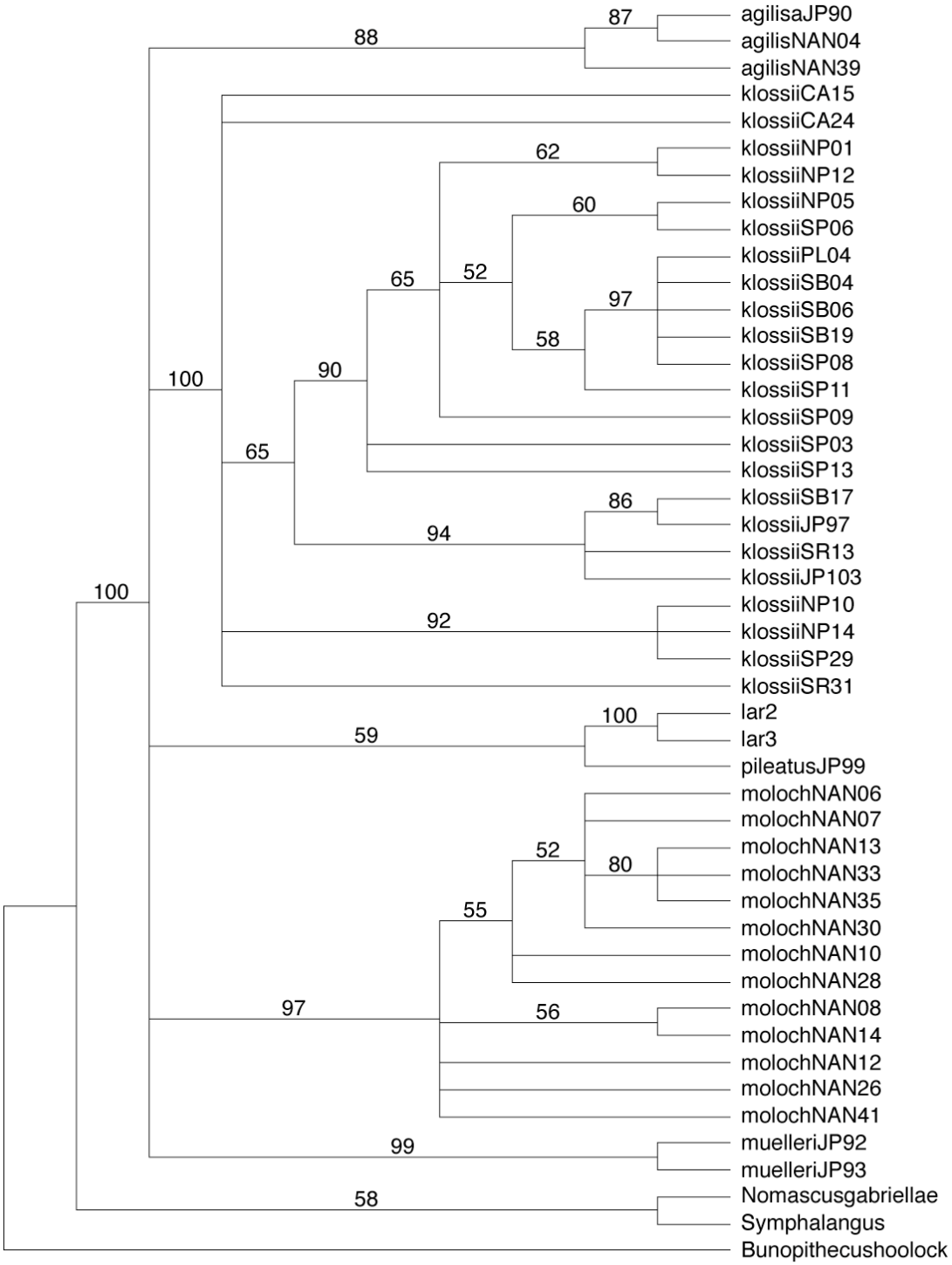

Figure 4.2: Weighted maximum parsimony tree, 1000 bootstrap replications. Branches with bootstrap values of less than 50% are collapsed.

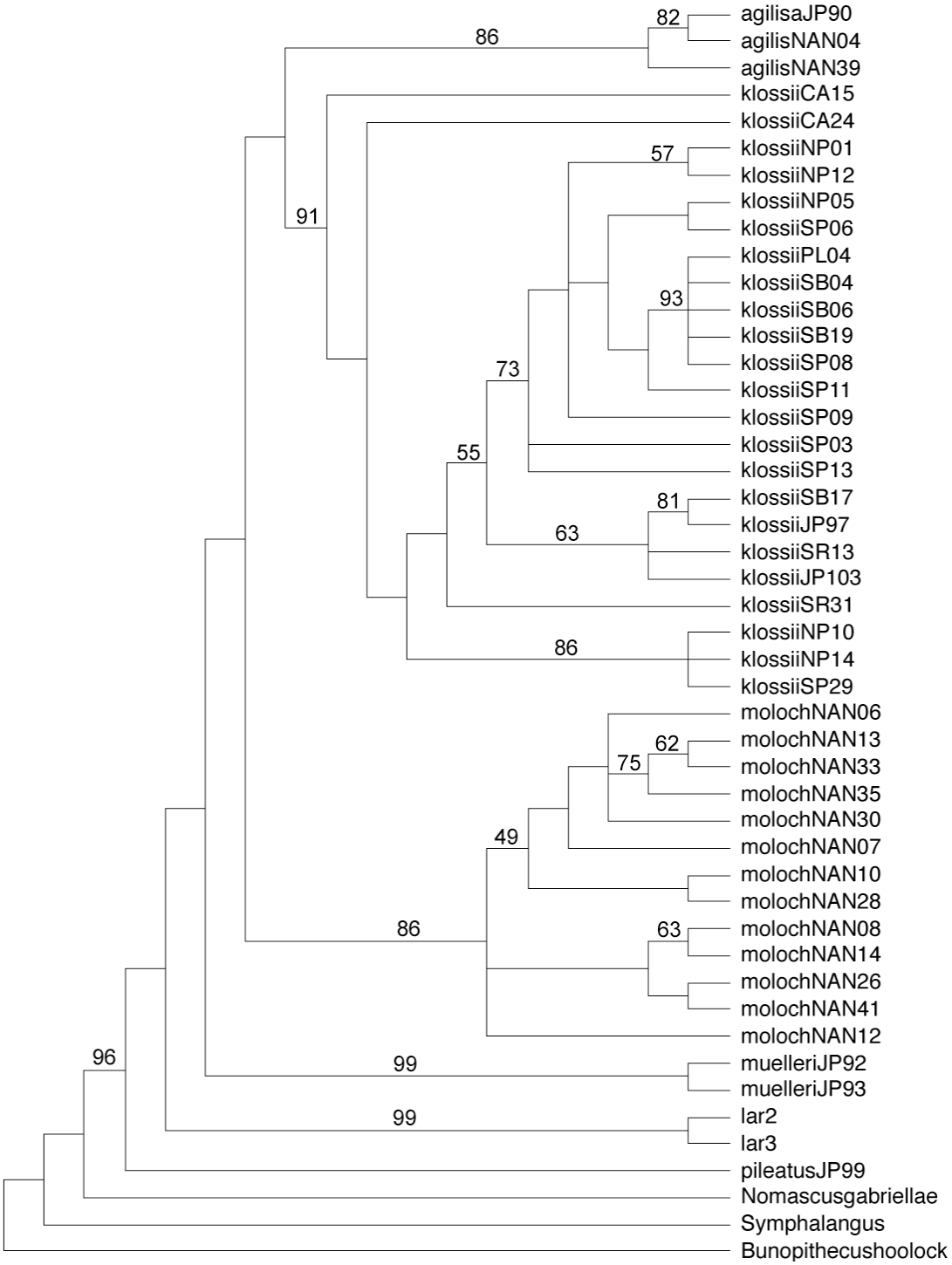

Figure 4.3: Maximum likelihood, strict consensus of three trees. Bootstrap values (100 replications) are indicated for clades with high support (over 50%).

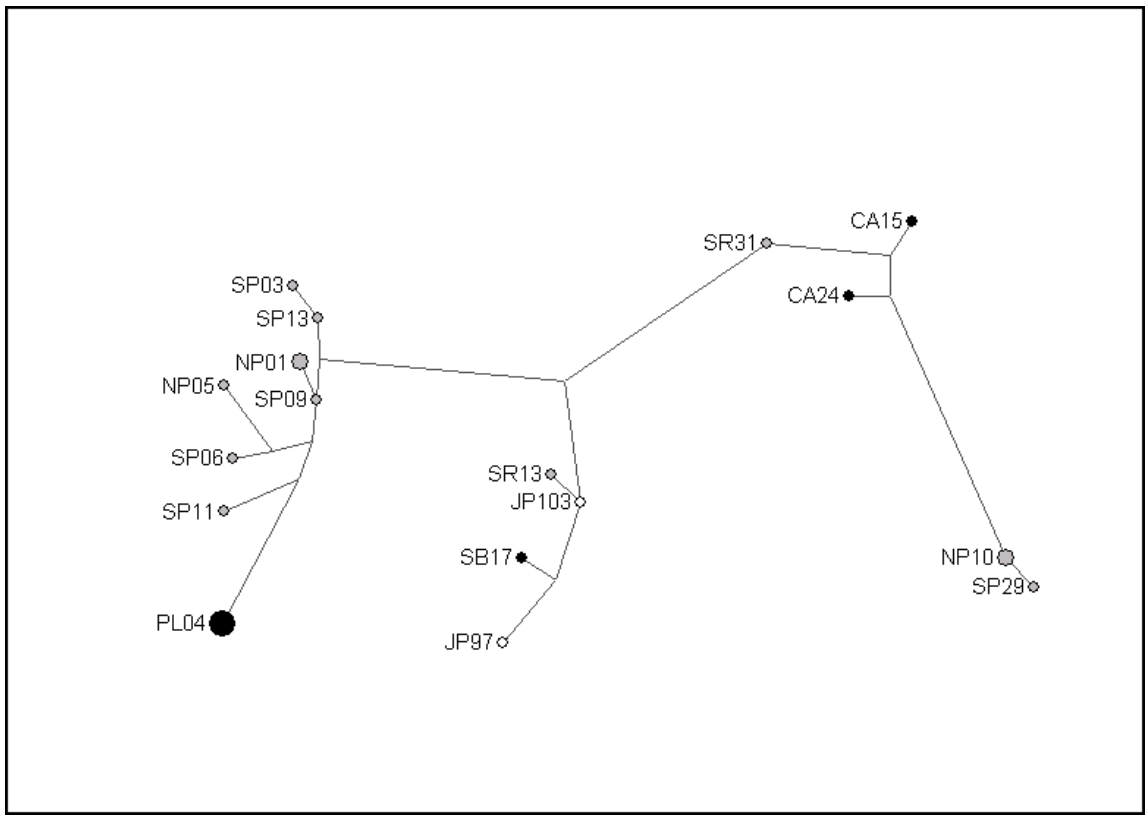

Figure 4.4: Median-joining network constructed with Network 4.1

Samples from Siberut are indicated by black circles; gray circles represent Sipora and Pagai samples. White circles represent blood samples from captive animals. Larger nodes indicate multiple individuals with identical haplotypes (such as PL04, which is identical to SB04, SB06, SB19, and SP08).

CHAPTER 5

Population Survey Results

5.1 Introduction

The goal of this chapter is to provide an estimate of the number of Kloss's gibbons throughout the Mentawai Islands, using a survey method based on gibbon loud calls and recent estimates of remaining forest cover. No surveys of Kloss's gibbon populations have been published since the World Wildlife Fund (1980) estimate of 36,000 gibbons on the island of Siberut. This study is the first attempt to survey Kloss's gibbons on all four Mentawai Islands.

The Kloss's gibbon is currently categorized by the World Conservation Union as "vulnerable," or at a high risk of extinction (IUCN 2004); however, researchers have recently suggested a change to "endangered" (very high risk of extinction) (Paciulli 2004) or even "critically endangered" (extremely high risk of extinction) (A. Eudey, pers. comm.) due to continuing, or perhaps increasing, threats of deforestation and hunting in the Mentawai Islands. Without updated population and habitat information, a species' conservation status cannot be adequately assessed. An evaluation must consider current population sizes, rate of decline (or increase), extent of area occupied, and whether the threats to the population are continuing or reversible. This chapter will present the results of the population survey, and Chapter 6 will evaluate the conservation status of the Mentawai primates based on the IUCN Redlist criteria and discuss conservation strategies.

5.1.1. Previous studies

The first attempt to assess the number of Kloss's gibbons in the Mentawai Islands was by Chivers (1977), who took estimates of Kloss's gibbon home range sizes from Tenaza (1974, 1975) and calculated the number of home ranges available in the forested area of the Mentawais. Using this method, he suggested that there could be 84,000 gibbons throughout the Mentawai Islands (Chivers 1977). Chivers (1977) states that these numbers are probably an overestimate, as they represent how many gibbons there "should" be in a roughly estimated 4,200 km^2 of hill and lowland forest. Furthermore, the gibbons in the area studied by Tilson (1974, 1975) and later by Tenaza (1980, 1981) apparently had unusually small home ranges, likely leading to an overestimate of gibbon density throughout the Mentawais. These studies report an average home range size of 7-11 hectares (Tenaza 1974; Tilson 1980).

Whitten's two-year study of a habituated group of Kloss's gibbons found a much larger home range of 20-35 ha, comparable to the home ranges of other gibbon species (Whitten 1982a, 1982d). Using his data, Whitten calculated that there were 36,000 Kloss's gibbons in Siberut (World Wildlife Fund 1980). This number was estimated in the following manner:

1. The average range size was calculated from several gibbon groups at a single study site as 20-35 ha (mean 27.5).
2. The area of suitable habitat in Siberut was estimated as 350,000 ha, a number arrived at by adding together the undisturbed forest (291,300 ha in 1977) and half of the area of moderately disturbed forest (71,700 ha) and forest disturbed by logging (49,300 ha).

3. The area of suitable habitat was divided by the average range size to determine the number of gibbon home ranges: 350,000/27.5=12,727.
4. This number was then multiplied by the average group size (3.8 individuals in Whitten's study): 12,727.27*3.8=48,363.
5. Finally, this number was multiplied by a correction factor of 0.75 to account for differences in hunting pressure and lack of continuity of ranges: 48,363*0.75=36,272.

This estimate assumes that all Kloss's gibbons have a similar home range, despite the earlier estimates of much smaller home ranges; and also that the average group size observed at Whitten's study site is typical throughout Siberut. It also assumes that Kloss's gibbons are less abundant in disturbed forest than in undisturbed forest. A later study (see below) suggests that Kloss's gibbons may actually maintain similar densities in disturbed and undisturbed forest (Paciulli 2004). The correction factor is an attempt to avoid overestimation; however, no justification is given for choosing this particular value.

In the last 25 years, logging and hunting have increased in the Mentawais, reducing the habitat and the primate populations. Fuentes (1996/1997) assessed the remaining habitat in the Mentawais through interviews with Mentawai Islanders and researchers and compiling data from the existing literature, as well as flying over the Mentawais to visually assess forest cover (Fuentes, pers. comm.). He suggests that 60% of Siberut (2,418 km^2), 10-15% of Sipora (85-127 km^2) and 15% of the Pagais (250 km^2) are forested. He further suggests there are 80,100-140,250 non-human primates in the

Mentawais; unfortunately, population estimates are not given for individual species (Fuentes 1996/1997).

Paciulli (2004) conducted line transect surveys in the Pagai Islands to determine the effects of logging, hunting, and vegetation on the densities of all four Mentawai primates. She found Kloss's gibbon densities to be 1.09-1.63 individuals/km^2, and suggests that there are 2,029 gibbons on the Pagai Islands, though it is unclear how she arrived at the area of occupancy estimate (Paciulli 2004). Paciulli reports that Kloss's gibbon densities seem to be unaffected by logging (densities are the same in forest that is unlogged, logged 10 years ago, or logged 20 years ago). Furthermore, there is no discernable difference in Kloss's gibbon density when examining the density of various tree species, including fig trees. These data suggest that Kloss's gibbons may be very flexible in their food choices, and change their diets based on the composition of the forest (Paciulli 2004).

Line transect surveys have been found to underestimate gibbon densities (Brockelman and Ali 1987; Brockelman and Srikosamatara 1993) and therefore Paciulli's study likely gives an underestimate of Kloss's gibbon density.

5.1.2. The current study

This study attempts to overcome the flaws of previous estimates, by using a method based on gibbon loud calls and surveying several sites on all four islands. Many of the earlier estimates were based on extrapolations of population densities from a single site. Primate densities often differ between habitat types and hunting and logging pressure. While Paciulli's (2004) study did investigate multiple sites and compared hunting and

logging pressure, she did not include the islands of Sipora and especially Siberut in her study. Siberut is the largest of the islands and the only island with a protected area.

Finally, great variation has been observed in Kloss's gibbon group size. While not published, there are many anecdotal reports of unusually large gibbon groups: groups of up to 8 individuals have been observed in North Pagai (Fuentes, pers. comm.; Delgado, pers. comm.), and up to 15 individuals in Siberut (Abegg, pers. comm.). I have observed groups of 8-10 individuals in North Pagai and groups of 10-15 in North Siberut. These larger group sizes suggest that estimates based on group sizes of 3-4 individuals underestimate the population density of Kloss's gibbons. This study incorporates observed group size estimates from each site.

5.2 Methods

Surveys were conducted throughout the Mentawai Islands at sites encompassing a range of forest types and disturbance (numbers correspond to sites in Figure 2.1):

1. Peleonan forest, North Siberut: a research area logged approximately 20 years ago with low hunting levels.
2. Simabuggai Biodiversity Research Station, Siberut National Park: a protected area subject to moderate hunting pressure by local people.
3. Taileleu, South Siberut: located near a logging concession, subject to heavy traditional use including hunting, extraction of forest products, and clearance for agriculture.
4. Saureinu, Sipora: subject to moderate levels of traditional use, but not logged because of local opposition.

5. Betumonga Research Station, North Pagai: visited during the pilot phase of the project (2001) but not surveyed; according to local reports the area has since been logged.
6. Muntei Research Area, North Pagai: also visited during pilot phase but not surveyed; heavily disturbed forest.
7. PT Minas Pagai Lumber concession South Pagai: 20-year selectively logged plots with some traditional use and high hunting pressure.

The sampling strategy aimed to sample each of the islands, and also to sample several forest types and levels of disturbance. Sites 1, 2, 5, 6, and 7 were chosen because previous researchers had worked there, or were still working there, and thus primate populations and research infrastructure existed. No previous research had been conducted in South Siberut or in Sipora. To find these sites, I talked with many local people to find areas with gibbon populations. These areas were used by local people for forest product extraction and hunting. Further details of each site are discussed in the Results section below.

