The *Long Calls* of Wild Male Orangutans: A Phylogenetic Approach

Marina Davila Roß 2004 Institut für Zoologie Tierärztliche Hochschule Hannover

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Supervised by Dr. Thomas Geissmann Prof. Dr. Elke Zimmermann

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Summary

Although several genetic, molecular, and morphological studies were carried out to clarify orangutan systematics, ongoing taxonomic controversies still exist. This project shows a new approach to orangutan phylogeny with focus on their *long calls*. Presented by numerous works, analyses on species-specific *loud calls* of primates can help to understand phylogenetic influences and to reconstruct taxonomy. Orangutan males produce *long calls* to regulate inter-male spacing and to attract mates.

Since samples needed to be pooled from dispersed orangutan populations and recordings from Northwest Borneo were not at my disposal, I collected the missing data myself in Batang Ai National Park, Sarawak. During this field work, 4.3 *long calls* were heard a day – at least 290% more calls than anywhere else reported. This rate reflects a high population density due to the profusion of empili fruit (*Lithocarpus* sp.). Additionally, compared to other populations, Batang Ai orangutans vocalize more often during the night. Presumably, this time offers males of lesser rank the opportunity to acoustically compete with more dominant individuals.

Prior to measuring sonagrams, the call structure needed to be examined. Unique among other non-human primates and as a result of high inter-male competition, orangutans are able to emit synchronic notes, possibly by means of their huge laryngeal sacs.

In this project, 64 variables (qualitative: n = 4; numerical: n = 26; metrical: n = 34) of 75 *long calls* from ten populations of wild orangutans (Borneo: n = 5; North Sumatra: n = 5) were analyzed. Hereby, all four possibly geographically isolated Bornean groups were represented. Their outcomes do not support nor reject island bifurcation. Monophyletic groups were found for Northwest Borneo (72-73%), Northeast-East Borneo (73-85%), and Ketambe (74-78%).

Although there are some inconsistencies that may be explained by further inquiries on *long calls, long call* analysis is an appropriate way to study orangutan phylogeny. As proposed by the Orangutan Action Plan, this study indicates for conservation management to separately deal with orangutans from geographically isolated areas (Northwest, Northeast, East, and Southwest Borneo; North and South Sumatra). Still, additional phylogeographic works are needed for more effective support.

Zusammenfassung

Trotz genetischer, molekularbiologischer und morphologischer Studien, bestehen weiterhin Uneinigkeiten über die Taxonomie der Orang-Utans. Diese Arbeit ist die erste phylogenetische Studie, die unterschiedliche Orang-Utan Populationen anhand ihrer *long calls* miteinander vergleicht. Bekanntlich können phylogenetische Studien über artspezifische *loud calls* von Primaten einen Beitrag zum Verständnis ihrer Systematik leisten. *Long calls* werden von männlichen Orang-Utans produziert um andere Männchen fernzuhalten und um Weibchen anzulocken.

Da es für dieses Projekt von größter Bedeutung war, *long calls* aus diversen Populationen miteinander zu vergleichen und Rufe aus Nordwest Borneo nicht verfügbar waren, habe ich die fehlenden Vokalisationen im Batang Ai National Park, Sarawak, selbst aufgenommen. Dort war es möglich, 4.3 *long calls* am Tag zu hören, was eine mindestens 290% höhere Rufrate als in den anderen Gebieten darstellt. Die hohe Populationsdichte ist vermutlich auf die Überfülle von Früchten (*Lithocarpus* sp.) zurückzuführen. Daten aus Batang Ai belegen auch häufige nokturne Rufe. Vermutlich ist die Nacht, für Männchen tieferen Ranges, die sicherste Zeit akustisch mit einanderen zu konkurrieren.

Vor den Messungen wurde die vokale Struktur der long calls untersucht. Dabei stellte sich heraus, dass der Orang-Utan, als einziger nicht-menschlicher Primat, die Fähigkeit besitzt, synchrone Rufeinheiten innerhalb eines Rufes zu produzieren. Eine Fähigkeit, die wohl auf die großen Kehlsäcke zurückzuführen ist.

In diesem Projekt wurden 64 Variablen (qualitative: n = 4; numerische: n = 26; metrische: n = 34) von 75 *long calls* wildlebender Orang-Utans aus zehn Populationen (Borneo: n = 5; Nord Sumatra: n = 5) anhand *OTU*'s untersucht. Hierbei wurde darauf geachtet, daß jede der vier eventuell geographisch isolierten Gruppen auf Borneo vertreten war. Die durchgeführten Analysen lieferten keine eindeutigen Ergebnisse, die eine eventuelle Borneo-Sumatra Dichotomie hinweisen könnten. In der phylogenetischen Rekonstruktion, wurden insgesamt drei monophyletische Gruppen festgestellt: Nordwest Borneo (72-73%), Nordost-Ost Borneo (73-85%) und Ketambe (74-78%) in Nord Sumatra.

Obwohl diese Studie neue Fragen aufwirft, die weitere Untersuchungen erforderlich macht, liefern die *long call* Analysen wichtige Resultate zur Phylogenie der Orang-Utans. Diese Arbeit unterstützt den Orangutan Action Plan, der Orang-Utans aus geographisch getrennten Gebieten (Nordwest, Nordost, Ost und Südwest Borneo; Nord und Süd Sumatra) unabhängig voneinander zu schützen vorsieht.

1. Introduction

Objectives of this study

Orangutan population estimates show merely 20,000 to 25,000 individuals still existing (cited in Andayani et al., 1998). Major threats to species' survival include natural disasters and human activities causing habitat loss and degradation and forcing their populations into fragmented forest pockets, where they may have to face lack of resources and inbreeding depression (Rijksen & Meijaard, 1999). Such dilemmas may be solved by displacing threatened orangutans into other habitats. However, translocations can also address a new serious problem — the hybridization of orangutan demes.

If possible, orangutans should not be brought into areas where wild populations reside. However, this kind of translocation takes place in emergency situations when fragmented groups face inbreeding depression. Unfortunately, once a population receives an influx of gene variability, hybridization of orangutan taxa may occur.

Hybridization possibilities often cannot be avoided in displacing actions due to the inadequate knowledge on orangutan systematics. Since taxonomists dispute strongly on the validity of "potential" orangutan taxa from Borneo and Sumatra (e.g. Muir et al., 2000; Röhrer-Ertl, 1984; Ryder & Chemnick, 1993; Xu & Arnason, 1996; Zhang et al., 2001; Zhi et al., 1996), it is difficult from the perspective of conservation management to decide on how to deal with fragmented populations declining in size.

Therefore, it is of utmost priority to achieve a better understanding on orangutan taxa and their boundary demarcation. More research projects should address orangutan phylogeny and systematics. This study on orangutan *long calls* is a new approach to already existing and ongoing genetic, molecular, and morphological works on phylogeography.

The objectives of this study are

- (1) to study the structure of orangutan *long calls*,
- (2) to compare *long calls* between different orangutan populations,
- (3) to enhance our knowledge of orangutan systematics, and
- (4) to contribute to orangutan taxon management and conservation.

Orangutans (Pongo)

Orangutans are the Asian representatives of the great apes (family Hominidae) and the largest arboreal primates (e.g. Geissmann, 2003; Groves, 2001).

