NICHE DIFFERENTIATION OF TWO SYMPATRIC COLOBINES
Simias concolor AND *Presbytis potenziani*
ON THE MENTAWAI ISLAND OF SIBERUT INDONESIA

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Earth provides enough to satisfy every man's need, but not every man's greed

Mohandas Karamchand Gandhi (1869 – 1948)

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Chapter 1.

GENERAL INTRODUCTION

1.1 . General principles of niche differentiation

Mechanisms which allow ecologically similar species to coexist are fundamental issues in community ecology. Gause (1934) identified the problem of a coexistence of two species, if both of them rely on the same kind of environmental conditions and resources. Therefore, two or more species that compete for exactly the same resources cannot permanently coexist – a phenomenon known as the “Competitive Exclusions Principle”.

The adaptive mechanisms enabling a sympatric coexistence of two closely related species within a habitat, which offers limited supplies of certain resources, later became clearer with the niche concept. A niche is described as a region in the multi dimensional hypervolume, in which a species can maintain a viable population (Hutchinson, 1957; Tokeshi, 1999). If resources are limited, different species with similar ecological requirements can coexist (i.e. are not forced to outcompete each other) only if they differ in at least one niche dimension (Gause, 1934). Hutchinson`s term “hypervolume” comprises abiotic factors, such as temperature, humidity, light intensity or salinity, which are combined with biotic factors, such as habitat type/size and food availability. Subsequently, Schoener (1974) identified the three factors habitat-type, food-type and differential activity patterns to further specify Hutchinsons idea of a multi-dimensional space in which competition between species can be reduced by niche differentiation. Furthermore Hutchinson (1959) also suggests that species can use the same type of resources if they differ in body mass or morphological characteristics. These mechanisms seem to operate in and to structure most sympatric primate communities (Rakotondranary and Ganzhon, 2011). Species that make use of the same resource in a similar way while they are in allopatry have to modify their modes of resource exploitation when their distribution ranges start to overlap, to be able to coexist. This adaptation results in behavioral, physiological or morphological divergence, termed character displacement (Rakotondranary, 2011). Possible competition seems to be aggravated between congeneric species and should be most pronounced in sister species because they share more genes with each other than they do with any other species (Simberloff and Dayan, 1991; Houlé, 1997).

The three factors in defining ecological niches of sympatric primates have been well demonstrated for a wide variety of primate taxa (Singh *et al.* 2000; Vasey 2000; Eckardt and Zuberbühler, 2004). Among the 56 species of colobine monkeys, all of which are known to be predominantly arboreal and morphologically specialized leaf eaters, shared habitats over major portions of their geographic distribution area are rare (Redmond 2008). Therefore, sympatrically living colobines represent a particularly interesting model to study the mechanisms of niche differentiation between closely related and similarly specialized primate species.

1.2. Colobines

a) Overview and general characteristics

Within the family Cercopithecidae and next to the Cercopithecinae, Colobine monkeys represent the large subfamily Colobinae. The colobine monkeys are divided into two groups, which are distributed on two different continents. The subtribe Colobina lives in Africa and is currently found in the forested areas of the sub-Saharan region. The distribution of the second subtribe, Presbytina or Semnopithecina, ranges from mainland south to south east Asia, including southeast Asian archipelagos (Delson 1975).

Compared to the Cercopithecinae, Colobine monkeys differ in several morphological aspects, such as: longer hindlimbs than forelimbs, a long tail, long phalangs but reduced or almost absent thumbs, an increased relief of molar teeth, enlarged salivary glands and a more complex gastrointestinal system to digest their fiber rich food (Oates and Davies, 1994).

A typical anatomical characteristic for colobine monkeys is represented by a complex gastrointestinal tract. The stomach has four chambers: presaccus, saccus, tubulus gastricus and pars pylorica (Kuhn, 1964). The presaccus and saccus make up an expanded and sacculated forestomach, in which microbial fermentation occurs. Thus, the digestive process of colobines is ruminant like, in which a large quantity of leaves, seeds and other plant material is detoxified and further processed to breakdown cellulose and secondary compounds/ingredients (Chiver, 1994). Hence, colobines can subsist on a heavily folivorous diet and exploit abundant food resources less usable by other primates (Oates and Davies, 1994). Although leaves make up a large portion of their diet, in some colobine species, such as the Thomas langur (Gurmaya, 1986) and the Red colobus (Clutton-Brock, 1977), fruits and seeds can be the dominant food resource.

b) Phylogenetic relationships.

The subfamily Colobinae most likely originated in western Africa (Ross *et al*, 2011). Firstly, *Colobus* split off from the main stem (~10.9 mya) followed shortly afterwards by the progenitor of *Piliocolobus* and *Procolobus* (~10.7 mya) (Ross *et al*, 2011). The ancestors of Asian colobines most likely invaded Eurasia in the late Miocene via a land bridge connecting Africa and the Arabian Peninsula (Stewart and Disotell, 1998). Subsequently, the populations dispersed into eastern Asia via a route north of the Himalaya. After their arrival at the Hengduan Mountains, Asian colobines diversifed into lineages comprising the progenitors of

Semnopithecus, the odd-nosed mokeys and *Presbytis/ Trachypithecus*. *Semnopithecus*, later colonized the Indian subcontinent. Shortly afterwards the progenitor of *Trachypithecus / Presbytis* split off from the group of odd-nosed monkeys and dispersed into southern mainland Asia, a process during which both genera diverged from each other (Ross *et al*, 2011).

The genus *Presbytis* diverged from *Trachypitecus* when they first entered the Malaysian Peninsula and subsequently Sundaland during periods of lowered sea levels (Miller *et al*, 2005). In the course of these migration events, the ancestor of *Presbytis potenziani*, most probably colonized the Mentawai islands during a major glacial in the late Pleistocene via a land bridge between Sumatra and the Mentawai archipelago between 3.4 and 1.9 mya (Ziegler *et al* 2007; Meyer 2011). A similar history of colonization can also be assumed for the odd nosed monkey *Simias concolor*. During the late Miocene, odd-nosed monkeys migrated from China to the South and expanded their range into Indochina and Sundaland (Meyer, 2011). This group of odd nosed monkeys split during the Pleistocene (1.1-1.9 mya), into *Simias*, today endemic to the Mentawai Islands, and *Nasalis*, the most closely related genus of *Simias*, which more recently colonized Borneo (Roos *et al*, 2011).

c) Ecology of African and Asian colobines

The vast majority of colobine species is strictly arboreal, whilst only a few species live semi-terrestrially. They are found in a relatively great variety of habitats and climate zones. African colobines show a wide distribution in tropical African forests from the Atlantic coast of the far west to the coasts of the Indian Ocean in Kenya and Tanzania. The majority of species lives in moist lowland forests, but some members of these primate taxa live in deciduous forests, savanna woodlands and montane forest zones (Oates *et al* 1994).

Asian colobines inhabit a wide variety of forest types, from tropical rain forest to montane, mangrove, temperate and highly seasonal forests. Hence they are distributed over a wide geographic range, from China to Java and from India to Borneo (Benett & Davies 1994).

Presently, colobine monkeys are almost absent in open habitats where considerable terrestrial locomotion is required (but see *Semnopithecus entellus*). However, fossil evidence suggests, that during the Miocene and Pliocene colobines were distributed over larger geographical areas, and many of these earlier colobines lived in relatively open woodlands and were at least partly terrestrial (Oates and Davies, 1994).

Today most colobine species live in relatively small social groups containing several adult females and a single adult male but some species form groups of over one hundred individuals with many adult males (Oates and Davies, 1994). Regarding their social behavior, colobine monkeys, exhibit less obvious dominance hierarchies and show less frequent interactions between the individuals of the groups, compared to many other group living primate taxa (Yeager and Kool, 2000).

The taxonomic group of colobine monkeys includes some of the most threatened primate species and sub species due to the fragmentation and destruction of their habitats. Their vulnerability largely derives from their ecological dependency on forested habitats, which are increasingly being cleared for commercial logging and agriculture (Marsh *et al* 1987). In addition, hunting poses a major threat for these primates in certain regions (Oates and Davies, 1994). Therefore, the continued survival of many colobine species will depend on a combination of an effective habitat protection and the elimination of hunting (Yeager and Kool, 2000).

d) Sympatry in colobines

There are relatively few examples of sympatric colobines. Sympatry among African colobines can be found in *Procolobus badius* and *Colobus guereza* in Central Africa (Struhsaker & Oates. 1975), and in *Procolobus badius* and *Procolobus verus* in West Africa (Struhsaker & Oates. 1975). Similarly, examples of sympatric colobines in Asia can be found in Sri Lanka, between *Semnopithecus entellus* and *Trachypithecus vetulus* (Hladik, 1977 and Bennett & Davies, 1994), on Borneo, between *Presbytis rubicunda* and *Presbytis hosei* (Medway, 1970) and on the Malayan peninsula between *Trachypithecus obscurus* and *Presbytis femoralis* (Curtin, 1980; Davis *et al*. 1988; Curtin and Chivers, 1978). These examples of colobine sympatry however, refer to species that have a wide geographic distribution and show a rather parapatric (or only partly overlapping) distribution.

In stark contrast, the Mentawaian colobines *Presbytis potenziani* and *Simias concolor* occur exclusively on a small archipelago (7000 km^2) off the west coast of Sumatra, where they coexist sympatrically across their entire distribution ranges.

1.3. Mentawai colobines

a) Species description

Simias concolor resembles a macaque-like body with relatively short arms and legs of similar length (Napier, 1985). The species exhibits sexual dimorphism in which males are on average 29% heavier than females (7.7: 7.1 kg, male: female; Rowe, 1996) and male canines are about twice as long as those of the females (Tenaza & Fuentes, 1995). *S. concolor* shows two colour phases, which are not related to sex, a blackish-gray coat and a golden coat (Tilson, 1977). The species also shows a small sexual swelling in females, which is a unique feature among Asian colobines (Tilson, 1977). Most of their social groups are relatively small (Tilson, 1977; Watanabe, 1981) with usually one male and one or more females and offspring (Mittermeyer *et al*, 2009). Based on IUCN`s Red List of threatened species (2011), the species is classified as Critically Endangered A2cd and listed as one of the 25 most endangered primate species worldwide (Mittermeyer *et al*, 2009).

In contrast, *Presbytis potenziani* has a slender body with hind limbs much longer than their forelimbs (Oates and Davies, 1994). The species does not exhibit a sexual dimorphism (Tilson & Tenaza 1976). The body mass of males and females is almost equal, showing 6.5 and 6.4 kg on average. Previously, *P. potenziani* was also reported to form small social groups of one adult male and one adult female and their offspring (Fuentes, 1996). Infants are born with a white coat and pale skin, which is the typical natal coat within the *aygula* group of *Presbytis* (Tilson, 1976). Similar to *S. concolor*, the conservation status of *P. potenziani* is Critically Endangered (IUCN, 2011).

b) Special situation of Mentawai colobines

As mentioned above, in contrast to all other recent colobines, the Mentawai colobines *P. potenziani* and *S. concolor* show a relatively small and geographically isolated distribution range confined to an archipelago of just about 7.000 km^2, where they coexist sympatrically across the entire area. Both species occupy all habitat types found on the Mentawai islands, such as primary forest, mixed forest, swamp forest, mangrove forest as well as secondary forests. The species coexist in low land forests near the shores as well as on forested slopes and ridges of hills. This unusual case of complete sympatry of the two Mentawaian colobines is probably closely related to the natural history of these islands, which created the special zoogeographic picture, seen today.

1.4. Geology and Mentawai island biogeography

a) Mentawai islands-biogeography.

The Mentawai islands represent a chain of four main islands (from north to south: Siberut, Sipora, North- and South Pagai), which are situated 85 - 135 km off the west coast of Sumatra. The total land area of these islands comprises about 7000 square kilometers. The northernmost island of Siberut is the largest Mentawai island, followed by North- and South Pagai, which are separated by a narow chanel, and Sipora, the central an smallest (main) island of the archipelago (WWF, 1980).

Based on paleo-geological data, the Mentawai archipelogo has been separated from main Sundaland by a 700-1700 m deep marine trough, since the Mid-Pleistocene, about 500 000 years ago (Verstappen, 1975, 1980; Brandon-Jones, 1978; Tilson, 1980). The only possible earlier connection to the mainland via a landbridge may have been through the Batu islands in the north, during low sea level stands. The Mentawai islands are considered to be oceanic islands, which were isolated from the dynamic evolutionary events on Sundaland during extended periods of time (WWF, 1980). Bathymetric data even suggest that the Mentawai islands were isolated from the mainland (today Sumatra), before the last Pleistocene separation of Sumatra from the Malay Penninsula, Kalimantan and Java (Tenaza, 1975).

Mentawai rainforests represent a unique element of south-east Asian forests, which are among the most biologically diverse areas in the world (Myers *et al.*, 2000). This island ecosystem and its biodiversity was considerably affected by Quaternary glaciations (van der Kaars & Dam, 1995; Morley, 2000). During major glaciation events most of the vegetation of Sundaland consisted probably of a mixture of savannah and patchy deciduous forests (Morley, 2000). Obligate rainforest species were most likely been confined to a few refuges in northern Borneo, northern Sumatra and the Mentawai islands (Brandon-Jones, 1998). Due to its long termed geographic isolation the Mentawai islands have undergone an evolutionary process, which resulted in a relatively high number of endemic plant and animal species. Today, it is estimated that about 15 % of the natural flora of Mentawai is endemic. Some of these plant species are also found elsewhere in South East Asia, however, the Mentawai forms of these species show an unusually increase in height or grow extraordinarily large (WWF, 1980).

About 65% of the mammals found on the Mentawais are recorded to be endemic at the genus or species level (WWF 1980). Although the rate of endemism in birds is much lower than in mammals, at least 12 out of 106 species were recorded to be endemic on a species or subspecies level (WWF, 1980).

The presence of nine endemic species of non-volant rainforest-obligate mammals on the Mentawais (WWF report 1980) indicates that these islands have been continually covered by evergreen and ever fruiting rain forest since they were separated from the mainland. Studies on termites also indicate that the islands have been an ancient rainforest refuge (Gathorne-Hardy *et al*., 2002; Gathorne-Hardy, 2003).

b) Mentawai primates and their evolutionary history

The most remarkable element of the endemic fauna on the Mentawai islands concerns the presence of five non-human primate species out of four genera. Representatives of all four genera live sympatrically across the entire area of the archipelago. In relation to Mentawais total land surface this represents the highest rates of primate endemism worldwide (WWF, 1980). Apart from the Kloss gibbon (*Hylobates klossii*) all Mentawaian primates can be divided into two populations, distinguishable on a subspecies or even species level. They are divided geographically between the southern islands (Sipora, North Pagai and South Pagai), and the northernmost and largest island of Siberut. The southern islands are inhabited by the

Mentawai macaque *Macaca pagensis* and the Mentawai langurs *Presbytis potenziani potenziani* and *Simias concolor concolor*. On Siberut the Mentawai langurs are distinguished as *Presbytis potenziani siberu* and *Simias concolor siberu* (WWF, 1980). Most recently, and based on molecular genetic studies the macaques on Siberut island were identified as a distinct species, *Macaca siberu*, which is more closely related to *Macaca nemestrina* on Sumatra than to *M. pagensis* on the southern Mentawai islands (Roos *et al*. 2003; Ziegler *et al*. 2007).

These recent molecular genetic studies on Mentawai macaques (Roos *et al*.2003; Ziegler *et al*. 2007) and also on the Mentawai langur *P. potenziani* (Meyer, 2011) suggest that the primate populations on the Mentawai islands were most probably formed by two distinct colonization events. During a first colonization event (sea level low stand 2.4-2.6 mya), ancestral forms of the Mentawai primates colonized the entire Mentawai archipelago via a landbridge, which most likely existed during a major glacial in the late Pleistocene between Sumatra and northern Siberut. During a second immigration event, about one million years later, another colonization of macaques from Sumatra occurred, but they were only able to outcompete (or hybridize with) the macaques on Siberut, their entrance island to the Mentawai archipelago, whereas the southern island populations remained unaffected (Roos *et al*.2003; Zielger *et al* 2007; Thinh *et al* 2010; Meyer 2011).

In contrast to the colobines and macaques of Mentawai, in which morphological and genetic differences could be identified, no such differences have been found for the Kloss gibbon. This lack of differentiation across islands may be linked to the fact, that these primates have longer life histories and generation times compared to the other genera (Whittaker 2009).

1.5. Lack of information

The absence of available data on niche differentiation between the two Mentawai colobines is in stark contrast to the high potential value of information on costs and benefits of such an ecological adaptation within a highly specialized primate genus, which comprises more than 50 species. Furthermore, the case of the two sympatric colobine species is of special scientific interest, as it can serve as a model to answer questions on the mechanisms of niche differentiation between closely related primates within a small island refuge.

The results of the study will yield information useful to evaluate the adaptive potential and flexibility of these primates and to assess the differential consequences of selected forest degradation and land conversion for the two sympatric Mentawaian langurs.

1.6. Objectives and specific questions

The main objective of this study is to identify the mechanisms of the ecological niche differentiation between the two sympatric colobines *P. potenziani and S. concolor* on the Mentawai island of Siberut. In order to reach this goal specific questions will be addressed and elaborated regarding their species specific i) habitat requirements/preferences ii) physical characteristics iii) group sizes iv) diet and v) activity patterns

Regarding the habitat, the present study was set up to:

a) characterize the Peleonan forest (i.e. the study area in northern Siberut) in order to assess specifics which support the coexistence of the two colobine species and compare these data to other forest habitats within the Mentawai islands.
b) describe how the species exploit their habitat using their biomass as a variable and compare those data to colobine populations living in other habitats within the Mentawais and to other sympatric colobines.
c) relate the different physical characteristics of the colobines to their species specific movements and three dimensional use of their habitat.

d) assess the food availability within the study area and the differential diet of the colobines on a monthly basis

   and

e) record the daily activity patterns of both species.

According to the specific questions presented above the following chapters present the results of the related studies in the form of three international publications:

Chapter two describes the forest i.e. the habitat in which the two colobine species live sypatrically, in order to get basic data on the forest type and habitat requirements. This assessment comprises data on tree diversity, species composition and richness as well as forest structure and represents the first publication, characterizing the mixed lowland rainforest in northern Siberut. The floristic data collected were based on three categories of growth phases and apart from a description of the canopy structure, the differential dominance of tree species and families was determined using the Important Value Index.

Chapter three elaborates the physical characteristics and group composition of *Simias concolor*. Previously, the mating system of *S. concolor* was disputed as showing either one male-one female, one male-multi female or one male–one- or multi female units. Here we could describe for the first time that the species exhibits a typical colobine mating system, represented by one male-multifemale groups (i.e. polygyny).

Chapter four deals with some important key questions, regarding the mechanisms of the ecological niche differentiation between these two colobines. The chapter describes how the two species share their natural resources in terms of space (home range size, canopy use), time (daily activity budgets) and species specific diets (food preferences and compositions). Based on the comprehensive and detailed datasets on the diets of the species, their ecological niche breadths and niche overlap could be calculated using the standardized Levin`s and Pianka`s indices.

In chapter five, the results of chapter 2-4 are discussed breadthwise and the role of habitat characteristics for the thriving of Colobine populations is described in a comparative approach. Furthermore, the relationship between physical characteristics and habitat use (threedimesional movements and exploitation of available food recourse) of the two species is described in greater detail. Finally, based on the results of the present study, some important recommendations for conservation strategies to be implemented on the Mentawai islands are being made.

Chapter 2.

TREE DIVERSITY AND FOREST STRUCTURE IN NORTHERN SIBERUT, MENTAWAI ISLANDS, INDONESIA

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Abstract

We assessed tree diversity, species composition and forest structure of 3.4 km² of primary rainforest in an important conservation area in N Siberut, Indonesia. We used floristic data from 34 20x20m plots for trees ≥20 cm diameter at breast height (dbh), 34 10x10m plots for poles (10-19 cm dbh) and 34 5x5m plots for saplings (<10cm dbh). In total, 136 species were recorded from 93 trees, 58 poles and 86 saplings, with an estimated total species richness of 180 (Michaelis Menten species richness estimator). Overall, 84 genera and 40 families were represented, with Euphorbiaceae, Lauraceae, Myrtaceae and Rubiaceae being most important in terms of species number and Myristicaceae in terms of individuals. At species level, species such as *Mallotus subpeltatus* and *Knema sumatrana,* as well as *Baccaurea deflexa* were most dominant in all dbh classes based on the Important Value index (IV), but only seven species reached IV indices of ≥ 5, reflecting the high evenness and low dominance of dipterocarps in the tree community. Among tress ≥20cm dbh, >50 % were within the 20-39 cm dbh class and 73% of trees formed a canopy between 6 and 20m in height, whereas emergent dipterocarps reached heights above 55 m (*Dipterocarpus elongatus*) and diameters above 230 cm (*Shorea pauciflora*). The mixed composition of this forest emphasizes its significance for the biodiversity of the region.

***Key words**:* Biodiversity hotspot, Evergreen lowland rainforest, Forest structure, Mentawai, Siberut island, Species richness, Tree diversity

2.1. Introduction

The Malesian region is considered to be one of the most diverse of the world's 152 floristic provinces, with about 40.000 vascular plants recorded (Baas *et al*. 1990; Roos 1993). About one third of these species are trees more than 10 cm in diameter (Jacobs 1974; Whitmore 1989). Due to their different biogeographical and palaeoecological histories, the islands of this region show extraordinary floristic differences.

A chain of four main islands represents the Mentawai archipelago, situated about 130 km off Sumatra's west coast. Siberut, the largest and northernmost island of the Mentawais, lost its last land-bridge connection to mainland Sumatra more than 500 000 years ago (Verstappen 1975). Due to this prolonged period of biogeographic separation, its fauna and flora have evolved in isolation since the mid-Pleistocene and this process has resulted in a relatively high number of endemic species. Some species are considered to be relicts of early Sundaland communities, whereas others have evolved into forms clearly distinct from the representatives found on the Asian mainland. Accordingly, seventeen out of thirty-four mammal species, including all four primate species found on Siberut, are known to be endemic (Whitten *et al*. 2000; Roos *et al*. 2003), whereas the number of endemic animal species on lower taxonomic level can only be estimated. Consequently, the protection of Siberut´s wildlife habitats ranks as a priority for conservation even within the "Sundaland Hotspot of Biodiversity" (Conservation International 2002).

Although the primary forests on the Mentawai islands represent the ecological refuge for the survival of most of these unique species, they have been under relentless pressure from logging and land conversion for several decades. Previously, the richness of plant species that make up these forests was reported to be relatively low compared to mainland forests on Sumatra (WWF 1980; Whitten 1982; Whitten *et al*. 2000) with several species of trees (e.g. Leguminosaceae) being completely absent. In general the tropical evergreen rainforests of Siberut can be categorized into five different forest types: primary dipterocarp and primary mixed forest, the less widespread peat swamp forest, mangrove forest and *Barringtonia* forest types. According to Whitten *et al*. (2000), up to 90% of Siberut`s forests are made up from primary dipterocarp and primary mixed forest. Many of the common plants found on the island are very similar to those found on mainland Sumatra, having evolved during the Tertiary when the Mentawais were still connected to the mainland (Paciulli 2004). Nevertheless, many of the woody plants and herbs remain to be described, despite the fact it is now over 80 years since the original floristic explorations of the Mentawai islands by Ridley (1926). Today Siberut‘s flora is reported to consist of 846 species out of 390 genera belonging to 131 families, but it is generally assumed that the list of plant species known to be endemic is incomplete, and that over time new species will be identified. (Unesco MAB 2004).