I used a loud-call monitoring to census gibbon populations at these sites, as described in detail in Chapter 2. I collected data on both male and female calls. At some sites, surveys of male and female calls indicated different densities, and thus suggest different estimates. Unmated "floating" male Kloss's gibbons are known to sing, perhaps even more frequently than mated males, indicating that male gibbon song may function for mate attraction (Tenaza 1976). I observed solitary males at several sites, but I never observed a solitary female. Female gibbons sing to defend a territory (Cowlishaw 1992); thus, female calls may be more likely to indicate the presence of a gibbon group. I

consider the estimates based on female calls more reliable; they are also a more conservative estimate, and thus I have chosen these numbers for the final population estimate.

5.3 Results

The raw survey data are presented in Appendix V, and are summarized for each site below. Table 5.1 presents the total population estimates, and table 5.2 compares estimates based on male and female calls. Data for both males and females are presented below.

5.3.1 Siberut

The Peleonan Forest. The Peleonan forest of North Siberut is an area of about 4,000 hectares of primary mixed forest. This area was surveyed near the village of Sigapokna in 2001 (Appendix V; sites 1-3) and 7 km away near the village of Policoman (4-5) in 2003.

Surveys were conducted on a total of 16 mornings. The highest number of female calls heard on any one day, within a 600 meter radius, that could be considered to be from different groups was three; for males, the highest number was also three. Thus, using the calculation D=n/p(m)A (details in Chapter 2), the group density in north Siberut is a minimum of 2.65 groups/km^2, and a maximum of 3.13 groups/km^2.

Eight groups were observed during sample collection, with an average group size of 10 individuals (range 4-15). Many of these groups contained 2-3 females singing together. Estimated individual density is thus 26.5-31.3 individuals/km^2.

The forested area of the Peleonan area is 40 km^2. This area is currently the site of the Siberut Conservation Project (Kobold et al. 2003), which is attempting to get recognition from the Indonesian government as a protected area. The Peleonan forest is thus estimated to be home to 1,060-1,252 Kloss's gibbons.

Siberut National Park. The gibbon population within the National Park was surveyed at the Simabuggai Biodiversity Research Station, located near the middle of the park within the Traditional Use Zone (Figure 2.2). I was unable to sample the Sanctuary Zones, as they were extremely difficult to access. However, due to hunting pressures and local disregard for park regulations, the Traditional Use Zone is likely to be representative of primate densities in most of the park, except for the Park Village Zones which are not included in the estimate of habitat area.

Surveys were conducted from this site on a total of four mornings. The highest number of gibbon groups heard within a 600m radius was two (females) or three (male calls). The estimated group density in this area is 1.77-2.08 groups/km^2 (females) or 2.65-3.13 groups/km^2 (males).

Average group size observed at Simabuggai was five individuals (n=4; range 3-5). Individual density is 8.9-10.4 individuals/km^2 (based on female calls) or 13.3-15.7 individuals/km^2 (based on male calls).

Siberut National Park has an area of 1926.4 km^2. However, the Park Village Zones on the west coast are inhabited and subject to intensive traditional use and hunting and probably do not support many primates. Furthermore, much of the west coast is *Barringtonia* beach forest, which is rarely used by gibbons (World Wildlife Fund 1980). The Park Village Zones have an area of 444 km^2. The Traditional Use Zones and Sanctuary Zones together are 1482.4 km^2, an area that is likely forested throughout and provides adequate gibbon habitat. Assuming this area supports similar gibbon densities as at Simabuggai, there are estimated to be 13,190-15,413 gibbons (or 19,711-23,267 gibbons, based on male calls) in Siberut National Park.

Taileleu. In South Siberut, outside of the National Park, I surveyed the forest near the village of Taileleu. This area is subject to heavy traditional use in the form of agriculture, forest product extraction (timber, rattan), and hunting.

A total of 10 surveys were conducted, at two different locations. The highest number of females heard was one; males, two. Group density based on the female calls is 0.88-1.04 groups/km^2; based on male calls, 1.77-2.08 groups/km^2.

No fecal samples were found at Taileleu. However, two gibbon groups were encountered, each with a group size of about five individuals. Individual density is thus 4.4-5.2 (females) or 8.9-10.4 (males) gibbons/km^2.

Assessing the extent of forest outside the National Park (excluding the Peleonan area) in Siberut is problematic, as reports on land use vary. According to newspaper articles, as well as personal communication with Siberut National Park personnel, all 2,065 km^2 has been granted as logging concessions or oil palm plantations – with a great deal of overlap, as more area has been granted than actually exists (Anonymous 2000). However, based on local newspaper articles and discussions with local politicians and citizens, about 900 km^2 of the area outside the park is heavily disputed based on land rights claims and allegedly illegal documentation, and so no logging has progressed in that area (Anonymous 2003). This figure of 900 km^2 seems reasonable; if it is added to the estimated forest area of the National Park (1,482 km^2) and the Peleonan forest (40 km^2), the total is 2,422 km^2, which agrees with Fuentes' (1996/1997) estimate of 2,418 km^2 of forest in Siberut. Thus, if 900 km^2 of Siberut outside the protected areas supports gibbon habitat, there are an estimated 3,960-4,680 (based on female calls) or 8,010-9,360 (based on male calls) gibbons in the area.

5.3.2 Sipora

On the island of Sipora, the forest near the village of Saureinu was visited. Because of time constraints and low gibbon encounter rates, surveys had to be combined with fecal sample collection, so replicating the surveys at each site was not possible (though three replications were conducted at site 1). The four sites are all within 2-3 km of each other. The house that served as a base camp was located in a valley surrounded by very high hills, and male pre-dawn calls were not heard from the base camp.

A total of six surveys were conducted in Sipora. The highest number of calls heard within a 600m radius was two male calls; no females were heard within 600 meters. Based on these male calls, the density at this site is estimated to be 1.77-2.08 groups/km^2.

Two groups were encountered during sample collection, each with an estimated four individuals. Individual density is thus estimated to be 7.1-8.3 gibbons/km^2.

Sipora is the most developed island of the Mentawais, and is home to the capital, Tuapejat. There are no protected areas in Sipora. The only estimate of forest cover for this island is Fuentes' (1996/1997) suggestion of 10-15% of the island's total area (845 km^2), which is 84.5-126.8 km^2. This estimate is probably reasonable, as Fuentes was able to fly over the island and visually assess forest cover, and his estimate of forest cover in the Pagais is similar to my estimate below. The mean of these figures was used for this study, for an estimate of 106 km^2 of forest. This area could support 753-880 gibbons, based on the above density estimates.

5.3.3 North Pagai

No surveys were conducted on North Pagai. However, I did undertake sample collection at Betumonga Research Station in 2001, and 5 gibbon groups were

encountered. Experienced field assistants at that site believed that those were all of the groups in the 6.23 km^2 study area, resulting in a density of .80 groups/km^2. Average observed group size in North Pagai (including samples collected at nearby Muntei Research Area) was 5.8 individuals (n=7, range 4-10), for an estimated density of 4.6 individuals/km^2. The Betumonga Research Area probably supported about 30-35 Kloss's gibbons. This area has since been logged, and was most likely clear-cut, eliminating the primate population in this forest (K. Meyers, pers. comm.).

5.3.4 South Pagai

Most of the area of North and South Pagai is within the PT Minas Pagai Lumber logging concession (83,330 ha). Of this area, 7,789 ha are designated as Buffer Zone and Conservation Area. Another 13,256 ha are Limited Production Forest, an area where selective logging is practiced, and where the surveys for this study were conducted. These two areas together account for a total of 21,045 ha (210 km^2) of suitable habitat for primates in the Pagai Islands (PT Minas Pagai Lumber Corporation 1996). This number is just slightly lower than Fuentes' (1996/1997) estimate of 15% of the island's land area, or 251 km^2.

My base camp in South Pagai was the logging base camp at KM37, which was completely cleared of forest. Surveys of pre-dawn male calls were not possible from the base camp, so density estimates are based only on post-dawn female calls. Surveys and sample collection were conducted in patches of limited production forest that had been logged about 20 years ago.

Two sites were surveyed, with four replications at each site. The highest number of females heard on any day was two, for a density of 1.77-2.08 groups/km^2.

Seven groups were encountered during sample collection in South Pagai, with an average group size of 4.5 individuals (range 4-5). The individual density is thus 8.0-9.4 gibbons/km^2.

Within the 210 km^2 area of suitable habitat within the PT Minas concession, there are estimated to be 1,680-1,974 gibbons.

5.4 Discussion

Estimates of forest cover presented here indicate that nearly 3,000 km^2 of adequate gibbon habitat remains in the Mentawai Islands. While the level of disturbance throughout these areas is uneven, Kloss's gibbons maintain similar population densities in unlogged forest, forests logged 10 years ago, and forests logged 20 years ago (Paciulli 2004). Table 5.1 combines the population density estimates (based on female calls only) with the estimates of forest extent to calculate total population sizes, indicating that there may be approximately 20,000-25,000 Kloss's gibbons remaining in the Mentawai Islands, most of which (13,000-15,500) are located in Siberut National Park.

The highest density (26.5-31.3 individuals/km^2) is found in the Peleonan forest of North Siberut, and is due to both high group density and large group sizes. The lowest density observed was in Taileleu, South Siberut (4.4-5.2 individuals/km^2), where hunting pressure and forest product use appears to be highest. The other three sites all had identical group densities (1.77-2.08 groups/km^2) with slightly different average group sizes resulting in different individual densities (range: 7.1-10.4 individuals/km^2). These three sites include protected, unlogged forest (Simabuggai, Siberut National Park), unlogged forest subject to moderate use (Saureinu, Sipora) and forest logged 20 years ago

(South Pagai). This finding supports Paciulli's (2004) suggestion that Kloss's gibbon densities are similar in logged and unlogged forest.

In Siberut National Park and South Siberut, very different estimates (differing by about 5,000-8,000 individuals) are found by using female and male calls in the calculations. These different totals results from small differences at the survey level: in Siberut National Park, two females and three males were heard within a 600m radius, while in South Siberut, one female and two males were heard. The difference becomes magnified when extrapolated over such a large area (1,482 and 900 km^2). I suggest the female calls are more likely to indicate the presence of gibbon groups, while the additional male heard may be a floating male, and thus the more conservative estimates provided by the survey of female calls may be more accurate. Kloss's gibbon females are stimulated to sing when they hear other females' songs; it seems unlikely that additional gibbon females were present and did not sing over several mornings. Additional sampling in Siberut may provide a better estimate.

5.4.1 Comparison with previous studies

Table 5.3 presents a comparison of the population estimates presented in this study with previous studies. These results suggest that there may have been a substantial decrease in numbers since 1980, when WWF estimated that there were 36,000 gibbons in Siberut alone (compared to 18,000-21,000 reported here). In 1977 it was estimated that there were 84,000 gibbons in the Mentawai Islands as a whole (Chivers 1977). However, this suggested decrease must be viewed with caution, as previous estimates were based on home range sizes of gibbon groups at a single study site. In particular, the 1977

estimate is based on gibbon groups with unusually small home ranges (Tenaza 1974), probably resulting in an overestimate of population size.

Paciulli's (2004) population survey used line transects, which as noted in other studies often provide an underestimate of gibbon densities. Her data suggest a density of only 1.08-1.63 individuals/km^2, compared to an average of 12 individuals/km^2 (range: 4.4 – 31.3) presented here. I believe the population estimate resulting from Paciulli's data (3,000-3,500 gibbons) is a large underestimate, highlighting the importance of using survey methods based on vocalizations when censusing hylobatids.

5.4.2 Unusually large group sizes

The Peleonan forest exhibits the highest density of Kloss's gibbons, due in part to unusually large group sizes. I directly observed eight groups, which ranged in size from four to 15 individuals (mean: 10 individuals). It may be that larger groups were easier to detect, so that I only observed the largest groups in the area, and that the actual average group size is smaller. Another possibility is that these large groups were actually two or more groups associating with each other. If the average group size were only five individuals as at other sites, the population estimate would only be reduced by 500-600 individuals. However, other researchers have observed unusually large groups of Kloss's gibbons, in North Siberut (C. Abegg, pers. comm.) and also in North Pagai (A. Fuentes, pers. comm.). These large groups could be explained by a number of phenomena: productivity of the Peleonan forest, dietary flexibility of the Kloss's gibbon, restricted area of the Mentawais, or an evolved response to hunting pressure by humans.

The Peleonan forest may differ from other areas of the Mentawais in vegetation and in hunting level, and thus is able to support larger groups than other sites. Most of the

forests in Asia and in the Mentawais are dominated by trees of the family Dipterocarpaceae (Whitten et al. 2000). These trees do not produce fleshy fruits and probably do not provide food for gibbons. The Peleonan forest is a mixed forest type, with a higher proportion of fruit trees, which may enable gibbons to live in larger groups. The Peleonan forest supports high densities of all four Mentawai primate species (C. Abegg, pers. comm.), suggesting higher productivity in this forest. Another contributing factor to these high densities may be reduced hunting in North Siberut.

It has been suggested that Kloss's gibbons may be more flexible in their diet than other gibbon species. One year after logging in Sarawak, the population density of *H. muelleri* was found to decrease by nearly 80% (Bennett and Dahaban 1995), while the density of *H. klossii* appears to be the same in logged or unlogged forest (Paciulli 2004), suggesting that Kloss's gibbons may switch to a more folivorous diet when necessary. Furthermore, the diet of Kloss's gibbons is more omnivorous than that of other gibbons, with up to 25% comprising insects and small animal prey (Whitten 1982b, 1984). This flexibility may allow Kloss's gibbons to live in larger groups than the more strictly frugivorous species, as food is relatively more abundant.

Kloss's gibbons are restricted to a very small geographic area compared to other gibbon species, and may live in larger groups because of this compression. In callitrichids, many species live at high population densities with little or no opportunities for dispersal. The maturing offspring stay, and in some cases reproduce, in their natal group (Roda and Mendes Pontes 1998; Lazaro-Perea et al. 2000). The Javan silvery gibbon (*H. moloch*) is restricted to very small forest patches in central and western Java, but live in much smaller groups than Kloss's gibbons, with an average size of 3.3

individuals (Kappeler 1984). However, the reduction of the Javan gibbon habitat is recent, whereas Kloss's gibbons have evolved in the small area of the Mentawais and thus may have adapted to larger group sizes.

Alternatively, the large groups sizes seen in Kloss's gibbons may be an evolved response to hunting by humans. One salient hypothesis for group living in primates live in groups is that it provides a defense against predation (Alexander 1974; van Schaik 1983). Living in a larger group provides more protection from predators through increased vigilance and reduced probability that any one individual will be the victim of predation. Red colobus monkeys (*Procolobus spp.*) have been observed to either live in larger groups or form polyspecific associations in the presence of predation by chimpanzees or crowned hawk eagles (Noe 1992; Struhsaker 2000). Humans have traditionally hunted gibbons in the Mentawai Islands, probably since their arrival 2,000-3,000 years ago (Whitten 1982e; Tenaza and Tilson 1985; Mitchell and Tilson 1986), and other aspects of Kloss's gibbon behavior such as sleep tree selection has been suggested to be the result of this hunting pressure (Tenaza 1974; Tenaza and Tilson 1985). Large group sizes can be a disadvantage due to increased intragroup feeding competition. However, if the habitat provides enough food to support larger groups, and if predation risk is high enough, the advantages of living in a larger group outweigh the disadvantages (van Schaik 1983).

5.4.3 Comparison with other gibbon species

Reported densities for other hylobatids range from 1-25 individuals/km^2, as summarized in table 5.4 (Rijksen 1978; Rodman 1978; Tilson 1979; Chivers 1980; Gittins 1984; Kappeler 1984; Mitani 1990; Nijman and van Balen 1998; Yanuar 2001;

McConkey et al. 2002; O'Brien et al. 2004). Average Kloss's gibbon population density presented here is 11-13 individuals/km^2, which is comparable to that found in other gibbon species. Density in Kloss's gibbons in North Siberut is much higher (27-31 individuals/km^2) than that seen in any other gibbon species, further suggesting that this forest may be unusually productive.

5.5 Conclusion

The data presented here suggest that there are 20,000-25,000 Kloss's gibbons remaining in the Mentawai Islands. While this estimate is up to 50% less than the World Wildlife Fund (1980) population estimate, it is considerably higher than that of recent line transect surveys (Paciulli 2004) and may be higher than expected, given reports of logging throughout the Mentawai Islands.

In the following chapter, I will assess the conservation status of the Kloss's gibbon based on the data presented here, and will make conservation recommendations for the Mentawai primates.

Location	LP[1]	Total Days[2]	Total Area (km^2)	Forested Area (km^2)	Group Density /km^2 (Min)	Group Density /km^2 (Max)	Observed Average Group Size	Individual Density /km^2 (Min)	Individual Density /km^2 (Max)	Total Population (Min)	Total Population (Max)
Peleonan, N. Siberut	5	16	40	40	2.65	3.13	10 *(n=8)*	26.5	31.3	1060	1252
Siberut National Park	1	4	1926	1482[3]	1.77	2.08	5 *(n=4)*	8.9	10.4	13190	15413
Siberut, outside park	2	10	2064	900[4]	0.88	1.04	5 *(n=2)*	4.4	5.2	3960	4680
Sipora	1	6	845	106[5]	1.77	2.08	4 *(n=2)*	7.1	8.3	753	880
North & South Pagai	2	8	1675	210[6]	1.77	2.08	4.5 *(n=13)*	8.0	9.4	1680	1974
TOTAL	11	44	**6550**	**2738**	*mean: 1.77*	*mean: 2.08*	*mean: 5.7*	*mean: 11.0*	*mean: 13.0*	**20643**	**24199**

Table 5.1: Summary of gibbon population density in remaining forest areas in the Mentawai Islands.

[1]Number of Listening Posts at each location

[2]Total days spent surveying each location

[3]Excludes Park Village Zones of the National Park, which are subject to heavy use by inhabitants.

[4]Area still unlogged due to disputed documents and land rights.

[5]Estimated 10-15% of area still forested (Fuentes, 1996/1997).

[6]Includes Conservation Area, Buffer Zone, and Limited Production Forest areas set aside by PT Minas Pagai Lumber.

	Population Size (Females)		Population Size (Males)	
Site	**Minimum**	**Maximum**	**Minimum**	**Maximum**
North Siberut	1,060	1,252	1,060	1,252
Siberut Nat'l Park	13,190	15,413	19,711	23,267
South Siberut	3,960	4,680	8,010	9,360
Sipora[1]	753	880	753	880
Pagais[2]	1,680	1,974	1,680	1,974
TOTAL	20,643	24,199	31,214	36,733

Table 5.2: Population estimates based on female and male Kloss's gibbon calls.