A striking characteristic of the genus *Pongo* is the extreme sexual dimorphism. Adult males possess impressive throat sacs, large canines, projecting cheek pads (flanges), and thickening of hair (e.g. Davila Ross, pers. obs.; Graham, 1988; MacKinnon, 1974). They weigh about 86.3 kg, more than twice as much as adult females (38.5 kg) (Markham & Groves, 1990; Schürmann & van Hooff, 1986). Additionally, both sexes differ in their behavior. While females raise their offspring in their natal areas, males are known to live dispersed and abandon the place where they grew up (e.g. Geissmann, 2003; Knott, 1999; Rijksen, 1978; Rodman, 1973; van Schaik & van Hooff, 1996). Moreover, *long calls* are only produced by males.

Bimaturism of physiologically adult males is another orangutan trait (e.g. Delgado & van Schaik, 2000; Schürmann & van Hooff, 1986; Knott, 1999). In smaller "unflanged" males (8 to 15 years of age in the wild), the exhibition of secondary sexual characteristics is delayed (\leq 9 years), which may be influenced by *long calls* and direct agonistic behavior of the nearby residing "flanged" males (Kingsley, 1982; Knott, 1998; cited in MacKinnon, 1974; Schürmann & van Hooff, 1986).

Males as well as females occupy ranges that overlap with those of others (e.g. Davila Ross, pers. obs.; Galdikas, 1995b; Rijksen, 1978). However, as fission-fusion species, their social organization may vary depending on ecological factors, e.g. mast fruiting (cited in Delgado & van Schaik, 2000).

The daily activity pattern of orangutans consists primarily of resting (44 %), feeding (41 %), and traveling between resting and feeding sites (13 %). During the remaining time, they build either tree nests (2 %) or engage in social activities (< 1 %) (Knott, 1999).

Besides their primary diet of pulp and seeds, orangutans eat leaves, shoots, flowers, bark, pithy plants, insects, and even small mammals (Knott, 1999; Rijksen, 1978; Rodman, 1988). Similar to chimpanzees, they may use tools (Lethmate, 1977a, 1977b, 1994; Rijksen, 1978; van Schaik & Knott, 2001).

Orangutan distribution and migration

During the Pleistocene, orangutans lived in China, Vietnam, Laos, Sumatra, Borneo, and Java (Kahlke, 1973; Muir et al., 2000; Smith & Pilbeam, 1980) (Figure 1.1). In the first of the last two glacial epochs, when the sea level was low, orangutans must have left the Asian mainland and arrived at the Sunda Shelf islands (Muir et al., 2000; Warren et al., 2001). Due to drastic climatic changes, times of land crossing alternated with periods of landmass separation (e.g. de Boer & Seuánez, 1982; MacKinnon et al., 1997; Muir et al., 2000). The last isolation occurred 8,000 to 10,000 years ago (de Boer & Seuánez, 1982; Muir et al., 2000; Seuánez et al., 1979). Yet, even during the glacial peaks, two wide rivers always dissected the direct migration routes between the Asian mainland, Borneo, and Java (Groves, 1986; MacKinnon et

al., 1997; Marshall & Sugardjito, 1986; Röhrer-Ertl, 1984; Warren et al., 2001). This way, Sumatra played the unique role of a land bridge in the mammal dispersion of Southeast Asia (Muir et al., 2000; Röhrer-Ertl, 1984).

Today wild orangutans solely live in rainforests of Borneo and Sumatra (Figure 1.1). On Sumatra, their distribution is mostly limited north of Lake Toba, although few small orangutan groups were found southward this region (e.g. Rijksen, 1995; Rijksen & Meijaard, 1999).



Figure 1.1. Contemporary orangutan distribution (dark-gray shaded areas) on Borneo and Sumatra with main rivers (from Orangutan Foundation International website) and insert with Pleistocene orangutan dispersion (from Rodman, 1988)

In contrast, Bornean orangutans are more widely spread throughout the island with exceptions of Southeast and Northcentral Borneo (Bennett, 1998; Rijksen & Meijaard, 1999). On Borneo, orangutan isolations are caused geographically by centered mountain ranges and the rivers Kapuas, Mahakam, Barito, and possibly Kayan (e.g. MacKinnon et al., 1997; Marshall & Sugardjito, 1986; Muir et al., 1998b; Zhi et al., 1996). Therefore, contemporary Bornean populations occupy three to four isolated regions – Northwest, Northeast, East, and Southwest Borneo (Andayani et al., 1998; Warren et al., 2001; Zhi et al., 1996). Due to lack of surveys, however, it is uncertain whether the two eastern fragments should not be considered as one (Rijksen, 1978; Rijksen & Meijaard, 1999). In historical times, further fragmentations were caused by habitat loss and poaching (Rijksen, 1995; Rijksen & Meijaard, 1999).

A division in four taxa would coincide more or less with the distribution of the four Bornean gibbon subspecies (*Hylobates agilis albibarbis*, *H. muelleri abbotti*, *H. muelleri funerus*, *H. muelleri muelleri*) (Marshall & Sugardjito, 1986). Also, a division (of orangutans) into either three or four fragments would equally closely resemble the distribution pattern of the Asian colobines of the genus *Presbytis* (*P. femoralis*, *P. comata*, *P. frontata*, *P. rubicunda*) (Brandon-Jones, 1996).

Phylogenetic studies on orangutans

Inter-island comparisons

Ever since differences in physical appearance and behavior between Sumatran and Bornean orangutans were published as a result of pioneer works (cited in Courtenay et al., 1988; MacKinnon, 1973, 1974, 1975; Rijksen, 1978), studies in search of taxonomic clarity for *Pongo* accumulated.

One of the earlier and most important works was carried out by de Boer & Seuánez (1982). Examining four chromosome pairs, they demonstrated the arrangement of chromosome 2 to be entirely different in Bornean and Sumatran orangutans.

Other evidence on a Borneo-Sumatra dichotomy were made by Meera Khan et al. (1982) with red cell enzymes and Wijnen et al. (1982) with Glucose6phosphate dehydrogenase. Unfortunately, both studies included only same small sample size for Sumatra (n = 2).

Dugoujon et al. (1984) measured immunoglobulin allotypes found in both islands and revealed Gm 10, 11, and 13 and Bm 7 to be present only in Sumatran orangutans. Their evaluations once again supported the occurrence of two lineages correlating with the two islands. However, their sample size does not represent the Bornean taxa (n = 4) appropriately.

Orangutan dichotomy was once more supported by an elaborate study of Ryder & Chemnick (1993) on mitochondrial DNA restriction endonuclease cleavage pattern of 14 orangutans. Interestingly, this study showed two phylogenetic lineages within each of the two islands (Figure 1.2b). Critique on its methods was made by Muir et al. (2000) because some Sumatran individuals were termed "misclassified" after their results revealed their "Bornean character". Including all data of the Ryder & Chemnick study would, consequently, result in a less stable Borneo-Sumatra dichotomy and in possibly more than two Sumatran lineages, of which at least one would show a close relationship to the Bornean cluster.