Due to the dramatic loss of rainforest habitat on the islands during the last three decades, all endemic forest wildlife of the Mentawais is under threat (e.g. primates: Eudey *et al*. 2000). According to Whittaker (2006) who compiled forest cover data for Siberut, the primary forests that covered almost all of the 4,030 km^2 island has been reduced to 3,500 km^2 by the 1980´s and in 1995 only 2,400 km^2 remained. Today most of the remaining intact forest is found within Siberut National Park on the western part of the island and in the North, while forest disturbance and fragmentation caused by legal and illegal logging as well as land conversion for local agriculture (Martin in prep.) is visibly increasing in the remaining parts of the island.

Although logging companies have operated systematically on Siberut since the early 70´s and the forest plays an important role in the traditions and daily life of the indigenous people, there is still very little published information on the tree communities and vegetation structure of the primary forests on this island. The only previous detailed study on primary forests of Siberut, using floristic and structural data, was conducted at Paitan and Sirimuri in central Siberut (Whitten 1982) as part of a study on the ranging behaviour of Kloss Gibbons (*Hylobates klossii*). Other research on forest structure and tree species composition was carried out mainly in secondary and disturbed forests of the southern Mentawai islands (Fuentes 1994; Paciulli 2004; Sangchantr 2004). No information exsists about the remaining evergreen rain forest in northern Siberut.

Here, we report on the tree community and forest structure of a largely undisturbed primary forest in northern Siberut. The study aims to determine the taxonomic and structural composition of the Peleonan forest. This forest is representing the core study area of an important field site for primate research and conservation (Waltert *et al.* 2008). The data presented here form an important basis for comparative ecological studies on this ecosystem. This includes not only the comparison of tree diversity and composition with mainland forests, but also the ecology and habitat use of Siberut´s endemic primates and the establishment of a biological database urgently needed for effective conservation strategies on Siberut island.

2.2. Materials and Methods

a) Study area

The study was conducted in a primary forest representing a tropical lowland evergreen rainforest, situated between the Peleonan and Sigep rivers at 0°58' and 1°03'S (latitude); and 98°48' and 98°51'E (longitude) in northern Siberut (Figure 1). Most of the study area is hilly with elevation measurements ranging from 2-182 meter above sea level. The forest area is drained by numerous small to medium sized creeks and rivers.

Due to their geographic location, the Mentawai islands are characterized by weak seasonal changes of an equatorial tropical climate. The mean annual rainfall on Siberut was measured at 4217 mm (Whitten 1982). In general, the drier season occurs from February to June and the wetter season from July to January (Mitchell 1982). Daily minimum and maximum temperatures range from 22°C to 31°C, while humidity levels range from 80 to 95 percent (Whitten 1982; WWF 1980).

b) Field sampling

The study site is accessible through 13 transects, ranging from 1 to 3 km in length and crossing riversides and hills (see also Waltert *et al.* 2008). For this study eight of these transects were selected randomly. On six of these transects four plots and on two of these transects five plots were marked measuring 20x20 m with a distance of 200m to each other, so that a total area of 3.41 km^2 was investigated. Within these plots all trees of ≥ 20 cm diameter in breast height (dbh; tree stage), were measured. Smaller trees (pole stage) were measured in smaller plots of 10x10m for dbh class 10-19 cm and 5x5m plots for saplings with dbh < 10 cm and a minimum height of 1.5 m. These smaller plots were nested within the 20x20 meter plots. Full spatial coverage of these smaller trees would have been impractical as the total sampling area encompassed 1.36 ha.

For each tree of any size within the plots, botanical name or local name was recorded. Local names were provided by three experienced natives of northern Siberut all of which were informed to rather leave a specimen unnamed instead of giving an unreliable information. Diameter at breast height (dbh) was measured using a meter tape and total heights of trees were taken as the distance from their base to the top of their crowns using a Leica LRF 800 digital rangefinder. From each tree recorded, three samples of terminal twigs were collected and preliminarily assigned to morphospecies. Occasionally fruits or flowers were collected to confirm identification in the field and to be used as additional references in the form of pictures or dried samples. From each specimen, one of the three dried twig samples were stored at research station facilities in the forest and in a dry storage room in Padang (West Sumatra), respectively, whereas the third sample was sent to the Herbarium of Andalas University in Padang for further scientific identification and storage.

Even without an existing Flora for the Mentawai archipelago, more than 90% of the specimen recorded could be identified on species or genus level using keys and descriptions of standard Malesian Floras (Whitmore 1972, 1973), the pilot study on the Mentawai Flora by Ridley (1926) and specimen references from the Herbarium of Andalas University.

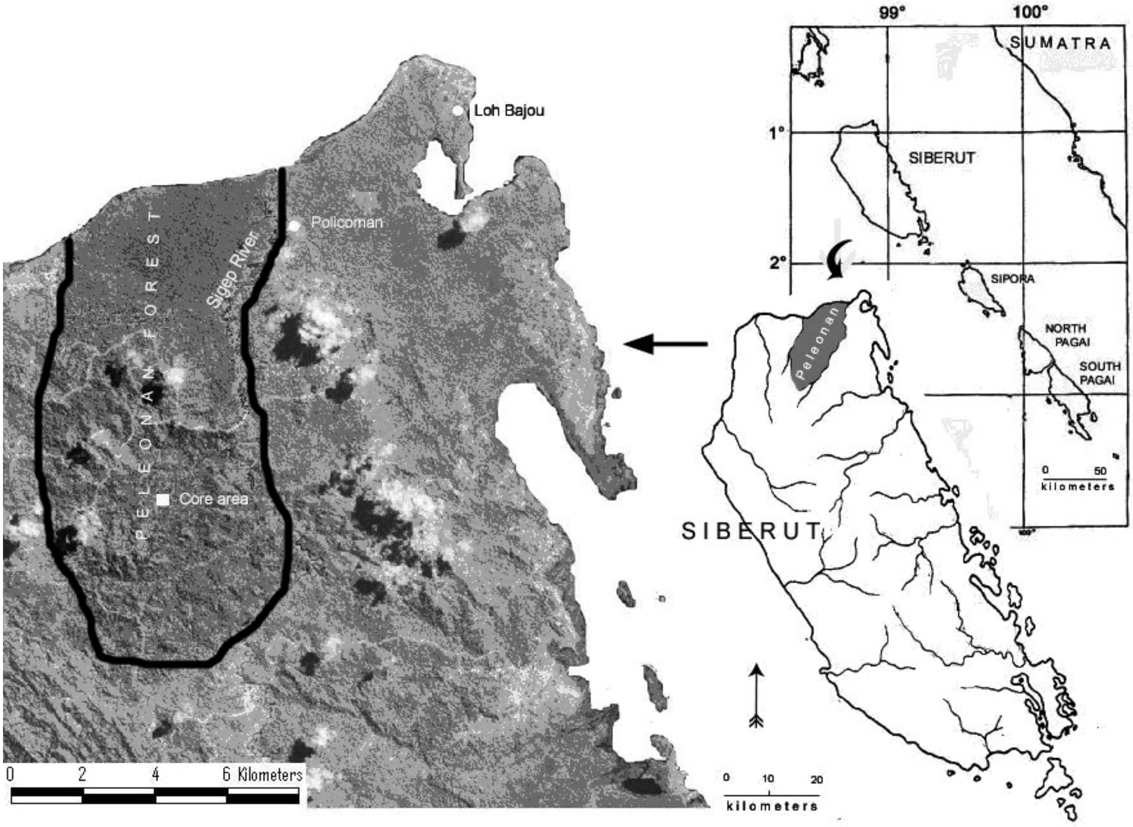

Figure 1. Map of the study area in Peleonan forest, North Siberut.

c) Data analysis

Based on the individuals recorded in the discrete plot samples, species richness was calculated using both, species accumulation curves and species richness estimators. Species accumulation curves were generated for three different sample sets: “Riverine-“, “Hillside-“ and “All plots”, in which the number of species found is shown in relation to the accumulating number of tree individuals or plots sampled.

Estimation of total richness was performed using the software *EstimateS* 6.0b1 (Colwell 2000). The MMMeans richness estimator was selected here, as it was shown to be the least biased estimator provided in the software package (Kessler *et al*. 2005), but the range of results from the other estimators in Colwell (2000) are also given.

Furthermore, floristic composition was assessed quantitatively by calculating the Important Value Index (IVI) for each species. The IV index represents the sum of the values for relative density (RD), relative frequency (RF) and relative dominance (RDo), which are determined by the following equations:

$$\text{Relative density} = \frac{\text{Number of individual of a taxon}}{\text{Total number of individuals}} \times 100$$

$$\text{Relative frequency} = \frac{\text{Number of plots containing a taxon}}{\text{Total frequencies of all taxa}} \times 100$$

$$\text{Relative dominance} = \frac{\text{Basal area of a taxon}}{\text{Total basal area of taxa}} \times 100$$

Structural analysis of the forest was made by comparing the distribution of canopy heights and trunk diameter classes. For the analysis of height distribution, all trees were allocated to one of ten height classes, arranged in 5 meter categories, covering all trees from 6 to 60 m height. To analyse diameter distribution, dbh measurements of trees with dbh $\geq$ 20cm were allocated to nine different categories arranged in 10 cm intervals.

2.3. Results

a) Floristic composition and species richness

Within the total area sampled, we recorded 93 trees, 58 poles and 86 saplings in our plots. They could be assigned to 136 tree species, representing 84 different genera out of 40 tree families. With regard to the number of species found within families, Euphorbiaceae was the most diverse tree family in the samples, being represented by 25 species, followed by Lauraceae (13 species), Myrtaceae (8 species) and Rubiaceae (8 species). Within the family Euphorbiaceae, *Aporosa* was the most common genus, being represented by 5 species. Whilst the family Lauraceae was dominated by the genus *Litsea* (6 species), the families Myrtaceae were dominated by *Eugenia* (4 species).

Calculations performed with the MMMeans richness estimator revealed a tree species richness for the 3.41 km^2 study area of an estimated total of 180 species. Results from other species richness estimators range from 169 to 187 (e.g. Jack1=182±5; Chao1=187±21; Chao2=178±16; ICE=176±0 ; ACE=169±0).

On average, 10.2±3.3 trees ≥ 20 cm dbh (mean ± s.d.) were recorded within one 20x20m plot, belonging to 8.29±2.38 species. Hill plots generally had about similar numbers of individuals (hill 10.48±3.58 and river 9.73± 2.53) (Mann-Whitney U test, U=116, p=0.70) and species (hill 8.35± 2.57 and river 8.18±2.04) (Mann-Whitney U test, U=125, p=0.96). There were also only slight differences between species accumulation curves from plots situated near rivers and those from plots in hilly areas, showing that species richness was only slightly lower near rivers (Figure 2a & 2b).

Species such as, *Durio graveolens, Mallotus subpeltatus* and *Pouteria duclitans* were mainly found in riverine plots , while *Baccaurea deflexa and Knema latifolia species* were common in hill plots. A similar topological preference was not found for *Baccaurea* *javanica*, *Dacryodes rostrata* and *Knema sumatrana*, which were found to be common in both, riverine and hill plots (Table 1).

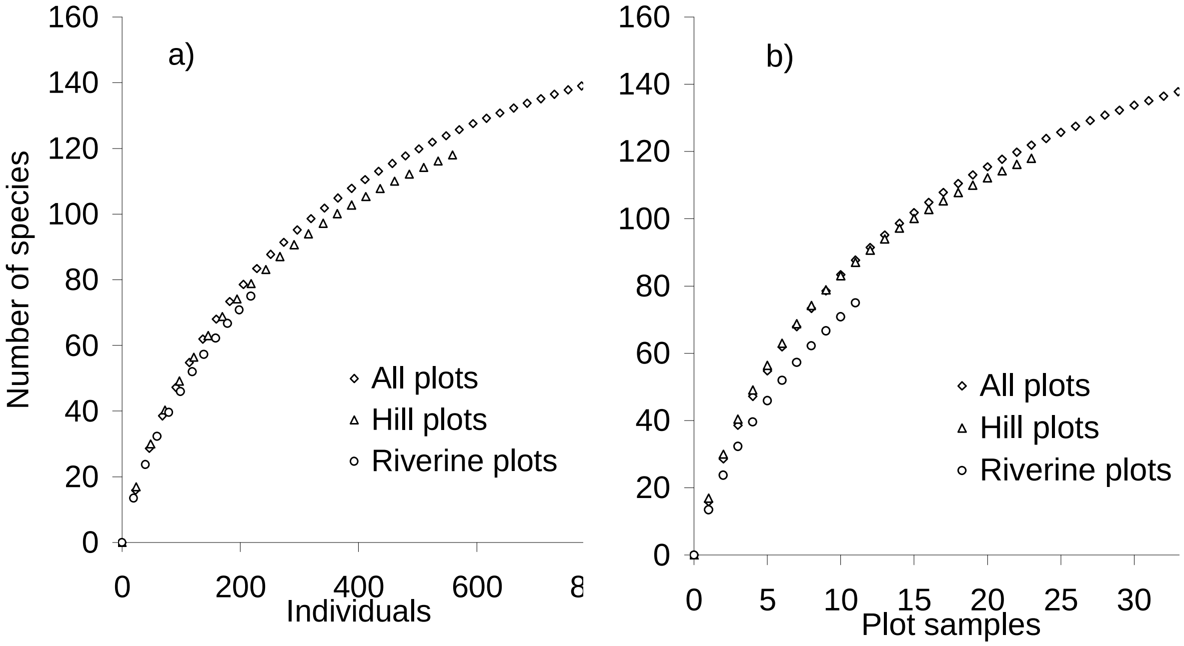

Figure 2. Species-accumulation curves based on numbers of individual trees (a) and on cumulative plot samples (b) in hill plots, riverine plots and all plots combined.

Table 1.: Important Value Index (IVI) of the ten most dominant species recorded for three different dbh classes in riverine and hill plots

Riverrine area		Hilly area	
Species (DBH < 10cm)	IVI	Species (DBH < 10cm)	IVI
Mallotus subpeltatus	29.57	*Urophyllum griffithianum*	13.21
Baccaurea javanica	11.36	*Croton laevifolius*	11.47
Pouteria duclitan	10.18	*Baccaurea javanica*	11.34
Dacryodes rostrata	9.99	*Popowia pisocarpa*	8.16
Artocarpus integer	9.99	*Anisophyllea disticha*	8.16
Bridelia stipularis	8.03	*Baccaurea deflexa*	7.71
Syzygium palembanicum	8.03	*Alangium ridleyi*	5.63
Galearia filiformis	7.44	*Knema latifolia*	5.18
Alangium ridleyi	6.66	*Knema sumatrana*	5.18
Aglaia argentea	6.66	*Psychotria robusta*	5.18
Species (DBH 10-19 cm)	IV	Species (DBH 10-19 cm)	IV
Mallotus subpeltatus	88.63	*Antidesma pentandrum*	67.47
Baccaurea javanica	54.85	*Baccaurea javanica*	26.89
Knema sumatrana	21.43	*Knema latifolia*	17.78
Pouteria duclitan	17.51	*Dacryodes rostrata*	12.79
Durio graveolens	16.29	*Knema sumatrana*	12.20
Dacryodes rostrata	15.57	*Baccaurea deflexa*	12.12
Aporosa lucida	14.67	*Aporosa arborea*	9.15
Antidesma pentandrum	7.45	*Durio graveolens*	7.98
Palaquium dasyphyllum	7.41	*Chionanthus laxiflorus*	7.53
Cinnamomum grandifolium	7.41	*Dipterocarpus elongatus*	6.12
Species (DBH ≥20 cm)	IV	Species (DBH ≥20 cm)	IV
Mallotus subpeltatus	60.41	*Antidesma pentandrum*	30.80
Knema sumatrana	24.48	*Santiria laevigata*	19.79
Santiria laevigata	17.25	*Baccaurea deflexa*	19.66
Bhesa paniculata	16.85	*Knema latifolia*	15.04
Eugenia grandis	14.96	*Artocarpus dadah*	13.49
Aporosa chondroneura	13.71	*Palaquium dasyphyllum*	13.34
Dillenia excelsa	11.26	*Dacryodes rostrata*	11.48
Artocarpus dadah	10.72	*Bhesa paniculata*	10.90
Horsfieldia irya	10.54	*Knema sumatrana*	9.41
Durio graveolens	8.66	*Shorea pauciflora*	8.92

Data based on the Important Value Index (IVI) ranked within the three different dbh classes (Appendix, Table A1) showed that species such as *Mallotus subpeltatus* (15.5%; 19.8% and 7.1%), *Knema sumatrana* (15.7%; 16.7% and 4.7%) and *Baccaurea deflexa* (15.0%; 8.4% and 5.9%) were quite abundant in all dbh classes. These species were followed by *Santiria laevigata* (22.1% and 5.7%), *Antidesma petandrum sp* (20.7% and 48.7%), *Baccaurea javanica* (41.8% and 11.3%), dominating two dbh classes. Species like *Artocarpus dadah* (14.3%), *Dacryodes rostrata* (14.9%), *Urophyllum griffithianum* (11.6%) and *Croton laevifolius* (9.5%), dominated only one dbh class.

According to their IVI, *Santiria laevigata* (Burseraceae), *Antidesma pentandrum* (Euphorbiaceae) and *Urophyllum griffithianum* (Rubiaceae) are the most dominant species within the dbh classes ≥ 20 cm, 10-19 cm and < 10 cm, respectively. Species of the family Dipterocarpaceae were not found to be dominant in any of the (sub) samples. The highest IV index for any species of this family was found for *Shorea pauciflora* (5.3%) with regard to the dbh class ≥ 20 cm only. Calculations by all dbh-classes pooled - i.e. all trees recorded - revealed that only seven species reached an IVI > 5 (*Santiria laevigata, Mallotus subpeltatus, Antidesma pentandrum, Knema sumatrana, Baccaurea deflexa, Baccaurea javanica* and *Urophyllum griffithianum).* On the other hand, for 84.21% of all species listed in the data set an IVI of < 2 was determined. These values indicate that there is no single species or genus of species clearly dominating the plotted areas, but a group of seven species, representing six different genera, show relatively high importance values.

b) Structural composition, diameters and height classes

A relatively high proportion of trees in the samples was represented by small individuals, i.e. belonging to the dbh classes 20-29 cm (36.4%) and 30-39 cm (17.5%). Hence more than 50% of the trees in the samples were represented by individuals with dbh values of less than 40cm. If the dbh class 10-19cm (pole stage) would be included (not shown in Figure 3a) here, the trees recorded for this category only would represent 61% of all individuals sampled.

If all trees with dbh-values between 50 and 100 cm are pooled together, this (mature) age class represents a fourth (24%) of all individuals plotted in Fig. 3a. About 15% of all trees in this figure belonged to the class of the largest trees with dbh values > 100 cm. A majority of these large trees is represented by species belonging to the genera *Shorea* and *Dipterocarpus*. The maximum dbh-value in the present sample is 235 cm recorded for *Shorea pauciflora*. Individuals of similar size were recorded for *Palaquium dasyphyllum, Mallotus subpeltatus* and *Camnosperma auriculata.*

c) Height distribution

As depicted in Fig. 3b. trees belonging to the first three height classes (measuring 6-20 m) accounted for 73% of all trees in the samples. The remaining 27% were distributed over seven height categories ranging from 21 to 60 m. The tallest tree (*Dipterocarpus elongatus*) was measured at 56 m. This figure also shows that the canopy of the Peleonan forest is predominantly built by trees, which are almost equally distributed over the first three height classes, i.e trees less then 21 m in height. The figure also shows that there is a major drop in the number of individuals reaching heights of more than 20 meter and a gradual decrease in numbers with increasing height class (Figure 3b).

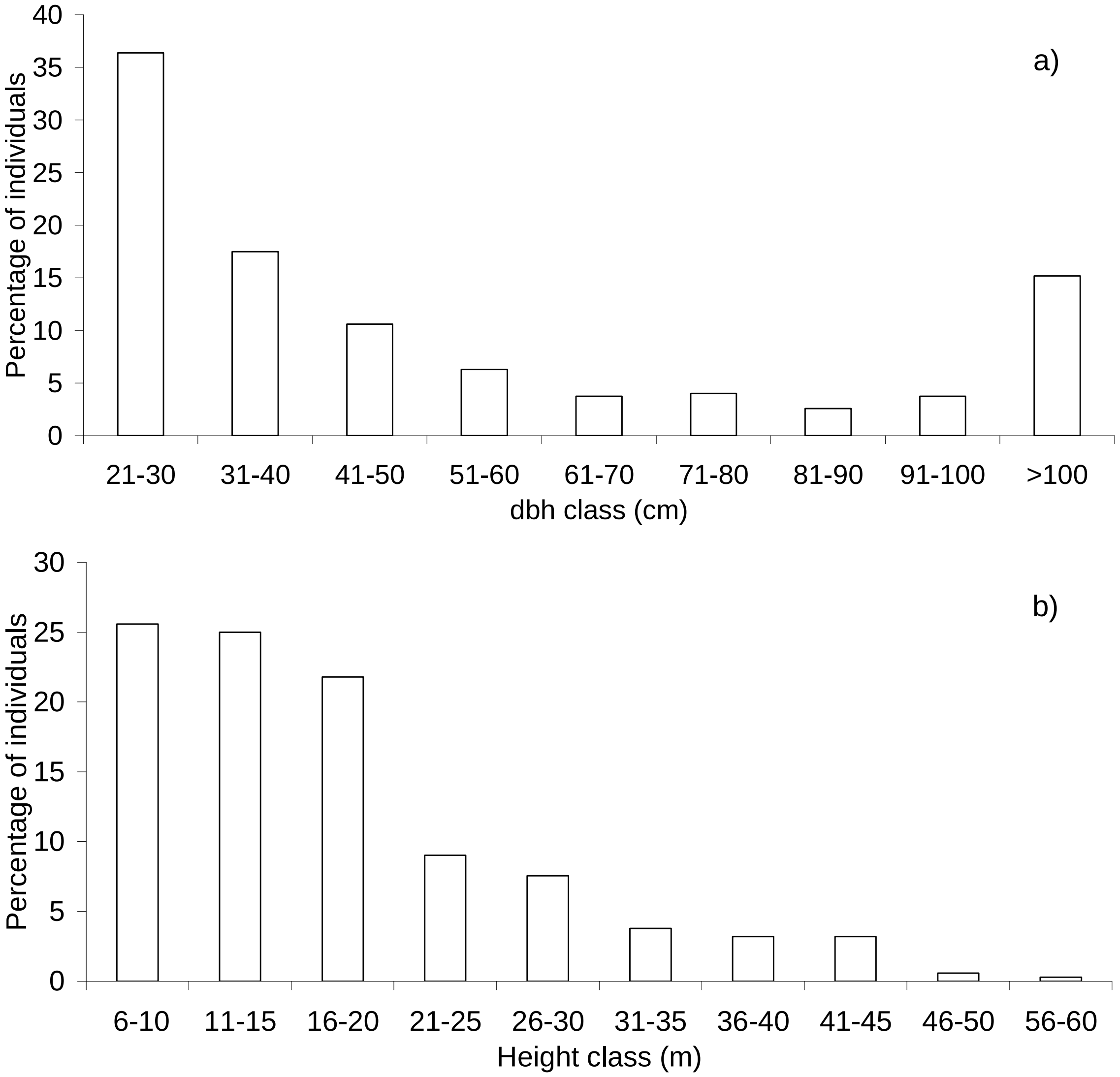

Figure 3. Distribution of trees to dbh-classes (a) and height classes (b)

2.4. Discussion

a) Floristic composition and species richness

This study characterizes a lowland evergreen rain forest of high conservation value in northern Siberut, providing a systematically collected data set that can be compared to a large number of similar plot inventories of other tropical rainforests. To date the only other quantitative floristic description of a primary forest area on Siberut was published by

Whitten (1982). He reports comparable data collected from two study areas located in the centre of the island, which became increasingly disturbed by legal logging activities. In total, he sampled 11.25 ha on which 162 “types” or “morpho”- species of trees ≥ 15 cm dbh were found. Similar to our study Euphorbiaceae were the most common tree families but in contrast to the present study, Dipterocarpaceae were also abundantly present. The latter is obviously the result of a relatively large proportion of samples from minor and major hill ridges, as these are the preferred ranging areas of the author’s main study subject, the Kloss Gibbon, and in general, Dipterocarpaceae are more common in elevated areas.