[1]Only males heard in surveys on Sipora.

[2]Only females heard in surveys in South Pagai.

Study	Siberut	All Mentawais
Chivers, 1977	55,440[1]	84,000
WWF, 1980	36,000	54,000[2]
Paciulli, 2004	3,000[3]	3,500[3]
This study	18,000-21,000	20,000-24,000

Table 5.3: Comparison of Kloss's gibbon population estimates.

[1]Chivers (1977) only provides an estimate for the Mentawai archipelago as a whole; since Siberut is about 2/3 the area of the Mentawais, this figure is 2/3 of the total population.

[2]World Wildlife Fund (1980) only gives an estimate for Siberut; this figure is based on the assumption that 2/3 of the total gibbon population are in Siberut.

[3]Figures calculated by multiplying Paciulli's (2004) average density estimate (1.27 individuals/km^2) by the forested area estimates presented here.

Study site	Species	Individual density	Reference
Mentawai, Indonesia	*H. klossii*	11-13	This study
Gunung Palung, Borneo, Indonesia	*H. agilis*	13.5-15.6	Mitani 1990
Bukit Barisan Selatan, Sumatra, Indonesia	*H. agilis*	1.4-2.8	O'Brien et al 2004
Kerinci-Seblat, Sumatra, Indonesia	*H. agilis*	6-11.4	Yanuar 2001
Barito Ulo, Borneo, Indonesia	*H. muelleri x agilis*	8.2	McConkey et al 2002
Kutai, Borneo, Indonesia	*H. muelleri*	15	Rodman 1977
Java, Indonesia	*H. moloch*	1-13	Kappeler 1984
Central Java, Indonesia	*H. moloch*	3.0-3.6	Nijman and van Balen 1998
Gunung Leuser, Sumatra, Indonesia	*H. lar*	11	Rijksen 1978
Krau, Malaysia	*H. lar*	13	Chivers 1980
Khao Yai, Thailand	*H. lar*	20	Brockelman and Reichard 1998
Krau, Malaysia	*S. syndactylus*	13	Chivers 1980
Gunung Leuser, Sumatra, Indonesia	*S. syndactylus*	15	Rijksen 1978
Bukit Barisan Selatan, Sumatra, Indonesia	*S. syndactylus*	4.2-10.3	O'Brien et al 2004
Kerinci-Seblat, Sumatra, Indonesia	*S. syndactylus*	7.2-24.6	Yanuar 2001
Hollongapar, India	*B. hoolock*	14	Tilson 1979
Bangladesh	*B. hoolock*	5	Gittins 1984

Table 5.4: Summary of hylobatid population density estimates

CHAPTER 6

Conservation Action Plan for Mentawai Primates

6.1 Introduction

The goal of this chapter is to review the conservation status and conservation history of the Mentawai primates, and to outline a conservation action plan based on the data presented in this dissertation, as well as the data and suggestions of others who have conducted research in the Mentawai Islands.

6.1.1 Overview of threats

The primates of the Mentawai Islands are forest-dependent species, and their forest habitats are threatened by legal and illegal logging, commercial conversion to oil palm plantations, and conversion for transmigration projects. The government-sponsored *transmigrasi* program has moved people from the densely populated islands of Java, Bali, Madura and Lombok to the more sparsely populated Outer islands (Sumatra, Kalimantan, Sulawesi, Irian Jaya) throughout the 1900s, but most intensely since 1970 (Hanson 1981; MacKinnon et al. 1996; Gillis 1998). Forest is cleared to make these settlements for the *transmigrasi* program, and the migrants themselves place additional pressure on the environment. Mentawai people also clear forest for gardens and gather forest products such as rattan for use and for sale.

A major additional threat to the Mentawai primates is hunting. All four species are traditionally hunted as food by local people, as they are the largest mammals on the islands. Technological advances have increased the rate of hunting, by increasing access to primate populations via logging roads and trucks, as well as the rate of success, as the

traditional bows and arrow have been replaced with .177 caliber air rifles. Possession of firearms by civilians is illegal in Indonesia, and air rifles larger than .177 caliber are restricted throughout Indonesia (Tenaza 1987, 1988).

Until recent times, hunting was regulated by rituals and taboos, most of which have been dropped along with the traditional animist religion in favor of Christianity (Tenaza 1974; Mitchell and Tilson 1986). For example, the Kloss's gibbon was considered sacred in the Mentawai religion, and could only be hunted for certain rituals, such as a boy's coming of age (Whitten 1982e). Catholic and Protestant missionaries have long had a presence in the Mentawais, and beginning under President Sukarno's doctrine of *Pancasila* (Five Principles) in the 1950s, all Indonesian citizens were required to adhere to one of five "accepted" religions: Catholicism, Christianity (*i.e.*, Protestantism), Islam, Buddhism, or Hinduism (Ricklefs 1993). The traditional animist religion of the Mentawais has all but disappeared, along with the associated hunting taboos. The traditional ethic has not been replaced by the view held by many Christians that humans are caretakers of the Earth; rather, many Mentawai people I spoke with informed me that "Now we know that we were created separately from the monkeys. They are just animals, and we can eat them just like we eat cows and chickens."

This combination of religious and technological change has increased the rate of wildlife removal far beyond that seen in traditional times. Unfortunately, the perception of wildlife abundance by local people has not changed: when I asked local people whether they could "run out" of primates to eat, they invariably replied, "There have always been primates, there will always be primates." Finally, the pet trade is another threat to Mentawai primates, especially gibbons, as the young of these popular primates

are sold cheaply by local people. Infant primates are obtained by killing the mother (Tenaza 1987, 1988).

6.1.2 Aims of this Action Plan

This action plan is intended to follow up on the recommendations made for Mentawai primates in the IUCN/SSC Primate Specialist Group's *Action Plan for Asian Primate Conservation: 1987-91* (Eudey 1987). Since that time, various conservation recommendations have been made by Fuentes (1996/1997), Tenaza (1987, 1988), Abegg (2004), and empirical studies on primate distribution and abundance have been conducted by Paciulli (2004) and Whittaker (this work).

This plan will first review the conservation status of each Mentawai primate species, and then recommend specific conservation action.

6.2 Review of conservation status of each species

The four Mentawai primates were last assessed for the IUCN Redlist in 2000, using version 2.3 (1994) of the Categories and Criteria (IUCN 2004). The Categories and Criteria have since been updated (v. 3.1, 2001), which could affect the categories assigned to these species. Most importantly, the criteria now distinguish between causes of decline that are "clearly reversible AND understood AND ceased" and those that "may not have ceased OR may not be understood OR may not be reversible" (IUCN 2004). This section will review the current categories assigned, the current population data, and the suggested changes to conservation status for each species.

6.2.1 *Hylobates klossii*

The IUCN Redlist currently lists the Kloss's gibbon as "Vulnerable," under criteria A1c+2c and B1+2ac. Under the 1994 version of Categories and Criteria, this means that

the species potentially faces "a high risk of extinction" because of a reduction in population size of ≥ 20% based on "a decline in area of occupancy, extent of occurrence, and/or quality of habitat", as well as a reduction in population size of ≥20% over the next ten years or three generations. Additionally, the extent of occurrence is less than 20,000 km^2, or the area of occupancy is less than 2,000 km^2, and the populations are severely fragmented and suffer from an observed, inferred, or projected continuing decline of extent of occurrence and area, extent, and/or quality of habitat (IUCN 2004).

The Kloss's gibbon was first evaluated as "Vulnerable" in 1986, elevated to "Endangered" in 1988, and downgraded back to "Vulnerable" in 1996 (IUCN 2004). However, some scientists have suggested that this species may be "Critically Endangered" due to a perceived increase in threat levels (A. Eudey, J. Supriatna, pers. comm.).

The current study suggests there are 20,000-25,000 gibbons in the Mentawai Islands, down from an estimated 54,000 in 1980 (see Chapter 5 for details). These numbers indicate a population decline of >50% in 25 years, which is approximately 3 generations in hylobatids (average generation time: 9.1 years) (Harvey et al. 1987). This decline is due to a decrease in both the area of occupancy and the quality of the habitat, due to extensive logging and forest product extraction, as well as some exploitation of the gibbons themselves for meat or pets. These causes have not ceased and may not be reversible. Therefore, under the new categories and criteria, I suggest that the status of *Hylobates klossii* should be upgraded to the category "Endangered", under the criteria A2cd. These criteria state that the species is facing a very high risk of extinction in the wild due to "(A) a reduction in population size based on… (2) an observed, estimated,

inferred, or suspected population size reduction of ≥50% over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on… (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat and (d) actual or potential levels of exploitation."

6.2.2 *Simias concolor*

The snub-nosed pig-tailed langur, or simakobu monkey, is currently listed on the IUCN Red List as "Endangered", on the basis of criteria A1cd+2c. This means the species is judged to be at a "very high risk of extinction" due to "(A1) a reduction in population size of ≥50% over the last ten years or three generations… due to (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat, and (d) actual or potential levels of exploitation"; as well as "(2) a projected decline over the next ten years or three generations… based on (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat." *Simias concolor* has been listed as "Endangered" since it was first evaluated in 1986 (IUCN 2004).

The most recent survey of *Simias* density was conducted in the Pagai Islands, where densities ranged from 5 individuals/km^2 in unlogged forest to 2.5 individuals/km^2 in forest patches logged 20 years ago (mean: 4 individuals/km^2) (Paciulli 2004). I have estimated that about 2,700 km^2 of primate habitat remains in the Mentawai Islands, for an estimated total of about 11,000 (range: 6,800-14,000) simakobu monkeys. Ten years ago, the mean population density for *Simias* throughout the Mentawais, based on home range sizes, was estimated as 21 individuals/km^2 (Tenaza and Fuentes 1995). If this estimate is accurate, there could have been 63,000 simakobus in 3,000 km^2 of forest in 1994,

indicating a possible loss of 80-90% of the population in ten years, even without taking into account the amount of forest that has probably been lost in that time. In 1980, the Siberut population of *Simias* was estimated as 19,000 individuals (World Wildlife Fund 1980). Based on the current mean estimate of 4 individuals/km^2 (range: 2.5-5) and about 2,400 km^2 of forest in Siberut, there may be about 9,600 (range: 6,000-12,000) simakobus remaining in Siberut alone – a possible decrease of 40-70% in 25 years. I suspect the loss has been greatest in the Pagai Islands, where logging has been more of a problem and hunting has been facilitated by logging roads.

The primary threat to *Simias* is hunting, as this species is the preferred prey item of most Mentawai hunters (Mitchell and Tilson 1986; Fuentes 2002; Paciulli 2004). Tenaza and Fuentes (1995) observed that a site in Siberut with an unusually high density of *Simias* (~220 individuals/km^2) (Watanabe 1981) had no *Simias* remaining at all when visited in 1990. The site had been logged, and after logging had ceased, local people reported that hunting the simakobus was easier because there were fewer places for the monkeys to hide (Tenaza and Fuentes 1995).

I recommend that the status of *Simias concolor* should be upgraded to "Critically Endangered," which means that the species faces an "extremely high risk of extinction" based on criteria A2cd: "(A) An observed, estimated, inferred or suspected population reduction (2) of ≥80% over the last 10 years or three generations… based on (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat and (d) actual or potential levels of exploitation."

6.2.3 *Presbytis potenziani*

The IUCN Red List currently categorizes the Mentawai langur as "Vulnerable," based on criteria A1c+2c and B1+2ac. Under the 1994 version of Categories and Criteria, this means that the species faces "a high risk of extinction" because of a reduction in population size of ≥20% based on "a decline in area of occupancy, extent of occurrence, and/or quality of habitat", as well as a predicted reduction in population size of ≥ 20% over the next ten years or three generations. Additionally, to meet these criteria, taxa should have an extent of occurrence that is less than 20,000 km^2, or an area of occupancy less than 2,000 km^2, with populations that are severely fragmented and suffer from an observed, inferred, or projected continuing decline of extent of occurrence and area, extent, and/or quality of habitat. In 1986, *P. potenziani* was listed as "Indeterminate", and then evaluated as "Endangered" in 1988. Its status was downgraded to "Vulnerable" in 1996 (IUCN 2004).

The most recent estimate of *P. potenziani* density is a mean of about 2 individuals/km^2 (range: 1-4 individuals/km^2) in the Pagai Islands (Paciulli 2004). Mentawai langurs appear to reach their highest densities in forest logged about 20 years ago, and their lowest densities in forest logged 10 years ago. Paciulli's population density estimates give a total population size of about 5,400 (range: 2,700-10,800) Mentawai langurs in the approximately 2,700 km^2 of remaining habitat, or 4,800 (range: 2,400-9,600) individuals in Siberut alone. In 1980, the Siberut population of *P. potenziani* was estimated (based on home range size) as 46,000 individuals: the most abundant species in Siberut. A later study suggested a population density of 13.5 individuals/km^2 at a site in

Siberut (Watanabe 1981). If these estimates are correct, then the Siberut *P. potenziani* population may have suffered an 80-95% loss.

However, behavioral studies of *P. potenziani* have found that this species is very difficult to habituate, possibly as an adaptation to human hunting, and may employ cryptic anti-predator behavior (Fuentes 1994; Sangchantr 2004). Such behavior would make Mentawai langurs difficult to observe on line transect surveys, and the densities presented in Paciulli (2004) may be an underestimate. Home range sizes in *P. potenziani* range from 11.5-38 ha throughout the Mentawais (Watanabe 1981; Tilson and Tenaza 1982; Fuentes 1994, 1996; Sangchantr 2004), with a mean home range size of 23.5 ha. Group size in *P. potenziani* is variable, as the species exhibits a flexible social organization with one-male one-female, one-male multi-female, and multi-male multi-female groups (Sangchantr 2004), though earlier studies suggested that the species lived only in one-male one-female groups throughout its range (Tilson 1980; Fuentes 1994). Average observed group size from all studies is 3.8 (range 2-8) (Watanabe 1981; Tilson and Tenaza 1982; Fuentes 1994, 1996; Sangchantr 2004). Based on these numbers, there could be 44,000 Mentawai langurs in the 2,700 km^2 of Mentawai forest, or 39,000 in Siberut alone – without accounting for the fact that *P. potenziani* home ranges exhibit 23-40% overlap (Sangchantr 2004). If a correction factor of 0.80 is applied to account for differences in hunting pressure and lack of continuity of ranges, as employed in the World Wildlife Fund's (1980) estimates, the results are about 35,000 langurs throughout the Mentawais or 31,000 in Siberut alone. These figures represent a 32% decrease from the 1980 estimate in Siberut.

While *S. concolor* is the preferred prey item of Mentawai hunters, *P. potenziani* is also a popular food and the second-most hunted Mentawai primate (Fuentes 1994; Fuentes 2002). *P. potenziani* also appears to be very sensitive to habitat disturbance (Paciulli 2004). Both hunting and habitat disturbance have occurred over a greater proportion of Sipora and the Pagais than of Siberut, so it seems probable that the decrease in population in these areas has also been greater than on Siberut.

I recommend that the status of *Presbytis potenziani* should be upgraded to "Endangered", under criteria A2cd, which state that the species is facing a very high risk of extinction in the wild due to "(A) a reduction in population size based on… (2) an observed, estimated, inferred, or suspected population size reduction of ≥50% over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on… (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat and (d) actual or potential levels of exploitation."

6.2.4 *Macaca pagensis*

The Mentawai macaque is currently listed as "Critically Endangered," under criteria A1cd+2c. These criteria state that the species is at "extremely high risk of extinction" due to "(A1) A reduction in population size of ≥80% over the last ten years or three generations… due to (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat, and (d) actual or potential levels of exploitation," as well as "(2) a projected decline of at least 80% over the next ten years or three generations… based on (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat." In

1986, *M. pagensis* was listed as "Indeterminate." The species was evaluated as "Endangered" in 1988, and upgraded to "Critically Endangered" in 1996 (IUCN 2004).

The most recent estimates of *M. pagensis* density suggest that there are 7-12 individuals/km^2 (Paciulli 2004), for a total of about 19,000-32,400 macaques throughout the Mentawais, or 16,800-28,800 in Siberut alone. The range of variation in density estimates is related to habitat quality: macaques live at much higher densities in logged than unlogged forest, and their highest density is in forest logged 20 years ago. In 1980, it was roughly estimated that there were 39,000 macaques in Siberut; this estimate was based on widely varying home range sizes and group sizes (World Wildlife Fund 1980). A possible range of loss is thus 25-55% of the population on Siberut. Because Mentawai macaques are found in higher densities in disturbed forest, and since very little of the Mentawai forest is undisturbed, I suggest that the larger population estimate is more accurate, which would imply that the population has suffered 25-30% loss since 1980.

While macaques are not a preferred food item because their meat is considered unpalatable, macaques still suffer from hunting because they are considered pests (Fuentes 2002; Paciulli 2004). While habitat disturbance appears to affect population sizes positively, macaques are found in lower densities near human settlements (Paciulli 2004).

I recommend that the status of *M. pagensis* should be downgraded to "Vulnerable", under criteria A2cd, which state that the species is facing a "high risk of extinction in the wild" due to "(A) reduction in population size based on… (2) an observed, estimated, inferred or suspected population size reduction of ≥ 30% over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have

ceased OR may not be understood OR may not be reversible, based on… (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat and (d) actual or potential levels of exploitation."

6.3 History of conservation action in the Mentawai Islands

6.3.1 Siberut National Park

The first protected area in the Mentawai Islands was established in 1976. This 6,500 ha Wildlife Reserve near the center of Siberut island, named "Teitei Batti," was the site of Richard Tenaza's doctoral dissertation research (Tenaza 1974). The reserve was expanded to 56,500 ha in 1979. In 1980, the World Wildlife Fund (1980) produced "Saving Siberut: A Conservation Master Plan," based primarily on the research of Anthony Whitten, Jane Whitten, and Alan House, who conducted their graduate research in Siberut on Kloss's gibbons, squirrels, and vegetation, respectively (Whitten 1980; Whitten 1982a, 1982b; Whitten 1982e). The recommendations in this publication attempted to reconcile the needs of the traditional societies living on Siberut with the need to protect the wildlife, and suggested 1) socio-economic development, to make the subsistence economy more efficient; 2) a system of land-use zones, allowing some traditional use in some areas while creating nature reserves in others; 3) naming Siberut Island as a UNESCO Man and the Biosphere Reserve; 4) more sustainable forestry practices; 5) ecotourism; 6) wildlife management, to allow for sustainable hunting practices; 7) conservation education; and 8) a system of evaluation and monitoring to ensure success (Whitten et al. 1979; World Wildlife Fund 1980).