Figure 1.2. Systematic trees of one morphological study derived by cluster analysis (a) and of six phylogenetic works (b-j): (a) Röhrer-Ertl (1984): craniometry; (b) Ryder & Chemnick (1993): mtDNA restriction endonuclease cleavage site; (c) Zhi et al. (1996): mt 16S rRNA; (d) Zhi et al. (1996): minisatellite data; (e) Zhi et al. (1996): mtDNA restriction fragment length polymorphisms; (f) Muir et al. (2000): mtDNA sequences of NADH subunit 3 and cytochrome B; (g) Warren et al. (2001): control region mtDNA. Numbers in parentheses indicate number of individuals; (h) Zhang et al. (2001): ND5 mtDNA.

Summarizing several studies, the divergence of Bornean and Sumatran taxa was estimated to range between 0.7 to 2.8 million years ago (Janczewski et al., 1990; Ryder & Chemnick, 1993; Warren et al., 2001; Zhang et al., 2001; Zhi et al., 1996). Strikingly, this suggests their historical separation may have occurred several hundred thousand years before the first submergence of Sunda Land (Muir et al., 2000).

As another approach the diversity of the genus *Pongo* was made compared with that of other species. A comparison of the complete mitochondrial DNA molecule revealed a greater difference between Bornean and Sumatran orangutans than between pygmy chimpanzees (*Pan paniscus*) and common chimpanzees (*Pan troglodytes*) (Xu & Arnason, 1996). Other molecular works came up with similar conclusions or showed just about the same diversity within *Pongo* and *Pan* (e.g. Bruce & Ayala, 1979; Janczewski et al., 1990; Zhi et al., 1996).

With these and later studies confirming two separate phylogenetic lineages, recognition of Bornean and Sumatran orangutans as two distinct species was proposed (e.g. Ryder & Chemnick, 1993; Groves, 1986, 2001; Warren et al., 2001; Xu & Arnason, 1996; Zhi et al., 1996).

Contrarily, other researchers disagreed with this classification (e.g. Courtenay et al., 1988; Muir et al., 1998a, 2000; Delgado & van Schaik, 2000). A major problem with these systematic works was that their analyses included solely captive individuals from zoos or research centers. Not only may such a sample choice possibly diminish valuable data on precise localities, but it can also lead to errors in origin determinations. Furthermore, the just mentioned studies mostly neglected the paleo-migration of orangutans caused by changing geographic boundaries (Muir et al., 2000). These two points of criticism, among others, lead to the urge for systematic analyses to include orangutans of various locations scattered throughout both islands. This perception was additionally emphasized by the impressive degree of variation found among orangutans from each of the two islands (de Boer & Meera Khan, 1982; de Boer & Seuánez, 1982; Janczewski et al., 1990; Meera Khan et al., 1982; Xu & Arnason, 1996).

A different approach

Although a new and more locality-conscious approach to investigate orangutan systematics has been carried out since the mid eighties, one hundred years earlier, Selenka made already use of exact locations in his morphological work and distinguished as many as two Sumatran and eight Bornean taxa (cited in de Boer & Seuánez, 1982). Mostly including the Selenka collection, Röhrer-Ertl (1984) analyzed cranial data from various samples with details on sites. The resulting dendrogram revealed not only a Borneo-Sumatra dichotomy, but also distinct Bornean clades (Figure 1.2a).

In another study on skulls, Groves et al. (1992) found clear differences between orangutans from Northwest-Northeast Borneo, Southwest Borneo, and Sumatra. When only

males were compared, data from Northwest and Northeast Borneo depicted discrepancies. The sample size from Northeast Borneo (n = 4) was, however, limited.

The first study on genomic differentiation of wild orangutans from Sumatra (n = 6) and the four geographically distinct Bornean areas (n = 33) was made by Zhi et al. (1996). Their phylogenetic trees were based on nuclear minisatellite loci, mitochondrial DNA restriction fragment length polymorphisms, and mitochondrial 16s rRNA sequences (Figures 1.2c-e). With each of the three data sets, the two island lineages resulted. Furthermore, mtDNA RFLP data showed two distinct Sumatran lineages. The other two analyses revealed even more Sumatran clades, but these exhibited lower bootstrap values. Concerning Borneo, orangutans of the four isolated areas were not significantly different from one another. Although high bootstrap values appeared randomly in all three dendrograms, the tree topology did not conform to geographic divisions. It should be noted, that data sets for East (n = 1) and Southwest Borneo (n = 1) were meager and that comparisons were made between haplotypes or nucleotide sequences instead of individuals or locations.

Applying analysis of variance and Scheffé's test, Uchida (1998) found equal differences in postcanine morphology between Northwest and Southwest Borneo when comparing interisland discrepancies. Samples from Northeast and East Borneo, however, were not included in his study.

Recently, Groves (2001) proposed to recognize Bornean and Sumatran orangutans as two distinct species and to split Bornean orangutans into three subspecies (Table 1.1). His division was based on his data of male crania resulting in three distinct clusters in multivariate analysis and on previous morphological findings (Röhrer-Ertl, 1984; Groves, 1986; Groves et al., 1992; Uchida, 1998). Groves's (2001) samples from East Borneo were clustering together with those from Northeast Borneo.

Species	Subspecies	Distribution
Pongo pygmaeus	P. p. pygmaeus	Northwest Borneo
(Linnaeus, 1760)	(Linnaeus, 1760)	(north of Kapuas River; West Sarawak)
	P. p. morio (Owen, 1837) P. p. wurmbii (Tiedemann, 1808)	Northeast-East Borneo
		(south of Mahakam River; Sabah)
		Southwest Borneo
		(south of Kapuas River; west of Barito River)
Pongo abelii		Sumatra
(Lesson, 1827)		

Table 1.1 Taxonomy of the genus *Pongo* according to Groves (2001).

Muir et al. (2000) came up with quite different conclusions by examining mitochondrial DNA sequences of NADH subunit 3 and cytochrome B. Their resulting dendrogram showed one Bornean and two Sumatran lineages (Figure 1.2f). The Bornean clade had no further distinct separations. Unfortunately, the partially estimated Bornean locations (Northwest, Northeast, East, and Southwest Borneo) could not be traced within their phylogeny which

was based on haplotypes. Interestingly, one of the two Sumatran lineages pictured a much closer relationship to the Bornean clade than to the other Sumatran lineage. The latter clade was further divided into two.

Analyzing microsatellite DNA of Kalimantan orangutans, Warren et al. (2000) concluded that no genetic distinction exists between East and Southwest Bornean individuals, but that these groups are subjected to genetic drift.

In their comprehensive study on mitochondrial DNA control region sequences, Warren et al. (2001) focused chiefly on Bornean orangutans (n = 41) of six different locations, but also included a small Sumatran sample (n = 5). Besides a clear island dichotomy, the resulting phylogeny exhibits distinct clades for Northwest, Northeast, East, and Southwest Bornean orangutans respectively with bootstrap values ranging from 52% to 71% (Figure 1.2g). Strikingly, all but one individual fit precisely into their geographic cluster. Moreover, Warren et al. (2001) calculated that these four Bornean taxa diverged 860,000 years ago, possibly right after their arrival on Borneo. As a result, the authors proposed to recognize four Bornean subspecies.