The results of this study are also comparable to similar studies, based on small plot inventories, conducted in other tropical rainforests. Our record of 136 species with dbh ≥ 10 cm found on 1.36 ha is within the range of 100-150 species recorded in studies using comparative methods to describe primary forest in SE Asia (Whitmore 1995). Considering the estimated total species richness of 180 species for such a relatively small study area, the tree flora of Siberut does not appear to be depauperate relative to other primary forests on small to medium sized SE-asian islands. For example, Whitmore (1974) found 184 species ≥ 10 cm in 13,.7 ha (22 non-contiguous plots) on the small Solomon island Kolombangara, whereas on a 1 ha plot on Negros Island (Philippines) Hamann *et al*. (1999) found 92 species representing 54 genera from 39 families. The fact that the latter study was conducted at about 1000 m above sea level explains the lower number of species found, since species richness generally declines with altitude. Surprisingly however, a study by Kessler *et al*. (2005), from a submontane area in Central Sulawesi, reported almost 150 tree species belonging to 82 genera from 42 families in one plot of 100 x 100m. In two smaller plots of 0.25 ha, about half the number of species was found.

On the family level, the primary forest investigated in that study was also dominated by Meliaceae and Lauraceae, whilst – in contrast to our study - members of the family Euphorbiaceae only dominated the understory.

On the other hand, compared to the geographically nearest and palaeoecologically most closely related forests on Malaya and the greater Sunda Islands Sumatra and Kalimantan, tree diversity on Siberut is definitely lower. A study in a lowland “mixed dipterocarp rainforest” in Riau, Sumatra, revealed an extraordinary diversity of trees, with 504 species being identified from 1885 trees sampled on a 3ha area (Renolls & Laumonier 2000). An almost equal diversity was found in a longer termed study by Newbery *et al.* (1992), conducted in a lowland forest of Danum Valley, Sabah, Malaysia. Here, 511 species ≥ 10 cm were identified on two plots of 4 ha each. The total sample of 17985 individuals comprised 164 genera from 59 families. Earlier studies on the Malayan peninsular found 164 and 176 species per ha, respectively (Wyatt-Smith 1966). For Wanariset on Kalimantan, Kartawinata *et al.* (1981) reported 239 species on a 1.6 ha plot. Similarly, Sidiyasa (2001) found 385 tree species within a 3,6 ha plot containing a tree density of 535 trees/ha at a protected forest site at Wain River, East Kalimantan. These species were allocated to 143 genera out of 49 families. Similar to our study, most of the species recorded belong to the family Euphorbiaceae but in contrast to the present results for North Siberut, this family was followed by Lauraceae, Myrtaceae and Rubiaceae. Like on Siberut, *Aporosa* and *Baccaurea* was recorded to be the most abundant genus within the family Euphorbiaceae. In general the studies on Sumatra and Kalimantan showed a greater diversity on all taxonomic levels and - similar to Siberut - a numerical prevalence of species from the families Euphorbiaceae and Lauraceae.

The difference in species richness between Sumatra and the island of Siberut fits into the species-area pattern from several studies in SE-Asia (MacArthur and Wilson 1967; Welzen *et al*. 2005) showing that the number of species found is positively correlated with the size of the island. However, it has to be noted that instead of complete species inventories only available plot sample analysis of various studies can be compared here, and lists of species only represent relatively small defined areas within these different ecosystems.

In our study, numerically, no species or group of species could be identified to dominate the forest investigated. If our study is representative of Siberut, it might show, that Siberut’s forests clearly differ from forests studied on Kalimantan, Sumatra and the Malayan Peninsula, where trees of the family Dipterocarpaceae can account for up to 21.9 % of all trees recorded and are considered to be the numerically dominant family (Ashton 1982; Kessler *et al*. 2005; see also: Manokaran 1995 for SE Asia and Vasanthraj & Chandrashekar 2006 for Western Ghats, India). Therefore, and in contrast to some early assessments which report dipterocarps being relatively common on Siberut (e.g. WWF 1980), the study area in the Peleonan forest can be described as a typical mixed primary forest.

b) Structural composition, diameters and height classes distribution.

The forest investigated in this study is characterized by a high abundance of relatively small trees with diameters in breast height below 40 cm (with 60.91% of all individuals sampled ranging between 10-19 cm). This pattern is not unusual for primary lowland forests, which are un- or only weakly affected by human exploitation and indicates a high potential for regeneration processes (Whitmore 1984, 1989). The relatively small number of high trees with dbh values ≥ 40 cm can be explained by two main, but not mutually exclusive, reasons. Firstly, there might be a limited number of species that naturally grow up to these heights/ diameters (Hartshorn 1980) and their seedlings need to meet optimal conditions/locations for growth, to out-compete other (especially fast growing) species. Secondly, the numbers of certain big tree species (i.e. members of the family Dipterocarpaceae) could have been already reduced by selective logging for local use, especially traditional construction of dugout-canoes and houses.

As commercial logging in northern Siberut was in the past restricted to only a few strips along the hill ridges accessible for heavy equipment, and the use of the Peleonan forest by locals has been rather negligible in the past, we consider natural causes to play a significant role in restricting the number of big trees in our study area. This assumption is based on the prevailing weather conditions and supported by the fact that Siberut` s geology is dominated by Miocene beds of unresistant shales, silts and marls (van Bemmelen 1949). Annual precipitation records for Siberut reach 4,420 millimeters (Tenaza & Fuentes 1995) and during heavy rain, the alluvial soil becomes soaked with water causing instability of the ground and even landslides (pers. observ.). Under these conditions, tall and heavy trees are more likely to fall during thunderstorms, causing a higher overall tree turnover and hence a higher proportion of regenerating trees.

The combination of these geological conditions with relatively frequent tropical thunderstorms, have probably influenced the structure of the Peleonan forest more than any anthropogenic factors so far. However, due to the ongoing loss of primary forest in the vicinity of the study area, the demand for big timber trees of high quality is rising and the remaining natural resources are becoming increasingly threatened.

The truly mixed composition of the forest studied, made up by an estimated 180 species, provides numerous important ecological niches, not only for plant-, but also (endemic) animal species and emphasizes the outstanding contribution of this forest to the biodiversity of the region. Hence, our data confirm that sustainable management of the remaining primary rainforests on Siberut is of major importance for the conservation of the “Sundaland biodiversity” (Conservation International 2002). The data presented here provide a basis for future studies on this ecosystem in general, the assessment of its present and potential threats and the implementation of effective conservation measures.

Chapter 3.

GROUP STRUCTURE AND PHYSICAL CHARACTERISTICS OF SIMAKOBU MONKEYS (*Simias concolor*) ON THE MENTAWAI ISLAND OF SIBERUT, INDONESIA

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Abstract

We present data on group structure and physical characteristics from free-ranging *Simias concolor*. Mean group size (N= 3) was 8.7 8 1.1 individuals with an average adult male:female sex ratio of 1: 3. All individuals were sexed and allocated into three categories (infants, juveniles plus subadults and adults) on the basis of their physical development. Within age categories, head-body lengths ranged from 19.6 to 25, 34 to 44 and 42 to 53 cm. Corresponding body weights ranged from 0.5 to 0.9, 2.35 to 4.4 and 5.2 to 7.85 kg, respectively; on average adult males were 13% larger and 23% heavier than adult females. Results indicate that for *S. concolor* living in undisturbed habitat (i) group sizes are larger than previously reported and (ii) polygyny is the most likely mating system. Both results support an earlier proposal that group size and social organization in Simakobu monkey are related to the degree of habitat disturbance.

Key Words: Social organization, Physical characteristics, Mating system, Sexual dimorphism, *Simias concolor,* Reproductive seasonality

3.1. Introduction

Having been separated from the Sunda shelf for more than 500,000 years, the four main islands comprising the Mentawai archipelago (Siberut, Sipora, North and South Pagai) (Verstappen, 1975, 1980) possess an unusual degree of biological diversity and species endemism. Of 16 mammal species found nowhere else, 5 are primates, all of which are officially listed as threatened (vulnerable, endangered or critically endangered) (Eudey *et al*., 2000). One of these, the pig-tailed langur *(Simias concolor)* , locally known as Simakobu, is listed as one of the World's 25 Most Endangered Primates (Mittermeier *et al*., 2007). Like most other areas in Sundaland, loss of suitable forest habitat through commercial logging and other non-sustainable land use practices is the main factor threatening populations of all the Mentawai primates, including Simakobu.

Despite the urgent need for scientifically based conservation measures for this species, basic information on the biology of the pig-tailed langur is very limited. Even data on group size and composition, as reported in studies conducted in the 1970s and 1980s (Tilson, 1977; Watanabe, 1981; Kawamura and Megantara, 1986) are contradictory and there is still no consensus on adult sex ratio and mating system of this species. For example, the monogamous mating system proposed for *S. concolor* by Tilson (1977) does not accord with the significant morphological differences between the sexes reported from field observations by Tenaza and Fuentes (1995). Furthermore, the only data on physical characteristics of the species derive from studies on relatively few specimens kept in museum collections (Napier, 1985) and direct measurements of animals living in the wild have never been recorded. Concerning pelage, *Simias* is asexually dichromatic (Chasen and Kloss, 1927), with the majority of animals having a greyish-black fur colour and less than one third of individuals being creamy-buff with brown (Tilson, 1977).

Despite widespread habitat destruction throughout most of the Mentawai Islands, Northern Siberut still possesses areas of relatively undisturbed rainforest cover and recent census data for the Peleonan forest (Waltert *et al*., 2008) indicate that *S. concolor* occurs in densities of up to 53.1 individuals/km^2 , considerably higher than estimates reported for other locations. Although hunting pressure in North Siberut is thought to be relatively low, and local inhabitants have traditionally shown considerable respect for their natural habitat and its resources, primates are still killed as an occasional source of animal protein. As part of our field research and conservation programme in Northern Siberut (SCP; www.siberut. island.org), which relies heavily on the support of and close interaction with local inhabitants, the opportunity arose for one of our team to passively attend a rare (1–2 per year) ceremonial hunt of *S. concolor*. In the course of this, three groups were hunted down and the majority of individuals were killed. Here we present data on size and composition of these groups as well as physical characteristics of most of the individuals killed by the local hunters.

3.2. Materials & Methods

The data presented here were collected in the Loh Bajou bay region of NE Siberut (0°55’46.41’’S and 98°53’17.98’E), which forms part of a largely undisturbed forested area (outside the 5,000 ha of forest protected by SCP), stretching between the village of Politcioman, next to the Sigep river in the West, and the village of Loh Bajou in the East (Figure. 1). The habitat can be described as an undisturbed peat swamp forest, dominated by the tree species *Terminalia phellocarpa*, *Elaeocarpus* sp. and *Alstonia angustiloba* M iq . All local traffic between the villages is restricted to boats going along the NE coast or a 12-km track along the beach.

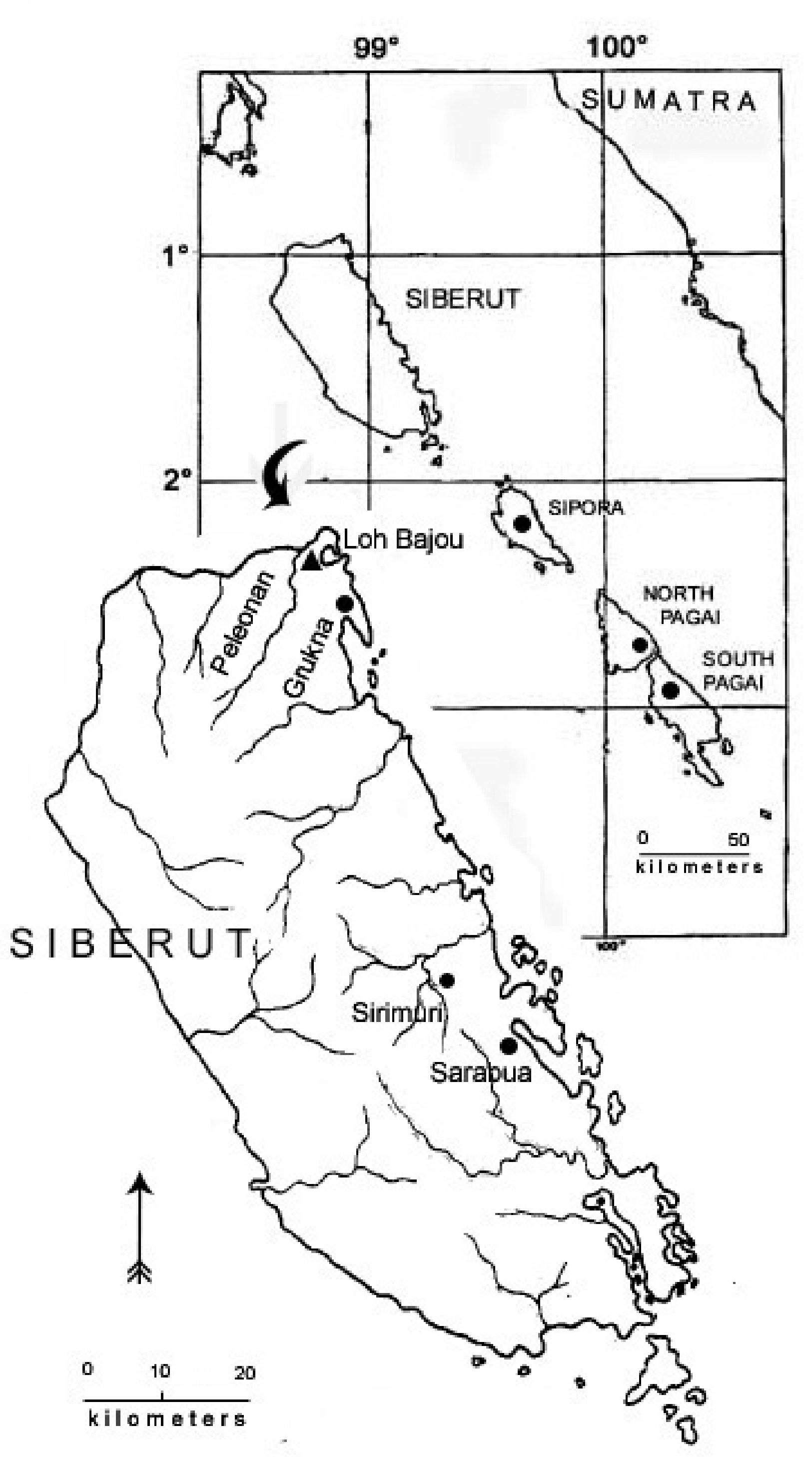

Figure 1. Map of Mentawai islands/Siberut, depicting the site of the present study at Loh Bajou (triangle) on Siberut and the sites of previous studies by Tenaza and Fuentes (1995) in North and South Pagai; Kawamura and Megantara (1986) on Sipora; Watanabe (1981) in Sarabua and Grukna and Tilson (1977) at Sirimuri (circles on Siberut island).

The ceremonial hunt took place in the 3rd week of December 2006, during which three Simakobu groups were encountered. For two of these groups, comprising 8 and 10 individuals, respectively, all but 1 member were killed. Data on sex, age class and measurements of body weight and crown-rump length were collected within 1 h by the first author. A third group was followed and its size determined, but culling was called off after the sighting of an individual with white (creamy buff) fur, the hunting of which is prohibited by a religious taboo. Data on sex, age class and reproductive status were collected, but were incomplete (Table 1), whereas for this third group, physical measurements of culled individuals were not possible at all.

After sexing of individuals in the first two groups (18 in total), animals were allocated to three age categories: infant, juvenile plus subadult and adult, according to their physical development (body size, reproductive status, parity, dental development). Additionally, measures of the head-body length (using hand-held tape measure) and body weight (using a portable digital balance) of these individuals were taken and the species-specific relationship between these parameters was analysed using a least-squares regression. Being genetically predisposed and unaffected by seasonal changes, head-body length was used as the independent variable. Differences in physical characteristics between adult males and adult females were analysed using the Student’s t test. The results were compared to data obtained from the only other comparable study by Tenaza and Fuentes (1995), which is based on measurements of museum specimens.

Table 1. Group composition and individual measurement of head-body length and body weight in *S. concolor.*

Group	Sex	Length (cm)	Weight (kg)	Remarks
I 1	M (adult)	53	7,85	
2	M (infant < 1 week)	19,6	0,5	
3	F (adult)	50	6,95	
4	F (adult)	45	6,3	
5	F (infant 1-2 weeks)	21,7	0,55	
6	F (adult)	44	5,55	
7	F (infant 2 weeks)	24,5	0,7	
8	F (sub adult)	42	5,2	
II 1	M (adult)	51	7,65	
2	M (juvenile)	39	3,75	
3	M (sub adult)	44	4,4	
4	M (embryo II/4)	13,6	0,18	
5	F (adult-pregnant)	47	7,0	with fetus-placenta 7.3kg
6	F (sub adult)	41	4,25	
7	F (juvenile)	34	2,35	
8	F (adult)	48	6,75	
9	F (infant < 1 month)	25	0,9	
10	F (infant < 1 month)	24	0,7	
11	F (adult)	-	-	survived
III 1	M (adult)	-	-	
2	M (sub adult)	-	-	
3	M (juvenile)	-	-	
4	F (adult- pregnant)	-	-	fetus 60% smaller than the one listed as II/4
5	F (adult-pregnant)	-	-	fetus 20% smaller than the one listed as II/4
6	F (adult)	-	-	
7	Sex? (infant)	-	-	survived
8	Sex? (sub adult - white phase)	-	-	survived

3.3. Results

Sizes and composition of the three groups are shown in table 1 . Individual group sizes were 8, 10 (without fetus) and 8 (mean group size was 8.7 8 1.1 individuals). The adult male:female sex ratio was on average 0.3 and similar in all groups (either 3 or 4 females per adult male). In each group only 1 adult male was present (Tables 1, 3). Of the 9 adult females killed, 3 were pregnant and 4 were accompanied by infants less than 1 month old. Within the three age categories infant, juvenile plus subadult and adult (sexes combined), head-body lengths ranged from 19.6 to 25, 34 to 44 and 42 to 53 cm, respectively. Corresponding body weight ranges were 0.5–0.9, 2.35–4.4 and 5.2–7.85 kg (Table 1, Figure 2). Head-body lengths and body weights showed significant differences between adult males and adult females. As shown in table 2, adult males were 13% ($p< 0.05$) larger and 23% ($p< 0.05$) heavier than adult females. Our data for wild animals compare well with those for museum specimens as published by Tenaza and Fuentes (1995). Based on measurements of 3 infants less than 2 weeks of age, we propose a neonatal body weight of 450–500 g and a head-body length of about 20 cm (Table 1). According to our physical measurements the relationship between head-body length and body weight for this species (Figure 2; sexes combined, N= 17) follows the equation $y = 0.24x– 4.91$ ($R^2 = 0.962$).

Table 2. Comparison of head-body length and body weight measurement between adult male female Simakobu monkeys.

Measurement	Male		Female		Student t Test		Sources
	Mean	Range	Mean	Range	t	two tailed *p*	
Head-body lenght (cm)	52±0,14 (N:2)	510-530	46,8±0.24 (N:5)	440-500	2,79	< ,05	This study
	53,11±2,61 (N:8)	480-571	47,61±1,38 (N:12)	460-500	5,82	< ,001	Tenaza RR & Fuentes A 1995
Body weight (kg)	7,75±0,14 (N:2)	7,65-7,85	6,51±0,6 (N:5)	5,55-7,0	2,73	< .05	This study
	8,8±0,2 (N:2)	8,6-8,9	6,8±0,5 (N3)	6,2-7,1	4,18	< ,05	Tenaza RR & Fuentes A 1995

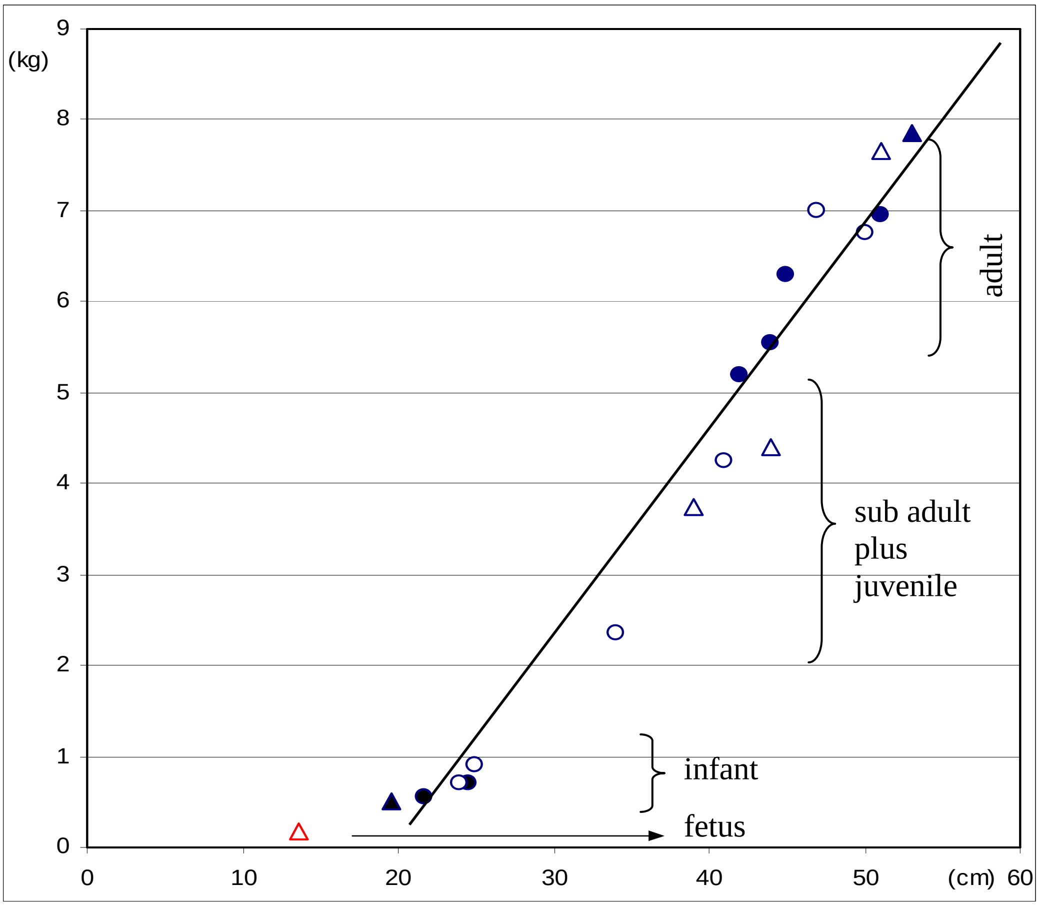

Figure 2. Relationship of physical characteristics (head-body length in centimetres and body weight in kilograms) across age categories of Simakobu monkeys. ▲=male, ●=female in group I; Δ= male fetus, Δ= male, ○= female in group II.