In 1981-2, many of these suggestions were met, expanding the protected area to 132,900 ha, creating land-use zones, and establishing a UNESCO Man and the Biosphere

(MAB) Reserve. This UNESCO (United Nations Education, Scientific, and Cultural Organization) program seeks to reconcile biodiversity and sustainable use by protecting areas while promoting economic development that is socio-culturally and ecologically sustainable (UNESCO 2005). The reserve remains under the jurisdiction of the country in which it is located, but UNESCO provides the initial planning and coordination of appropriate authorities, and in some cases provides representatives who assist in conservation and economic development.

The nature reserve was granted National Park status in the Indonesian National Parks system in 1993, and was increased to 190,500 ha (PHPA 1995). The Park is currently 1,926 km^2, and is divided into three land-use zones: sanctuary (465 km^2), traditional use (1017 km^2), and park village (444 km^2) (Figure 2.2). Hunting is strictly prohibited within the sanctuary zones, and while limited traditional hunting is allowed by permit in the traditional-use zones, hunting of *H. klossii* and *S. concolor* is banned. Logging is not permitted in the sanctuary or traditional-use zones. The three park village zones are inhabited by native Mentawai people, and no restrictions are placed on their land-use (PHPA 1995).

In 1995, an Integrated Conservation and Development Management Plan was produced by the Biodiversity Conservation Project in Flores and Siberut, funded by the Asian Development Fund of the World Bank (PHPA 1995). This plan aimed to continue the objectives first set out in the World Wildlife Fund (1980) plan, as well as to promote further research in the area. The Simabuggai Biodiversity Research Station, in the center of Siberut, was established as a result of this plan run by the Directorate General of Forest Protection and Nature Conservation within Indonesia's Ministry of Forestry. This

plan also proposed the implementation of a Community Awareness, Mobilization and Extension Program (CAMEP) to improve social and economic conditions. Unfortunately, due to lack of visible success, the World Bank stopped funding this project in 2001.

Socio-economic development has taken the form of educating and empowering local Mentawai people to produce and market their own goods, as well as education about land rights and the impact of logging companies on the local economy. A UNESCO representative, Koen Meyers, has lived in Siberut for several years and is working in conjunction with Siberut National Park to educate local people about their land rights and economics. This work is part of the UNESCO Man and the Biosphere program.

A cessation of all logging, plantations, and migrant settlement on the island of Siberut was enacted in 1993 as a condition of funding for Siberut National Park. However, logging began again a few years later (Anonymous 2000), and by 2001, the entire area outside of Siberut National Park had been granted as overlapping logging concessions and oil palm plantations (Management of Siberut National Park, pers. comm.). When the Mentawai Islands were granted the status of independent regency (*kabupaten*) within the province of West Sumatra by the Indonesian government in 1999, illegal logging permits began to be issued. The *kabupaten* does not have the authority to issue such permits; only the central Ministry of Forestry in Jakarta has this authority, but the local offices can make money by allowing illegal activities. However, in 2004, the Mentawai regency reported zero income from forestry, despite a projected target of Rp. 2.5 billion (US$277,777), apparently due to the timber companies' refusal to pay agreed-upon fees (Bachyul Jb 2005). In April 2005, the Jakarta Post (Indonesia's English-language

newspaper) reported that the *Bupati* (regent) revoked all permits for concessions granted in 2004-2005, possibly because of the lack of revenue (Anonymous 2005).

Local Mentawai people have begun to fight back against the *Bupati* and timber companies, asserting their own land rights and refusing to allow logging (Anonymous 2003). Such disputes have slowed the pace of logging in Siberut, but have not stopped it.

6.3.2 The Peleonan Forest in North Siberut

The Peleonan Forest in northern Siberut has recently been recognized for its unusually high density of all four primate species and its accessibility. While Siberut National Park is very remote, has very rugged terrain, and attracts few visitors, the 4,000 ha Peleonan forest is relatively flat and easy to reach from the North Siberut port of Muara Sikabaluan. In 2000, a team of European researchers, headed by Christophe Abegg and Thomas Ziegler, presented a proposal to begin the Siberut Conservation Project with plans to conduct research on the wildlife and support sustainable economic development. Since 2002, the team has leased the forest from the local clan, established a research station and improved local river transportation by purchasing speedboats and engines to assist local people with transportation of goods for sale (Kobold et al. 2003).

6.3.3 Sipora

Sipora is the most developed of all the Mentawai Islands, and is home to the regency capital, Tua Pejat. Despite its popularity with tourists as a surfing destination, no conservation action has ever been attempted, and only 10-15% of the original forest cover remains (Fuentes 1996/1997).

6.3.4 The Pagai Islands

In recognition of the possibly unique subspecies of primates living in the southernmost islands, researchers have suggested a few sites in the Pagai Islands for protected area status. Much of the area of the Pagai Islands is managed by a single logging company, PT Minas Pagai Lumber Corporation. The southernmost portion of South Pagai, Sinakak islet (600 ha) was undisturbed due to its inaccessibility, and was suggested as a potential wildlife reserve (Tenaza 1987, 1988; Fuentes 1996/1997). Unfortunately, in recent years smaller logging companies have found a way to access this area and extract lumber.

A second area was suggested on North Pagai Island in the Betumonga region. This 623 ha forest was the site of dissertation research by Agustin Fuentes (1994), Sasimar Sangchantr (2004), and Lisa Paciulli (2004). In the late 1990s, Paciulli succeeded in gaining protected status from the government; the area was named Betumonga Research Area. A "research area" has very little actual protection compared to a nature reserve or national park, and after Paciulli's return to the United States in 2002, local people sold the forest to a logging company.

So far, attempts to protect undisturbed areas in the Pagai Islands have not been successful, as local villages are often eager to sell forest to small, often foreign, timber companies who clear-cut the area in exchange for a relatively small sum of cash, food supplies, and televisions. The PT Minas Pagai Lumber Corporation, an Indonesian timber company based in Padang, has controlled a large logging concession (83,330 ha) that encompasses much of the interior of North and South Pagai (total area of the islands: 1675 km^2). PT Minas has controlled this concession since 1971; the current permit

expires in 2012 but may be extended. Unlike most logging companies in the Mentawais, which usually practice clear-cutting following by conversion to plantations, PT Minas manages the area with selective logging and replanting, and rotating logging areas over a few decades. An area of 7,789 ha is designated by the corporation as a Buffer Zone and Conservation Area, and another 13,256 ha as a Limited Production Forest where selective logging is practiced (PT Minas Pagai Lumber Corporation 1996). While the corporation's primary conservation interest is trees, these two areas together account for a total of 21,045 ha (210 km^2) of suitable habitat for primates in the Pagai Islands. However, logging roads have made these forest patches far more accessible, and thus hunting has become a primary concern in the Pagais.

6.4 Recommended conservation action

This section will first review the progress made on recommendations from the 1987 Action Plan for Asian Primates, and then list new recommendations for conservation in the Mentawai Islands.

6.4.1 Review of recommendations from 1987-91 Asian Primate Action Plan

Four recommendations were made that specifically addressed the Mentawai Islands (Eudey 1987):

Development of the Biosphere Reserve on Siberut Island: This objective was fully accomplished with the 1995 ICDP plan (see section 6.4.1). However, local enforcement is weak, and hunting of all four primates and forest product extraction occurs in all management zones.

Creation of a primate reserve on South Pagai Island and off-shore islands: Despite several attempts to establish such a reserve, this objective has not been accomplished. Areas suggested for conservation have been logged (see section 6.4.4).

Survey of primates on Sipora Island: While a survey of Kloss's gibbon density was conducted on Sipora in the present study, no survey has been conducted of the macaques or colobines.

Captive breeding program to recover the endemic subspecies of Mentawai primates on the southern islands, Sipora and Pagais: This expensive recommendation has not been included in any other plans for conservation in the Mentawai Islands, and no progress has been made.

6.4.2 New recommended conservation action

I suggest two general recommendations: first, to increase existing protection by enforcing the laws of the existing National Park, extending formal protected area status to the Peleonan forest, and working with existing "Conservation Areas" set aside by PT Minas Pagai Lumber Corporation in the Pagais; and second, to begin a campaign of education and law enforcement against hunting of endangered primates throughout the Mentawais.

Increased protection of Siberut National Park. Siberut National Park already encompasses nearly half of the island of Siberut, and is home to the largest populations of all four primate species. This area has the potential to adequately protect the Mentawai wildlife; unfortunately, the laws are not enforced. Hunting beyond that allowed by the land-use regulations occurs throughout the park, and logging companies outside the park boundaries frequently encroach upon park forest. The park has few employees, and funds

from park headquarters in Padang infrequently reach Siberut (a problem for workers throughout the Mentawais, including government employees and teachers), giving employees little motivation to perform their jobs. The park needs funding to hire more park guards, and better infrastructure to ensure that guards receive their pay in a timely manner. A system of penalties for breaking park regulations should be developed and implemented.

Formal protection of the Peleonan forest**.** While the National Park has enough space for conservation of the Mentawai primates, the park suffers from inaccessibility. About 2,000 tourists visit Siberut each year to observe the traditional lifestyle of the local people, but none of them ever enter the remote National Park. Similarly, few researchers work within the park boundaries. Formally protecting the 40 km^2 Peleonan forest in North Siberut will provide opportunities for Siberut to generate income from ecotourism and research, as well as increasing awareness about the Mentawai Island forests and primates.

Protected areas in the Pagai Islands. While the Kloss's gibbons do not exhibit any differentiation between the Pagais and Siberut, the other primate species show phenotypic differentiation that has led to subspecific designations (described in Chapter 1). Protection of primates in Pagai Islands is essential to conserve these variations in addition to the Siberut population. Because attempts to conserve undisturbed areas in the Pagais have not been successful, and because PT Minas Pagai Lumber Corporation has established its own "conservation areas" within its concession, I propose that a conservation program collaborates with this corporation to conserve primates. The corporation has been very open to allowing researchers to study primates in the

concession, and has even provided accommodations, transportation and field assistants. The administrative heads of the company have expressed great interest in the results of both the current study and Paciulli's (2004) dissertation study. Furthermore, most employees of this corporation appear to have an understanding of the concepts of sustainable use and conservation, an attitude that is rare in the Mentawais. I recommend working with the logging company, requesting the continued conservation of those areas, perhaps in exchange for some kind of benefits for the company or its employees.

Conservation education, especially regarding hunting. An educational campaign throughout the Mentawais, but especially in the Pagais, is essential to the survival of the Mentawai primates. New technologies for forest product extraction and hunting, as well as a cash-based economy (making the prospect of selling land to companies very attractive), are relatively new to the Mentawai people. As is evident in the attitude towards hunting primates (see Introduction), a full understanding of the concept of sustainability has not really arrived. While no data are available to quantify how much hunting is sustainable, a reduction in hunting is crucial and cessation is unrealistic. A conservation education campaign should begin with the schools and perhaps the churches. In addition, educating the hundreds of people who work with PT Minas to reduce hunting could be very effective, as they already express an understanding of sustainability with regard to the trees.

Alternative economic development. Major educational campaigns are underway in Siberut by UNESCO and Siberut National Park to inform local people about land rights, economics, and alternative, sustainable methods of supporting themselves, such as the planting and harvesting of cinnamon. These efforts should be supported and continued, as

well as expanded to the Pagais. More personnel are needed for these efforts. I recommend that local Mentawai people be trained as educators and compensated for their work.

6.5 Conclusion

The Mentawai primate populations have declined dramatically in the last 25 years, and recent data necessitate updating the conservation status of each species. Action must be taken to conserve populations of these species; while much of the infrastructure for conservation (e.g., Siberut National Park) is already in place, further involvement is necessary to ensure the success of these measures. The long-term success of conservation in the Mentawai Islands will depend on the involvement of the local people, which in turn will depend on changes in the current attitudes about sustainability.

CHAPTER 7

Summary and Conclusions

This dissertation was the first study of the Kloss's gibbon in two decades. During that time, many suggestions have been made about southeast Asian primate biogeography, such as the importance of the Mentawai Islands as a Pleistocene refuge (Brandon-Jones 1998); gibbon social organization, including references to lack of duetting and other pair-bonding behaviors in *H. klossii* giving rise to questions about monogamy (Fuentes 2002); and Mentawai conservation, such as suggestions that the Kloss's gibbon may be critically endangered (A. Eudey, J. Supriatna, pers. comm.). The data I have presented here have important implications for all of these hypotheses. Additionally, the Conservation Action Plan presented in this dissertation provides new direction for conservation planning that can benefit all four endemic Mentawai primates.

7.1 Phylogenetic position of the Kloss's gibbon

Using the rapidly mutating mitochondrial D-loop and a more extensive sample size than has been used in previous studies, I conclude that the Kloss's gibbon is most closely related to the agile gibbon (*H. agilis*) and to the Javan silvery gibbon (*H. moloch*). These two species are geographically the closest to *H. klossii*, and the Javan gibbon shares derived vocal features with the Kloss's gibbon that are not observed in other gibbon species (Geissmann 1993). The biogeographic pattern inferred in this study suggests a single southward migration pattern from the north, where the most basal members of the genus (*H. lar* and *H. pileatus*) occur, to the south, where the most derived species (*H. klossii*, *H. agilis*, and *H. moloch*) are found.

While the many molecular systematics studies of gibbons all provide somewhat different conclusions, the D-loop data may be the most reliable guide to evolutionary history as this rapidly mutating locus has the potential to identify rapid, recent speciation events. However, the phylogenetic trees in this study all have very low bootstrap support values, leading to questions about their reliability. I suggest that the genus *Hylobates* may not have speciated in a bifurcating, branching pattern that phylogenetic analyses attempt to reconstruct, and further research using these methods may never elucidate this pattern satisfactorily.

7.2 Phylogeography of Kloss's gibbons

While populations of Kloss's gibbons have been separated on different islands, these populations do not display genetic differentiation. This lack of differentiation is likely due to historical gene flow when the islands were last connected (about 7,000 years ago), followed by incomplete lineage sorting. The other Mentawai primate species display phenotypic variation, and subspecies on Siberut and the southern islands have been named on the basis of this variation. However, generation times for gibbons are twice as long as for the cercopithecoids, so different biogeographic histories need not be inferred. Additional sampling and genotyping of microsatellite loci would possibly identify the straits separating the islands as being recent barriers to gene flow in gibbons.

7.3 Directions for future research

Comparative Mentawai phylogeography. The data presented here about Kloss's gibbon genetic variation are in contrast with the proposition that the other three Mentawai primates (*M. pagensis*, *P. potenziani*, and *S. concolor*) have differentiated subspecies. While some genetic analysis has been conducted on mtDNA variation in *M. pagensis*,

genetic analysis of intraspecific variation should also be conducted in *P. potenziani* and *S. concolor* to test whether these species have differentiated genetically. As mentioned above, because of different generation times it is possible for the Kloss's gibbon and these cercopithecoids to share the same biogeographic history but to display different patterns of genetic variation. This hypothesis should be tested with genetic data from the Mentawai monkeys.

Gibbon population genetics. No study has been conducted of genetic population structure in any gibbon species. While questions have been raised about the "typical" pattern gibbon social organization, few researchers have studied the dispersal patterns of maturing gibbons (but see Lappan 2005). In all gibbon species, both males and females disperse, but it is not known how far each sex typically travels, how frequent group transfers are later in life, or how genetic variation is patterned within a population. Future research should compare the distribution of maternally (mitochondrial DNA and X-chromosome), paternally (Y-chromosome), and biparentally inherited (autosomal) genetic markers to examine male and female dispersal patterns. Hypotheses concerning the effects of gibbon social organization on population substructuring should be tested as well. Ideally this research would be conducted with data from several gibbon species, including Kloss's gibbons, before any further conclusions are drawn about the "typical gibbon pattern."

Gibbon social structure. Unusually large group sizes were observed in Kloss's gibbons during the population survey. Gibbon groups observed throughout the Mentawai Islands ranged in size from 4-15 individuals, with an average size of 10 individuals at one site, the Peleonan forest in North Siberut. These observations raise interesting questions

about gibbon biology and behavior. These large group sizes may be an ecological response of this species to productive forests, to compressed habitat, or to human hunting. The ability of Kloss's gibbons to respond to ecological pressures by adjusting group size has implications for the study of gibbon social structure.

The typical model of a gibbon social group, consisting of a pair-bonded male and female and their offspring (Leighton 1987), has been challenged by recent research that has found significant departures from this model in many populations (Srikosamatara and Brockelman 1987; Bleisch and Chen 1991; Palombit 1994a, 1994b; Reichard 1995; Brockelman et al. 1998; Jiang et al. 1999; Lappan 2005). The large groups observed here (several with more than one infant) further challenge this model. Several authors have suggested that monogamy results when females, territorial and intolerant of other females, space themselves out in relationship to resources in such a way that a male cannot monopolize more than one female (Emlen and Oring 1977; Rutberg 1983). Others have suggested that male gibbons assist females in defending their territories in order to increase their own reproductive success (Raemakers and Chivers 1980; Brockelman and Srikosamatara 1984), or to prevent infanticide by other males (van Schaik and Dunbar 1990; van Schaik and Kappeler 1997), though there is little evidence to support these hypotheses (Palombit 1999; Palombit 2000; van Schaik and Kappeler 2003). In cases where gibbon habitats are productive enough to reduce food competition and support multiple breeding females in a single group, then perhaps the ecological basis of monogamy is relaxed, resulting in larger groups. Future research on gibbon monogamy should incorporate hypotheses about ecological constraints on group size, comparing populations with habitats of different levels of productivity.

Gibbon social structure may be best studied from a population level, as behavioral data have suggested that gibbon social groups have a more fluid membership than previously supposed, and that gibbons may operate as members of local communities rather than as members of an exclusive, small social group (Fuentes 2000; Reichard 2003). Fuentes (2000) has proposed that gibbons may exhibit a "supragroup" structure in which "variable communities" (rather than "social groups," a term that implies a degree of permanence) of 3-5 individuals cluster together. Reichard (2003) has suggested that male gibbons pursue reproductive opportunities as members of a local community, and proposed that some gibbons exhibit "local-community social-monogamy combined with mating polygyny," as evidenced by frequent observations of extra-pair copulations. Models of the evolution of monogamy could benefit greatly from an understanding of the overall population structure of gibbons, by incorporating population-level processes rather than focusing solely on the social group.

Gibbon conservation genetics. The HV-I region of the mitochondrial D-loop appears to unambiguously identify gibbon species, and therefore could be used as a "DNA barcode" (Hebert et al. 2003). Such a tool would be useful for identifying the origin of bushmeat and captive gibbons, and would greatly assist efforts to enforce hunting and pet trade laws. Furthermore, while this locus did not identify multiple populations for conservation in the Kloss's gibbon, greater variation was found in this locus within other gibbon species, most notably the agile gibbon (*H. agilis*), and so it has the potential to be used to identify populations for conservation action.