Zhang et al.'s (2001) analysis ND5 mitochondrial DNA sequences also resulted in a clear Borneo-Sumatra dichotomy (Figure 1.2h). Within the Sumatran cluster, two lineages were supported by 93% of the bootstrap replicates. Additionally, the authors analyzed 16S rRNA sequences (partially from Zhi et al., 1996) and microsatellite data, and found no evidence of island distinction. All samples, however, came from zoo animals, and should, therefore, be looked at with caution.

Results supporting the existence of more than one Sumatran lineage (e.g. Karesh et al., 1997; Muir et al., 2000; Ryder & Chemnick, 1993; Zhi et al., 1996) were often thought to be related to Rijksen's (1978) observations on sympatric long-fingered, dark-haired and short-fingered, light-haired orangutans, and their intermediates. Differing models on paleo-dispersal, causing multiple origins, were proposed. Most commonly accepted is the migration from the western and eastern side of the Asian mainland to North and South Sumatra respectively (Rijksen & Meijaard, 1999). Röhrer-Ertl (1984), on the other hand, suggested that a split into two distinct populations may have occurred right after the arrival of *Pongo* on Sumatra.

A more unconventional model was portrayed by Muir et al. (2000). About 74,000 years ago, the second largest volcanic eruption (Toba Volcano) on earth took place in North Sumatra destroying its surroundings with most larger mammals (see Lake Toba, Figure 1.1). The explosion may have initiated the following glacial epoch that lasted 50,000 years. During this period, genetically distinct orangutans from the Asian mainland as well as Borneo and Java may have migrated to Sumatra, forming at least three distinct lineages on this island.

As one can easily see, all morphological, molecular, and chromosomal studies on orangutan phylogeny cannot be summarized to provide a clear picture on orangutan systematics. As a result, there is a need for more phylogeographic studies with different, independent approaches and with more consideration on regional information, both for Borneo and Sumatra. Therefore, by comparing *long calls* from ten different populations, this project might help to give us an insight on orangutan systematics.

Orangutan long calls

Long calls or *loud calls* are far-carrying sounds of great intensity produced by numerous primates (e.g. Fossey, 1972; Gautier, 1988; Geissmann, 2003; Hohmann & Fruth, 1994; Snowdon et al., 1986). Because of their species' distinction, *long call* analyses are most reliable in reconstructing phylogeny successfully, as was the case for Asian gibbons (Hylobatidae: e.g. Geissmann, 1993), African guenons (Cercopithecini: e.g. Gautier, 1988, 1989) African bushbabies (Galagonidae: e.g. Zimmermann, 1990), African Colobus monkeys (Colobini: e.g. Oates & Trocco, 1983), Madagascan lemurs (Lemuriformes: Macedonia & Stanger, 1994; Stanger, 1995), and South American marmosets and tamarins (Callitrichidae: Wittiger, 2002). Often, the results corroborate with those of molecular works (Geissmann, pers. comm.). Surprisingly, any phylogenetic approaches on orangutan *long calls* are absent.

Among all types of orangutan vocalizations, *long calls* are the loudest and one of the most frequently uttered (Davila Ross, pers. obs.; Galdikas, 1983; MacKinnon, 1971, 1974; Mitani, 1985). First to investigate their acoustic structure, MacKinnon (1971, 1974) distinguished between three gradually merging successional segments of call unit series: A deep bubbly introduction, a high climax of full roars, and a bubbly tail off with low sighs. Also during the inhalation of these notes, bubbling sounds may be produced (e.g. Rijksen, 1978). *Long call* duration varies from twenty seconds to four minutes. Usually, however, calls last one or two minutes (Table 1.2) (Davila Ross, pers. obs.; Galdikas, 1983; MacKinnon, 1971, 1974; Mitani, 1985; Rijksen, 1978).

Orangutan *long calls* are solely emitted by flanged males (e.g. Galdikas & Insley, 1988; MacKinnon, 1971; Mitani, 1985). Besides their body size, two dimorphic features may effect these sounds. Inflated during calling (e.g. Davila Ross, pers. obs.; MacKinnon, 1971; Rodman, 1973), throat pouches can amplify and resonate the acoustics (Rodman, 1973). Furthermore, cheek pads may help recipients to locate *long call* directions (Galdikas 1983) or may concentrate the caller's vocal energy in a particular direction (Rodman & Mitani, 1987).

Table 1.2. Long call data of measured variables from previous field studies (abbreviations: Max. = maximum; min = minutes; no. = number; n.u. = no unit, Hz = hertz. s = seconds)

Variable	East Borneo	Northeast Borneo	Southwest Borneo	Sumatra	Sumatra
	(Mitani, 1985)	(MacKinnon, 1971)	(Galdikas, 1983; Galdikas & Insley, 1988)	(MacKinnon, 1974)	(Rijksen, 1978)

No. calls per day (n.u.)		0.6	1.5		
Duration of call (min)	1-2	≤ 3	1-2	≤ 1	1-2
No. of sounds (n.u.)		≤ 50	≤ 33	≤ 25	
Max. frequency (Hz)		< 1300	< 1200	< 700	
Sound distances (s)		3.0	2.3	1.5	

Characterizing orangutan dimorphism and bimaturism and linked with inter-male encounters (Rijksen, 1978; MacKinnon, 1974) and copulations (e.g. Galdikas, 1983; Schürmann, 1982), *long calls* may have resulted as part of the male-to-male competition over numerous resources, such as females and food (e.g. Galdikas, 1983; MacKinnon, 1974; Mitani, 1985).

Inter-male spacing

Long calls function in keeping males apart over long distances (e.g. Galdikas, 1983; Mitani, 1985; MacKinnon, 1971, 1974; Rijksen, 1978). Reacting most of all sex-age classes when hearing *long calls* (Galdikas, 1983; MacKinnon, 1971; Mitani, 1985), adult males vary in their responses depending on their hierarchical status (Galdikas, 1983; Mitani, 1985; Rijksen, 1978).

Males of lower rank mostly avoid meeting dominant individuals by moving quickly away from their call directions (Galdikas, 1983; Mitani, 1985). As an additional reaction, *kiss-squeaks* (MacKinnon, 1974) are occasionally vocalized by subordinate flanged males (Mitani, 1985). These were, however, never heard by unflanged males in similar situations (Galdikas, 1983; Mitani, 1985).

Dominant flanged males, on the other hand, approach subordinate callers and were found to counter-call in six of eleven playback experiments (Mitani, 1985). Although such behavior should lead to numerous confrontations among males with overlapping home ranges, encounters of this kind are surprisingly rare (Galdikas, 1983: Four contacts in 6,804 hours; MacKinnon, 1971: One contact in 1200 hours).

This could be the result of long-distance communication. In fact, dominant males (two to four calls per day) vocalize more often than subordinates (Galdikas, 1983; Mitani, 1985), placing the lower ranking orangutans in a position to react rather than act. Furthermore, with decreasing call distances, acoustic recipients respond stronger and, specifically for adult males, observed patterns margin within four hundred meters (Galdikas, 1983; Mitani, 1985). Thus, by means of individual hierarchical status in calling behavior and in keeping safety regions, spacing between males is obtained.

Mate attraction

Besides inter-male spacing, some researchers hypothesize *long calls* to attract sexually receptive females over far distances (Galdikas, 1983; Horr, 1972, 1975; MacKinnon, 1969; Rodman, 1973). However, due to the long-term offspring investments by females (e.g. MacKinnon, 1974; Rijksen, 1978) and lack of estrous signals during field observations (Dahl, 1988), such data are limited (Mitani, 1985).