3.4. Discussion

The present study provides an important contribution to the limited dataset for *S. concolor*, one of the 25 most endangered primates worldwide (Mittermeier *et al*., 2007). The data, collected in an undisturbed swamp forest of North Siberut, indicate a mean group size (8.7 individuals) higher than that reported previously from various locations throughout the Mentawai archipelago (Table 3). Interestingly the present figure for group size is most similar to that reported by Watanabe (1981), based on a total of 23 groups encountered (mean group size: 7.1 individuals). In his publication, Watanabe (1981) notes that large groups of Simakobu can only be found in the North of Siberut island and that local people often see relatively large groups of this langur species in inaccessible swamp forest areas. The present study confirms these earlier observations on group size and, since our own study was carried out in a peat swamp forest region, it also provides further support that peat swamp forest represents an important habitat for *S. concolor* (see also: Quinten, 2008). These findings, together with the high abundance of *S. concolor* in the adjacent (mixed) primary rainforest of North Siberut (53.1 individuals/km 2) shown by Waltert *et al*. (2008), indicate a relatively high carrying capacity of both habitats, situated in the northern periphery of the distribution range of *S. concolor* . The comparatively low level of forest degradation in this region combined with the relatively low hunting pressure exerted on *S. concolor* by the locals living in this area most likely explain the abundance of these primates in the Peleonan forest and emphasise the conservation significance of this region for this critically endangered species.

Consideration of our data together with those from earlier studies also allows us to comment on group composition and mating system in this species. One of the first scientific publications on *S. concolor* describes the mating system as monogamous and therefore unique among Asian colobines (Tilson, 1977). These initial observations, however, were made on non-habituated groups, living in a disturbed secondary forest near Sirimuri, where hunting pressure was relatively high. Based on counts during relatively short sightings, group sizes reported ranged from 2 to 5 individuals. Some years later, Watanabe (1981) studied *S. concolor* at two different sites on Siberut, at one of which he observed much larger single male/ multi-female groups near Grukna, in a relatively undisturbed area. Subsequently, Tenaza and Fuentes (1995) proposed the revised term ‘monandrous’ (i.e. 1 adult male and 1 or more adult females) to describe the mating system of *S. concolor*, and since then the species has been considered to be organized into both monogamously and polygynously breeding groups. However, Watanabe (1981) was the first to propose that in the absence of large predators on the Mentawai Islands, group size and composition in Simakobu monkeys is strongly influenced by human hunting pressure. In contrast to the earlier studies conducted in disturbed or secondary forests, where relatively high hunting pressure existed (Tilson, 1977; Kawamura and Megantara, 1986; Tenaza and Fuentes, 1995), our study in an undisturbed swamp forest found only 1-male/multifemale groups of Simakobu monkeys.

This result is not only in line with the findings of Watanabe (1981), but is also supported by our own long-term observation of an all-male band of *S. concolor* near our field station in northern Siberut a phenomenon, not yet described for *S. concolor*, but to be expected as a consequence of a heavily biased sex ratio in polygynous groups (see also Watanabe, 1981; Kawamura and Megantara, 1986). An additional indication contradicting a monogamous mating system in this species is the significant sexual dimorphism found in this species on the basis of museum specimens (Tenaza and Fuentes, 1995) and direct measurements from the present study (Table 2). Thus, combining all available evidence, we propose that the mating system of Simakobu monkeys be reassigned as polygynous. Furthermore, we consider the local occurrence of 1-adult male/1-adult female units as an unusual social organization caused by increased human hunting pressure in combination with the degradation of the natural habitat of these langurs due to commercial logging and the conversion of primary forest into agricultural fields.

The conservation significance of local hunting of *S. concolor* and its effect on the overall population size of the species is difficult to assess. Historically, hunting for food probably had a low impact, especially in the light of the traditional animistic religion of the Mentawaians, in which all creatures of the forest possess a soul and are considered valuable. Currently, however, with much less forest habitat available and a more widespread use of non-sustainable land use practices, the additional impact of hunting may, at least locally, represent a more serious threat to already vulnerable populations of the species than previously envisaged.

Table 3. Comparison of group size and range, sex ratio and mating status with previous studies.

Parameter	N. Siberut Loh Bajou1) (N:3)	S. Siberut Sirimuri2) (N:15)	S. Siberut Sarabua3) (N:7)	N. Siberut Grukna3) (N:23)	Sipora4) (N:2)	Pagai5) (N:20)
Group size	8,7 ± 1,1	3,5 ± 1,1	3,0 ± 1,0	7,1 ± 6,4	3,0 ± 0,0	4,1 ± 2,1
Group size range	8 - 11	2 - 5	2 - 5	2 - 20	3	2 - 7
Adult M:F ratio	1 : 3	1 : 1	1 : 1	1 : 2	1 : 2	1 : 1,8
Proportion number of						
1adult M : 1 adult F	-	100%	100%	39%	-	45%
1 adult M : > 1 adult F	100%	-	-	61%	100%	55%

Sources
1) This study (2006)
2) Tilson (1977)
3) Watanabe (1981)
4) Kawamura and Megantara (1986)
5) Tenaza and Fuentes (1995)

Although our data are limited, certain inferences on postnatal development and reproductive seasonality can also be made. Based on its size and the presence of visible remains of the umbilical cord (1.5 cm in length with dry blood on the tip), the youngest infant of group I can be assumed to have been born a few (2–3) days prior to the hunting event. Its body weight and head-body length are therefore likely to fit closely to those of newborn Simakobu monkeys. The other infants of the same group were estimated to be 1–2 and about 2 weeks of age, being 50 and 200 g heavier than the newborn. As referred from their physical measurements (Table 1) and information from the local hunters, both infants found in group II were no older than about 1 month. These data suggest a growth rate for newborn Simakobu infants of approximately 1.5 cm and 0.15 kg per week and provide the first information of this nature for the species.

Based on their estimated age, infants were most probably born in the first and second week of December and the third or fourth week of November 2006. The mature fetus found in group II would most probably have been born in the second half of January 2007, and the 2 other fetuses (found in group III) from which exact measurements could not be collected were estimated to have reached 80 and 40% of the size of the mature embryo (13.6 cm/0.18 kg), giving a prospected time of birth around late February to April (Kirkwood, 1885; Tarantal and Hendrickx, 1988; Martin and MacLarnon, 1988, 1990; Ross, 1991). Since Tilson (1977) reported births in June/July, collectively the data indicate that the period during which births occur extends from at least November to July. Thus, in contrast to the earlier suggestion of a restricted birth season for Simakobu monkeys (Tilson, 1977), we propose that only a weakly seasonal, if not an aseasonal pattern of reproduction can be expected for this species.

Chapter 4.

HABITAT USE AND TROPIC NICHE OVERLAP OF TWO SYMPATRIC COLOBINES, *Presbytis potenziani* AND *Simias concolor* ON SIBERUT ISLAND, INDONESIA

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Abstract

According to ecological theory, the concept of niche differentiation is essential to our understanding of how sympatric species can limit competition over resources. We here examine ecological niche differentiation in 2 sympatric Asian langurs, *Presbytis potenziani* and *Simias concolor*, both endemic to the Mentawai Islands off the west coast of Sumatra. We collected data (home range size, canopy use, activity budgets, diet, and niche breadth and overlap) using GPS and scan/focal animal sampling methods on 2 groups of *Presbytis potenziani* and 3 groups of *Simias concolor* living in a mixed primary rain forest in northern Siberut. Results show that home ranges of the 2 species overlapped completely and that the home range size of *Presbytis potenziani* was ca. 4 times larger than that of *Simias concolor*. Lower canopy levels (<20 m) were used more often by *Simias concolor,* whereas *Presbytis potenziani* preferred the canopy >20 m. Apart from foraging and other activities, there was little difference in overall activity budgets of the 2 species. Regarding diet, although 60% of all food species examined were used by both langur species, they shared only 3 of the 10 most commonly eaten species. *Presbytis potenziani* fed more selectively on fruits, whereas *Simias concolor* fed predominantly on leaves. Levins niche breadth indices revealed that the diet of *Simias concolor* is more general (0.34) than that of *Presbytis potenziani* (0.22). Based on a Pianka index of 0.32, we conclude that there is a relatively small food niche overlap between the 2 colobine species and that diet represents an important mechanism enabling their coexistence.

Keywords: Activity budget, Diet, Habitat use, Mentawai islands, Niche separation, *Simias concolor, Presbytis potenziani*

4.1. Introduction

A niche is a region in the multidimensional hypervolume representing a combination of environmental factors necessary for growth, survival, and reproduction of a species (Hutchinson 1957; Tokeshi 1999). According to ecological theory, the niche concept and the concept of resource competition are central to our understanding of how sympatric species coexist. While the niche concept refers to all resources relevant for the existence of a species, competition theory posits that ≥2 species cannot coexist if they rely on the same resources, given that these are limited in supply (Gause 1934; Hutchinson 1957; Tokeshi 1999). Thus, in sympatric species, niche differentiation appears to have evolved as a mechanism to reduce resource competition to enable coexistence. In this context, 3 major niche dimensions — habitat type, temporal differentiation and food type— have been identified as being the principal determining factors (Schoener 1974).

Among sympatric primates, the importance of these 3 factors in defining ecological niches has been well demonstrated. For example, a study of 7 lemur species from the eastern of Madagascar demonstrated niche separation with respect to microhabitat characteristics and food chemistry; species occupying the same habitat chose foods with different chemical properties and those eating the same food showed differences in habitat use (Ganzhorn 1989). Data exist for a wide variety of other taxa —Agostini *et al*. (2010) on *Alouatta guariba clamitans* and *A. caraya*; Eckardt and Zuberbühler (2004) on *Cercopithecus nictitans* and *C. diana*; Heymann and Buchanan-Smith (2000) on *Saguinus labiatus labiatus* and *Callimico goeldii*; Heymann *et al*. (2000) on *Saguinus mystax* and *S. fuscicollis*; Mitani (1991) on *Cercopithecus neglectus* and *Colobus badius*; Reed and Bidner (2004) on *Colobus polykomos* and *Piliocolobus badius*; Singh *et al*. (2000) on *Macaca silenus* and *Presbytis johnii*; Vasey (2000) on *Varecia variegata rubra* and *Eulemur fulvus albifrons*— but to date most of the studies have concerned species that 1) have a wide geographic distribution, 2) show a parapatric (partly overlapping) distribution, or 3) are more stereotypically frugivorous than most colobines, or all of these.

We here describe the mechanisms of coexistence in 2 sympatrically living colobines that are both specialized leaf eaters and that coexist across their entire distribution range. Among the 56 species of colobines in general and the Asian colobine taxa in particular, shared habitats over major portions of the geographic range are rare (Redmond 2008). For example, the distribution ranges of *Colobus guereza* and *Procolobus rufomitratus* overlap extensively in central Africa (Chapman *et al*. 2010) and for all other sympatrically living Asian colobines; i.e., *Semnopithecus entellus* and *Trachypithecus vetulus* on Sri Lanka (Napier 1985; Oates and Davies 1994), *Presbytis rubicunda* and *Presbytis hosei* on the island of Borneo (Medway 1970), and *Trachypithecus obscurus* and *Presbytis* (*melalophos*) *femoralis* (Fleagle 1977) along the eastern Malaysian peninsula (Curtin 1980) distribution overlaps exist only partially (ca. 20–60%). In stark contrast, the Mentawaian colobines *Presbytis potenziani* and *Simias concolor* occur exclusively on a small archipelago (6000 km2) off the west coast of Sumatra, where they coexist sympatrically across their entire distribution ranges.

Although several studies of the general ecology of the Mentawaian langurs exist (Tenaza 1987; Tilson 1977; Watanabe 1981), they are based on a very limited number of contact hours with individuals not habituated to human observers. Tilson and Tenaza (1982) described aspects of feeding and home range competition between *Presbytis potenziani* and *Hylobates klossii*, and more recent systematic studies of Mentawai langur socioecology are restricted to *P. potenziani* (Fuentes 1994; Sangchantr 2004).

Based on differences in morphology between the 2 langur species, certain predictions concerning niche differentiation can, however, be made. First, *Presbytis* *potenziani* has a slender body, with hind limbs that are much longer than the forelimbs (Oates and Davies 1994), whereas *Simias concolor* is of a stockier build, with hind and forelimbs of very similar length (Hadi *et al*. 2009a; Tenaza and Fuentes 1995). Consequently, we would predict that *Presbytis potenziani* has a greater ability to perform long-distance leaping, important in using higher forest canopy levels, and *Simias concolor* to be better suited to the use of lower canopy and ground levels. Second, important differences in the digestive systems between the 2 species exist. As do other members of the genus, *Presbytis potenziani* has a 3-chamber sacculated stomach (Bennett and Davies 1994), whereas the similarly locular stomach of *Simias concolor* possesses a presaccus as an additional compartment, thought to be a preliminary storage area that helps to ensure that there is always sufficient substrate available for fermentation (Caton 1998; Kuhn 1964). Thus, we expect a difference in diet composition to exist, whereby *Presbytis potenziani* feeds predominantly on low-fiber food, e.g., fruits, whereas high-fiber leaves form the major part of the diet of *Simias concolor*.

To test these predictions and investigate ecological niche differentiation between the 2 Mentawai langurs, we collected data on home range, canopy use, activity budgets, and diet from habituated individuals of both langur species living in a primary mixed rain forest in northern Siberut.

4.2. Methods

a) Study site

We conducted the study in the Peleonan forest, located at 0°58′ and 1° 03′S (latitude) and 98°48' and 98° 51′E (longitude) in North Siberut, Mentawai, West Sumatra (Figure 1). The forest represents the study area of the Siberut Conservation Programme (SCP: www.siberut-island.org) and encompasses ca. 5000 ha. The area is confined by coastal forest in the north and the Tateiku River in the south, while the western and eastern borders are formed by the Peleonan and the Sigep rivers, respectively (Figure 1).

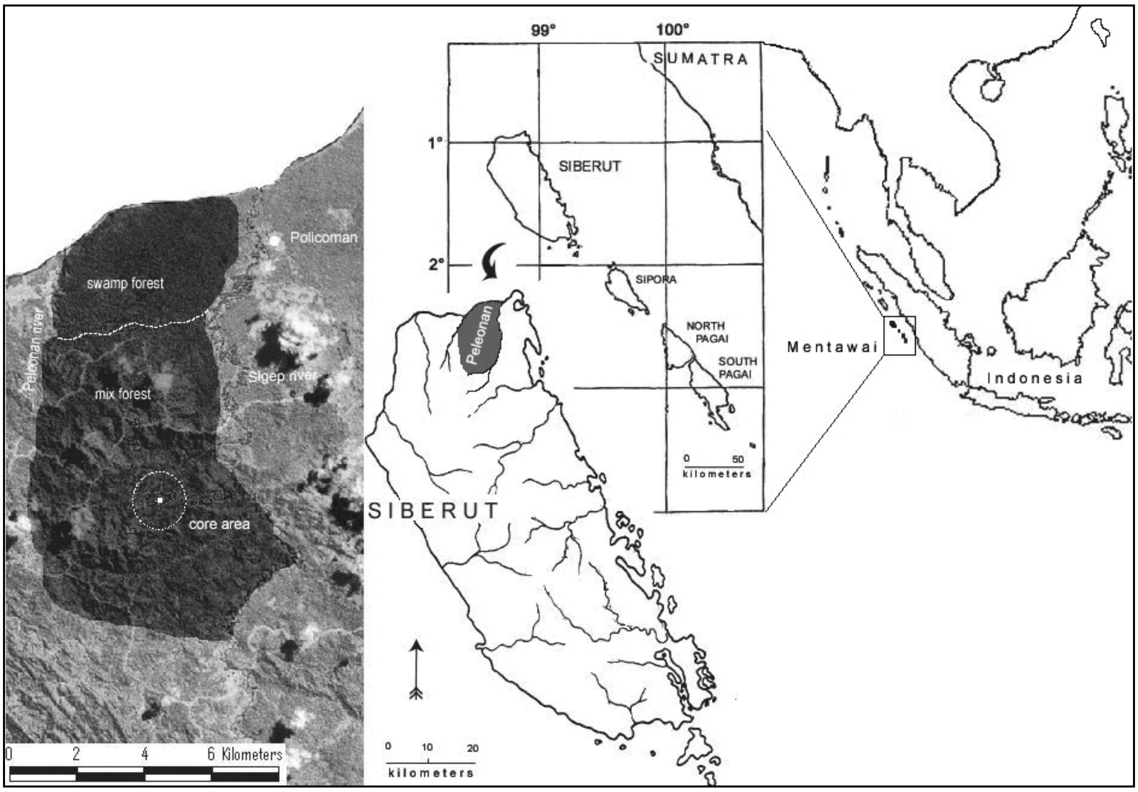

Figure 1. Map of the study site, the Peleonan mixed rainforest in North Siberut.

The Peleonan forest consists partly of peat swamp forest, making up the northernmost part, as well as of mixed forest representing the much larger part toward the south. The study area, located in the center of this mixed forest, is composed of ca. 70 tree genera from 35 families, with Euphorbiaceae, Myrtaceae, Lauraceae, and Moraceae being the dominant taxa. The forest structure consists of >50% trees with diameter at breast height (DBH) between 21 and 40 cm, and 50% of trees 6–15 m high and 35% 16–30 m high (Hadi *et al*. 2009b).

The climate at the study site is typically equatorial, with high rates of precipitation throughout the year. The monthly rainfall from January through September 2008 varied from 120 to 568 mm, with fluctuation between months of low and high rates of precipitation being unpredictable. Temperatures recorded between March and December 2007 ranged between 20.6°C and 33.6°C (mean 25.6°C), with a mean relative humidity of 89.4%.

b) Focal subjects

At the beginning of the observations, *Presbytis potenziani* group A consisted of 7 individuals, including 1 adult male and 3 adult females. The number of group members increased to 8 after a birth in 2008. Maximum group size from earlier studies in North Pagai (Fuentes 1996; Sangchantr 2004) was 6 individuals. We conducted focal animal sampling on 5 individuals of our study group (group A: 1 adult male, 2 adult females, 1 subadult male, and 1 subadult female).

For *Simias concolor* we collected data from individuals originally living in 2 groups, a 1 male–multifemale group (Aldran; here, we used 1 adult male and 1 adult female for focal animal sampling) and an all-male band (2 adult males used for focal animal sampling). In August 2008, 1 focal individual of the all-male band left to form a 1-male–multifemale group (Aldo group, 4 individuals in total). All individuals (of both species) were fully habituated to human observers.

We collected home range size data from *Presbytis potenziani* group A, and an adjacent group B, which was also habituated to human observers. For *Simias concolor*, we collected home range data from the 2 1 male–multifemale groups (Aldran and Aldo) and an adjacent *S. concolor* group B that was also habituated.

Data Collection and Analysis

We collected data daily between 06:00 h and 18:00 h from January 2008 to July 2009 during >4000 contact hours.

To determine home range sizes, we used a GPS to collect geographic positions of the groups. We collected GPS points at 30-min intervals, from a position at the spatial center of the group, i.e., at a position where the majority of group members gathered. Data collection in *Presbytis potenziani* group B and *Simias concolor* group B was sufficient to use the mimimum convex polygon (MCP) analysis, whereas in all other groups we collected additional data from March to July 2009 to use the fixed kernel contours (FKC) analysis also (Boyle *et al*. 2009; White *et al*. 2010), which provides additional information on the internal size structure of home ranges. This information allows identification of the most intensively used areas within a particular home range. We used GIS Quantum GIS 0.9.1 Ganymede and ESRI's ArcGIS, version 9.3 to convert GPS data points (fixes) into maps and the Hawth tool for ArcGIS to calculate the range size.

To assess the species-specific use of canopy, we collected height position data for individuals every 30 min using scan sampling. We measured absolute vertical heights using laser rangefinders and grouped them into 7 strata: 0–5 m, 6–10 m, 11–15 m, 16–20 m, 21–25 m, 26–30 m, and >30 m.

To compare canopy use between *Presbytis potenziani* (N=5 individuals; 5502 scan data points) and *Simias concolor* (N=4 individuals; 3040 scan data points), we allocated all individual scan sampling data to 1 of 7 horizontal strata categories and standardized data samples for a given individual by dividing the total number of observations (events) of this individual in a certain height category by its total number of scans.

To obtain comparable behavioral data for activity budgets and food compositions, in total, we compiled 722 focal animal sampling protocols for *Presbytis potenziani* (based on 5 individuals) and 639 protocols for *Simias concolor* (based on 4 individuals). Each focal animal sampling protocol was composed of instantaneous sampling at 20-s intervals, covering a total length of 30 min, resulting in 90 data points (or events) per protocol.

To gain representative behavioral data, we generated 12 focal animal sampling protocols per individual per month, each representing a different hour of the daylight period (06:00–18:00 h).

The behavioral data collected include 6 activity categories: resting, feeding, foraging, traveling, social behaviour, and other (such as solitary play, autogrooming, agonistic and sexual behavior). We also recorded the food species and the parts of these species consumed, distinguishing leaves, flowers, fruits, and others (bark, fungi, lichen, animal matter). For further identification of plants used by primates, we collected herbarium samples, which we sent to the Herbarium of Andalas University, Padang and to the Herbarium Bogoriense, LIPI Bogor, Indonesia.