7.4 Mentawai conservation

My surveys indicate that there are an estimated 20,000-25,000 gibbons, and 3,000 km^2 of tropical rainforest habitat in the Mentawai Islands. Compared with the results of past estimates (World Wildlife Fund 1980), these data suggest a population decline of >50% in three generations (estimated as equivalent to about 27 years), and thus I recommend that the status of the Kloss's gibbon be upgraded from "Vulnerable" to "Endangered." The mitochondrial sequence data suggest that the species should be managed as a single unit, and that Siberut National Park should be sufficient to preserve the present genetic variation of the species. The first action needed to conserve Mentawai primates is to increase protection of the National Park by enforcing the existing laws to reduce hunting and prevent illegal logging. More park guards are needed, and officials must ensure that they receive their pay in a timely manner.

However, possibly unique populations of the other Mentawai primates have been identified, and therefore I recommend working to preserve populations on the Pagai Islands as well. My research and that of Paciulli (2004) suggest that there are potentially viable populations of primates in previously logged and regenerating patches managed by PT Minas Pagai Lumber Corporation, an Indonesian company that has practiced selective logging and replanting throughout the Pagai Islands for over thirty years. I recommend that conservationists collaborate with this corporation to reduce hunting and preserve populations in areas that the company has already set aside as buffer and conservation zones.

Hunting is a major threat to all four species of Mentawai primates. A conservation education campaign, beginning in schools and perhaps churches, is crucial to educate

Mentawai people about the endangered status of the primates and the principle of sustainable use. Furthermore, PT Minas employees are currently major consumers of primates, yet the corporation uses the concept of sustainable use in their logging techniques. By extending this concept from the exploitation of timber to the exploitation of primates, educating these workers may substantially decrease the rate of hunting in the Pagai Islands.

Because of their long period of isolation and high level of endemism, the Mentawai Islands have been described as an "evolutionary laboratory" in which a "unique experiment" on change, isolation, and adaptation is taking place (Fuentes 2002). Action must be taken to preserve this unusual fauna. The survey results presented here show unexpectedly large primate populations in logged forests, and even larger populations in unlogged areas. The history of the Mentawai people and the sustainable practices of the largest logging concession on the islands provide a cultural background in which an education program could lead to significant changes in behavior. The conservation action plan and data presented here offer hope, not that the primate populations will survive on their own, but that saving them is possible.

APPENDIX I

Complete Sample List

Site	Sample ID	Date	Island	Location	GPS	Group composition	D-loop	M-sats	Notes
1	PL01	4/2/01	Siberut	Peleonan	S0º58.3' E98º49.1'	4 individuals			
1	PL02	4/5/01	Siberut	Peleonan	S0º57.6' E98º48.9'	7 individuals; incl. 1 infant			
1	PL03	4/5/01	Siberut	Peleonan					
1	PL04	4/5/01	Siberut	Peleonan			X		
1	PL05	4/5/01	Siberut	Peleonan					
1	PL06	4/5/01	Siberut	Peleonan	S0º57.8' E98º49.3'	5 individuals			
1	CA01	9/17/03	Siberut	Policoman	S01º01.176' E98º50.495'	at least 15 individuals: at least 2 adult females; 1 adult male heard 2 females heard 1 male before dawn			
1	CA02	9/17/03	Siberut	Policoman					
1	CA03	9/17/03	Siberut	Policoman					
1	CA04	9/17/03	Siberut	Policoman					
1	CA05	9/17/03	Siberut	Policoman					
1	CA06J	9/17/03	Siberut	Policoman					
1	CA07	9/17/03	Siberut	Policoman					
1	CA08J	9/17/03	Siberut	Policoman					
1	CA09	9/17/03	Siberut	Policoman					
1	CA10	9/17/03	Siberut	Policoman					
1	CA11	9/17/03	Siberut	Policoman					
1	CA12	9/17/03	Siberut	Policoman					
1	CA13	9/17/03	Siberut	Policoman					
1	CA14	9/18/03	Siberut	Policoman	S1º01.744' E98º50.898'	heard 2 females sing together; 10-15 individuals			
1	CA15	9/18/03	Siberut	Policoman			X	X	Identical genotypes
1	CA16	9/18/03	Siberut	Policoman			X	X	
1	CA17J	9/18/03	Siberut	Policoman					
1	CA18	9/18/03	Siberut	Policoman					
1	CA19FJ	9/19/03	Siberut	Policoman	S1º01.220' E98º50.585'	3-6 individuals			
1	CA20F	9/19/03	Siberut	Policoman					
1	CA21J	9/22/03	Siberut	Policoman	S1º01.239' E98º49.985'	At least 10-12 individuals; 3 females singing together; 1 infant			
1	CA22FJ	9/22/03	Siberut	Policoman					
1	CA23F	9/22/03	Siberut	Policoman					
1	CA24	9/22/03	Siberut	Policoman			X	X	Identical genotypes
1	CA25	9/22/03	Siberut	Policoman			X	X	
1	CA26J	9/23/03	Siberut	Policoman	S1º01.475' E98º50.041'	At least 5 individuals; 2-3 females singing together			
1	CA27	9/23/03	Siberut	Policoman					
1	CA28	9/23/03	Siberut	Policoman					
1	CA29J	9/23/03	Siberut	Policoman					
2	SB01	4/21/01	Siberut	Simabuggai	S1º22.8' E098º56.8'	2 adults, 2 infants			
2	SB02	4/23/01	Siberut	Simabuggai	S1º22.5' E098º56.9'	3 individuals			
2	SB03	4/23/01	Siberut	Simabuggai					
2	SB04	4/23/01	Siberut	Simabuggai			X	X	
2	SB05	4/23/01	Siberut	Simabuggai					

Site	Sample ID	Date	Island	Location	GPS	Group composition	D-loop	M-sats	Notes
2	SB06	4/23/01	Siberut	Simabuggai	S1°22.4' E098°57.1'	3 adults, 2 adolescents, 1 juvenile	X	X	Non-identical genotypes
2	SB07	4/23/01	Siberut	Simabuggai					
2	SB08	4/23/01	Siberut	Simabuggai			X	X	
2	SB09	4/23/01	Siberut	Simabuggai					
2	SB10	4/25/01	Siberut	Simabuggai	S1°23.1 E098°56.9'	4 individuals (1 juvenile)	X		Identical genotypes
2	SB11	4/25/01	Siberut	Simabuggai					
2	SB12	4/25/01	Siberut	Simabuggai					
2	SB13	4/25/01	Siberut	Simabuggai					
2	SB14	4/25/01	Siberut	Simabuggai					
2	SB15	4/25/01	Siberut	Simabuggai					
2	SB16	4/25/01	Siberut	Simabuggai					
2	SB17	4/25/01	Siberut	Simabuggai			X		
2	SB18	4/25/01	Siberut	Simabuggai	S01°22.2 E098°57.3'	solitary male?	X	X	Identical genotypes
2	SB19	4/25/01	Siberut	Simabuggai			X	X	
3	TL01	11/15/03	Siberut	Taileleu	S1°42.749' E99°08.351'	unknown	X		Flying squirrel
3	TL02	11/15/03	Siberut	Taileleu					
3	TL03	11/15/03	Siberut	Taileleu					
3	TL04	11/17/03	Siberut	Taileleu	S1°42.749' E99°08.351'	unknown	X		Civet
3	TL05FJ	11/17/03	Siberut	Taileleu					
3	TL06F	11/17/03	Siberut	Taileleu					
3	TL07FJ	11/17/03	Siberut	Taileleu					
3	TL08F	11/17/03	Siberut	Taileleu					
3	TL09FJ	11/17/03	Siberut	Taileleu					
3	TL10FJ	11/17/03	Siberut	Taileleu					
	MG01	4/9/01	Siberut	Madobag		captive female			
	ML01	4/10/01	Siberut	Malancan		captive			
	ML02	4/10/01	Siberut	Malancan					
	ML03	4/10/01	Siberut	Malancan					
	ML04	4/10/01	Siberut	Malancan					
4	SR01FJ	12/13/03	Sipora	Saureinu	S2°07.946' E99°37.851'	heard 1 female call but did not see group			
4	SR02F	12/13/03	Sipora	Saureinu					
4	SR03F	12/13/03	Sipora	Saureinu					
4	SR04F	12/15/03	Sipora	Saureinu	S2°07.732' E99°37.768'	unknown - could be M. pagensis			
4	SR05F	12/15/03	Sipora	Saureinu					
4	SR06FJ	12/15/03	Sipora	Saureinu					
4	SR07FJ	12/15/03	Sipora	Saureinu					
4	SR08J	12/15/03	Sipora	Saureinu					
4	SR09	12/15/03	Sipora	Saureinu					
4	SR10J	12/15/03	Sipora	Saureinu					
4	SR11	12/15/03	Sipora	Saureinu					
4	SR12	12/16/03	Sipora	Saureinu	S2°07.263' E99°36.660'	1 adult male singing; saw 2 other adults	X	X	Identical genotypes
4	SR13	12/16/03	Sipora	Saureinu			X	X	
4	SR14J	12/16/03	Sipora	Saureinu					
4	SR15FJ	12/16/03	Sipora	Saureinu					
4	SR16FJ	12/16/03	Sipora	Saureinu	S2°07.842' E99°37.614'	2 individuals; heard female call			
4	SR17F	12/16/03	Sipora	Saureinu					
4	SR18FJ	12/16/03	Sipora	Saureinu					
4	SR19F	12/16/03	Sipora	Saureinu					
4	SR20	12/18/03	Sipora	Saureinu	S2°07.742' E99°37.702'	Unknown, Macaques?			
4	SR21J	12/18/03	Sipora	Saureinu					

Site	Sample ID	Date	Island	Location	GPS	Group composition	D-loop	M-sats	Notes
4	SR22J	12/18/03	Sipora	Saureinu					
4	SR23J	12/18/03	Sipora	Saureinu					
4	SR24J	12/18/03	Sipora	Saureinu					
4	SR25	12/18/03	Sipora	Saureinu					
4	SR26	12/18/03	Sipora	Saureinu					
4	SR27	12/18/03	Sipora	Saureinu					
4	SR28	12/18/03	Sipora	Saureinu					
4	SR29	12/18/03	Sipora	Saureinu	S2º07.854' E99º37.627'	2 individuals; 1 male calling			
4	SR30J	12/18/03	Sipora	Saureinu					
4	SR31	12/18/03	Sipora	Saureinu			X	X	
4	SR32J	12/18/03	Sipora	Saureinu					
4	SR33	12/18/03	Sipora	Saureinu					
4	SR34	12/18/03	Sipora	Saureinu					
4	SR35	12/18/03	Sipora	Saureinu					
4	SR36	12/18/03	Sipora	Saureinu					
4	SR37	12/18/03	Sipora	Saureinu					
4	SR38J	12/18/03	Sipora	Saureinu					
4	SR39J	12/18/03	Sipora	Saureinu					
4	SR40	12/18/03	Sipora	Saureinu					
5	NP01	3/5/01	N Pagai	Betumonga	S2º46.97' E100º01.96'	7 individuals	X		
5	NP02	3/5/01	N Pagai	Betumonga					
5	NP03	3/5/01	N Pagai	Betumonga					
5	NP04	3/5/01	N Pagai	Betumonga					
5	NP05	3/6/01	N Pagai	Betumonga	S2º46.8' E100º01.6'	unknown	X		
5	NP06	3/6/01	N Pagai	Betumonga					
5	NP07	3/6/01	N Pagai	Betumonga	S2º46.6' E100º01.55'	8-10 individuals			
5	NP08	3/6/01	N Pagai	Betumonga	S2º47.0' E100º01.9'	5 individuals (1 juvenile)			
5	NP09	3/6/01	N Pagai	Betumonga					
5	NP10	3/7/01	N Pagai	Betumonga	S2º46.6' E100º01.49'	5 individuals	X		
5	NP11	3/7/01	N Pagai	Betumonga					
6	NP12	3/6/01	N Pagai	Muntei	S2º47.7' E100º00.6'	4-5 adults	X	X	
6	NP13	3/11/01	N Pagai	Muntei	S2º47.7' E100º00.7'	3 adults, 1 juvenile, 1 infant			
6	NP14	3/11/01	N Pagai	Muntei			X		
7	SP01	2/12/01	S Pagai	KM 34	S2º58.3' E100º17.2'	3 adults, one infant			
7	SP02	2/12/01	S Pagai	KM 34					
7	SP03	2/12/01	S Pagai	KM 34			X	X	
7	SP04	2/14/01	S Pagai	KM 32	S2º57.4' E100º18.6'	unknown			
7	SP05	2/15/01	S Pagai	KM 45	S3º02.9' E100º20.6'	1 adult male, 1 adult female 1 juvenile			
7	SP06	2/15/01	S Pagai	KM 45			X	X	Non-identical genotypes
7	SP07	2/15/01	S Pagai	KM 45					
7	SP08	2/15/01	S Pagai	KM 45			X		
7	SP09	2/19/01	S Pagai	KM 38	S3º00.9' E100º17.4'	at least 3 adults, 1 infant	X	X	Non-identical genotypes
7	SP10	2/19/01	S Pagai	KM 38					
7	SP11	2/19/01	S Pagai	KM 38			X	X	
7	SP12J	10/13/03	S Pagai	KM 34	S2º58.197' E100º17.516'	1 adult female, 1 adolescent (at least)			
7	SP13	10/13/03	S Pagai	KM 34			X	X	
7	SP14J	10/13/03	S Pagai	KM 34					
7	SP15	10/13/03	S Pagai	KM 34					

Site	Sample ID	Date	Island	Location	GPS	Group composition	D-loop	M-sats	Notes
7	SP16	10/15/03	S Pagai	KM 32	S2º57.973' E100º18.568'	1 adult male, 1 adult female 2 juvenile/ adolescent (at least one female) and 1 infant			
7	SP17J	10/15/03	S Pagai	KM 32					
7	SP18	10/15/03	S Pagai	KM 32					
7	SP19J	10/15/03	S Pagai	KM 32					
7	SP20J	10/15/03	S Pagai	KM 32					
7	SP21	10/15/03	S Pagai	KM 32					
7	SP22J	10/15/03	S Pagai	KM 32					
7	SP24FJ	10/20/03	S Pagai	KM 34	S2º57.979' E100º17.294'	3 adults, 1 infant			
7	SP25FJ	10/20/03	S Pagai	KM 34					
7	SP26F	10/20/03	S Pagai	KM 34					
7	SP27F	10/20/03	S Pagai	KM 34					
7	SP28	10/20/03	S Pagai	KM 34					
7	SP29	10/20/03	S Pagai	KM 34			X	X	
7	SP30	10/20/03	S Pagai	KM 34					
7	SP31J	10/20/03	S Pagai	KM 34					
7	SP32J	10/20/03	S Pagai	KM 34					
7	SP33F	10/20/03	S Pagai	KM 32	S2º57.841' E100º18.581'	5 individuals			

Site numbers correspond to sites in Figure 2.1.

Samples marked with “F” are chewed fruit pieces. All other samples are fecal samples.

Samples marked with “J” are stored in Jakarta with collaborators at As-Syafi’iyah Islamic University.