Alternatively, *long calls* can signal nulliparous females to initiate mating with flanged males, who are aroused by vocalizing (Galdikas, 1983, 1995a; Schürmann, 1982) and who seem to be sexually more interested in adult females (e.g. Galdikas, 1983, 1995a; Mitani, 1985; Schürmann, 1982).

Inter-population comparisons

Within a distance of 400 m, Galdikas (1983) could acoustically identify four different *long callers* in Tanjung Puting, Southwest Borneo. Idiosyncrasies in call structures were also suggested for Kutai, East Borneo, (Mitani, 1985) and Ketambe, Sumatra, (Rijksen, 1978) populations. The latter findings, however, lack confirmation.

The circadian spectra of numerous studies show maximum *long call* rates during 04:00 to 10:00 and 15:00 to 19:00 (Figure 3.1) (Galdikas, 1983; MacKinnon, 1974; Mitani, 1985). Their histograms vary in numbers of peaks (1-3), peak positions, and general temporal dispersion. Interestingly, MacKinnon (1974) found orangutans to compete acoustically with other species on temporal preferences based on differences between Ulu Segama, Borneo, and Ranun, Sumatra. According to him, Sumatra had a higher primate density than Borneo and, furthermore, the presence of *loud calling* leaf-monkeys (*Presbytis aygula*) and siamangs (*Symphalangus syndactylus*) (Geissmann, 2003).

Notably, calls are emitted during day and night (Figure 3.1); however, nocturnal data was limited (Galdikas, 1983; MacKinnon, 1974; Mitani, 1985).

Long calls vary in rates from less than once a month (Ancrenaz, pers. comm.; Meredith, 1993) to 1.5 per day (Galdikas, 1983) (Table 1.2). In East and Southwest Borneo, calls are mostly produced spontaneously (Galdikas, 1983; Mitani, 1985), but in Northeast Borneo and Sumatra, these are more often triggered by crashing trees, breaking branches, and other *long calls* (MacKinnon, 1971; Rijksen, 1978).

Although no study has ever focused on comparing *long call* structures between different populations, an attempt has been made on these grounds by MacKinnon (1974), who found discrepancies between the Ulu Segama, Northeast Borneo, and Ranun, Sumatra, populations (Table 1.2). According to him, Northeast Bornean calls lasted longer and consisted of more notes which, in addition, were timed farther apart and reached higher frequencies than those

from Sumatra. Moreover, Galdikas & Insley (1988) presented their acoustic data from Tanjung Puting, Southwest Borneo (Table 1.2).

2. Methods

Field study in Batang Ai National Park

For this study, it is essential to include vocal data from a wide range of different locations. Since field studies on the Northwest Bornean fauna are extremely rare and since I was not aware of anyone ever having tape-recorded orangutan *long calls* in this area, I collected the missing data myself in the Batang Ai National Park, Sarawak, Malaysia (Figures 2.1 & 2.2).



Figure 2.1. Three research sites Kota Enggam, Bukit Spantu, and Nanga Rirong (plots) in Batang Ai National Park (from Meredith, 1993)

Material

Long calls were tape-recorded with a Sennheiser ME66 microphone, a Sennheiser K6 adapter, and a Sony Professional Walkman WM-D6C. A GPS receiver Garmin Etrex and a simple compass were used for orientation purposes.

Long call data

The field study was carried out from the 6th of August to the 1st of October, 2001. Its recording method was simple. We waited hours and sometimes days for indications on the presence of flanged male orangutans. Hereby, *long calls* were most helpful. Then, estimating the distance and direction, we tried silently to trace the male and tape-record any following *long calls*. Data of all *long calls* heard always included the date and time, the location, the direction and distance of the calling male, possible behavioral observations, and the weather. Data were collected at all hours of the day and the night (318 hours total) (Table 2.1).

Time of day and night	Hours of survey
00:00-01:00	4.00
01:00-02:00	4.17
02:00-03:00	5.00
03:00-04:00	4.00
04:00-05:00	5.00
05:00-06:00	6.67
06:00-07:00	14.83
07:00-08:00	22.00
08:00-09:00	24.33
09:00-10:00	23.00
10:00-11:00	20.50
11:00-12:00	19.83
12:00-13:00	20.25
13:00-14:00	18.75
14:00-15:00	19.00
15:00-16:00	18.00
16:00-17:00	21.17
17:00-18:00	16.25
18:00-19:00	11.33
19:00-20:00	10.50
20:00-21:00	10.50
21:00-22:00	9.00
22:00-23:00	5.75
23:00-00:00	4.25
Total hours	318.08

Table 2.1. Hours of research conducted within temporal dispersion in Batang Ai

Observational methods

Besides collecting data concerning orangutan vocalization in Batang Ai National Park, ethological observations on *Pongo* were recorded *ad libitum*. Hereby, the behavioral context, the identification of each individual, age, sex, exact position, and time were reported. Additionally, the number of nests were noted at all sites.

Study sites

The Batang Ai National Park (24,040 ha) is mainly a dipterocarp primary forest located in the southern portion of the state Sarawak, Malaysia, close to the Lanjak-Entimau Wildlife Sanctuary (Sarawak) and the Bentuang Karimun National Park (West Kalimantan) (Meredith, 1993). It is known to have the highest orangutan density in the state (Bennett, 1998).

For this project, Kota Enggam, Bukit Spantu, and Nanga Rirong were chosen as study locations because of their high population density of orangutans and the absence of loud rivers nearby when conducting tape-recordings (Figure 2.1).

Eighteen days of research (08.08.01 and 11.-27.08.01) were spent at two sites in Kota Enggam (N 01°18.156-201', E 112°05.883-910', elevation 290-348m; N 01°18.086-155', E 112°06.327-516', elevation 326-386m). As the forest is dense and steep, my following of orangutans was limited to 2 paths.

In Bukit Spantu, data were collected for eleven days during two different time frames (01.-07.09.01 and 15.-18.08.01) and at five recording plots forming a semicircular track (N 01°14.518-996', E 112°05.500-769', elevation 397-525m). Bukit Spantu and surrounding areas offered excellent research possibilities for ethological work because its trees are farther apart and more small paths lead to different directions than in most other areas visited in Batang Ai National Park.

In the third area, Nanga Rirong, survey methods were carried out for 6 days (26.09.-01.10.01) at 6 different plots which connected to a straight pathway (N 01°19.036-195', E 112°05.097-916', elevation 320-440m). The forest environment was similar to that of Bukit Spantu, thus ideal for ethological studies. However, good tape-recordings were collected here as walks were limited by surrounding rivers.

Recording collection

In this study, a total number of 75 *long calls* of wild living orangutans from 10 different populations on Borneo and Sumatra have been analyzed (Figure 2.2). Information on these recordings (e.g. location, recording equipment, date, recordist name) are listed in Appendix 1. More details on research sites may be found in the following works: For Batang Ai: Meredith, 1993; for Kutai: Mitani, 1985; Rodman, 1973; For Ulu Segama: MacKinnon, 1973; for Gunung Palung: Knott, 1998; for Tanjung Puting: Galdikas, 1979, 1985a, 1985b; for Ketambe: Rijksen, 1978; for Ranun: MacKinnon, 1973, 1974; for Sikundur: MacKinnon, 1973; and for Suaq Balimbing: Singleton & van Schaik, 2001.