To obtain comparable standardized values for activity budgets and diet, we divided the sums of focal animal samples (events) for each category by the number of focal animal sampling protocols made. First we did this separately for each individual and month. Second we calculated the overall individual means by dividing the sum of monthly means by the number of observation months. Finally we summarized all these individual mean values for each category and divided them by the number of individuals observed in this species to obtain mean values for each category representing the species. Because all calculations are based on observation events taken from focal animal sampling protocols, representing a certain daylight hour each, we present the species-specific mean values as event/h.

The assumptions for normality were not met in our data set; thus we used the 2 tailed Mann–Whitney U-test to compare the values for canopy use, activity budget, and diet between *Presbytis potenziani* and *Simias concolor*. We determined significance at a p-level of ≤ 0.05.

We used the standardized Levin's index to calculate the values for niche breadth, applied to the proportions of food items consumed:

$$B = 1/\,\Sigma p_i^2$$

where B is Levin's niche breadth and pi is the proportion of a single resource category (food item) in relation to the overall consumption. Subsequently we calculated the standardized Levin's niche breadth (Bsta) by computing:

$$B_{sta} = B\text{-}1/\,B_{max}\text{-}1$$

where B is Levin's niche breadth and Bmax is the total number of food items recognized. The standardized Levin's index varies between 0 (minimal niche breadth) and 1 (maximal niche breadth) (Colwell and Futuyma 1971; Levins 1968).

Finally, to calculate trophic niche overlap between *Presbytis potenziani* and *Simias concolor*, we used Pianka's index with the formula:

$$Ojk = \Sigma pij\ pik\ /\ \sqrt{}\Sigma pij^2\ \Sigma pik^2$$

where Ojk is the overlapping index between species j and k, and pi is the proportion of a single food item i in the diet of species j and k. Pianka's index varies between 0 (total separation) and 1 (total overlap) (Pianka 1973).

4.3. Results

Home Ranges

Home range sizes of *Presbytis potenziani* based on MCP and FKC analysis were 20.2 and 30.3 ha (N=2 groups) and were on average ca. 4 times larger than those of *Simias concolor* (4.1–10.0 ha; N=3 groups; Table I). The internal size structure calculated via the FKC method showed that both species used their home range unevenly. The area covered by the FKC 50% probability contour indicated that *Presbytis potenziani* spent half of its activity in an area covering only 18% (5.5 ha) of their total home range. Similarly, the area used intensively (FKC, 50% probability contour) by *Simias concolor* represented 12% (1.2 ha, group Aldran) and 18% (1.0 ha, group Aldo) of the total home range (Fig. 2, Table I).

Table 1. Total number of fixes (GPS position records) per group studied and home range size based on MCP and FKC analysis.

Group	Fixes	Home range area (Ha)		
		MCP	FKC 95%	FKC 50%
P. potenziani A	1411	30.53	30.31	5.47
P. potenziani B	403	20.24	-	-
S. concolor B	432	4.1	-	-
S. concolor Aldran	553	8.4	9.96	1.2
S. concolor Aldo	370	4.9	5.59	1.01

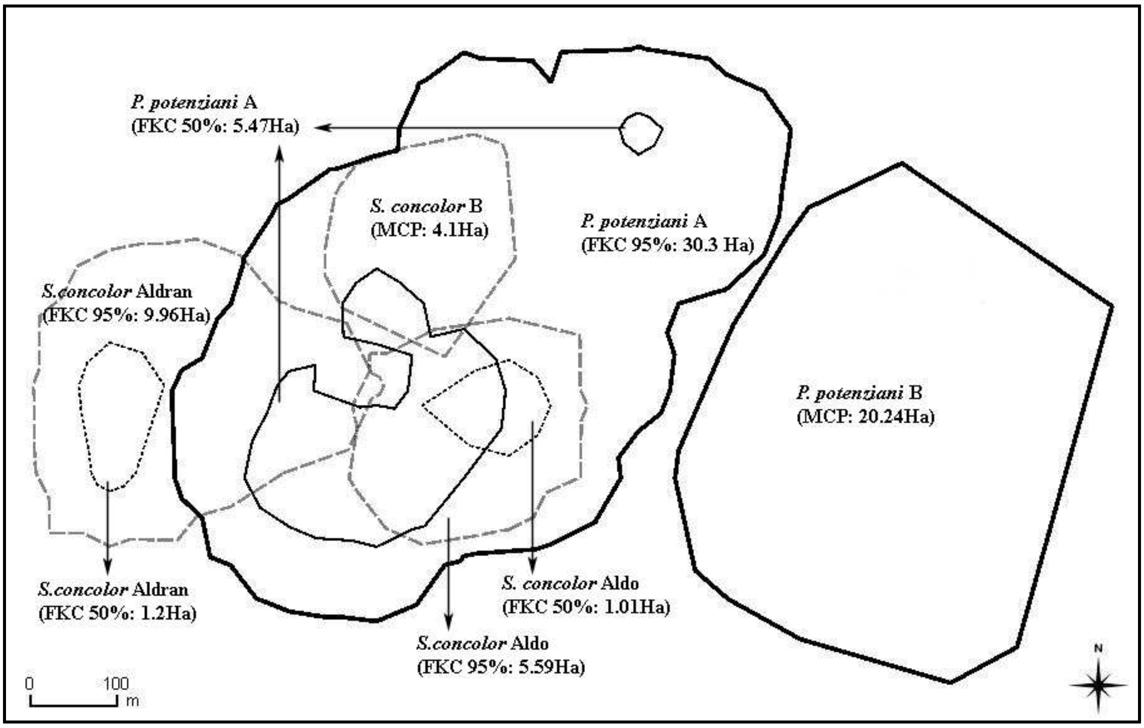

Figure 2. GPS-mapped home ranges of *Presbytis potenziani* (N=2) and *Simias concolor* (N=3) based on minimum convex polygons (MCP) and fixed kernel contours (FKC) 95% and 50% analyses. Bold line= FKC 95% of *Presbytis potenziani*; thin line=FKC 50% of *P. potenziani*; bold dashed line=MCP of *P. potenziani*; thin dashed line=FKC 95% of *Simias concolor*; dotted line=FKC 50% of *S. concolor*; dasheddotted line: MCP of *S. concolor*.

Although there was no intraspecific overlap of home ranges in *Presbytis potenziani*, *Simias concolor* home ranges overlapped on average by 5%. In contrast, the interspecific overlap of home ranges *between Presbytis potenziani* and *Simias concolor* was up to 100%. Because we collected data only on focal groups, it is not known to what extent home range overlap occurred with other groups.

Canopy Use

We found both species most often (0.62–0.65 events per scan) in the 16–25 m canopy height range. We observed *Presbytis potenziani* more often at heights >20 m (21–25 m, 0.31 event/scan, MW U-test: Z=−1.97; p=0.049, N=9 and >30 m, 0.01 event/scan, MW U-test: Z=−2.24, p=0.025, N=9), whereas *Simias concolor* used the lower strata of the canopy including the ground level more frequently than *Presbytis potenziani* (16–20 m, 0.4 event/scan, MW U-test: Z=−2.49, p=0.013, N=9 and 0–5 m, 0.03 event/scan, MW U-test: Z=−2.19, p=0.028, N=9; Figure 3).

Activity Budgets

Overall activity budgets for the 2 colobine species were similar. Both species devoted the majority of their average daily time budget to resting (45.7 and 49.8 events/h in *Presbytis potenzinai* and *Simias concolor*, respectively) and feeding (31.8 and 27.7 events/h in *P. potenzinai* and *S. concolor*, respectively). Traveling represented 6.2 and 5.6 events/h and social behavior 0.6 and 2.1 events/h in *Presbytis potenzinai* and *Simias concolor*, respectively. Although foraging (4.4 events in *Presbytis potenziani* and 2.2 events in *Simias concolor*, MWU-test: Z=−2.2, p=0.03, N=9) and other activities (1.3 events in *P. potenziani* and 2.5 events in *S. concolor*, MWU-test: Z=−2.2, p=0.03, N=9), differed between the species, we rarely observed these behaviors (Figure 4).

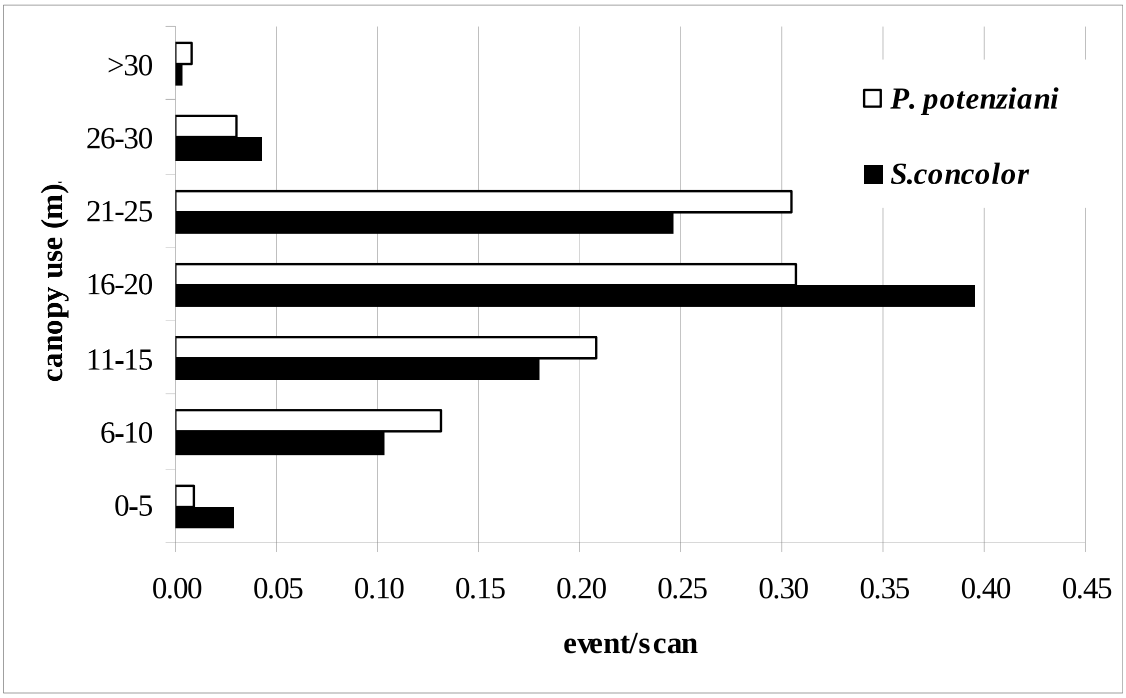

Figure 3. Distribution of the use of canopy level (event/scan) between *P. potenziani* (N:5) and *S. concolor* (N:4).

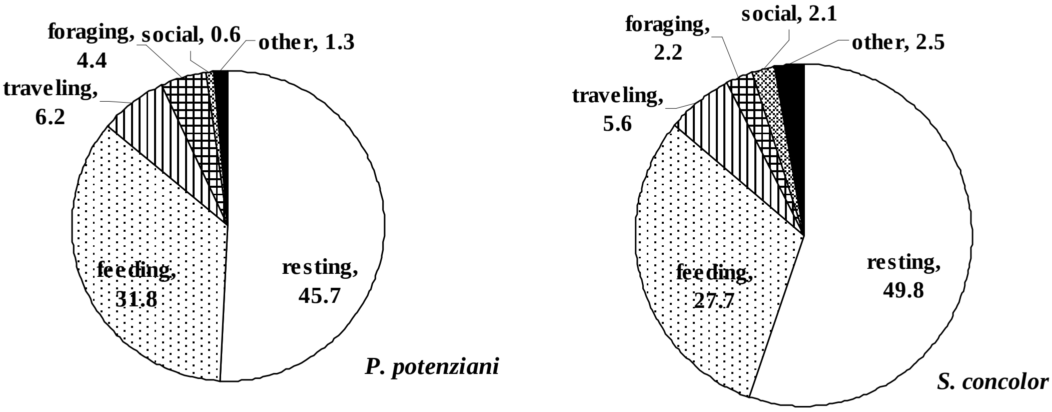

Figure 4. Average daily time budgets (event/ hour) between *P. potenziani* (N:5) and *S. concolor* (N:4).

Diet

Based on both identified and unidentified taxa, *Presbytis potenziani* and *Simias concolor* ate 118 and 99 plant species respectively, with 62 species being used by both. While this overlap in food species composition represents >50% for both langurs, our analysis of 1) the top 10 food species used and 2) food preferences with regard to leaves, flowers, fruits, etc. for each individual showed differences between the species.

The top 10 food species used by *Presbytis potenziani* and *Simias concolor* accounted for 41% and 48% of their overall diets. Of the top 10 food species, only 3 were used by both primate species (Table 2).

Table 2. Ranked proportions (event/ hour) of the top 10 plant species used by *P. potenziani* and *S.concolor*.

Food composition (species)	Habitus	Event/hour & rank on *P. potenziani*	Event/hour & rank on *S. concolor*
Xanthophyllum vitellinum	tree	2.23 (1)	-
Artocarpus integer	tree	1.48 (4)	-
Antidesma velutinosum	tree	1.26 (5)	-
Chisocheton divergens	tree	1.13 (6)	-
Gnetum latifolium	tree	0.85 (8)	-
Palaquium gutta	tree	0.71 (9)	-
Mangifera macrocarpa	tree	0.68 (10)	-
Mallotus subpeltatus	tree	-	2.43 (2)
Arenga obtusifolia	palm	-	2.08 (3)
Endospermum malacense	tree	-	1.67 (6)
Artocarpus dadah	tree	-	1.28 (7)
Poikilospermum suaveolens	tree	-	1.05 (8)
Carallia brachiata	tree	-	0.93 (9)
Durio zibethinus	tree	-	0.85 (10)
Argyreia sp.	**liana**	**1.73 (2)**	**1.72 (5)**
Bhesa paniculata	**tree**	**1.55 (3)**	**2.49 (1)**
Syzygium palembanicum	**tree**	**1.11 (7)**	**1.95 (4)**
Total event/hour (Proportion in overall diet)		12.82 (41.01%)	16.45 (47.96%)

Mean values for food preferences for certain parts of food species indicated that *Presbytis potenziani* fed predominantly on fruit (17.3 events/h), followed by leaves (10.8

events/h), flowers (1.6 events/h), and other items (1.5 events/h). In contrast, *Simias concolor* mainly fed on leaves (15.8 event/h, MW U-test: Z=−2.2, p=0.027, N=9), followed by fruits (6.3 events/h, MW U-test: Z=−2.45, p=0.014, N=9), flowers (4.9 events/h, MW U-test: Z=−2.45, p=0.014, N=9), and other items (0.6 events/h; MW U-test: Z=−2.2, p=0.027, N=9) (Figure 5).

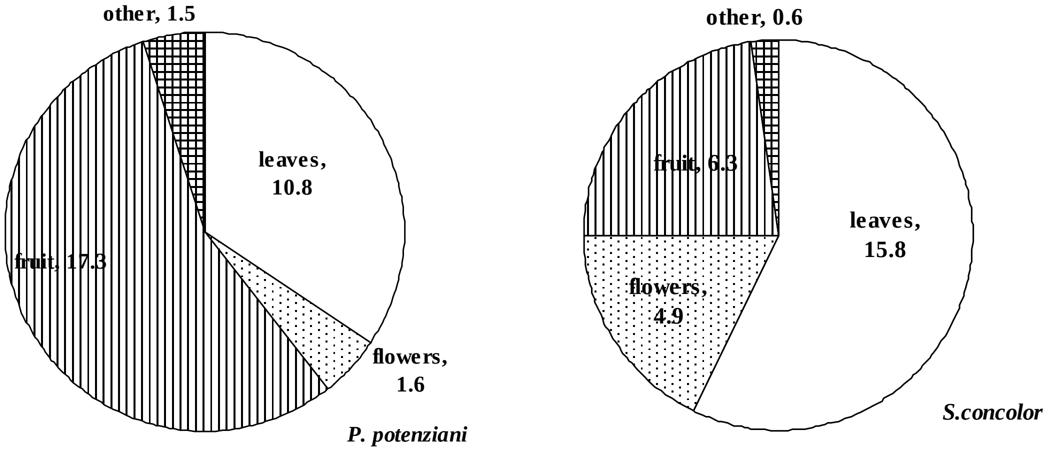

Figure 5. Proportion of food preferences (event/hour) between *P. potenziani* (N:5) and *S. concolor* (N:4).

Detailed analysis of all food items (including all parts of different plant species eaten) revealed 256 food items in total, 176 and 143 of which were eaten by *Presbytis potenziani* and *Simias concolor*, respectively. Of these, 63 items (36% in *Presbytis potenzinai* and 44% in *Simias concolor*) were used by both species (see Appendix Table A3). Based on these different compositions in their overall diet, calculated niche breadths (Levin’s index) were 0.22 for *Presbytis potenziani* and 0.34 for *Simias concolor*. Finally, the Pianka’s index, describing the dietary overlap between the 2 langur species, was 0.32.

4.4. Discussion

Our data on ecological niche differentiation in the Mentawaian colobines show that within the relatively undisturbed habitat of our study area, home ranges of *Presbytis potenziani* are ca. 4 times larger than those of *Simias concolor*. This finding is similar to that reported earlier by Watanabe (1981) for nonhabituated individuals in a secondary forest in Eastern Siberut. Other data from the literature also suggest home ranges to be larger for *Presbytis potenziani* than *Simias concolor*, although actual size varies considerably according to habitat quality (Fuentes 1994; Sangchantr 2004; Tenaza and Fuentes 1995; Tilson 1977).

Our results indicate very little intraspecies overlap of home ranges for *Simias concolor* and none for *Presbytis potenziani*, a finding supported by our observations of a high degree of aggression and vocalization behaviors in intergroup encounters for *P. potenziani*, but a much lower level for *S. concolor* (unpubl. data). In contrast, the degree of overlap between the 2 species was almost complete. However, although living in close sympatry, the Mentawai langurs do not form stable polyspecific associations as observed, e.g., in *Cercopithecus nictitans* and *Cercopithecus diana* (Eckardt and Zuberbühler 2004), probably due to differences in home range size requirements and a much lower natural predation pressure on the Mentawai islands. However, the low levels of interspecific agonistic behavior, frequently observed during group encounters, are in line with results from a study of lion-tailed macaques (*Macaca silenus*), bonnet macaques (*M. radiata*), and Hanuman langurs (*Semnopithecus entellus*) living sympatrically in the Western Ghats of SW India (Singh *et al*. 2011), and in contrast to observations in sympatrically living frugivorous primates such as blue monkeys (*Cercopithecus mitis*) and red-tailed monkeys (*C. ascanius*) (Houle *et al*. 2006).

Our finding of low competition over resources among the Mentawai langurs is further supported by our results on species-specific habitat use. Although home ranges of *Presbytis potenziani* and *Simias concolor* overlap completely, their species-specific use of the forest canopy shows differences. Thus, in contrast to *Presbytis potenziani*, which showed preferences for elevated strata and avoided extremely low positions, *Simias concolor* was more often found in lower strata and at ground level (Fig. 3), where it foraged on mushrooms growing on decaying wood and in scrub vegetation. The canopy use of *Presbytis potenziani* corresponds well with data for this species collected previously by Fuentes (1996) and has also been described for other members of *Presbytis* and *Trachypithecus* (Bennett and Davies 1994; Curtin 1976; Davies 1984; Ruhiyat 1983).

The differences in canopy use and the accompanying locomotive behavior support our hypothesis relating these behaviors to the morphological differences between the species (Ankel-Simons 2000). Whereas the relatively slender body of *Presbytis potenziani* with longer hind limbs supports long-distance leaping and traveling in the upper canopy to explore widely scattered and patchy food resources, i.e., fruiting trees, the stockier (macaque-like) body of *Simias concolor*, in which hind and forelimbs are similar in length, is better suited to a more intensive use of the lower canopy, including the ground level. In this regard, it is of interest to note that *Simias concolor* was repeatedly observed by local inhabitants crossing creeks by wading and swimming (Hadi pers. comm.), a behavior somewhat unusual for langurs, but that has also been described for the closely related proboscis monkeys (*Nasalis larvatus*: Bennett and Davies 1994; Bennett and Sebastian 1988; Yeager 1993).

Activity budgets for both species follow patterns observed in other folivorous monkeys in Africa, e.g., *Colobus guereza*, *C. satanas*, and *Procolobus badius* (Rowe 1996; Struhsaker and Oates 1975) and in other Asian colobines such as *Presbytis comata* (Ruhiyat 1983), *P. thomasi* (Gurmaya 1994), *Trachypithecus cristatus* (Brotoisworo and

Dirgayusa 1991), *T. leucocephalus* (Li and Rogers 2004), *T.pileatus* (Islam and Husain 1982), and *Nasalis larvatus* (Matsuda *et al*. 2009), in which only small proportions of time are spent on social behavior, but >80% of mean daily activity is devoted to resting and feeding. This activity pattern is typical for colobines that consume diets largely based on leaves, seeds, and unripe fruits, which require prolonged periods of resting to support digestion (fermentation) in their sacculated stomachs (Folk 2000; Kuhn 1964; Oates and Davies 1994). The interspecific differences in time spent foraging found here can be explained by the more efficient use of abundant food resources such as leaves and flowers by *Simias concolor*, compared to the extensive foraging on scattered fruit resources by *Presbytis potenziani*.

Our findings on dietary separation between the 2 Mentawai langurs agree well with those on other sympatric Asian colobines: Among the colobines of Malaysia, for example, *Trachypithecus obscurus* prefers to feed on leaves, whereas *Presbytis femoralis* feeds more on fruits (Curtin 1980; Davies *et al*. 1988) and in Kalimantan, *P. hosei* feeds predominantly on leaves (Mitchell 1994), while *P. rubicunda* prefers fruits (Davies 1991). Likewise, *Trachipithecus vetulus* feeds much more on leaves (60%; Hladik 1977) than *Semnopithecus entellus* (39%), both living sympatrically on Sri Lanka (Bennett and Davies 1994). Thus, collectively the data suggest that feeding on a leaf- or fruit-based diet represents an ecological tradeoff among sympatrically living colobines generally. The digestion of a predominantly leafbased (high-fiber) diet may be supported by the presence of a presaccus, which is thought to function as a preliminary storage area, ensuring that there is plenty of substrate continuously available for fermentation (Caton 1998; Kuhn 1964). This specific anatomical characteristic can be found in *Simias concolor* but not in *Presbytis potenziani*, which accordingly prefers a fruit-dominated diet, as predicted by our hypothesis.