APPENDIX II

Sequence alignment

```
                                10        20        30        40        50
                                .         .         .         .         .

agilisaJP90                     TATTCTCATGTGGAAGCGGTTTTGAGTACGACCCCAGTACCAACCCACCC
agilisNAN04                     ................T.............................
agilisNAN39                     ................T.....................T....T.G...
klossiiCA15                     ................T...........A.........TT.....GTT.
klossiiCA24                     ................T...........A.........TT.....GTT.
klossiiNP01                     .............G..T...........A.........TT.....GTT.
klossiiNP05                     .............G..T...........A.........TT.....GTT.
klossiiNP10                     .............GA.T...........A.........TT.....GTT.
klossiiNP12                     .............G..T...........A.........TT.....GTT.
klossiiNP14                     .............GA.T...........A.........TT.....GTT.
klossiiPL04                     .............G..T...........A.........TT.....GTT.
klossiiSB04                     .............G..T...........A.........TT.....GTT.
klossiiSB06                     .............G..T...........A.........TT.....GTT.
klossiiSB17                     ................T.....A.....A.........TT.....GTT.
klossiiSB19                     .............G..T...........A.........TT.....GTT.
klossiiSP03                     .............G..T...........A.........TT.....GTT.
klossiiSP06                     .............G..T...........A.........TT.....GTT.
klossiiSP08                     .............G..T...........A.........TT.....GTT.
klossiiSP09                     .............G..T...........A.........TT.....GTT.
klossiiSP11                     .............G..T...........A.........TT.....GTT.
klossiiSP13                     .............G..T...........A.........TT.....GTT.
klossiiSP29                     .............GA.T...........A.........TT.....GTT.
klossiiSR13                     ................T...........A.........TT.....GTT.
klossiiSR31                     ................T...........A.........TT.....GTT.
klossiiJP103                    ................T...........A.........TT.....GTT.
klossiiJP97                     ................T...........A.........TT.....GTT.
lar2                            ................CA.....G....A..........T.......TT
lar3                            ................CA.....G....A..........T...T...T.
molochNAN06                     ................T...........A..........T....TGTT.
molochNAN07                     ................T...........A..........T....TGTT.
molochNAN08                     ................T...........A..........T....TGTT.
molochNAN10                     ................T...........A..........T....TGTT.
molochNAN12                     ................T...........A..........T....TGTT.
molochNAN13                     ................T...G.......A..........T....TGTT.
molochNAN14                     ................T...........A..........T....TGTT.
molochNAN26                     ................T...........A..........T....TGTT.
molochNAN28                     ................T...........A.........TT....TGTT.
molochNAN30                     ................T...........A..........T....TGTT.
molochNAN33                     ................T...........A..........T....TGTT.
molochNAN35                     .............A.T.......A...A..........T....TGTT.
molochNAN41                     ................T...........A..........T....TGTT.
muelleriJP92                    ................TA..........A..............AGTT.
muelleriJP93                    ................TA.....G....A..............AGTT.
pileatusJP99                    ................T...........A...................T.
Bunopithecushoolock             .......G........TAA.....G....A.........T.G.T.T.-T.
Nomascusgabriellae              C................CA....A.....A..........T.G....-..
Symphalangus                    ................T...........A....T....-.......TTT
```

```
                                60        70        80        90        100
                                .         .         .         .         .

agilisaJP90                     TCCCACAACTCTATGTACTTCGTACATTACTGCCAGCCCCC-ATGAATAT
agilisNAN04                     ........................................-........
agilisNAN39                     ..........T..................T...T..T....-........
klossiiCA15                     ..T.....................................T....-...G....
klossiiCA24                     ..T.....................................T....-...G....
klossiiNP01                     ..T.....................................T....-...G....
klossiiNP05                     ..T.....................................T....-........
klossiiNP10                     ..T.....................................T....-........
klossiiNP12                     ..T.....................................T....-...G....
klossiiNP14                     ..T.....................................T....-........
klossiiPL04                     ..T.....................................T....-........
klossiiSB04                     ..T.....................................T....-........
klossiiSB06                     ..T.....................................T....-........
klossiiSB17                     ..T.....................................T....-...G....
klossiiSB19                     ..T.....................................T....-........
klossiiSP03                     ..T.....................................T....-...G....
klossiiSP06                     ..T.....................................T....-........
klossiiSP08                     ..T.....................................T....-........
klossiiSP09                     ..T.....................................T....-...G....
klossiiSP11                     ..T.....................................T....-........
klossiiSP13                     ..T.....................................T....-...G....
klossiiSP29                     ..T.....................................T....-........
klossiiSR13                     ..T.....................................T....-...G....
klossiiSR31                     ..T.....................................T....-...G....
klossiiJP103                    ..T.....................................T....-...G....
klossiiJP97                     ..T.....................................T....-...G....
lar2                            CT......................................T....-...C....
lar3                            CT......................................T....-...C....
molochNAN06                     .T.......C..............................-........
molochNAN07                     .T.......C..............................-........
molochNAN08                     .T.......C.............................T....C........
molochNAN10                     .T.......C.......T.....................-...G....
molochNAN12                     .T.......C..............................-........
molochNAN13                     .T.......C..............................-........
molochNAN14                     .T.......C..............................-........
molochNAN26                     .T.......C..............................-........
molochNAN28                     .T.......C.........................T.....-........
molochNAN30                     .T.......C.........................T.....-........
molochNAN33                     .T.......C..............................-........
molochNAN35                     .T.......C..............................-........
molochNAN41                     .T.......C..............................-........
muelleriJP92                    ..T......CT.......................T..T....-........
muelleriJP93                    ..T......CT.......................T..T....-........
pileatusJP99                    ...T..............................T.....-...G....
Bunopithecushoolock             C..T.T..T.T.......................T.....-...G....
Nomascusgabriellae              C..ACG.TT........T...........A...T..T....-...G....
Symphalangus                    .....TG..CT.......................T..T....-........
```

```
                                  110       120       130       140       150
                                  .         .         .         .         .

agilisaJP90                  TGTACAGTACTACAA--TCACTTAAATAACTACAATACATTAA-CCATCA
agilisNAN04                  ..C..G....C.T..--..G...G..C....GT.G........-...C..
agilisNAN39                  ............T..--......G....G...T..C....C..-...C..
klossiiCA15                  ..............--..........G...T..........-T..CT.
klossiiCA24                  ..............--..........G...T..........-T..CT.
klossiiNP01                  ............T..--..........G...T..........-..G.T.
klossiiNP05                  ............T..--..........G...T..........-..G.T.
klossiiNP10                  ..............--..........G...T..........-...CT.
klossiiNP12                  ............T..--..........G...T..........-..G.T.
klossiiNP14                  ..............--..........G...T..........-...CT.
klossiiPL04                  ............T..--..........G...T..........-..GCT.
klossiiSB04                  ............T..--..........G...T..........-..GCT.
klossiiSB06                  ............T..--..........G...T..........-..GCT.
klossiiSB17                  ..............--..........G...T........G.-....T.
klossiiSB19                  ............T..--..........G...T..........-..GCT.
klossiiSP03                  ............T..--..........G...T..........-..G.T.
klossiiSP06                  ............T..--..........G...T..........-..G.T.
klossiiSP08                  ............T..--..........G...T..........-..GCT.
klossiiSP09                  ............T..--..........G...T..........-..G.T.
klossiiSP11                  ............T..--..........G...T..........-..G.T.
klossiiSP13                  ............T..--..........G...T..........-..G.T.
klossiiSP29                  ..............--..........G...T..........-...CT.
klossiiSR13                  ..............--......G....G...T..........-....T.
klossiiSR31                  ..............--..........G...T..........-T..CT.
klossiiJP103                 ..............--..........G...T..........-....T.
klossiiJP97                  ..............--..........G...T.G......G.-....T.
lar2                         ............T..--........G.....GT.G.......C-...C..
lar3                         ............T..--..............GT.G.......C-...C..
molochNAN06                  ..C.........T..--..................G.....C.C-T..CT.
molochNAN07                  ..............--..................G.....C.C-T...T.
molochNAN08                  ..............--.........C.......G.......C-...C..
molochNAN10                  ..............--.........C.......G.....C.C-...CT.
molochNAN12                  ..............--........GC.......G.......C-...C..
molochNAN13                  ..C.........T..--..................G.....C.C-....T.
molochNAN14                  ..............--.........C.......G.......C-...C..
molochNAN26                  ............T..--.........C.......G.......C-...C..
molochNAN28                  C.............--........GC.......G.....C.C-...CT.
molochNAN30                  ..C.........T..--..................G.....C.C-T..CT.
molochNAN33                  ..C.........T..--..................G.....C.C-....T.
molochNAN35                  ..C.........T..--..................G.....C.C-....T.
molochNAN41                  ..............--..................G.......C-...C..
muelleriJP92                 ............T..--.........C.G...T..C.......-.T.C..
muelleriJP93                 ...C...........--...T...G.........G........-.T.C..
pileatusJP99                 ..............--........GC.G...T.C.......G-.T..T.
Bunopithecushoolock          ...........TT..--........C.....GT.G.....A..C...-..
Nomascusgabriellae           .....G......G..AA.T......CC.....T.GA...G..CA...C..
Symphalangus                 .......C....T..--.TG.A...C......T.GA....A.C-......
```

```
                                 160       170       180       190       200
                                 .         .         .         .         .

agilisaJP90                      AACGTACATACAAACATCCCCAACATGCTTACAAGCAAGCACTAGAATAC
agilisNAN04                      ..........T......TT.......................C.......
agilisNAN39                      ..................................................
klossiiCA15                      .....G..........A............................G......
klossiiCA24                      .....G..........A............................G......
klossiiNP01                      ...........G....A..T..G.....................G......
klossiiNP05                      ...........G....A............................G......
klossiiNP10                      .....G..........A.....................G.....G......
klossiiNP12                      ...........G....A..T..G.....................G......
klossiiNP14                      .....G..........A.....................G.....G......
klossiiPL04                      ...........G.G..A.TT........................G......
klossiiSB04                      ...........G.G..A.TT........................G......
klossiiSB06                      ...........G.G..A.TT........................G......
klossiiSB17                      ................A..T........................G......
klossiiSB19                      ...........G.G..A.TT........................G......
klossiiSP03                      ...........G....A..T........................G......
klossiiSP06                      ...........G....A..T........................G......
klossiiSP08                      ...........G.G..A.TT........................G......
klossiiSP09                      ...........G....A..T........................G......
klossiiSP11                      ...........G....A.TT........................G......
klossiiSP13                      ...........G....A..T........................G......
klossiiSP29                      .....G..........A.....................G.....G......
klossiiSR13                      ................A..T........................G......
klossiiSR31                      .....G..........A..T........................G......
klossiiJP103                     ................A..T........................G......
klossiiJP97                      ................A..T........................G......
lar2                             ................GA..........................C..C.C.T
lar3                             ................GA..........................C.AC....
molochNAN06                      G...............A........C.....................
molochNAN07                      G...............A..............................
molochNAN08                      ................A..............................
molochNAN10                      GG..............A.........A....................-
molochNAN12                      ................A..............................
molochNAN13                      G...............A........C.....................
molochNAN14                      ................A..............................
molochNAN26                      ................A.......................T......
molochNAN28                      GG..............GA.............................
molochNAN30                      G...............A........C.....................
molochNAN33                      G...............A........C.....................
molochNAN35                      G...............A........C.....................
molochNAN41                      ................A.T.........................-.....
muelleriJP92                     G...............A.T.....................T..C.AC.C.T
muelleriJP93                     ................A.......................T.TC.AC....
pileatusJP99                     G....G..........A...T................G..GTC..CTC..
Bunopithecushoolock              .T.........C..GCAAT......C................C.A.....
Nomascusgabriellae               .C.........C..GTAAGA...................A..C..C....
Symphalangus                     .C........TC..GCAAG......A.....T................C.
```

```
                                  210       220       230       240       250
                                  .         .         .         .         .

agilisaJP90                -CTCAATCAACTGTAAAGCATCCACTTCACTCTCAC--------------
agilisNAN04                -.............G.....................--------------
agilisNAN39                -..........A...G.....................--------------
klossiiCA15                -.............G.....A......GT......--------------
klossiiCA24                -.............G.....A..T...GT......--------------
klossiiNP01                -.............G.....A...C..GT......--------------
klossiiNP05                -.............G.....A...C..G.......--------------
klossiiNP10                -.............G.....A...C..GT......--------------
klossiiNP12                -.............G.....A...C..GT......--------------
klossiiNP14                -.............G.....A...C..GT......--------------
klossiiPL04                -.............GC....A...C..GT......--------------
klossiiSB04                -.............GC....A...C..GT......--------------
klossiiSB06                -.............GC....A...C..GT......--------------
klossiiSB17                -.............G.....A...C..GT......--------------
klossiiSB19                -.............GC....A...C..GT......--------------
klossiiSP03                -.............G.....A...C..GT......--------------
klossiiSP06                -.............G.....A......GT......--------------
klossiiSP08                -.............GC....A...C..GT......--------------
klossiiSP09                -.............G.....A...C..GT......--------------
klossiiSP11                -.............G.....A...C..GT......--------------
klossiiSP13                -.............G.....A...C..GT......--------------
klossiiSP29                -.............G.....A...C..GT......--------------
klossiiSR13                -.............G.....A...C..GT......--------------
klossiiSR31                -.............G.....A...C..GT......--------------
klossiiJP103               -.............G.....A...C..GT......--------------
klossiiJP97                -.............G.....A......GT......--------------
lar2                       -..TG.C........G.....................--------------
lar3                       -..TG.CT.......G....C...T...........--------------
molochNAN06                -..............C.....................--------------
molochNAN07                -..............C.......T...........--------------
molochNAN08                -..............C....T...........T..--------------
molochNAN10                -..............CA....................--------------
molochNAN12                -..............CA....................--------------
molochNAN13                -..............C.......T..........G--------------
molochNAN14                -..............C....T...........T..--------------
molochNAN26                -..............C....T...C..........--------------
molochNAN28                -.............GC....T...............--------------
molochNAN30                -..............C.....................--------------
molochNAN33                -............T.C.......T...........--------------
molochNAN35                -..............C.......T...........--------------
molochNAN41                -..............C....T...C..........--------------
muelleriJP92               -..T.GCT...A...G.....................--------------
muelleriJP93               -..TGGCT...A...G.....T..............--------------
pileatusJP99               T...G.CT......GT.....T..........C.C.--------------
Bunopithecushoolock        -..T..C...T....G.A........C..AC.C...TAC---AATCCTCC
Nomascusgabriellae         -...C.A.....A....A.......CATTACTC..ACATTCCAAGCCCGA
Symphalangus               -..T..CT.........A...T..TCC..A..C...CAT-CAAATTCTTA
```

```
                                260       270       280       290       300
                                .         .         .         .         .

agilisaJP90                  --GACATACAAACCAACCACCA--------------AAGACCGCCCATCT
agilisNAN04                  --....................--------------..............
agilisNAN39                  --............CCA.CAGG--------------.G....CT......
klossiiCA15                  --..................G..--------------....TT.T......
klossiiCA24                  --..................G..--------------....TT.T......
klossiiNP01                  --..................G..--------------G...TT.T......
klossiiNP05                  --..................G..--------------G...TT.T......
klossiiNP10                  --..................G..--------------....TT.T......
klossiiNP12                  --..................G..--------------G...TT.T......
klossiiNP14                  --..................G..--------------....TT.T......
klossiiPL04                  --..................G..--------------....TT.T......
klossiiSB04                  --..................G..--------------....TT.T......
klossiiSB06                  --..................G..--------------....TT.T......
klossiiSB17                  --..................G..--------------....TT.T......
klossiiSB19                  --..................G..--------------....TT.T......
klossiiSP03                  --..................G..--------------G...TT.T......
klossiiSP06                  --..................G..--------------G...TT.T......
klossiiSP08                  --..................G..--------------....TT.T......
klossiiSP09                  --..................G..--------------G...TT.T......
klossiiSP11                  --..................G..--------------G...TT.T......
klossiiSP13                  --..................G..--------------G...TT.T......
klossiiSP29                  --..................G..--------------....TT.T......
klossiiSR13                  --..................G..--------------....TT.T......
klossiiSR31                  --..................G..--------------....TT.T......
klossiiJP103                 --..................G..--------------....TT.T......
klossiiJP97                  --..................G..--------------....TT.T......
lar2                         --......A.C.G......GT.--------------....TA.T......
lar3                         --......A.C.G......GT.--------------....TA.T......
molochNAN06                  --..................G..--------------....TT.T......
molochNAN07                  --..................G..--------------....TT.T......
molochNAN08                  --..................G..--------------....TT.T......
molochNAN10                  --..................G..--------------....TT.T......
molochNAN12                  --.............G...G..--------------....TT.T......
molochNAN13                  --..................G..--------------....TT.T......
molochNAN14                  --..................G..--------------....TT.T......
molochNAN26                  --..................G..--------------....TT.T......
molochNAN28                  --................T..G..--------------....TT.T......
molochNAN30                  --..................G..--------------....TT.T......
molochNAN33                  --..A...............G..--------------....TT.T......
molochNAN35                  --..................G..--------------....TT.T......
molochNAN41                  --..-...............G..--------------....TT.T......
muelleriJP92                 --.......GC.T......G..--------------.......T......
muelleriJP93                 --..................G..--------------.......T......
pileatusJP99                 -G....C...C.TTG....GT.--------------....T.TTT..CT.
Bunopithecushoolock          CCA....G.TT........G..--------------......AT.....A
Nomascusgabriellae           CTA...CG.GT.T.....GA..--------------....TA.T...CTC
Symphalangus                 CTA....G.GT.T.....GAT.GGCTCCTTCCATAACGT.ATT..AC.AC
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```
                                 310        320        330        340        350
                                 .          .          .          .          .

agilisaJP90                AAAGGGCATCCTGCACTCGTTTATTTATCACACATACCAAACCCTTACCG
agilisNAN04                .....A.............C.............T.......CT...
agilisNAN39                ...................C.............T......CCT..A
klossiiCA15                ...................C.............-......C....A
klossiiCA24                ...................C.............-......C....A
klossiiNP01                ..................CC.............-..........A
klossiiNP05                ..................CC.............-.G........A
klossiiNP10                ...................C.............-......C....A
klossiiNP12                ..................CC.............-..........A
klossiiNP14                ...................C.............-......C....A
klossiiPL04                ..................CC.............-..........A
klossiiSB04                ..................CC.............-..........A
klossiiSB06                ..................CC.............-..........A
klossiiSB17                ..................CC.............-..........A
klossiiSB19                ..................CC.............-..........A
klossiiSP03                ..................CC.............-......C....A
klossiiSP06                ..................CC.............-.G........A
klossiiSP08                ..................CC.............-..........A
klossiiSP09                ..................CC.............-..........A
klossiiSP11                ..................CC............TT..........A
klossiiSP13                ..................CC.............-..........A
klossiiSP29                ..................CC.............-......C....A
klossiiSR13                ..................CC.............-..........A
klossiiSR31                ...................C.............-......C....A
klossiiJP103               ..................CC.............-..........A
klossiiJP97                ..................CC.............-..........A
lar2                       .........GA.......A..CG..C.C.G.......A..CT..C....A
lar3                       .........AA.......A..C...C.C.G.......A..CT..C....A
molochNAN06                .......G.............-C.....C.G.......-.....TC....A
molochNAN07                .......G.............C.....C.G.......-.....TC....A
molochNAN08                .......G.............C.....C.G.......-.....TCC...A
molochNAN10                .......G.............C.....C.G.......-.....TCC...A
molochNAN12                .......G.............C.....C.G.......-.....TCC...A
molochNAN13                .......G.............C.....C.G.......-.....TCC...A
molochNAN14                .......G.............C.....C.G.......-.....TCC...A
molochNAN26                .......G.............C.....C.GT......-.....TCC...A
molochNAN28                .......G.............C.....C.GT......-.....TC....A
molochNAN30                .......G.............C.....C.G.......-.....TC....A
molochNAN33                ......GG.............C.....CGCA......-.....TCC...A
molochNAN35                .......G.............C.....C.G.......-.....TCC...A
molochNAN41                .......G.............C.....C.G.......-.....TCC...A
muelleriJP92               .......G..........A..C...C...G.......-.G...T.C...A
muelleriJP93               .......G..........A..C...C...G.......-.....TAC...A
pileatusJP99               .GT......AA....T..A..C...C.C.GT......-......CC...A
Bunopithecushoolock        TT-..A...GGCA..T.....C.....C.GT....G.-.G...T..C..A
Nomascusgabriellae         C--..A...GGCA..T.AAAC.G..C...GT.....A..TGTTACAT..A
Symphalangus               GT.......GGCA..TA....C.......GT......T......AAT..A
```

```
                                360       370       380       390       400
                                .         .         .         .         .

agilisaJP90                     AAATCAACTCACGATCCATAC--ACAGCCTATTTCAGATAGAAGTCCCCT
agilisNAN04                     ......................--...A.............G........
agilisNAN39                     ................---..--...CA...C.......G.G........
klossiiCA15                     ..G.........A........--..TA............G.GG..TT...
klossiiCA24                     ..G.........A........--..CA............G.GG..TT...
klossiiNP01                     ..G.........A........--..TA............G.G........
klossiiNP05                     ..G.........A........--..TA............G.G........
klossiiNP10                     ..G.........A........--..CA............G.GG..TT...
klossiiNP12                     ..G.........A........--..TA............G.G........
klossiiNP14                     ..G.........A........--..CA............G.GG..TT...
klossiiPL04                     ..G.........A........--..TA............G.G........
klossiiSB04                     ..G.........A........--..TA............G.G........
klossiiSB06                     ..G.........A........--..TA............G.G........
klossiiSB17                     ..G..................--..C.............G.GG.......
klossiiSB19                     ..G.........A........--..TA............G.G........
klossiiSP03                     ..G.........A........--..TA............G.G...T....
klossiiSP06                     ..G.........A........--..TA............G.G........
klossiiSP08                     ..G.........A........--..TA............G.G........
klossiiSP09                     ..G.........A........--..TA............G.G........
klossiiSP11                     ..G.........A........--..TA............G.G........
klossiiSP13                     ..G.........A........--..TA............G.G...T....
klossiiSP29                     ..G.........A........--..CA............G.GG..TT...
klossiiSR13                     ..G..................--..CA............G.GG.......
klossiiSR31                     ..G.........A........--..TA............G.GG..T....
klossiiJP103                    ..G..................--..CA............G.GG.......
klossiiJP97                     ..G..................--..C.............G.GG.......
lar2                            C.C.........A........--...A.........C..G.....TT..C
lar3                            C.C.........A........--...A.........C..G.....TT..C
molochNAN06                     .CG.........A........--.................G.-...TT..C
molochNAN07                     .CG.........A........--..-A.............G.-.TT..C
molochNAN08                     .CG.........A........--...A............G.G...TT..C
molochNAN10                     .CG.........A........--...A............G.GT..TT..C
molochNAN12                     .CG.........A........--...A............G.G...TT..C
molochNAN13                     .CG..T......A.C......--...A............G.G...TT..C
molochNAN14                     .CG.........A........--...A............G.GG..TT..C
molochNAN26                     .CG.........A........--...A............G.G...TT..C
molochNAN28                     .CG.........A........--...A..................TT..C
molochNAN30                     .CG.........A........--...A............G.G...TT..C
molochNAN33                     .CG..T......A........--..GAA...........G.G...TT..C
molochNAN35                     .CG.........A........--..GA............G.G...TT..C
molochNAN41                     .CG.........A........--...A............G.G.A.TT..C
muelleriJP92                    ............A........--...A...........AG.GG..TT..C
muelleriJP93                    ............A.....C..--...A....C......AG.GGA.TT..C
pileatusJP99                    ..G.........A........--.T.A....C.......G...A.TT..C
Bunopithecushoolock             C...........AC.......GAGT.AT....................T.
Nomascusgabriellae              ............AC.......GAGT.AT.............GG.....T.
Symphalangus                    C....T......AT.......GAGT.AT.............G......TC
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                                410       420       430       440       450
                                .         .         .         .         .

agilisaJP90                     GCCCAGCATCCTCCGTGAAATCACCAACCCGCCCAAAGAATACTAACTCC
agilisNAN04                     ........................G............G.............
agilisNAN39                     --.......................G.........................
klossiiCA15                     ........................G........A...-..G...CC.....
klossiiCA24                     ........................G........A...-..G...CC.....
klossiiNP01                     .T......................G........A...-..G...CC.....
klossiiNP05                     .T......................G........A...-..G...CC.....
klossiiNP10                     ........................G........A...-..G...CC.....
klossiiNP12                     .T......................G........A...-..G...CC.....
klossiiNP14                     ........................G........A...-..G...CC.....
klossiiPL04                     .T......................G........A...-..G...CC.....
klossiiSB04                     .T......................G........A...-..G...CC.....
klossiiSB06                     .T......................G........A...-..G...CC.....
klossiiSB17                     ........................G........A...-..G...CC.....
klossiiSB19                     .T......................G........A...-..G...CC.....
klossiiSP03                     ........................G........A...-..G...CC.....
klossiiSP06                     .T......................G........A...-..G...CC.....
klossiiSP08                     .T......................G........A...-..G...CC.....
klossiiSP09                     .T......................G........A...-..G...CC.....
klossiiSP11                     .T......................G........A...-..G...CC.....
klossiiSP13                     ........................G........A...-..G...CC.....
klossiiSP29                     ........................G........A...-..G...CC.....
klossiiSR13                     ........................G........A...-..G...CC.....
klossiiSR31                     ........................G........A...-..G...CC.....
klossiiJP103                    ........................G........A...-..G...CC.....
klossiiJP97                     ........................G........A...-..G...CC.....
lar2                            ........................G........A...-..G..........
lar3                            .T......................G........A...-..G..........
molochNAN06                     .T.............................A...-..G..........
molochNAN07                     .T.............................GA...-..G..........
molochNAN08                     .T.............................A...-..G..........
molochNAN10                     .T.............................A...-..G..........
molochNAN12                     .T.............................A...-..G..A.......
molochNAN13                     .T.............................A...-..G..........
molochNAN14                     .T.............................A...-..G......T...
molochNAN26                     .T.............................A...-..G..........
molochNAN28                     .T.............................A...-..G..........
molochNAN30                     .T.............................A...-..G..........
molochNAN33                     .T.............................A...-..-..........
molochNAN35                     .T.............................A...-............
molochNAN41                     .T.............................A...-............
muelleriJP92                    ........................T............-..G..........
muelleriJP93                    .T......................T.............AGG..........
pileatusJP99                    .T......................A........A...-..G..........
Bunopithecushoolock             ........................A..T.....A...-..G..........
Nomascusgabriellae              ..........-......................T..G-A...G....T..A
Symphalangus                    .T..................G..A..T.....A...-..G....G.T.AT
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                                460       470       480       490       500
                                .         .         .         .         .

agilisaJP90                     CCTCGCTCCGGGCTTACAACACCTGGGGGTAGCTATAGTGAGCTGTATCC
agilisNAN04                     .........................................
agilisNAN39                     ...................................C.A...
klossiiCA15                     ..................T......................
klossiiCA24                     ..................T............C.........
klossiiNP01                     ..................T............C.........
klossiiNP05                     ..................T............C.........
klossiiNP10                     .....................................C...
klossiiNP12                     ..................T............C.........
klossiiNP14                     .....................................C...
klossiiPL04                     ..................T............C.........
klossiiSB04                     ..................T............C.........
klossiiSB06                     ..................T............C.........
klossiiSB17                     .....................................C...
klossiiSB19                     ..................T............C.........
klossiiSP03                     ..................T............C.........
klossiiSP06                     ..................T............C.........
klossiiSP08                     ..................T............C.........
klossiiSP09                     ..................T............C.........
klossiiSP11                     ..................T............C.........
klossiiSP13                     ..................T............C.........
klossiiSP29                     .....................................C...
klossiiSR13                     .....................................C...
klossiiSR31                     ..................T............C.........
klossiiJP103                    .....................................C...
klossiiJP97                     .....................................C...
lar2                            .....................................C...
lar3                            ...........C.........................C...
molochNAN06                     ..............A.CA..........A..............
molochNAN07                     ............................TA..............
molochNAN08                     .........................................
molochNAN10                     ..................T......................
molochNAN12                     .............AC.A........................
molochNAN13                     .........................................
molochNAN14                     .........C...............................
molochNAN26                     .........................................
molochNAN28                     ...........C.............................
molochNAN30                     .........................................
molochNAN33                     ....................-....................
molochNAN35                     .TC.................................A.....
molochNAN41                     .TC......................................
muelleriJP92                    .........................................
muelleriJP93                    .....................................C...
pileatusJP99                    .....................................C...
Bunopithecushoolock             ...........C.............................
Nomascusgabriellae              ...........C.......T.....................
Symphalangus                    .T.........C.............................
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                                 510       520
                                 .         .

agilisaJP90                 GGCATCTGGTTCTTACCTCACGGCCATA
agilisNAN04                 ............................
agilisNAN39                 ...................T........
klossiiCA15                 ...................T........
klossiiCA24                 .................C.T........
klossiiNP01                 ...................T........
klossiiNP05                 ...................T........
klossiiNP10                 ...................T........
klossiiNP12                 ...................T........
klossiiNP14                 ...................T........
klossiiPL04                 ...................T........
klossiiSB04                 ...................T........
klossiiSB06                 ...................T........
klossiiSB17                 ...................T........
klossiiSB19                 ...................T........
klossiiSP03                 ...................T........
klossiiSP06                 ...................T........
klossiiSP08                 ...................T........
klossiiSP09                 ...................T........
klossiiSP11                 ...................T........
klossiiSP13                 ...................T........
klossiiSP29                 ...................T........
klossiiSR13                 ...................T........
klossiiSR31                 ...................T........
klossiiJP103                ...................C........
klossiiJP97                 ...................T........
lar2                        ...................C........
lar3                        ...................T........
molochNAN06                 ...................T........
molochNAN07                 ...................T........
molochNAN08                 ...................T........
molochNAN10                 ...................T........
molochNAN12                 ...................T........
molochNAN13                 ...................T........
molochNAN14                 ...................T........
molochNAN26                 ...................T........
molochNAN28                 ...................T........
molochNAN30                 ...................T........
molochNAN33                 ...................T........
molochNAN35                 ...................T........
molochNAN41                 ...................T........
muelleriJP92                ............................
muelleriJP93                ............................
pileatusJP99                ...................T........
Bunopithecushoolock         ............C......T........
Nomascusgabriellae          ..............T...G.......
Symphalangus                ...................T........
```