Figure 2.2. Recording sites (dots) on Borneo and Sumatra with current orangutan distribution (dark-gray shaded areas) and main rivers (from Orangutan Foundation International website)

Orangutans isolated from each other due to geographic barriers were grouped into five areas: Northwest (NW) Borneo, Northeast (NE) Borneo, East (E) Borneo, Southwest (SW) Borneo, and North Sumatra. Within most of these areas, however, it was still obscure whether individuals of different locations shared at least recently the same gene pool (e.g. Gunung Palung and Tanjung Puting). Therefore, orangutans were furthermore grouped into populations.

As part of the data matrix in the phylogenetic evaluation, the *operational taxonomic unit* (*OTU*) was defined as either one identified individual or all unidentified orangutan(s) within one population (Table 2.2). "Unidentified" meant, that the individual could not be recognized later on, making it uncertain if his call was recorded once or more often.

Besides orangutan *long calls*, chimpanzee (*Pan troglodytes*) *pant hoots* were included in the recording collection as the *outgroup* (Table 2.2) (Appendix 2.1). An *outgroup* is required in the phylogenetic analyses in order to polarize the resulting clades. Since *Pongo* has no living ancestors, it was essential to look for a close relative whose *loud call* shows the greatest resemblance to the orangutan *long call*. Of all *loud calls* emitted by apes, chimpanzee *pant hoots* seemed to be most suitable to be included in this work. The structure of chimpanzee *pant hoots* has been described and analyzed in several previous studies (e.g. Arcadi, 1996; Marler & Hobbett, 1975; Marshall et al., 1999). *Pant hoot* recordings of males were collected from 3 different populations.

Area	OTU no.	OTU name	No. of calls	No. of indiv.	Identification
NW Borneo	1	Batang Ai 1	5	1	identified
	2	Batang Ai 2	2	1-2	unidentified
	3	Batang Ai 3	2	1	identified
	4	Batang Ai 4	2	1-2	unidentified
NE Borneo	5	Ulu Segama	2	1-2	unidentified
E Borneo 6 Kutai		Kutai	3	1-3	unidentified
SW Borneo	7	Gunung Palung 1	4	1	identified
	8	Gunung Palung 2	12	1	identified
	9	Tanjung Puting 1	3	1	identified
	10	Tanjung Puting 2	1	1	identified
	11	Tanjung Puting 3	5	1	identified
	12	Tanjung Puting 4	1	1	unidentified
Sumatra	13	Ketambe 1	5	1	identified
	14	Ketambe 2	5	1	identified
	15	Ketambe 3	5	1	unidentified
	16	Ranun	3	1-3	unidentified
	17	Sikundur	1	1	unidentified
	18	Soraya	1	1	unidentified
	19	Suaq Balimbing 1	3	1	identified
	20	Suaq Balimbing 2	3	1	identified
	21	Suaq Balimbing 3	2	1	identified
	22	Suaq Balimbing 4	3	1	identified
	23	Suaq Balimbing 5	2	1	unidentified
Africa	24	Chimpanzee 1	1	1	unidentified
	25	Chimpanzee 2	2	1	identified
	26	Chimpanzee 3	5	1-5	unidentified

Table 2.2. List of *operational taxonomic units* (*OTU*'s) of orangutans and chimpanzees with number of calls, number of individuals, and individual identification status respectively (no. = number; indiv.= individuals)

Sonagrams

The recordings were digitized (11025 Hz sampling rate, 16 bits sample size) using the Canary 1.2.4 program (Cornell Laboratory of Ornithology) on a Power Macintosh G3. Sonagrams were established by *Fast-Fourier-Transformation* (FFT) of the sound software with parameter adjustments listed in Table 2.3 (Charif et al., 1995). Appendix 2 presents a representative *long call* sonagram for every population of the reduced *OTU* data matrix (see Methods: Data matrix).

Table 2.3. List for sonagram options using parameters of Canary 1.2.4.

Parameter	Adjustment	
Filter bandwidth	87.42 Hz	
Frame length	512 Points	
Time	128 Points	

Overlap	75 %
Frequency	21.53 Hz
FFT size	512 Points
Window function	Hamming
Clipping level	- 80 dB
Display style	Smooth
Amplitude	Logarithmic

Data matrix

For the evaluation, a total of 64 variables were measured (Appendix 3). In order to characterize the *long call*, the variables were chosen to describe not only the call (*long call* in its entirety), but also the sounds (all call units in general), and the three most common note types (R, S, I) in their uniqueness. Therefore, first of all, the acoustic structure of the *long call* needed to be examined (see Results & Discussion: Call structure).

The characters consist out of a qualitative (n = 4), a numerical (n = 26), and a metrical part (n = 34). The qualitative variables described the sonagraphical structure for each call and are made up of binary data. An example would be the absence or presence of note type H within the call (Variable 4). The numerical variables characterize calls and sounds. They were obtained by counting (e.g. Variable 6: Number of sounds). Furthermore, percentages (e.g. Variable 14: Number of note types R x 100 / total number of sounds) and positions (e.g. Variable 17: Sound with maximum frequency found either in beginning, middle, or end of call) of certain sounds in a *loud call* were measured. The metric data include calls, sounds, and 3 note types (R, S, I). Their data were derived by using the Canary 1.2.4 measuring features.

A *loud call* data matrix was applied to compare calls in the multidimensional scaling and to find the averages for each *OTU* of the *OTU* data matrix. Since the qualitative variables were of binary kind (e.g. absent = 0%, present = 100%), their means were simply be calculated (e.g. absent = < 50%, present = $\ge 50\%$).

The *OTU* data matrix was applied in two different ways. One of the applications included all *OTU*'s of the recording collection and was used for the multidimensional scaling and the phylogenetic analyses (Table 2.2). The other application was a reduced form of the prior and consisted only out of *OTU*'s with two or more *loud calls*. In this reduced data set, five calls (Tanjung Puting 2 & 4, Sikundur, Soraya; Chimpanzee 1 for the dendrograms) were excluded. Its matrix was used in the multidimensional scaling, the discriminant analysis, and the phylogenetic methods.

All calculations were generated by Microsoft Excel 98.

Statistics

Multidimensional scaling (MDS)

The nonmetric multidimensional scaling (MDS) is a method that depicts plotted data relative to similarities and dissimilarities of numerous variables within one graph (SYSTAT, 1992).

To enable comparisons between samples, firstly, data sets of each character were *standardized* by changing their values to average zero and making their standard deviation equal to one (Sneath & Sokal, 1973; SYSTAT, 1992). Secondly, the matrix was transposed and the *Eucledian distance* was chosen (r = 2) (Sneath & Sokal, 1973; SYSTAT, 1992). Thirdly, the *Kruskal Monotonic method* was applied (SYSTAT, 1992). The MDS analyses were generated by SYSTAT. 5.2.1.