In total, we identified 118 and 99 food species as being eaten by *Presbytis potenziani* and *Simias concolor*, respectively, of which 62 species (>50% for each) were used by both langur species. This degree of dietary overlap is roughly similar to that of 43% reported for the African colobines *Procolobus badius* and *Colobus guereza* living sympatrically in the Kibale National Park (Chapman and Pavelka 2005). However, in the present study, when only the 10 most frequently consumed items are considered, the overlap is lower (30%). Further, when leaves, fruits, flowers, etc. of the same food plant species are considered as separate items (see Appendix A3), a clear separation of food preferences becomes visible, with only ca. 25% of all food items recorded being used by both species. This small degree of overall dietary overlap is reflected by the relatively low values of Levin's (niche breadth) and Pianka's (niche overlap) indices for the Mentawai langurs. The slightly higher Levin's index in *Simias concolor* than in *Presbytis potenziani* reflects a more even use of food items compared to the latter. Hence, *Simias concolor* seems to be able to exploit a greater variety of food items within their smaller home ranges vs. *Presbytis potenziani*, which spend more time for traveling and foraging to assort their diet.

In a similar study on sympatric howler monkeys (*Alouatta guariba clamitans* and *A. caraya*) in the Atlantic forests of northeast Argentina, a trophic overlap index of 0.6 was obtained. This represents a much higher proportion of dietary overlap than that found in the present study and may play an important role in maintaining the essentially parapatric distribution of howler species throughout the Neotropics (Agostini *et al*. 2010). Similarly, Sushma and Singh (2006) found a dietary overlap value of 0.56 between *Macaca silenus* and *M. radiata* in the rain forests of the Central Western Ghats, South India, combined with behavioral intolerance between these species. In contrast, the relatively low trophic niche overlap index (0.32) calculated for the two colobines in this study confirms our initial assumption that the ecological niche separation, allowing a sympatric distribution of *Presbytis potenziani* and *Simias concolor* on the Mentawai islands, is determined predominantly by the species-specific diet.

In summary, the present study shows that home ranges of the sympatric langurs *Presbytis potenziani* and *Simias concolor* differ markedly in size and overlap completely. Although their overall daily activity budgets are quite similar, we identified the species-specific differences in diet (food species, food preferences, and food items), as reflected by a relatively low dietary overlap value, linked with a differential use of the canopy/home range, as the main mechanisms by which ecological niche separation of the two langur species is achieved.

Chapter 5.

GENERAL DISCUSSION

Colobines or leaf eating monkeys are characterized by a specialized digestive system and hence, rather specialized dietary requirements. Therefore, the resulting competition over suitable food would favor a parapatric distribution of leaf eating monkeys as observed in the majority of the species within this genus. However, there are sympatrically living leaf-eating monkeys in Africa as well as in Asia. An extreme example for the latter is represented by the the two colobine monkeys *Presbytis potenziani* and *Simias concolor,* which live sympatrically throughout their entire distribution range, an archipelago of only 4000km^2 off the west coast of Sumatra. Within this restricted distribution, the two poorly studied Colobine species share all types of habitats found on these Mentawai islands.

This is the first study, which was set up to identify the behavioral-ecological mechanisms that enable these food specialists to coexist within an isolated and spatially restricted habitat. To investigate the ecological niche differentiation between the two colobines *P. potenziani* and *S. concolor* on the Mentawai islands, the studies were focused on the characterization of their joint habitat as well as on the physical characteristics, group- and home range sizes, diet and the spatial and temporal habitat use of these species.

Most of the data presented in this thesis were collected during a long term field study, conducted, from January 2008 to July 2009, which included more than 4000 hours of close contact with the study groups. These data, collected in the Peleonan forest in northern Siberut were compared and complemented with the sparse data available from the literature.

5.1 Habitat

As forest dwellers, primates benefit from their habitat in numerous aspects such as food supply, the provision of sleeping and resting sites, cover against predators and substrate for three-dimensional locomotion. Therefore, the presence of primates is closely related to the forest structure of their habitat, i.e. the diversity of trees present (Brown, 1981).

The Peleonan forest, home to the sympatric Mentawai colobines, is a mixed forest type (Hadi *et al*, 2008a), which is characterised by dipterocarp trees at the hilly sites, while in the valleys, which makes up almost two-thirds of this forest area, overgrown stands of secondary forest elements such as Euphorbiacease, Myrtaceae, Lauraceae and Moraceae are dominant.

A primate survey in 2006 and 2010 indicated that the forest carries a high population density of all four primate species found on Siberut island including the two Colobines (Waltert *et al.* 2008; A. Höing, personal communication). The survey data also suggest a higher population density of the Colobines in the Peleonan forest compared to other habitats on the Mentawai islands, e.g. primary dipterocarp (Tilson 1977; Watanabe 1981; Paciulli, 2004), secondary (Watanabe, 1981) and peat swamp forest (Quinten, 2008; Tenaza & Fuentes, 1995), and hence indicate, that these populations are doing relatively well.

The latter can be due to i) a high tree species diversity of the forest in which the Colobines have more option regarding various food resources, and ii) the absence of human disturbance, including hunting.

Regarding habitat use, the data of this study clearly show that the Mentawai Colobines use the entire area of the forest and that the home ranges of the two species completely overlap. *P potenziani*, however, uses significant larger home ranges than *S. concolor* (Hadi *et al*., 2012). Although the home range sizes for both species considerably vary according to habitat types (Fuentes, 1994; Sangchantr, 2004; Tenaza and Fuentes, 1995; Tilson, 1977, this study), the home range size ratio between both species is always about the same. This indicates that the two Colobines use different strategies to exploit the same habitat.

Whilst *S. concolor* uses smaller home range sizes in the Peleonan forest, the species shows a relatively high biomass (419 kg/km^2), suggesting that they are more efficient in exploiting the resources of this forest compared to *P. potenziani*, showing a biomass of 53 kg/km^2 (Waltert *et al.*, 2008). In this forest, the biomass value for *S. concolor* is also higher compared to other populations of this species living in the peat swamp forest (Tenaza & Fuentes, 1995), primary forest (Tilson 1977; Watanabe 1981; Tenaza & Fuentes, 1995) and secondary forest (Watanabe, 1981).

A comparison to other habitats of sypatrically living colobines, such as the site in Polonnaruwan, Sri Lanka (a habitat for *Trachipithecus vetulus* and *Semnopithecus entellus*), Kuala Lompat, Peninsular Malaysia (a habitat for *Trachipithecus. obscurus* and *Presbytis femoralis*) and Sepilok, Borneo (a habitat for *Presbytis rubicunda* and *Presbytis hosei*), reveals some interesting similarities and differences:

1) Like the Peleonan forest, the forest of Polonnaruwan is characterized as a semi-deciduous tropical forest type with trees not exceeding 20-25 meters, and, as a heterogeneous forest, it is also dominated by families such as Euphorbiaceae, Myrtaceae and Moraceae (Hladik, 1977). However, the total biomass of the sympatric colobines in Polonnaruwan is much higher (1820 kg/km^2) than that of the sympatric Mentawai colobines (472 kg/km^2). According to Waterman (1988, see below) a different ratio between nitrogen and fiber contents of the present food plants may be responsible for the difference in Colobine biomass.

2) Although Kuala Lompat is described as lowland evergreen dipterocarp forest, it is

relatively poor in dipterocarps, and unusually rich in large leguminous trees (Lambert, 1998). Phytochemical studies suggest that the forest as a whole is rich in nitrogen but relatively poor in phenolics and fibre. As a consequence, the foliage of the Kuala Lompat forest is comparatively easy to digest for the primates. This is in stark contrast to the conditions in the Sepilok forest, wich is characterized by a predominance of dipterocarpaceae and a lack of leguminosaceae, similar to other sites on Borneo (Waterman *et al* 1988).

Furthermore, Waterman *et al* (1988) showed a positive relationship between the ratio of nitrogen to fiber in the forest and the biomass of Colobines. When comparing three different study sites at which sympatrically living colobine can be found, the highest total biomass is reported for the Kibale forest, where *Colobus guereza* and *Procolobus badius* coexist (1849 kg/km^2), followed by Kuala Lompat (876 kg/km^2) and Sepilok (64 kg/km^2) (Waterman *et al* 1988). Compared to these studies, the total biomass value of the Mentawai colobines in the Peleonan forest (472 kg/km^2) has to be considered as moderate. However, this value from a restricted habitat on a small island is still much higher than that found at Sepilok (Borneo). Hence it can be concluded that the quality of a forest habitat is one important factor to support a coexistence of leaf eating primates.

5.2 Physical characteristics

According to Tokeshi (1999) the physical characteristics are associated with, or even defining the ecological niche of a species. Differences in the use of horizontal areas and vertical strata of the forest are related to a species` body size, and can explain in part the coexistence of species on a local scale. Furthermore, as locomotion is closely linked to habitat use and foraging strategies, these differences are also consistent with an ecological separation in canopy use (McGraw, 1998). As an example, a large primate can dwell in the canopy by moving quadrupedally on large branches, whereas smaller species can leap between narrow branches in the understory (Cunha *et al* 2006).

As presented in the previous chapter, the physical characteristics (body shape and locomotory appendages) of the two Mentawai colobines fit well to the differences observed in their three dimensional use of space (range size and canopy use) in the forest. Although both species can move quadrupedally, *P. potenziani* also shows leaping locomotion in the middle and upper part of the canopy, whereas *S. conc*olor is better adapted to a more intensive use of the lower canopy including the ground level (Hadi *et al*, 2012).

The present study also found a different preference of the two species with regard to their horizontal use of trees branches. In contrast to *P. potenziani* which showed a clear preference for the middle section of the branches, *S. concolor* occupied all three sections of the tree branches to a more similar extent, with a tendency to be found more often at the tip of the branches than elsewhere (Figure A2). Those preferences seem to be correlated with the species specific postural modes of sitting in a tree, which are also associated with physical characteristics (Eakins 2010). According to our observations, *P. potenziani*, having longer hind limbs than forelimbs, prefers to extend its legs (hips and knees largely extended) while sitting on relatively broad branches, free of twigs and leaves. In contrast, *S. concolor*, having hind limbs and forelimbs of similar length prefers to sit with both, hips and knees flexed so that it can use any section of the branches for resting.

This study could also show clear differences in the daily travel distance of the two species. Based on our long term data, *P. potenziani* travels farther (773.8 m) than S. *concolor* (572.4 m), which is possibly related to their differences in home range sizes.

In conclusion, as the anatomical structure determines function, the two Colobines are an example of how differences in locomotion are reflected in morphology. As locomotion is closely linked to habitat use in general and foraging in particular (McGraw`s, 1998), these differences are consistent with an ecological separation.

5.3 Group size

Primates form social groups that vary in size from small family units to large complex, multi-tiered units. This variation of group size has been attributed to multiple factors such as feeding competition and predation pressure (Porter & Garber, 2007; van Schaik, 1983).

The social organization in the two Mentawai colobines has been long debated in primatological research. *P. potenziani*, e.g. was reported as being the only Old World monkey living in monogamous family groups (Tilson & Tenaza 1976; Fuentes 1994; Watanabe 1981). Although the species does appear to live in groups of two adults plus offspring, the general behavioral profile of adult male and female Mentawai Island langurs appear to be quite similar to that of other polygynous members of the genus Presbytis (Fuentes 1994). The latter statement was supported by Sangchantr, (2004), who studied a population of *P.potenziani* on North Pagai, where she found one male/one female groups, one male/ multi female groups and multi/male-multi female groups. Moreover, our long term study on group dispersal of *P. potenziani* in the Peleonan forest clearly shows that the species forms one male/ multi female groups, ranging from 3-8 individuals per group, including 2-3 adult females.

Similar to *P. potenziani, S.concolor* was initially reported to form one male/one female groups (Tilson, 1977). Tenaza and Fuentes (1995) recently labeled this species as monandrous, i.e. living in social groups composed of one male and one or more females. There are no reports, however, saying that this species would exhibit any pair bond related behavior (Fuentes, 1998). Furthermore, the present study indicates that for *S. concolor,* living in an undisturbed habitat, one male/multifemale groups are the most common social organization (Hadi *et al* 2009b). According to the latest data, this species occurs in groups ranging from 2 to 11 individuals consisting of either one male and one or more females (up to 5 adult females) and their offspring or all male bands (Hadi *et al*, 2009b; Paciulli, 2004; Tenaza and Fuentes 1995; Tilson 1977; Watanabe 1981).

In sum it can be concluded that both langur species on the Mentawai islands show a social organization which is typical for colobines in terms of i) group composition and ii) group size. Nevertheless, the two species differ in various aspects, particularly in home range size, density and biomass, as previously described. These differences obviously reflect species specific strategies to adapt to their ecological niches.

5.4 Diet

The present study suggests, feeding on a leaf- or fruit-based diet represents an ecological tradeoff between *P. potenziani* and *S. concolor*. *P. potenziani* feeds predominantly on fruits, whereas in contrast, *S.concolor* mainly feeds on leaves. *S. concolor* also consumes fewer species than *P. potenziani* (Hadi *et al.*, 2012). In addition *S. concolor* groups spread out during foraging, whereas *P. potenziani* forages predominantly in spatially confined units.

This study also addressed the question whether the food composition of the species changes throughout the year and it became clear, that both P. *potenziani* as well *S. concolor* showed considerable variation in their diet during the observation period (Figure A4). Diet components, such as fruits, flowers and leaves where seen to fluctuate quantitatively from month to month in both species, without showing a certain pattern. However, a consistent observation regarding food preference was, that *P. potenziani* prefers to feed on fruits, while leaves where used as a second option. In contrast, *S. concolor* prefers to feed on leaves, while either fruit or flowers where used as an alternative choice of feeding.

The unpredictable pattern of food composition over time in *P. potenzianin* and *S. concolor* is presumably related to an irregular pattern of fruit, flower and leaf production in this forest (see Erb, 2012). This observation is also supported by the quantitative data on rainfall (Figure A5), which show an unclear pattern between dryer (actually less wet) and wetter periods during a one year period. Regarding rainfall it has to be noted here that even during the relatively drier season, Siberut is characterised by frequent and sometimes heavy rainfalls (WWF, 1980).

The present study also shows that the production of fruits, flowers and leaves by the different plant species differs in timing throughout the year. This phenomenon is reflected by the traveling and foraging pattern of *P. potenziani*. This species, which mainly feeds on fruits was observed feeding in the same fruiting tree for several days, before it moved (occasionally long distances) to another food tree in their relatively large home range. In contrast, *S. concolor* was not observed to make fruiting-tree oriented travels over long distances. Presumably this is related to their preference for leaves as their main food resource, which is more evenly distributed and abundant in the forest compared to fruits.

An important ecological factor for both Colobines is the abundance of preferred food tree species in their habitat. The data on the main food species eaten by *P. potenziani* and *S. concolor* (see Hadi *et al*, 2012) show, that these species are relativly common in the study area (see Hadi *et al* 2009a). This refers for example to species belonging to the family Moraceae (*Artocarpus integer* and *A. dadah),* Euphorbiaceae *(Mallotus subpeltatus* and *Endospermum malacense)* and Meliaceae *(Chisocheton divergensma)* which are mainly used by either *P. potenziani* or *S. concolor,* or to those species, which are used by both langurs such as *Bhesa paniculata* (Centroplacaceae) and *Syzygium palembanicum*

(Myrtaceae). These fast growing species are typical for secondary or selectively logged forests.

In sum it can be concluded, that in addition to the observed differences in food preferences (fruits, flowers and leaves) throughout the year between the two Colobines, the overall abundance of their most important food species seems to play an important role for their successful ecological niche differentiation.

5.2 Activity patterns

In general, activity budgets for the two colobine species were similar. Both species devoted the majority of their average daily time budget to resting and feeding, while traveling, foraging, social- and other activities represented a minor proportion (Hadi *et al* 2012). These activity budgets are typical for Colobine monkeys. The relatively high proportion of feeding seems to be connected to less nutritious food eaten, such as leaves or young and often unripe fruits, while the high proportion of resting is a consequences of the low rate of digestion. Nevertheless, a distinctive flexibility in the use of the different food resources available can explain the low proportion of traveling and foraging in the activity budgets of the two Colobines. The small proportion of social activity may be connected to the relatively small group sizes and the lack of social complexity as seen in other primate species, forming larger groups with more individuals of different age classe and hence more complex relationships based on individual social rankings.

A more detailed picture of the activity budget can be drawn when looking at the daily activity patterns (Figure A3). The highest proportion of feeding occurs in the first two hours of the daily activity when the two colobines have moved out of their sleeping trees in the morning, and in the last two hours before they return to sleeping trees in the evening.

When comparing the activity patterns in more detail, it appears that *P. potenziani* spents more time feeding in the morning and in the late afternoon i.e. at times when *S. concolor* can afford to spent relatively more time for resting. Differences in time spent traveling were also seen during the first half of the day, when *P. potenziani* was more active than *S. concolor*. The longer feeding times of *P. potenziani* may be related to a higher energy demand of this species, as a result of their longer travel distances during foraging, compared to *S. concolor*.

The extended time for feeding in the morning and afternoon seen in *P. potenziani*, however, seems not to be related to an avoidance of feeding competition with *S. concolor* as described for *P. potenziani* with respect to *Hylobates klosii* by Tilson and Tenaza (1982). So far, there is no record of aggressive interactions between the two colobine species during group encounters. Previous studies also reported that both species were seen to behave tolerant towards each other within their common habitats of primary, secondary and swamp forests. (Fuetes, 1994; Watanabe 1981). In general, *S. concolor* seems to represent the most tolerant species towards all other primates in the study area.

5.6 Implications for conservation strategies

The following implications can be drawn from this study for the conservation of the Mentawai colobines in particular and the Mentawai primates in general:

1. The present study in connection with primate surveys shows that a mix forest like the Peleonan harbours a tree species richness that supports the coexistence and high population densities of *P. potenziani*, *S. concolor* and the two other primates species *Macaca siberu* and *Hylobates klossi*. Therefore, it is important to consider that the Peleonan and comparable forests on the Mentawai islands should be promoted as Nature Reserves.

2. *S. concolor* appears to be the most flexible and adaptive species regarding the use of food resources. However, survey data show that the population of this species has a tendency to decline rapidly. A weak species specific anti-predation strategy and a high human hunting pressure are thought to be the main reasons for this decline. In addition to conservation education efforts for local people, any program aiming to substitute protein derived from primates, such as animal husbandry and fisheries programmes, should be intensified and promoted.
3. Globalization of agriculture commodities such as cocoa and palm oil plantation are likely to become the main reason for large-scale forest clearing instead of selective logging. The revitalization of traditional agroforesty practicies of the Mentawaian people, the so called *pumonean*, which resembles a form of a secondary forest, needs to be supported to i) preserve the forest and ii) create income for the local households and the village communities.
4. Cultural-based conservation should be conducted during the implementation of any conservation programme in the Mentawai region. Right from the beginning, this approach puts value to a culture, which is based on local wisdom and traditional laws as well as to the traditional religion and certain tabus. This approach is needed to avoid misunderstandings during the implementation of any conservation programme in the community. For example, the establishment of stricly protected areas to maintain primate conservation can result in resistance from the community because it can be misinterpreted as a form of occupation of customary land and the loss of traditional land use rights.

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APPENDIX

Table A1: Floristic composition and Important Value Index (IVI) in three different dbh classes: ≥ 20cm, 10-19 cm and <10 cm.

dbh ≥ 20cm		dbh = 10 - 19cm		dbh < 10cm	
Species	IVI	Species	IVI	Species	IVI
Santiria laevigata	22.07	*Antidesma pentandrum*	48.74	*Urophyllum griffithianum*	11.63
Antidesma pentandrum	20.67	*Baccaurea javanica*	41.78	*Baccaurea javanica*	11.31
Knema sumatrana	15.69	*Mallotus subpeltatus*	19.77	*Croton laevifolius*	9.50
Mallotus subpeltatus	15.47	*Knema sumatrana*	16.66	*Mallotus subpeltatus*	7.13
Baccaurea deflexa	15.01	*Dacryodes rostrata*	14.86	*Popowia pisocarpa*	7.00
Bhesa paniculata	14.87	*Knema latifolia*	11.93	*Anisophyllea disticha*	6.21
Artocarpus dadah	14.31	*Durio graveolens*	11.16	*Alangium ridleyi*	5.87
Eugenia grandis	11.88	*Baccaurea deflexa*	8.37	*Baccaurea deflexa*	5.87
Palaquium dasyphyllum	11.11	*Aporosa arborea*	6.31	*Shorea ovalis*	5.53
Knema latifolia	9.76	*Santiria laevigata*	5.62	*Knema sumatrana*	4.74
Dacryodes rostrata	8.32	*Chionanthus laxiflorus*	5.40	*Eugenia grandis*	4.63
Cryptocarya crassinervia	5.72	*Dipterocarpus elongatus*	4.16	*Dacryodes rostrata*	3.95
Dillenia excelsa	5.56	*Pouteria duclitan*	4.16	*Psychotria robusta*	3.95
Shorea pauciflora	5.26	*Phoebe grandis*	4.02	*Palaquium dasyphyllum*	3.84
Chisocheton divergens	5.12	*Diplospora malaccensis*	3.81	*Pouteria duclitan*	3.63
Durio graveolens	5.07	*Palaquium dasyphyllum*	3.81	*Meliosma nervosa*	3.50
Pometia pinnata	4.37	*Aglaia korthalsii*	3.76	*Gardenia tubifera*	3.39
Gymnocranthera paniculata	4.35	*Strombosia javanica*	3.76	*Galearia filiformis*	3.39
Aporosa chondroneura	4.27	*Beilschmiedia kunstleri*	3.70	*Aglaia argentea*	3.16
Platea excelsa	4.17	*Bhesa paniculata*	3.67	*Endospermum malacense*	3.16
Shorea ovalis	3.97	*Garcinia rigida*	3.67	*Blumeodendron elateriospermum*	3.16
Pentace floribunda	3.13	*Polyalthia glauca Boerl.*	3.66	*Artocarpus integer*	3.16
Carallia brachiata	3.08	*Aporosa lucida*	3.56	*Antidesma pentandrum*	3.16
Blumeodendron tokbrai	3.04	*Eugenia grandis*	3.55	*Semecarpus heterophylla*	3.16
Syzygium palembanicum	3.03	*Syzygium rostratum*	3.53	*Litsea firma*	3.05
Dipterocarpus elongatus	3.02	*Chisocheton divergens*	1.81	*Bridelia stipularis*	3.05
Horsfieldia irya	3.00	*Gironiera subequalis*	1.80	*Chisocheton divergens*	2.71
Litsea noronhae Blume	2.96	*Cinnamomum grandifolium*	1.80	*Garcinia rigida*	2.37
Artocarpus elasticus	2.80	*Eugenia sp.(pakapeula)*	1.79	*Ardisia lanceolata*	2.37
Endospermum malacense	2.64	*Aporosa antenifera*	1.78	*Ostodes macrophyllus*	2.37
Aporosa grandistipula	2.52	*Pleomele angustifolia*	1.78	*Santiria laevigata*	2.15
Phoebe grandis	2.32	*Pometia pinnata*	1.77	*Bhesa paniculata*	1.92
Baccaurea javanica	2.31	*Durio zibethinus*	1.77	*Phoebe grandis*	1.92
Artocarpus sp (kabit raba)	2.13	*Cryptocarya crassinervia*	1.75	*Ficus vriseana*	1.92
Polyosma integrifolia	2.00	*Ormosia sumatrana*	1.74	*Syzygium palembanicum*	1.92
Baccaurea lanceolata	2.00	*Ficus variegata*	1.74	*Diospyros bornensis*	1.92
Litsea sp (sibuluk boiko)	1.96	*Nauclea purpurascens*	1.74	*Dysoxylum excelsum*	1.58
Camnosperma auriculata	1.85	*Dillenia excelsa*	1.73	*Aporosa antenifera*	1.58
Chisocheton patens	1.83	*Diospyros sumatrana*	1.73	*Dehaasia caesia*	1.58
Palaquium gutta	1.63	*Symplocos costata*	1.72	*Garcinia maingayi*	1.58
Plectronia didyma	1.56	*Meliosma nervosa*	1.72	Canarium oleosum	1.58
Myristica maxima	1.54	*Evodia macrocarpa*	1.71	*Pternandra galeata*	1.58