APPENDIX III

Pairwise Sequence Distances

	agilisaJP90	agilisNAN04	agilisNAN39	klossiiCA15	klossiiCA24	klossiiPL04
agilisaJP90						
agilisNAN04	0.0530					
agilisNAN39	0.0864	0.0885				
klossiiCA15	0.0921	0.1083	0.1073			
klossiiCA24	0.0982	0.1145	0.1094	0.0082		
klossiiPL04	0.1023	0.1104	0.1116	0.0389	0.0429	
klossiiSB04	0.1023	0.1104	0.1116	0.0389	0.0429	0.0000
klossiiSB06	0.1023	0.1104	0.1116	0.0389	0.0429	0.0000
klossiiSB17	0.0860	0.1104	0.1074	0.0327	0.0327	0.0348
klossiiSB19	0.1023	0.1104	0.1116	0.0389	0.0429	0.0000
klossiiSR13	0.0860	0.1022	0.1012	0.0286	0.0286	0.0307
klossiiSR31	0.0962	0.1124	0.1073	0.0082	0.0123	0.0307
klossiiNP01	0.1003	0.1165	0.1137	0.0368	0.0409	0.0143
klossiiNP05	0.0941	0.1104	0.1075	0.0389	0.0429	0.0164
klossiiNP10	0.0962	0.1125	0.1074	0.0184	0.0184	0.0368
klossiiNP12	0.1003	0.1165	0.1137	0.0368	0.0409	0.0143
klossiiNP14	0.0962	0.1125	0.1074	0.0184	0.0184	0.0368
klossiiSP03	0.1003	0.1165	0.1115	0.0286	0.0327	0.0184
klossiiSP06	0.0962	0.1124	0.1096	0.0368	0.0409	0.0143
klossiiSP08	0.1023	0.1104	0.1116	0.0389	0.0429	0.0000
klossiiSP09	0.0982	0.1145	0.1116	0.0348	0.0389	0.0123
klossiiSP11	0.1020	0.1123	0.1135	0.0409	0.0450	0.0102
klossiiSP13	0.0982	0.1145	0.1135	0.0307	0.0348	0.0164
klossiiSP29	0.0982	0.1145	0.1095	0.0204	0.0204	0.0348
klossiiJP103	0.0839	0.1043	0.1053	0.0286	0.0286	0.0307
klossiiJP97	0.0839	0.1042	0.1053	0.0307	0.0307	0.0368
lar2	0.1286	0.1347	0.1547	0.1186	0.1206	0.1349
lar3	0.1326	0.1388	0.1505	0.1206	0.1186	0.1329
molochNAN06	0.0965	0.1192	0.1307	0.0843	0.0905	0.0966
molochNAN07	0.0904	0.1191	0.1328	0.0782	0.0802	0.0967
molochNAN08	0.0879	0.1043	0.1178	0.0716	0.0778	0.0860
molochNAN10	0.1025	0.1189	0.1326	0.0778	0.0840	0.0983
molochNAN12	0.0961	0.1125	0.1281	0.0859	0.0920	0.1002
molochNAN13	0.1002	0.1166	0.1302	0.0900	0.0920	0.1002
molochNAN14	0.0920	0.1084	0.1260	0.0757	0.0818	0.0941
molochNAN26	0.0920	0.1043	0.1219	0.0798	0.0859	0.0859
molochNAN28	0.1043	0.1248	0.1323	0.0879	0.0941	0.1022
molochNAN30	0.0941	0.1105	0.1199	0.0757	0.0818	0.0900
molochNAN33	0.1069	0.1232	0.1328	0.0945	0.0966	0.1048
molochNAN35	0.1022	0.1187	0.1281	0.0941	0.0961	0.1043
molochNAN41	0.0904	0.1070	0.1246	0.0822	0.0884	0.0884
muelleriJP92	0.1206	0.1187	0.1260	0.1125	0.1186	0.1268
muelleriJP93	0.1265	0.1388	0.1340	0.1227	0.1247	0.1391
pileatusJP99	0.1558	0.1701	0.1718	0.1432	0.1453	0.1657
Bunopithecus	0.1723	0.1703	0.1990	0.1892	0.1954	0.1932
Nomascus	0.2281	0.2281	0.2597	0.2412	0.2473	0.2472
Symphalangus	0.2089	0.2069	0.2149	0.2175	0.2196	0.2134

	klossiiSB04	klossiiSB06	klossiiSB17	klossiiSB19	klossiiSR13	klossiiSR31
agilisaJP90						
agilisNAN04						
agilisNAN39						
klossiiCA15						
klossiiCA24						
klossiiPL04						
klossiiSB04						
klossiiSB06	0.0000					
klossiiSB17	0.0348	0.0348				
klossiiSB19	0.0000	0.0000	0.0348			
klossiiSR13	0.0307	0.0307	0.0082	0.0307		
klossiiSR31	0.0307	0.0307	0.0245	0.0307	0.0204	
klossiiNP01	0.0143	0.0143	0.0286	0.0143	0.0245	0.0286
klossiiNP05	0.0164	0.0164	0.0348	0.0164	0.0307	0.0348
klossiiNP10	0.0368	0.0368	0.0307	0.0368	0.0266	0.0184
klossiiNP12	0.0143	0.0143	0.0286	0.0143	0.0245	0.0286
klossiiNP14	0.0368	0.0368	0.0307	0.0368	0.0266	0.0184
klossiiSP03	0.0184	0.0184	0.0286	0.0184	0.0245	0.0204
klossiiSP06	0.0143	0.0143	0.0327	0.0143	0.0286	0.0327
klossiiSP08	0.0000	0.0000	0.0348	0.0000	0.0307	0.0307
klossiiSP09	0.0123	0.0123	0.0266	0.0123	0.0225	0.0266
klossiiSP11	0.0102	0.0102	0.0328	0.0102	0.0287	0.0328
klossiiSP13	0.0164	0.0164	0.0266	0.0164	0.0225	0.0225
klossiiSP29	0.0348	0.0348	0.0286	0.0348	0.0245	0.0204
klossiiJP103	0.0307	0.0307	0.0082	0.0307	0.0041	0.0204
klossiiJP97	0.0368	0.0368	0.0061	0.0368	0.0102	0.0266
lar2	0.1349	0.1349	0.1329	0.1349	0.1288	0.1226
lar3	0.1329	0.1329	0.1349	0.1329	0.1308	0.1247
molochNAN06	0.0966	0.0966	0.1007	0.0966	0.1007	0.0925
molochNAN07	0.0967	0.0967	0.0966	0.0967	0.0925	0.0864
molochNAN08	0.0860	0.0860	0.0900	0.0860	0.0859	0.0798
molochNAN10	0.0983	0.0983	0.1004	0.0983	0.0963	0.0860
molochNAN12	0.1002	0.1002	0.1043	0.1002	0.1002	0.0941
molochNAN13	0.1002	0.1002	0.1043	0.1002	0.1002	0.0982
molochNAN14	0.0941	0.0941	0.0941	0.0941	0.0900	0.0838
molochNAN26	0.0859	0.0859	0.0941	0.0859	0.0900	0.0838
molochNAN28	0.1022	0.1022	0.1063	0.1022	0.1022	0.0961
molochNAN30	0.0900	0.0900	0.0982	0.0900	0.0941	0.0838
molochNAN33	0.1048	0.1048	0.1110	0.1048	0.1069	0.1027
molochNAN35	0.1043	0.1043	0.1084	0.1043	0.1043	0.1022
molochNAN41	0.0884	0.0884	0.0966	0.0884	0.0925	0.0863
muelleriJP92	0.1268	0.1268	0.1268	0.1268	0.1227	0.1207
muelleriJP93	0.1391	0.1391	0.1350	0.1391	0.1309	0.1268
pileatusJP99	0.1657	0.1657	0.1576	0.1657	0.1535	0.1473
Bunopithecus	0.1932	0.1932	0.1931	0.1932	0.1891	0.1933
Nomascus	0.2472	0.2472	0.2410	0.2472	0.2410	0.2390
Symphalangus	0.2134	0.2134	0.2174	0.2134	0.2134	0.2175

	klossiiNP01	klossiiNP05	klossiiNP10	klossiiNP12	klossiiNP14	klossiiSP03
agilisaJP90						
agilisNAN04						
agilisNAN39						
klossiiCA15						
klossiiCA24						
klossiiPL04						
klossiiSB04						
klossiiSB06						
klossiiSB17						
klossiiSB19						
klossiiSR13						
klossiiSR31						
klossiiNP01						
klossiiNP05	0.0102					
klossiiNP10	0.0389	0.0368				
klossiiNP12	0.0000	0.0102	0.0389			
klossiiNP14	0.0389	0.0368	0.0000	0.0389		
klossiiSP03	0.0082	0.0143	0.0307	0.0082	0.0307	
klossiiSP06	0.0082	0.0061	0.0389	0.0082	0.0389	0.0123
klossiiSP08	0.0143	0.0164	0.0368	0.0143	0.0368	0.0184
klossiiSP09	0.0020	0.0082	0.0368	0.0020	0.0368	0.0061
klossiiSP11	0.0082	0.0103	0.0389	0.0082	0.0389	0.0123
klossiiSP13	0.0061	0.0123	0.0327	0.0061	0.0327	0.0020
klossiiSP29	0.0368	0.0348	0.0020	0.0368	0.0020	0.0286
klossiiJP103	0.0245	0.0307	0.0266	0.0245	0.0266	0.0245
klossiiJP97	0.0307	0.0368	0.0327	0.0307	0.0327	0.0307
lar2	0.1349	0.1308	0.1206	0.1349	0.1206	0.1268
lar3	0.1329	0.1288	0.1227	0.1329	0.1227	0.1288
molochNAN06	0.1027	0.0966	0.0925	0.1027	0.0925	0.0986
molochNAN07	0.0987	0.0925	0.0864	0.0987	0.0864	0.0946
molochNAN08	0.0921	0.0859	0.0757	0.0921	0.0757	0.0880
molochNAN10	0.1004	0.0983	0.0901	0.1004	0.0901	0.0963
molochNAN12	0.1063	0.1002	0.0900	0.1063	0.0900	0.1022
molochNAN13	0.1022	0.0961	0.0941	0.1022	0.0941	0.0982
molochNAN14	0.1002	0.0941	0.0798	0.1002	0.0798	0.0961
molochNAN26	0.0920	0.0859	0.0798	0.0920	0.0798	0.0879
molochNAN28	0.1084	0.1022	0.0920	0.1084	0.0920	0.1043
molochNAN30	0.0961	0.0900	0.0838	0.0961	0.0838	0.0920
molochNAN33	0.1069	0.1007	0.1007	0.1069	0.1007	0.1028
molochNAN35	0.1063	0.1002	0.0941	0.1063	0.0941	0.1022
molochNAN41	0.0987	0.0925	0.0822	0.0987	0.0822	0.0946
muelleriJP92	0.1329	0.1227	0.1166	0.1329	0.1166	0.1288
muelleriJP93	0.1411	0.1350	0.1227	0.1411	0.1227	0.1391
pileatusJP99	0.1596	0.1576	0.1433	0.1596	0.1433	0.1555
Bunopithecus	0.1933	0.1891	0.1972	0.1933	0.1972	0.1933
Nomascus	0.2473	0.2472	0.2493	0.2473	0.2493	0.2431
Symphalangus	0.2113	0.2072	0.2174	0.2113	0.2174	0.2134