Discriminant analysis

The discriminant analysis is a parametric multivariate method with a discriminant function, that depicts weighted characters identifying discrepancies for defined sample groups without clear separation (Sneath & Sokal, 1973; SYSTAT, 1992). Hereby, characters may be pooled into a smaller set (Lamprecht, 1992; Sneath & Sokal, 1973).

The discriminant function 1 does most of the discrimination (SYSTAT, 1992).

For this work, samples were grouped reflecting the MDS outcome and orangutan demes. Moreover, the group centroids, the mean values for the discriminant scores for each given category, were measured. STATISTICA 5.5 was used to carry out the statistical analysis on a DOS computer.

Phylogenetic analyses

Setup

In order to apply the *OTU* data matrix to the phylogenetic programs, data had to be coded for each variable (Appendices 4 & 5) (Maddison & Maddison, 2000). The coding process resulted in a set of conditions known as character states (Maddison & Maddison, 2000). For binary variables, codes were simply congruent to its values (e.g. character state 0 = absent, character state 1 = present). Most quantitative characters, however, included continuous data, which had to be grouped before coding. Decisions on the value ranges of each character state were made by searching for aggregations in the linear function of each variable (Maddison & Maddison, 2000).

In MacClade 4.0, quantitative variables were labeled *ordered*, since their character states and their uncoded values showed the same continuity respectively. For example, character state 1 (of a variable with 4 character states) needed 1 step to reach character state 4, but only

0.25 step to reach character state 2. Although qualitative variables were termed *unordered*, such labeling was actually inessential because of their binary data. *Unordered* meant that the distance from any character state to another was always equal.

Moreover, characters were termed to have an *equal weight*. Hereby, all variables had the same value in the analysis independent to their number of character states (Swofford, 1990).

Variables inapplicable to certain taxa were recorded as missing.

With these settings established, the coded matrix was placed into PAUP 4.0 for calculating clades.

Cladistics

Cladistic analysis arranges taxa in a hierarchical manner using the concept of *maximum parsimony* and resulting hereby in branching diagrams with shortest tree lengths of alternative hypotheses (Geissmann, 2003; Swofford, 1990).

After stating the *outgroup*, the heuristic method and the bootstrap analysis were carried out. The heuristic method is ideal for a large set for data (Kitching et al., 1998). Starting off with three taxa, it applies trial-and-error whereby taxa are added one by one to an evolving *phylogram* (Kitching et al., 1998). *Phylograms* are phylogenetic trees with branch lengths congruent with the number of character changes (Kitching et al., 1998). *Cladograms*, on the other hand, picture no such evidence on their branch lengths (Kitching et al., 1998). In this work, *cladograms* represent *strict consensus trees* of *phylograms*. *Cladograms* with multiple simultaneous branching (*polytomous* nodes) resulted, when combining *phylograms* with different taxa alignments (Maddison & Maddison, 2000).

To evaluate the stability of clustered taxa in clades, the bootstrap method was applied (Maddison & Maddison, 2000). For this particular analysis, 1000 tree pseudoreplicates to make up a 50% majority-rule consensus tree were chosen. Every pseudoreplicate was produced by randomly deleting and repeatedly adding characters while maintaining the same number of characters the data matrix offered. The resulting *cladogram* presented only grouped taxa with more than a 50% support of all pseudoreplicates (Kitching et al., 1998).

For the quality of the resulting dendrograms, tree length, *consistency index* (*CI*), and *retention index* (*RI*) were noted (Kitching et al., 1998). The tree length is the total number of evolutionary steps of every character in a tree (Swofford, 1990). Looking at a particular character, the number of evolutionary steps indicate the number of times the character states have evolved within the clade (Maddison & Maddison, 2000). Although it indicates inconsistency in a clade, tree length plays chiefly a role in the selection of the most parsimonious trees.

The *CI* is a more accurate measure of inconsistency than tree length. It measures the degree of *homoplasy*, which takes place when a character state evolves more than once in a

clade (Kitching et al., 1998; Maddison & Maddison, 2000). The *CI* of a dendrogram is defined as M/S (M: The sum of minimum numbers of steps from each character in any tree; S: The sum of minimum numbers of steps from each character in a particular tree) (Kitching et al., 1998; Maddison & Maddison, 2000). It ranges from 0 to 1 with 1 being the best value because it portrays no *homoplasy* and with 0.5 having twice as many evolutionary steps as 1 (Maddison & Maddison, 2000). For the *CI*, it is important to be aware of the following. In the first place, the number of evolutionary steps is most likely to increase with every additional character or taxa and vice versa. Secondly, all *missing* data are excluded in the counting of steps, which could make the results look more favorable than reasonable (Kitching et al., 1998). To avoid these problems, the *RI*, which evaluates the consistency of a phylogenetic tree was also measured (Kitching et al., 1998).

The *RI* shows the amount of *synapomorphies* or derived character states united in a group of taxa (Geissmann, 2003; Kitching et al., 1998). It is the result of (G-S)/(G-M) (G: The sum of maximum numbers of steps from each character in any tree) (Kitching et al., 1998). As it is the case of *CI*, the values of *RI* range from 0 to 1 with 1 being the most favorable value for the tree because its characters coincide perfectly with each other.

3. Results

Findings of Batang Ai National Park

Orangutans in Batang Ai National Park

During field work, I had the chance to see a total of 22 orangutans (7 flanged males, 6 adult females, 1 unflanged male, 2 adolescents, 5 juveniles, 1 infant) and 63 of their nests (Table 3.1). Nine individuals were observed eating empili fruit (*Lithocarpus* sp.) (Meredith, 1993). The pea-sized, black empili fruit kept falling from the trees during four consecutive days continuously and were spread on the grounds while I was stationed at the first two sites.

duit ferriale, I – infant, J – juvernie, J – unite				
	Subgroup composition	No. of occurrences	No. of individuals	
	Μ	5	5	
	FJ	3	6	
	А	2	2	
	MFJ	1	3	
	MFI	1	3	
	UFJ	1	3	
	Total	13	22	

Table 3.1. Subgroup compositions for 22 orangutans in Batang Ai (A = adolescent; M = flanged male; F = adult female; I = infant; J = juvenile; U = unflanged male)

No orangutan was ever directly observed calling. Only 2 males whose calls were recorded could later on be identified. Efforts to trace wild orangutans were mostly dissolved because orangutans were not habituated. Furthermore, the tracking of an orangutan sometimes meant ending up in the proximity of a river which could have compromised tape-recordings due to high background noise. And last, the forest was often too steep or too dense for any successful follow-ups.

Call rates and temporal dispersion

During the field study, 4.3 calls a day (151 long calls) were heard.

Vocal findings depict a bimodal circadian distribution in Batang Ai (Figure 3.1). Call rates peak from 05:00 to 06:00 hours and from 18:00 to 19:00 hours. Contrarily, no acoustic data was collected between 00:00 and 01:00 hours.

Batang Ai results show orangutans to emit nocturnal calls. These orangutans vocalize more spread throughout the temporal spectrum than males from other populations (Galdikas, 1983: Tanjung Puting; MacKinnon, 1974: Ulu Segama & Ranun; Mitani, 1985: Kutai).