Artocarpus integer	1.52	*Litsea sp (sibulukboiko)*	1.70	*Durio graveolens*	1.58
Ormosia sumatrana	1.46	*Nephelium cuspidatum*	1.70	*Xanthophyllum vitellinum*	1.58
Evodia macrocarpa	1.39	*Artocarpus sp (kabitraba)*	1.69	*Drypetes macrophylla*	1.58
Ficus variegata	1.36	*Pentace floribunda*	1.69	*Artocarpus dadah*	1.47
Actinodaphne glomerata	1.36	*Blumeodendron elateriospermum*	1.68	*Pentace floribunda*	1.13
Rhodamnia cinerea	1.36	*Alangium ridleyi*	1.68	*Dipterocarpus elongatus*	1.13
Strombosia javanica	1.33	*Elaeocarpus stipularis*	1.68	*Elaeocarpus petiolatus*	1.13
Nephelium cuspidatum	1.32	*Gymnocranthera paniculata*	1.67	*Gymnocranthera paniculata*	0.79
Saurania nudiflora	1.31	*Rhodamnia cinerea*	1.67	*Polyalthia lateriflora*	0.79
Beilschmiedia kunstleri	1.31	*Litsea sp (Eneu)*	1.66	*Nephelium cuspidatum*	0.79
Dysoxylum parasiticum	1.29	*Carallia brachiata*	1.66	*Beilschmiedia kunstleri*	0.79
Litsea elliptica	1.02	*Dysoxylum excelsum*	1.65	*Calophyllum soulattri*	0.79
Gonystylus macrophyllus	0.95	*Horsfieldia irya*	1.65	*Myristica maxima*	0.79
Pterospermum javanicum	0.95	*Memecylon ovatum*	1.64	*Diplospora malaccensis*	0.79
Octomeles sumatrana	0.84	*Diospyros polyalthoides*	1.64	*Knema latifolia*	0.79
Firmiana malayana	0.82	*Urophyllum griffithianum*	1.64	*Mallotus dispars*	0.79
Dysoxylum excelsum	0.74			*Semecarpus heterophylla*	0.79
Artocarpus sp.(kopkap)	0.70			*Polyalthia glauca*	0.79
Alangium ridleyi	0.68			*Chionanthus laxiflorus*	0.79
Acmena acuminatissima	0.68			*Ormosia sumatrana*	0.79
Garcinia nervosa	0.68			*Acmena acuminatissima*	0.79
Astronia macrophylla	0.67			*Aporosa chondroneura*	0.79
Dysoxylum arborescens	0.67			*Eugenia sp.(pakapeula)*	0.79
Dehaasia caesia	0.66			*Garcinia nervosa*	0.79
Diospyros buxifolia	0.66			*Dillenia reticulata*	0.79
Xanthophyllum vitellinum	0.66			*Eugenia formosa*	0.79
Elaeocarpus stipularis	0.66			*Litsea sp.(sibeukanang)*	0.79
Eugenia filiformis	0.65			*Cleistanthus myrianthus*	0.79
Polyalthia rumpfii	0.65			*Litsea noronhae*	0.79
Garcinia rigida	0.65			*Litsea sp (sibulukboiko)*	0.79
Mangifera parvifolia	0.65			*Baccaurea lanceolata*	0.79
Popowia pisocarpa	0.65			*Polyalthia rumpfii*	0.79
Litsea sp (Eneu)	0.65			*Aglaia korthalsii*	0.79
Symplocos costata	0.65			*Aporosa arborea*	0.79
Symplocos fasciculata	0.65			*Diospyros sumatrana*	0.79
Beilschmiedia lucidula	0.65			*Plectronia sumatrana*	0.79
Astronia specabilis	0.65			*Platea excelsa Blume.*	0.79
(Umankaleak)	0.65			*Aporosa grandistipula*	0.79
Mangifera foetida	0.65			*Dysoxylum parasiticum*	0.79
Aporosa arborea	0.65			*Baccaurea dulcis*	0.79
Antidesma velutinosum	0.65			*Mallotus peltatus*	0.79
Pouteria duclitan	0.65			*Syzygium rostratum*	0.79
Nauclea orientalis	0.65			*Radermachera gigantea*	0.79
Calophillum javanicum	0.65			*Gironiera subequalis*	0.79
Meliosma nervosa	0.65				
Plectronia sumatrana	0.65				
Gironiera subequalis	0.65				
Drypetes macrostigma	0.65				
Garcinia forbesii	0.65				
Diplospora malaccensis	0.65				
Aporosa lucida	0.65				
Total	300.0		300.0		200.0

Table A2: Proportion (event/ hour) of food composition (species or items) in the diet of *P. potenziani* and *S. concolor*. Of all species, 62 species are used by both.

No.	*P. potenziani*	part eaten	event/ hour	*S. concolor*	part eaten	event/ hour
1	*Xanthophyllum vitellinum*	le,fl,f	2.7652	*Bhesa paniculata*	le fl f	2.486
2	*Argyreia sp.*	le	1.7309	*Mallotus subpeltatus*	le fl f	2.434
3	*Bhesa paniculata*	le,f	1.5622	*Arenga obtusifolia*	fl f	2.080
4	*Artocarpus integer*	fl, f	1.5269	*Syzygium palembanicum*	le fl f	1.948
5	*Antidesma velutinosum*	f	1.2601	*Argyreia sp.*	le	1.721
6	*Chisocheton divergens*	le,f	1.2304	*Endospermum malacense*	le fl f	1.674
7	*Syzygium palembanicum*	le,f	1.1905	*Artocarpus dadah*	le f	1.278
8	*Gnetum latifolium*	f	0.8484	*Poikilospermum suaveolens*	le f	1.046
9	*unknown*	le f	0.8309	*Carallia brachiata*	le fl f	0.926
10	*Palaquium gutta*	f	0.7139	*Durio zibethinus*	le fl	0.851
11	*Mangifera macrocarpa*	fl,f	0.6796	*Aporosa arborea*	le f	0.850
12	*Knema sumatrana*	le,fl,f	0.6411	Liana	le,f	0.716
13	*Sarcotheca diversifolia*	le,fl,f	0.5796	*Antidesma velutinosum*	le	0.681
14	*Knema latifolia*	f	0.5659	unknown	le f fl	0.667
15	*Strombosia javanica*	fl,f	0.5448	*Oncosperma horridum*	fl	0.638
16	*Tetrastigma lanceolarium*	le,fl,f,ba	0.5387	*Gironiera subequalis*	fl f	0.608
17	*Polyosma integrifolia*	le,ba	0.5356	*Dillenia excelsa*	le fl	0.524
18	*Litsea noronhae*	f	0.5346	*Artocarpus integer*	le f	0.516
19	*Leuconotis eugeniifolia*	le,fl,f,ba	0.5098	*Strombosia javanica*	le	0.481
20	*Fungi*	pil	0.4997	*Blumeodendron elateriospermum*	le fl f	0.472
21	*Endospermum malacense*	le,fl,f	0.4883	*Desmos glauca*	le	0.452
22	*Durio zibethinus*	le	0.4788	*Semecarpus heterophylla*	le fl f	0.449
23	*Liana*	le, f	0.4667	*Ficus variegata*	f	0.438
24	*Agelaea trinervis*	le	0.4113	*Palaquium dasyphyllum*	le f	0.424
25	*Alangium ridleyi*	fl, f	0.3934	*Bauhinia semibifida*	le f	0.411
26	*sipu apela*	f	0.3841	*Camnosperma auriculata*	le f	0.405
27	*Symplocos costata*	f	0.3774	*Bauhinia integrifolia*	le	0.399
28	*Horsfieldia irya*	le,f	0.3319	*Uncaria gambir*	le	0.391
29	*Garcinia forbesii*	le,fl,f	0.3229	*Platea excelsa*	le	0.385
30	*Lichen*	mos	0.3148	*Ficus pumila*	le	0.347
31	*Ficus sagittata*	le,f	0.2947	*Sloetia elongata*	le f	0.316
32	*Semecarpus heterophylla*	le,fl,f	0.2926	*Santiria laevigata*	le f	0.312
33	*Baccaurea deflexa*	le,f	0.2898	*Knema sumatrana*	le fl f	0.299
34	*Baccaurea javanica*	le	0.2829	Lichen	mos	0.283
35	*Anthocephalus chinensis*	le,fl,f	0.2809	*Octomeles sumatrana*	le	0.273
36	*Desmos glauca*	le,f	0.2580	*Tetrastigma lanceolarium*	le	0.264
37	*Platea excelsa*	f,ba	0.2505	Pteridophyta	f	0.250
38	*Ficus pumila*	le	0.2293	*Myrmecodia tuberosa*	le tb	0.248
39	*Myristica maxima*	le,f	0.2252	*Baccaurea javanica*	le fl f	0.245
40	*Artocarpus sp.*	f	0.2148	*Beilschmiedia lucidula*	le f	0.235
41	*Piper ungaranense*	le	0.2129	*Chisocheton patens*	le f	0.231
42	*Chionanthus laxiflorus*	le,f	0.2031	*Ormosia sumatrana*	le	0.226
43	*Bauhinia sembifida*	le,fl,f	0.1999	Animal	am	0.209
44	*Myrmecodia tuberosa*	le,tb	0.1776	*Nephrolepis cordifolia*	le	0.192
45	*Poikilospermum suaveolens*	le,f	0.1773	*Alangium ridleyi*	le fl f	0.190
46	*Rhaphidophora montana*	le,f	0.1741	*Lomariopsis cochinchinensis*	le	0.184
47	*Timonius wallichianus*	le,f	0.1724	*Ficus microcarpa*	le	0.183
48	*Polyalthia rumpfii*	le,f	0.1643	*Ficus montana*	le	0.176
49	*Glochidion zeylanicum*	fl,f	0.1625	*Canarium oleosum*	f	0.171
50	*Uvaria purpurea*	f	0.1596	*Blumeodendron tokbrai*	le fl	0.170
51	*Glochidion sp.*	le,f	0.1574	*Durio graveolens*	fl	0.164
52	*Artocarpus dadah*	le, f	0.1463	*Antidesma pentandrum*	le f	0.142
53	*Acmena acuminatissima*	le f	0.1423	*Nephelium lappaceum*	le fl	0.141
54	*Canthium glabrum*	f	0.1411	*Xanthophyllum vitellinum*	le	0.139
55	*Bauhinia integrifolia*	le	0.1410	*Polyosma integrifolia*	le	0.122
56	*Saurania nudiflora*	le	0.1251	*Diplazium esculentum*	le	0.118

57	*Ormosia sumatrana*	f	0.1179	*Polyalthia glauca*	le f	0.118
58	*Santiria laevigata*	le,f	0.1013	*Gymnacranthera forbesii*	le	0.118
59	*Freycinetia javanica*	le,fl	0.1007	*Nothaphoebe macrocarpa*	fl	0.115
60	*Meliosma nervosa*	f	0.0989	*Ficus sagittata*	le	0.101
61	*pela*	le,f	0.0956	*Sarcotheca diversifolia*	fl	0.093
62	*Diospyros buxifolia*	f	0.0923	*Pometia pinnata*	le f	0.088
63	*beletbeu*	fl	0.0876	*Sterculia rubiginosa*	le f	0.088
64	*Schefflera sp.*	le,f	0.0773	*Symplocos fasciculata*	le	0.083
65	*Firmiana malayana*	le,f	0.0769	*Horsfieldia irya*	le fl	0.082
66	*Plectronia sumatrana*	le,fl,f	0.0767	*Knema latifolia*	le fl	0.081
67	*Vitex quinata*	le	0.0766	*Casearia flavovirens*	le	0.068
68	*Drymoglossum heterophyllum*	le	0.0760	*Nauclea macrophylla*	le	0.064
69	*Calamus sp.*	le,fl,f	0.0730	soi-soi	le	0.063
70	*Blumeodendron tokbrai*	f	0.0693	*Gnetum latifolium*	f	0.061
71	*Sterculia rubiginosa*	le	0.0667	*Polyalthia lateriflora*	le	0.059
72	*Chisocheton patens*	f	0.0624	*Artocarpus elasticus*	f	0.055
73	*Rhodamnia cinerea Jack*	le	0.0623	Fungi	pil	0.055
74	*Baccaurea lanceolata*	le, fl	0.0622	*Leuconotis eugeniifolia*	le	0.048
75	*Psychotria robusta*	le,fl	0.0597	*Intsia palembanica*	le	0.047
76	*Artocarpus elasticus*	f	0.0578	*Litsea noronhae*	le	0.047
77	*Dillenia reticulata*	le	0.0500	*Eugenia grandis*	fl	0.042
78	*Pentace floribunda*	f	0.0467	*Korthalsia sp.*	f	0.042
79	*Sloetia elongata*	f	0.0467	*Horsfieldia glabra*	le	0.041
80	*Macaranga hypoleuca*	le	0.0445	*Memecylon ovatum*	le f	0.041
81	*Carallia brachiata*	le	0.0398	*Gigantochloa apus*	le	0.039
82	*Horsfieldia glabra*	f	0.0397	*Ficus consociata*	f	0.037
83	*Ficus montana*	f	0.0354	*Baccaurea deflexa*	le	0.034
84	*Aporosa grandistipula*	f	0.0350	*Liana kecil*	le	0.034
85	*paipailumendeu*	f	0.0343	*Willughbeia coriacea*	le	0.033
86	*sipu tarosi*	le	0.0303	*Cleistanthus myrianthus*	le	0.029
87	*Pometia pinnata*	le	0.0284	*Litsea firma*	fl	0.026
88	*Aglaia korthalsii*	le	0.0283	*Baccaurea lanceolata*	fl	0.022
89	*Garcinia rigida*	le,fl	0.0263	*Daemonorops sp.*	le	0.022
90	*Litsea firma*	le	0.0245	*Ficus padana*	ba	0.022
91	*Mallotus subpeltatus*	le	0.0239	*Dillenia reticulata*	le	0.018
92	*Elaeocarpus petiolatus*	le	0.0237	*Elaeocarpus glaber*	le	0.016
93	*Dillenia excelsa*	f	0.0234	*Chisocheton divergens*	le	0.013
94	*Palaquium dasyphyllum*	f	0.0234	*Freycinetia javanica*	le	0.013
95	*sipu rimbu*	f	0.0233	*Medinilla sp.*	le	0.013
96	*Aporosa arborea*	le	0.0225	*Pentace floribunda*	f	0.013
97	*Beilschmiedia kunstleri*	le	0.0222	Soil	sl	0.009
98	*Korthalsia sp.*	f	0.0216	*Actinodaphne procera*	le	0.009
99	*Ficus consociata*	f	0.0211	*Mallotus dispars*	le	0.007
100	*liana kecil*	le	0.0211			
101	*Dehaasia caesia*	le,fl	0.0178			
102	*Ficus trichocarpa Blume.*	f	0.0167			
103	*uman kaleak*	le	0.0143			
104	*Allophylus cobbe*	fl	0.0133			
105	*Vitis trifolia*	le	0.0122			
106	*Antidesma pentandrum*	le	0.0122			
107	*Asplenium nidus*	le	0.0108			
108	*Durio graveolens*	le	0.0100			
109	*Nauclea orientalis L.*	f	0.0094			
110	*Millettia sericea*	le	0.0069			
111	*Dacryodes rostrata*	le	0.0063			
112	*Popowia pisocarpa Endl.*	f	0.0047			
113	*Daemonorops verticillaris*	f	0.0044			
114	*Gymnacranhera forbesii*	f	0.0034			
115	*Piper baccatum*	le	0.0031			
116	*Pternandra galeata*	f	0.0022			
117	*Blumeodendron elateriospermum*	le	0.0011			
118	*urat-urat*	le	0.0010			

le: leaves; fl: flower; f: fruit; ba: bark; tb: tuber; phil: phileus; mos: lichen; am: animal

Table A3. Proportion (event/hour) of food categories in the diet of *P. potenziani* and *S. concolor*. Of all categories, both species use 64 items in commons.

No.	Species	part eaten	*P. potenziani* (event/hour)	*S. concolor* (event/hour)
1	urat-urat*)	le	0.001	-
2	*Plectronia sumatrana*	le	0.001	-
3	*Pternandra galeata*	f	0.002	-
4	*Piper baccatum*	le	0.003	-
5	*Mangifera macrocarpa*	fl	0.003	-
6	*Gymnacranhera forbesii*	f	0.003	-
7	*Daemonorops verticillaris*	f	0.004	-
8	*Popowia pisocarpa Endl.*	f	0.005	-
9	*Dacryodes rostrata*	le	0.006	-
10	*Millettia sericea*	le	0.007	-
11	*Schefflera sp.*	f	0.007	-
12	*Garcinia rigida*	le	0.007	-
13	*Dehaasia caesia*	le	0.009	-
14	*Dehaasia caesia*	fl	0.009	-
15	*Nauclea orientalis L.*	f	0.009	-
16	*Strombosia javanica*	fl	0.010	-
17	*Durio graveolens*	le	0.010	-
18	*Acmena acuminatissima*	le	0.011	-
19	*Asplenium nidus*	le	0.011	-
20	*Platea excelsa*	ba	0.011	-
21	*Vitis trifolia*	le	0.012	-
22	*Allophylus cobbe*	fl	0.013	-
23	*uman kaleak*	le	0.014	-
24	*Plectronia sumatrana*	fl	0.014	-
25	*Myristica maxima*	le	0.015	-
26	*Chionanthus laxiflorus*	le	0.016	-
27	*Ficus trichocarpa Blume.*	f	0.017	-
28	*Calamus sp.*	f	0.017	-
29	Pela*)	le	0.018	-
30	*Xanthophyllum vitellinum*	f	0.018	-
31	*Firmiana malayana*	le	0.018	-
32	*Psychotria robusta*	fl	0.019	-
33	*Garcinia rigida*	fl	0.019	-
34	*Leuconotis eugeniifolia*	fl	0.019	-
35	*Bauhinia sembifida*	fl	0.020	-
36	*Beilschmiedia kunstleri*	le	0.022	-
37	*Calamus sp.*	fl	0.023	-
38	sipu rimbu*)	f	0.023	-
39	*Dillenia excelsa*	f	0.023	-
40	*Elaeocarpus petiolatus*	le	0.024	-
41	*Litsea firma*	le	0.025	-
42	*Aglaia korthalsii*	le	0.028	-
43	*Garcinia forbesii*	f	0.028	-
44	*Tetrastigma lanceolarium*	fl	0.030	-
45	*Freycinetia javanica*	fl	0.030	-
46	sipu tarosi*)	le	0.030	-
47	*Polyalthia rumpfii*	le	0.031	-
48	*Calamus sp.*	le	0.034	-
49	*paipailumendeu*	f	0.034	-
50	*Ficus sagittata*	f	0.034	-
51	*Aporosa grandistipula*	f	0.035	-
52	*Ficus montana*	f	0.035	-
53	*Baccaurea deflexa*	f	0.036	-
54	*Timonius wallichianus*	le	0.038	-
55	*Horsfieldia glabra*	f	0.040	-
56	*Psychotria robusta*	le	0.041	-
57	*Macaranga hypoleuca*	le	0.045	-
58	*Tetrastigma lanceolarium*	f	0.045	-
59	*Artocarpus integer*	fl	0.049	-
60	*Glochidion zeylanicum*	fl	0.052	-

61	*Baccaurea lanceolata*	le	0.057	-
62	*Glochidion sp.*	le	0.057	-
63	*Garcinia forbesii*	le	0.058	-
64	*Firmiana malayana*	f	0.059	-
65	*Anthocephalus chinensis*	fl	0.059	-
66	*Anthocephalus chinensis*	le	0.059	-
67	*Plectronia sumatrana*	f	0.061	-
68	*Rhodamnia cinerea Jack*	le	0.062	-
69	*Blumeodendron tokbrai*	f	0.069	-
70	*Polyosma integrifolia*	ba	0.070	-
71	*Schefflera sp.*	le	0.070	-
72	*Drymoglossum heterophyllum*	le	0.076	-
73	*Vitex quinata*	le	0.077	-
74	*Rhaphidophora montana*	f	0.078	-
75	Pela*)	f	0.078	-
76	Beletbeu*)	fl	0.088	-
77	*Diospyros buxifolia*	f	0.092	-
78	*Rhaphidophora montana*	le	0.096	-
79	*Meliosma nervosa*	f	0.099	-
80	*Glochidion sp.*	f	0.100	-
81	*Glochidion zeylanicum*	f	0.110	-
82	*Desmos glauca*	f	0.114	-
83	*Ormosia sumatrana*	f	0.118	-
84	*Saurania nudiflora*	le	0.125	-
85	*Acmena acuminatissima*	f	0.132	-
86	*Polyalthia rumpfii*	f	0.134	-
87	*Timonius wallichianus*	f	0.134	-
88	*Leuconotis eugeniifolia*	f	0.135	-
89	*Canthium glabrum*	f	0.141	-
90	*Tetrastigma lanceolarium*	ba	0.146	-
91	*Uvaria purpurea*	f	0.160	-
92	*Anthocephalus chinensis*	f	0.163	-
93	*Sarcotheca diversifolia*	le	0.185	-
94	*Chionanthus laxiflorus*	f	0.187	-
95	*Myristica maxima*	f	0.211	-
96	*Piper ungaranense*	le	0.213	-
97	*Artocarpus sp.*	f	0.215	-
98	*Sarcotheca diversifolia*	f	0.234	-
99	*Garcinia forbesii*	fl	0.237	-
100	*Platea excelsa*	f	0.240	-
101	*Horsfieldia irya*	f	0.261	-
102	*Leuconotis eugeniifolia*	ba	0.300	-
103	*Symplocos costata*	f	0.377	-
104	sipu apela*)	f	0.384	-
105	*Agelaea trinervis*	le	0.411	-
106	*Xanthophyllum vitellinum*	fl	0.517	-
107	*Litsea noronhae*	f	0.535	-
108	*Strombosia javanica*	f	0.535	-
109	*Knema latifolia*	f	0.566	-
110	*Mangifera macrocarpa*	f	0.676	-
111	*Palaquium gutta*	f	0.714	-
112	*Chisocheton divergens*	f	1.133	-
113	*Antidesma velutinosum*	f	1.260	-
114	***Xanthophyllum vitellinum***	**le**	**2.230**	**0.139**
115	***Argyreia sp.***	**le**	**1.731**	**1.721**
116	***Bhesa paniculata***	**f**	**1.554**	**0.072**
117	***Artocarpus integer***	**f**	**1.478**	**0.508**
118	***Syzygium palembanicum***	**f**	**1.107**	**1.220**
119	***Gnetum latifolium***	**f**	**0.848**	**0.061**
120	**unknown**	**le fl f**	**0.831**	**0.667**
121	***Knema sumatrana***	**f**	**0.609**	**0.046**
122	**Fungi**	**pil**	**0.500**	**0.055**
123	***Durio zibethinus***	**le**	**0.479**	**0.592**
124	**Liana**	**le, f**	**0.467**	**0.716**
125	***Polyosma integrifolia***	**le**	**0.466**	**0.122**
126	***Endospermum malacense***	**f**	**0.461**	**0.185**
127	***Alangium ridleyi***	**f**	**0.337**	**0.035**