	klossiiSP06	klossiiSP08	klossiiSP09	klossiiSP11	klossiiSP13	klossiiSP29
agilisaJP90						
agilisNAN04						
agilisNAN39						
klossiiCA15						
klossiiCA24						
klossiiPL04						
klossiiSB04						
klossiiSB06						
klossiiSB17						
klossiiSB19						
klossiiSR13						
klossiiSR31						
klossiiNP01						
klossiiNP05						
klossiiNP10						
klossiiNP12						
klossiiNP14						
klossiiSP03						
klossiiSP06						
klossiiSP08	0.0143					
klossiiSP09	0.0061	0.0123				
klossiiSP11	0.0082	0.0102	0.0062			
klossiiSP13	0.0102	0.0164	0.0041	0.0103		
klossiiSP29	0.0368	0.0348	0.0348	0.0369	0.0307	
klossiiJP103	0.0286	0.0307	0.0225	0.0287	0.0225	0.0245
klossiiJP97	0.0307	0.0368	0.0286	0.0348	0.0286	0.0307
lar2	0.1329	0.1349	0.1329	0.1388	0.1288	0.1227
lar3	0.1309	0.1329	0.1309	0.1367	0.1309	0.1247
molochNAN06	0.0986	0.0966	0.1007	0.1028	0.1007	0.0925
molochNAN07	0.0946	0.0967	0.0967	0.0988	0.0967	0.0884
molochNAN08	0.0880	0.0860	0.0900	0.0922	0.0900	0.0777
molochNAN10	0.1003	0.0983	0.0983	0.1045	0.0983	0.0922
molochNAN12	0.1022	0.1002	0.1043	0.1064	0.1043	0.0920
molochNAN13	0.0982	0.1002	0.1002	0.1024	0.1002	0.0961
molochNAN14	0.0961	0.0941	0.0982	0.1003	0.0982	0.0818
molochNAN26	0.0920	0.0859	0.0900	0.0921	0.0900	0.0818
molochNAN28	0.1043	0.1022	0.1063	0.1085	0.1063	0.0941
molochNAN30	0.0920	0.0900	0.0941	0.0962	0.0941	0.0859
molochNAN33	0.1028	0.1048	0.1048	0.1069	0.1048	0.1027
molochNAN35	0.1022	0.1043	0.1043	0.1064	0.1043	0.0961
molochNAN41	0.0986	0.0884	0.0966	0.0946	0.0966	0.0843
muelleriJP92	0.1247	0.1268	0.1309	0.1290	0.1268	0.1186
muelleriJP93	0.1370	0.1391	0.1391	0.1412	0.1391	0.1247
pileatusJP99	0.1596	0.1657	0.1575	0.1638	0.1575	0.1453
Bunopithecus	0.1892	0.1932	0.1913	0.1934	0.1913	0.1993
Nomascus	0.2493	0.2472	0.2452	0.2489	0.2452	0.2472
Symphalangus	0.2113	0.2134	0.2092	0.2087	0.2134	0.2195

	klossiiJP103	klossiiJP97	lar2	lar3	molochNAN06	molochNAN07
agilisaJP90						
agilisNAN04						
agilisNAN39						
klossiiCA15						
klossiiCA24						
klossiiPL04						
klossiiSB04						
klossiiSB06						
klossiiSB17						
klossiiSB19						
klossiiSR13						
klossiiSR31						
klossiiNP01						
klossiiNP05						
klossiiNP10						
klossiiNP12						
klossiiNP14						
klossiiSP03						
klossiiSP06						
klossiiSP08						
klossiiSP09						
klossiiSP11						
klossiiSP13						
klossiiSP29						
klossiiJP103						
klossiiJP97	0.0102					
lar2	0.1247	0.1268				
lar3	0.1308	0.1288	0.0286			
molochNAN06	0.1007	0.0945	0.1169	0.1149		
molochNAN07	0.0925	0.0905	0.1191	0.1129	0.0248	
molochNAN08	0.0859	0.0839	0.1042	0.1022	0.0349	0.0308
molochNAN10	0.0963	0.0942	0.1187	0.1188	0.0371	0.0329
molochNAN12	0.1002	0.0982	0.1124	0.1145	0.0349	0.0391
molochNAN13	0.1002	0.0982	0.1206	0.1145	0.0267	0.0267
molochNAN14	0.0900	0.0879	0.1124	0.1104	0.0390	0.0349
molochNAN26	0.0900	0.0920	0.1083	0.1063	0.0349	0.0349
molochNAN28	0.1022	0.1002	0.1165	0.1145	0.0452	0.0390
molochNAN30	0.0941	0.0920	0.1104	0.1083	0.0123	0.0205
molochNAN33	0.1068	0.1048	0.1315	0.1253	0.0372	0.0351
molochNAN35	0.1043	0.1022	0.1267	0.1206	0.0328	0.0308
molochNAN41	0.0925	0.0946	0.1151	0.1108	0.0413	0.0350
muelleriJP92	0.1207	0.1247	0.1185	0.1226	0.1191	0.1190
muelleriJP93	0.1288	0.1288	0.1287	0.1205	0.1232	0.1169
pileatusJP99	0.1535	0.1535	0.1310	0.1311	0.1500	0.1415
Bunopithecus	0.1891	0.1870	0.1748	0.1728	0.1879	0.1878
Nomascus	0.2390	0.2431	0.2261	0.2343	0.2584	0.2544
Symphalangus	0.2134	0.2155	0.2212	0.2149	0.2146	0.2040

	molochNAN08	molochNAN10	molochNAN12	molochNAN13	molochNAN14
agilisaJP90					
agilisNAN04					
agilisNAN39					
klossiiCA15					
klossiiCA24					
klossiiPL04					
klossiiSB04					
klossiiSB06					
klossiiSB17					
klossiiSB19					
klossiiSR13					
klossiiSR31					
klossiiNP01					
klossiiNP05					
klossiiNP10					
klossiiNP12					
klossiiNP14					
klossiiSP03					
klossiiSP06					
klossiiSP08					
klossiiSP09					
klossiiSP11					
klossiiSP13					
klossiiSP29					
klossiiJP103					
klossiiJP97					
lar2					
lar3					
molochNAN06					
molochNAN07					
molochNAN08					
molochNAN10	0.0266				
molochNAN12	0.0204	0.0307			
molochNAN13	0.0327	0.0348	0.0409		
molochNAN14	0.0082	0.0287	0.0245	0.0368	
molochNAN26	0.0123	0.0307	0.0245	0.0327	0.0164
molochNAN28	0.0368	0.0389	0.0450	0.0491	0.0409
molochNAN30	0.0266	0.0287	0.0348	0.0184	0.0307
molochNAN33	0.0432	0.0432	0.0514	0.0227	0.0472
molochNAN35	0.0389	0.0410	0.0470	0.0225	0.0429
molochNAN41	0.0185	0.0371	0.0309	0.0391	0.0226
muelleriJP92	0.1002	0.1107	0.1125	0.1166	0.1043
muelleriJP93	0.0961	0.1168	0.1125	0.1206	0.1002
pileatusJP99	0.1331	0.1395	0.1412	0.1453	0.1372
Bunopithecus	0.1851	0.1875	0.1871	0.1890	0.1891
Nomascus	0.2369	0.2351	0.2430	0.2572	0.2368
Symphalangus	0.1974	0.2120	0.2076	0.2013	0.2013

	molochNAN26	molochNAN28	molochNAN30	molochNAN33	molochNAN35
agilisaJP90					
agilisNAN04					
agilisNAN39					
klossiiCA15					
klossiiCA24					
klossiiPL04					
klossiiSB04					
klossiiSB06					
klossiiSB17					
klossiiSB19					
klossiiSR13					
klossiiSR31					
klossiiNP01					
klossiiNP05					
klossiiNP10					
klossiiNP12					
klossiiNP14					
klossiiSP03					
klossiiSP06					
klossiiSP08					
klossiiSP09					
klossiiSP11					
klossiiSP13					
klossiiSP29					
klossiiJP103					
klossiiJP97					
lar2					
lar3					
molochNAN06					
molochNAN07					
molochNAN08					
molochNAN10					
molochNAN12					
molochNAN13					
molochNAN14					
molochNAN26					
molochNAN28	0.0368				
molochNAN30	0.0266	0.0348			
molochNAN33	0.0410	0.0575	0.0288		
molochNAN35	0.0389	0.0552	0.0245	0.0267	
molochNAN41	0.0185	0.0473	0.0329	0.0454	0.0329
muelleriJP92	0.1002	0.1207	0.1063	0.1273	0.1227
muelleriJP93	0.1002	0.1206	0.1104	0.1314	0.1267
pileatusJP99	0.1331	0.1351	0.1392	0.1521	0.1515
Bunopithecus	0.1809	0.1727	0.1768	0.1961	0.1951
Nomascus	0.2327	0.2450	0.2470	0.2627	0.2614
Symphalangus	0.1931	0.2011	0.2013	0.2081	0.2072

	molochNAN41	muelleriJP92	muelleriJP93	pileatusJP99	Bunopithecus	Nomascus
agilisaJP90						
agilisNAN04						
agilisNAN39						
klossiiCA15						
klossiiCA24						
klossiiPL04						
klossiiSB04						
klossiiSB06						
klossiiSB17						
klossiiSB19						
klossiiSR13						
klossiiSR31						
klossiiNP01						
klossiiNP05						
klossiiNP10						
klossiiNP12						
klossiiNP14						
klossiiSP03						
klossiiSP06						
klossiiSP08						
klossiiSP09						
klossiiSP11						
klossiiSP13						
klossiiSP29						
klossiiJP103						
klossiiJP97						
lar2						
lar3						
molochNAN06						
molochNAN07						
molochNAN08						
molochNAN10						
molochNAN12						
molochNAN13						
molochNAN14						
molochNAN26						
molochNAN28						
molochNAN30						
molochNAN33						
molochNAN35						
molochNAN41						
muelleriJP92	0.1088					
muelleriJP93	0.1005	0.0593				
pileatusJP99	0.1399	0.1413	0.1434			
Bunopithecus	0.1856	0.1808	0.1993	0.2074		
Nomascus	0.2419	0.2388	0.2593	0.2533	0.2120	
Symphalangus	0.1979	0.2175	0.2298	0.2292	0.1684	0.2194

APPENDIX IV

Microsatellite Genotypes

	D3S1766		D5S1457		D11S1366	
Sample Name	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**
DJW	204	216	116	120	222	238
CA11			136	136		
CA15/CA16	280	284	136	140	242	246
CA24/CA25	256	272	106	136	238	242
JP103	268	268			242	242
NP12					238	238
PL04			132	132	242	242
SAS1			132	144		
SB04					230	242
SB06/SB08					230	234
SB18/SB19					230	238
SP03	276	276			206	246
SP06	272	272				
SP09	276	276			230	238
SP10						
SP11					234	238
SP13	280	280	132	136	234	238
SP29	268	276	124	132		
SR12/13	268	296	106	152	234	238
SR31	276	296	132	132	234	238
RANGE	256	296	106	152	206	246

Highlighted cells have been confirmed by 2 or more replications.
Highlighted homozygotes have been confirmed by 3 or more replications.

	D12S391		D14S306		D19S714	
Sample Name	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**
DJW	204	216	196	208	220	236
CA11			208	212		
CA15/CA16	220	224	204	208	244	276
CA24/CA25			204	208	236	240
JP103			204	208	240	240
NP12	220	240			284	284
PL04	216	240			236	240
SAS1	216		204	204		
SB04	220	244	204	208		
SB06/SB08	220	244	200	204	284	284
SB18/SB19	220	228	220	228		
SP03	216	216	216	216	244	284
SP06			208	216		
SP09			216	216	284	284
SP10						
SP11	208	208	212	216	288	288
SP13	208	208	208	212	240	280
SP29			204	212	240	276
SR12/13	216	224	208	216	280	284
SR31	216	220	208	212	288	292
RANGE	208	244	200	228	236	292

Highlighted cells have been confirmed by 2 or more replications.
Highlighted homozygotes have been confirmed by 3 or more replications.

APPENDIX V

Raw Survey Data

North Siberut

Site 1: Base camp "Pondok", GPS 0º58.128' S, 98º48.536' E

Date	Time	Direction	Distance	Sex
4/1/01	300	165	300-500	M
	500	90	800	M
	530	30	800	M
4/2/01	459	180	1000	M
	513	90	800	M
	522	140	800	M
	548	160	1000	M
4/4/01	616*	140	1000	M
	620*	160	900	M
4/6/01	240*	160	800	M
	343	40	800	M
	347*	180	700	M
	350**	140	700	M
	353**	120	900	M

** calls are presumed to be from same group*
*** calls are presumed to be from same group*

Site 2: "Voc1", 0º58.409' S, 98º49.471' E

Date	Time	Direction	Distance	Sex
4/2/01	814	40	1000	F
	814	160	1000	F
	818	300	1000	F

Site 3: “Voc2”, 0º58.036' S, 98º49.649' E

Date	Time	Direction	Distance	Sex
4/4/01	750	355	800	F
	757*	280	500	F
	758	45	700	F
	800*	300	400	F
	802	45	700	M
	803	95	400	F
	820	190	300	F
	828	280	500	M
	835	95	400	M
4/5/01	900	160	1000	F
	905	90	800	F
	1008	120	300	M
	1008	20	250	M
	1040	120	900	M
	1044	220	800	M

** calls are presumed to be from same group*

Site 4: Siberut Conservation Project field station, GPS: 1º01.070' S, 98º50.297' E

Date	Time	Direction	Distance	Sex
9/17/03	440	110	500	M
	445	150	1000	M
	455	170	900	M
	500	230	500	M
9/18/03	445	130	1000	M
	450	110	500	M
	500*	300	300	M
	520*	340	300	M
9/19/03	445	0	1000	M
	500	170	400	M
	505	300	600	M
	510	120	750	M
9/20/03	515	140	500	M
	545	30	300	M
9/22/03	505	110	1000	M
	510	90	700	M
9/23/03	no calls			
9/24/03	415	70	300	M
	415	220	600	M
	430	150	1000	M
	440	320	600	M

** calls are presumed to be from same group*

Site 5: "Voc3", GPS: 1º01.234' S, 98º50.043' E

Date	Time	Direction	Distance	Sex
9/22/03	740	80	1000	F
	745	310	300	F
	745	0	500	F
	750	270	100	F
9/25/03	800	70	1000	F
	805	90	800	F
	805‡	310	750	F
	807‡	280	600	F
	817	340	500	F
	830	125	750	F

‡ calls are 400 meters apart but may be different groups

Siberut National Park

Base camp, GPS 1º22.599' S, 98º56.975' E

Date	Time	Direction	Distance	Sex
4/17/01	525	90	500	M
	528	320	700	M
	532	40	900	M
	534	210	1000	M
	544	0	700	M
4/18/01	414	20	1000	M
	414	310	800	M
	458	120	1000	M
	508	160	1000	M
	510	70	600	M
	511*	0	400	M
	520	250	600	M
	529*	30	500	M
4/20/01	545	320	1000	M
	550	340	1000	M
	752	290	1000	M
4/24/01	756	50	1000	F
	803	30	300	F
	825	210	300	F
	840	300	800	F
	930	60	800	M
	935	30	600	M

** calls are presumed to be from same group*

Taileleu, South Siberut

Site 1: Base camp, GPS 1º42.621' S, 99º08.738' E

Date	Time	Direction	Distance	Sex
11/10/03	150	0	300	M
	230*	240	500	M
	230*	260	600	M
11/11/03	515	30	1000	M
	515	250	700	M
	540	0	900	M
11/12/03	500	0	200	M
	505	240	900	M
	520	290	500	M
	643	0	500	F
11/15/03	520	240	1000	M
	710	10	750	F
11/16/03	500	30	600	M
	500*	260	400	M
	515*	240	400	M
	800	250	750	F
	800	20	600	F
	810	310	800	F
11/18/03	no calls			
11/19/03	no calls			

** calls are presumed to be from same group*

Site 2: “Boats”, GPS: 1º42.597' S, 99º08.410' E

Date	Time	Direction	Distance	Sex
11/14/03	825	140	800	F
	833	290	1000	F
	836	340	600	F
11/15/03	no calls			
11/17/03	no calls			

Sipora

Site 1: “Clearing”, GPS 2º07.464' S, 99º37.711' E

Date	Time	Direction	Distance	Sex
8/25/03	1045	150	500	M
	1045	220	600	M
12/11/03	826	225	1000	F
	832	200	800	F
12/12/03	no calls			

Site 2: GPS 2º07.032' S, 99º37.903' E

Date	Time	Direction	Distance	Sex
12/11/03	832*	200	1000	F
	832*	270	1000	F

** calls are presumed to be from same group*

Site 3: GPS 2º07.263' S, 99º36.660' E

Date	Time	Direction	Distance	Sex
12/16/03	915	0	0	M
	915	210	500	M
	915	320	1000	M

Site 4: GPS 2º07.854' S, 99º37.627' E

Date	Time	Direction	Distance	Sex
12/18/03	500	0	0	M
	530	160	1000	M
	530	350	1000	M

South Pagai

Site 1: KM34 GPS 2º58.197' S, 100º17.516' E

Date	Time	Direction	Distance	Sex
10/13/03	620*	0	800	F
	620	90	500	F
	620*	330	700	F
	625	190	200	F
10/14/03	810	250	600	F
	810*	200	300	F
	815*	230	200	F
	815	0	1000	F
10/18/03	no calls			
10/20/03	827	305	300	M

** calls are presumed to be from same group*

Site 2: KM 32, GPS 2º57.980' S, 100º18.482' E

Date	Time	Direction	Distance	Sex
10/15/03	750	120	150	F
10/16/03	no calls			
10/17/03	620	310	200	M
	625	320	500	M
	730	275	700	F
	731	345	1000	F
	740	230	1000	F
	745	360	500	F
10/20/03	no calls			

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