128	***Tetrastigma lanceolarium***	**le**	**0.317**	**0.264**
129	**Lichen**	**mos**	**0.315**	**0.283**
130	***Baccaurea javanica***	**le**	**0.283**	**0.209**
131	***Ficus sagittata***	**le**	**0.260**	**0.101**
132	***Baccaurea deflexa***	**le**	**0.254**	**0.034**
133	***Ficus pumila***	**le**	**0.229**	**0.347**
134	***Semecarpus heterophylla***	**fl**	**0.226**	**0.083**
135	***Bauhinia sembifida***	**f**	**0.168**	**0.159**
136	***Sarcotheca diversifolia***	**fl**	**0.161**	**0.093**
137	***Desmos glauca***	**le**	**0.144**	**0.452**
138	***Bauhinia integrifolia***	**le**	**0.141**	**0.399**
139	***Artocarpus dadah***	**f**	**0.140**	**0.677**
140	***Myrmecodia tuberosa***	**le**	**0.125**	**0.042**
141	***Poikilospermum suaveolens***	**le**	**0.112**	**0.562**
142	***Chisocheton divergens***	**le**	**0.097**	**0.013**
143	***Syzygium palembanicum***	**le**	**0.084**	**0.083**
144	***Freycinetia javanica***	**le**	**0.070**	**0.013**
145	***Horsfieldia irya***	**le**	**0.070**	**0.056**
146	***Sterculia rubiginosa***	**le**	**0.067**	**0.046**
147	***Poikilospermum suaveolens***	**f**	**0.065**	**0.484**
148	***Chisocheton patens***	**f**	**0.062**	**0.055**
149	***Semecarpus heterophylla***	**f**	**0.062**	**0.009**
150	***Artocarpus elasticus***	**f**	**0.058**	**0.055**
151	***Alangium ridleyi***	**fl**	**0.057**	**0.050**
152	***Leuconotis eugeniifolia***	**le**	**0.056**	**0.048**
153	***Santiria laevigata***	**le**	**0.055**	**0.283**
154	***Myrmecodia tuberosa***	**tb**	**0.052**	**0.206**
155	***Dillenia reticulata***	**le**	**0.050**	**0.018**
156	***Pentace floribunda***	**f**	**0.047**	**0.013**
157	***Sloetia elongata***	**f**	**0.047**	**0.197**
158	***Santiria laevigata***	**f**	**0.046**	**0.029**
159	***Carallia brachiata***	**le**	**0.040**	**0.195**
160	***Pometia pinnata***	**le**	**0.028**	**0.018**
161	***Mallotus subpeltatus***	**le**	**0.024**	**1.202**
162	***Palaquium dasyphyllum***	**f**	**0.023**	**0.186**
163	***Knema sumatrana***	**fl**	**0.023**	**0.157**
164	***Aporosa arborea***	**le**	**0.023**	**0.041**
165	***Korthalsia sp.***	**f**	**0.022**	**0.042**
166	***Ficus consociata***	**f**	**0.021**	**0.037**
167	**Liana kecil***	**le**	**0.021**	**0.034**
168	***Endospermum malacense***	**le**	**0.016**	**0.769**
169	***Antidesma pentandrum***	**le**	**0.012**	**0.005**
170	***Bauhinia sembifida***	**le**	**0.012**	**0.251**
171	***Endospermum malacense***	**fl**	**0.012**	**0.719**
172	***Knema sumatrana***	**le**	**0.009**	**0.096**
173	***Bhesa paniculata***	**le**	**0.008**	**1.967**
174	***Artocarpus dadah***	**le**	**0.006**	**0.601**
175	***Baccaurea lanceolata***	**fl**	**0.006**	**0.022**
176	***Semecarpus heterophylla***	**le**	**0.004**	**0.356**
177	***Blumeodendron elateriospermum***	**le**	**0.001**	**0.301**
178	*Arenga obtusifolia*	fl	-	1.477
179	*Mallotus subpeltatus*	f	-	1.033
180	*Aporosa arborea*	f	-	0.809
181	*Antidesma velutinosum*	le	-	0.681
182	*Oncosperma horridum*	fl	-	0.638
183	*Arenga obtusifolia*	f	-	0.603
184	*Syzygium palembanicum*	le	-	0.568
185	*Gironiera subequalis*	f	-	0.491
186	*Strombosia javanica*	le	-	0.481
187	*Bhesa paniculata*	fl	-	0.447
188	*Ficus variegata*	f	-	0.438
189	*Uncaria gambir*	le	-	0.391
190	*Platea excelsa*	le	-	0.385
191	*Carallia brachiata*	f	-	0.382
192	*Carallia brachiata*	fl	-	0.349
193	*Camnosperma auriculata*	f	-	0.299
194	*Dillenia excelsa*	le	-	0.273

195	*Octomeles sumatrana*	le	-	0.273
196	*Durio zibethinus*	fl	-	0.259
197	*Dillenia excelsa*	fl	-	0.251
198	Pteridophyta	f	-	0.250
199	*Palaquium dasyphyllum*	le	-	0.237
200	*Ormosia sumatrana*	le	-	0.226
201	Animal	am	-	0.209
202	*Mallotus subpeltatus*	fl	-	0.200
203	*Nephrolepis cordifolia*	le	-	0.192
204	*Lomariopsis cochinchinensis*	le	-	0.184
205	*Ficus microcarpa*	le	-	0.183
206	*Chisocheton patens*	le	-	0.177
207	*Ficus montana*	le	-	0.176
208	*Canarium oleosum*	f	-	0.171
209	*Durio graveolens*	fl	-	0.164
210	*Syzygium palembanicum*	fl	-	0.160
211	*Blumeodendron elateriospermum*	fl	-	0.147
212	*Antidesma pentandrum*	f	-	0.137
213	*Beilschmiedia lucidula*	le	-	0.135
214	*Diplazium esculentum*	le	-	0.118
215	*Sloetia elongata*	le	-	0.118
216	*Gironiera subequalis*	fl	-	0.118
217	*Gymnacranthera forbesii*	le	-	0.118
218	*Nothaphoebe macrocarpa*	fl	-	0.115
219	*Camnosperma auriculata*	le	-	0.105
220	*Alangium ridleyi*	le	-	0.105
221	*Nephelium lappaceum*	fl	-	0.101
222	*Blumeodendron tokbrai*	fl	-	0.101
223	*Beilschmiedia lucidula*	f	-	0.100
224	*Polyalthia glauca*	f	-	0.099
225	*Pometia pinnata*	f	-	0.070
226	*Blumeodendron tokbrai*	le	-	0.069
227	*Casearia flavovirens*	le	-	0.068
228	*Knema latifolia*	fl	-	0.067
229	*Nauclea macrophylla*	le	-	0.064
230	soi-soi*)	le	-	0.063
231	*Polyalthia lateriflora*	le	-	0.059
232	*Intsia palembanica*	le	-	0.047
233	*Litsea noronhae*	le	-	0.047
234	*Sterculia rubiginosa*	f	-	0.042
235	*Eugenia grandis*	fl	-	0.042
236	*Horsfieldia glabra*	le	-	0.041
237	*Nephelium lappaceum*	le	-	0.039
238	*Gigantochloa apus*	le	-	0.039
238	*Willughbeia coriacea*	le	-	0.033
240	*Baccaurea javanica*	f	-	0.031
241	*Cleistanthus myrianthus*	le	-	0.029
242	*Litsea firma*	fl	-	0.026
243	*Horsfieldia irya*	fl	-	0.026
244	*Blumeodendron elateriospermum*	f	-	0.024
245	*Memecylon ovatum*	f	-	0.022
246	*Ficus padana*	ba	-	0.022
247	*Daemonorops sp.*	le	-	0.022
248	*Polyalthia glauca*	le	-	0.019
249	*Memecylon ovatum*	le	-	0.019
250	*Elaeocarpus glaber*	le	-	0.016
251	*Knema latifolia*	le	-	0.014
252	*Medinilla sp.*	le	-	0.013
253	Soil	sl	-	0.009
254	*Actinodaphne procera*	le	-	0.009
255	*Artocarpus integer*	le	-	0.008
256	*Mallotus dispars*	le	-	0.007
257	*Baccaurea javanica*	fl	-	0.005

Note: le: leaves; fl: flower; f: fruit; ba: bark; tb: tuber; phil: fungi; mos: lichen; am: animal

*): local name

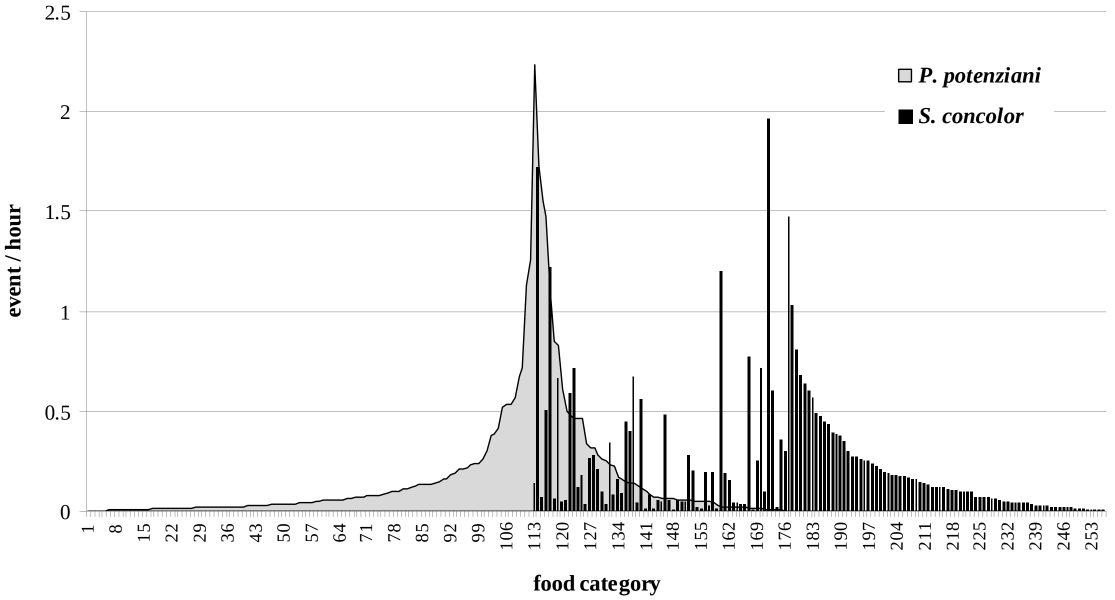

Figure A1. Distribution of food categories (species and part of plant) used by *P. potenziani* and *S. concolor*. Numbers of food categories refers to the list on Table A3.

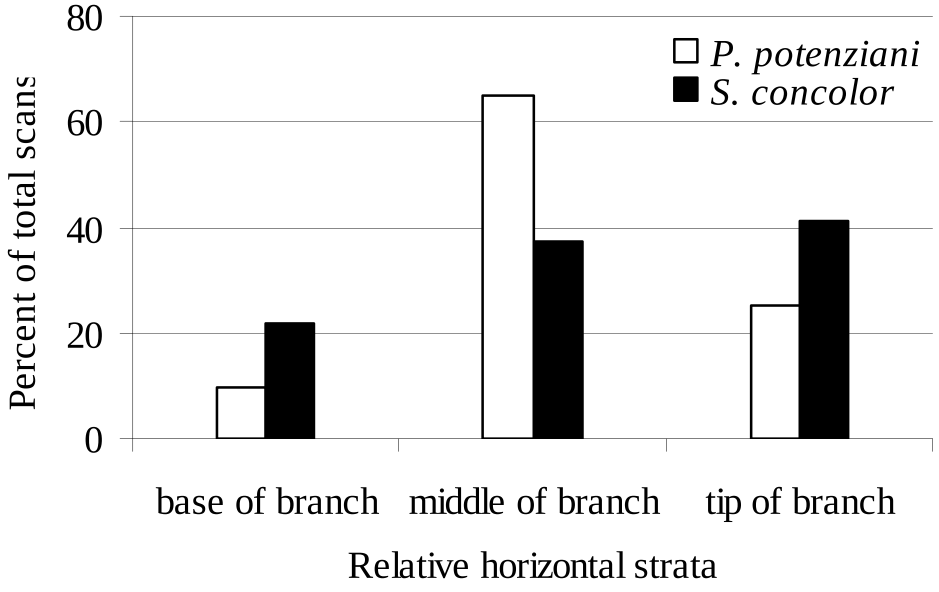

Figure A2. Distribution of the use of relative horizontal positions in the tree branch in *P. potenziani* and *S. concolor*

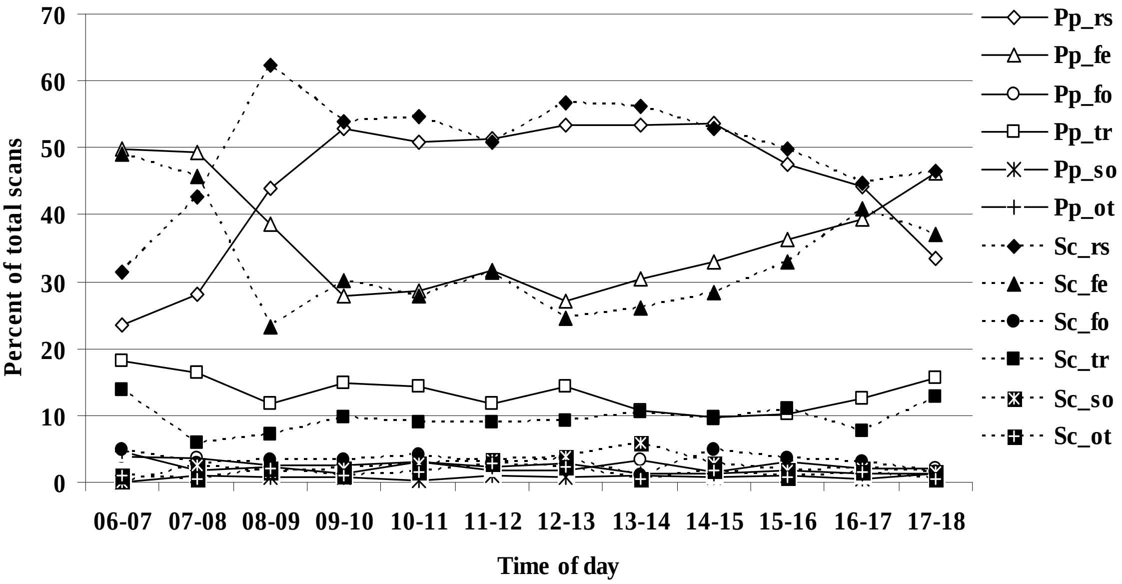

Figure A3. Mean daily activity patterns of *P. potenziani,* and *S.concolor* from 06.00-18.00. Abbreviations: *Pp* = *P. potenziani*; *Sc* = *S. concolor*; *rs* = resting; *fe* = feeding; *fo*= foraging; *tr* = traveling; *so* = social behaviour; *ot* = other.

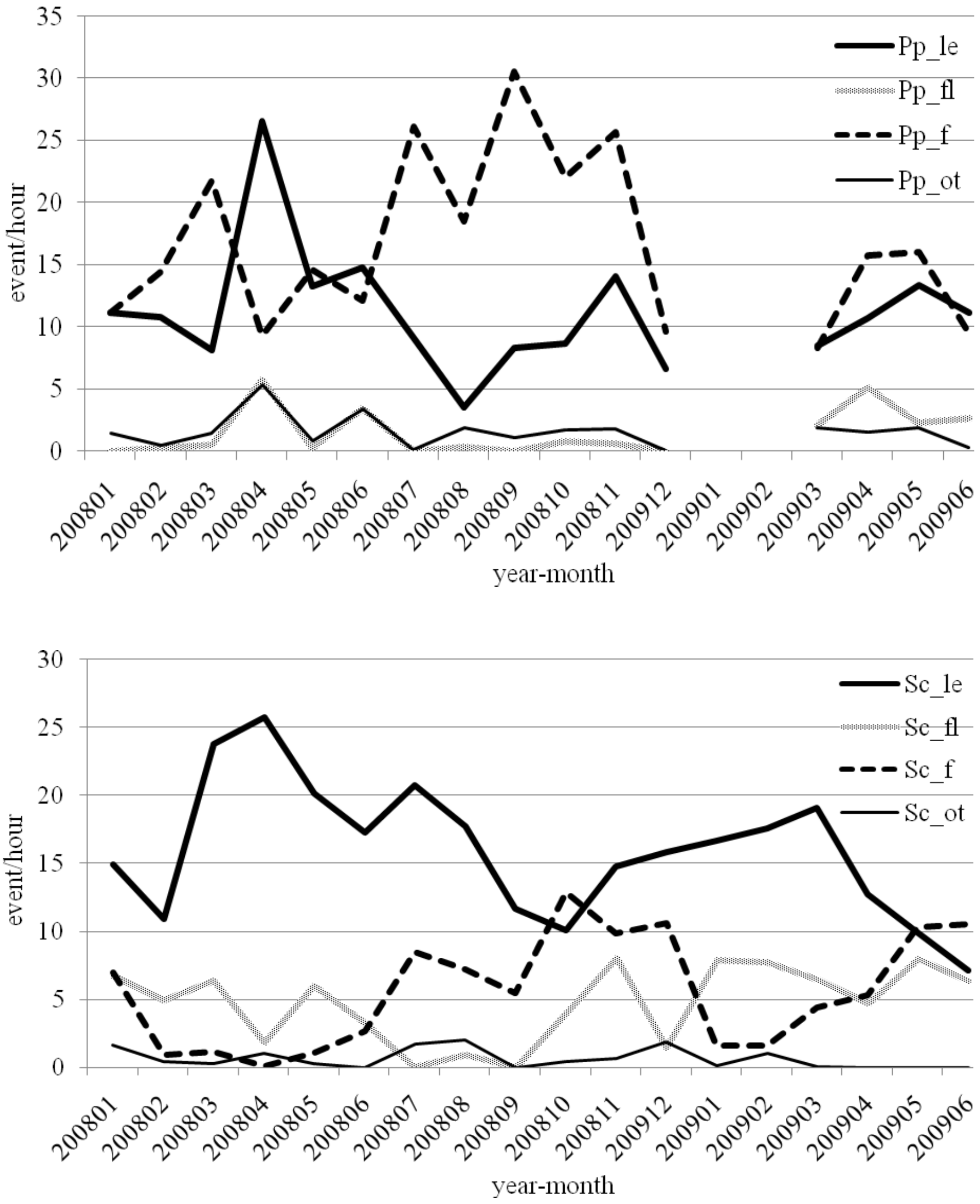

Figure A4. Monthly distribution of food preferences (le: leaf; fl: flower; f: fruit; ot: other) in *P. potenziani* (Pp) and *S. concolor* (Sc).

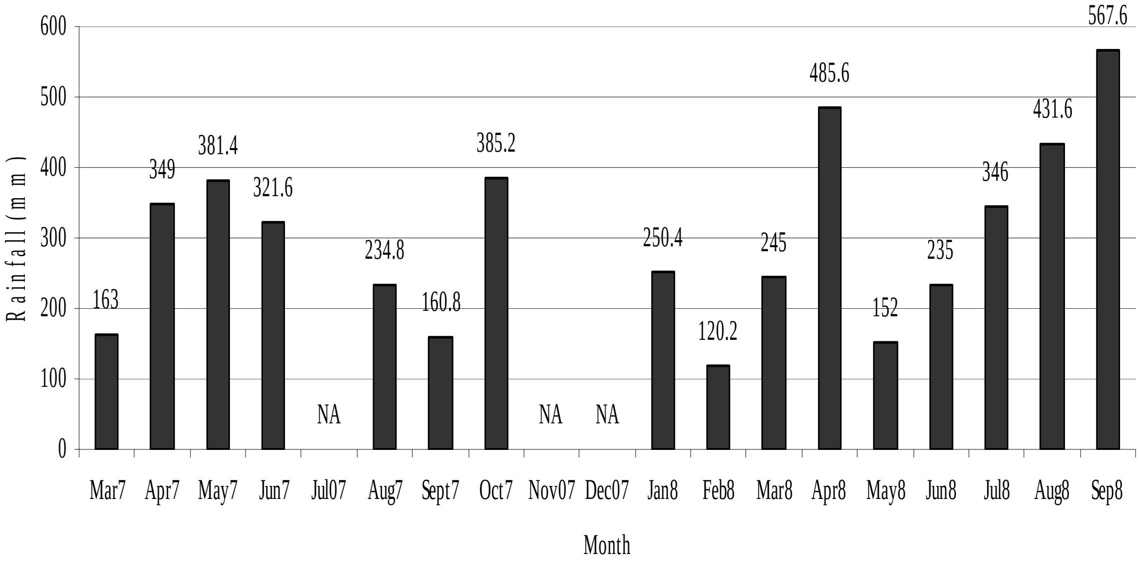

Figure A5. Rainfall measured in Peleonan forest from March 2007 through September 2008 (NA: no data available).

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Göttingen October 2012

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Basic Education

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High Education

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Promotion

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Publication

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Hadi S, Ziegler T, Waltert M, Syamsuri F, Muehlenberg M, Hodges JK. 2012. Habitat use and niche overlap of two sympatric colobines, *Presbytis potenziani* and *Simias concolor* on Siberut, Indonesia. *International Journal of Primatology,* 33:218–232

Hadi S, Ziegler T, Hodges JK. 2009. Group structure and physical characteristics of Simakobu Monkeys (*Simias concolor*) on the Mentawai island of Siberut Indonesia. *Folia Primatologica,* 80: 74-81

Hadi S, Ziegler T, Waltert M, Hodges JK . 2009. Tree diversity and forest structure in northern Siberut, Mentawai islands, Indonesia. *Tropical Ecology,* 50(2): 315-327

Waltert M, Abegg C, Ziegler T, **Hadi S**, Priata D, Hodges JK. 2008. Abundance and community structure of Mentawai primate in the Peleonan Forest, North Siberut, Indonesia. *Oryx*, 42(3), 1–5

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August 2008: Niche differentiation of two sympatric colobines (*Simias concolor* &

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