Time of day

Figure 3.1. Circadian call spectra of the geographically isolated areas from (a) Northwest (Davila Ross, this study), (b) Northeast (MacKinnon, 1974), (c) East (Mitani, 1985), and (d) Southwest Borneo (Galdikas, 1983) and (e) Sumatra (MacKinnon, 1974)

Hearing numerous calls nearby coming from different directions in Batang Ai, I got the impression, that these individuals had very small and overlapping home ranges. This belief was best supported by the *long calls* emitted from their sleeping nests during nights. Calls from up to four different directions could be heard no more than 100 meters away from my tent.

Tape-recordings

In Batang Ai, orangutan *long calls* were tape-recorded within an acoustic distance ranging between 50 and 500 meters The value of several calls, however, was partially or fully reduced due to one or more of the following problems encountered during the field work. Roughly stated, orangutan *long calls* may only be entirely useful for sound analysis when recorded no farther than 100 meters away from the focal animal. Beyond this radius, data on call frequency may get lost. As the sound intensity of *long calls* could differ, this also played a role in the evaluation.

Moreover, acoustic interferences decreased the value of numerous recordings. Especially one species of cicadas (6 hours/day) and one species of crickets (5 hours/day), besides other insects, produced extremely noisy and continuous sounds that were often heard during *long call* recordings. Although they were heard at all hours, their acoustic peaks were during the night. Other loud calls were produced by Argus pheasants, *Argusianus argus*, and Bornean gibbons, *Hylobates muelleri abbotti*. Argus pheasants vocalized day and night, while Bornean gibbons were heard solely from 06:00 to 10:00 hours.

Call structure

When comparing *long calls* in this study, I found some exceptions in the occurrence of their three parts (introduction, climax, tail-off) as defined by MacKinnon (1974). Any of these segments may repeat, differ in its sequential position, or be absent.

Callers produce exhalation as well as inhalation sounds. During the exhalation, various note types may be heard, the most common being huitus (H), roars (R), sighs (S), intermediaries (I) and bubbling (B) (Appendices 2 & 6). These occur at different rates, depending on the calling male.

The tonal "huitu"-sounding units (frequency: 55 to 1700 hertz; duration: 0.106 to 1.072 seconds) are composed of steeply ascending and descending concave slopes. Their two parts appear not to be connected to each other, although this may have more technical reasons. Marked by constantly highest frequencies, huitus characterize the climaxes of the *long calls*. At times, however, they are not present (56% presence). Tonal roaring sounds (frequency: 18 to 1411 hertz; duration: 0.064 to 1.637 seconds) are elements of convex rising and falling shapes connected at their highest points (99% presence). With strongly varying bandwidths,

these elements may occur in any of the three *long call* parts. Depending on the call, roars of high frequencies are emitted during the climax whereas those of low frequencies are positioned either in the introduction or the tail-off. Sighing notes (frequency: 21 to 804 hertz; duration: 0.120 to 1.094 seconds) have descending tonal shapes (88% presence). With relatively small bandwidths, they occur mostly in the introduction or the tail-off. As their name already implies, intermediary sounds (frequency: 28 to 903 hertz; duration: 0.342 to 1.129 seconds) have transitional shapes of roaring and sighing elements (77% presence). Furthermore, their sequential position lies between the two characteristic note types. Thus, intermediaries may be found in any of the three defined *long call* parts. Bubbling is the only atonal sound produced in the *long call* (89% presence). Due to their linear, quickly repeating, vertical shapes which often are not interrupted by inhalation pauses, they cannot be measured as single units but rather as segments. Bubbling occurs during the introduction and tail off – mostly at the very beginning or the very end respectively. However, parts of these sounds may now and then be attached to other elements. In recordings of low quality, bubbling may be mistaken for background noise or go under.

Less frequently, ascending and multi-modulated note types appear in a call. Note types, occurring in two or less *OTU*'s are not mentioned.

Between two sounds of exhalation, orangutans produce often purring during inhalation, that looks sonagraphically similar to bubbling, yet with regular duration. Because purring has less intensity than any other elements, it may not always be noticed sonagraphically or acoustically.

Interestingly, two elements produced at the same temporal interval are often visible in the *long call* sonagrams (Figure 3.2). Thus, notes overlapped. Although this was undoubtedly best visible in Ketambe sonagrams (12 of 15 calls: All, but 1K, 1N, 1O), synchronic calling occurred in numerous populations.



Figure 3.2. Sonagrams of synchronically emitted sounds (manual scaling with 0.7 s/cm and 0.2 kHz/cm)

To make calls even more complex, both elements of synchronic sounds were occasionally alternating in their intensity (Figure 3.3). Thus, a dominating form of one interval may hardly be visible in its following exhalation phase, when the other, previously less visible element is most intense. In numerous sonagrams, however, notes of the transitional phase are not traceable with certainty.



Figure 3.3. Sonagram segment of transitional intensity by two synchronic forms (KE 1I: manual scaling with 0.7 s/cm and 0.2 kHz/cm)

Statistical results

Results of multidimensional scaling

In the MDS diagram, polygons of NW, NE-E, and SW Borneo and Sumatra were marked with respect to geographic isolation for the two *OTU* and the single *long call* data sets (Figure 3.4). Because of the uncertainty regarding separation caused by the Kayan River, their thin sample sizes (*OTU*'s: n = 2; *long calls*: n = 5), and close distances in the MDS diagram, NE and E Bornean data were grouped together.

Common to all three diagrams, the SW Bornean and Sumatran polygons partially overlap. Furthermore, data of NW Borneo accumulate with those of SW Borneo and Sumatra on two occasions (Figures 3.4b & c). The NE and E Bornean plots stand closer to SW Bornean than to any other clusters (Figures 3.4a & b). Contrarily, NW and NE-E Bornean data have a distinct space between each other (Figures 3.4a & b).

Distinctions of samples exist for the single standing NE-E Bornean group of the reduced *OTU*'s (Figure 3.4b) and for the NW and NE-E Bornean data of all *OTU*'s (Figure 3.4a). All remaining forms accumulate partially two-fold, with two exceptions of partially three-fold piling ups in the *long call* graph (Figure 3.4c).



Figure 3.4. Diagrams of multidimensional scaling for (a) all *OTU*'s, (b) reduced *OTU*'s, and (c) individual *long calls* with polygons as NW Borneo, NE-E Borneo, SW Borneo, and Sumatra

Island comparisons for the complete and reduced *OTU* and *long call* data portray 17%, 21%, and 43% of the plots sharing the same space respectively.

Results of discriminant analysis

The resulting scatter plot of the discriminant analysis was carried out for NW, NE-E, and SW Borneo and Sumatra, in accordance with the MDS groups (Figure 3.5).



Figure 3.5. Scatterplot for discriminant functions 1 and 2 of all OTU data and group centroids (crosses) for NW, NE-E, and SW Borneo and Sumatra

It shows clear separations of all four sets. The NW Bornean sphere depicts most distinction. The plots of NW and SW Borneo were the farthest apart from one another, whereas the shortest distance existed between SW Bornean and Sumatran groups.

Concerning the coordinate axes, the NW Bornean sphere scores highest on discriminant function 1 and the Sumatran samples on discriminant function 2. Contrarily, SW Bornean data score lowest on function 1 while those from NE-E Borneo score the lowest on function 2. Within the clusters, the Sumatran data had the tightest assemblage based on function 1, neglecting hereby the two samples of NE-E Borneo. All other plots were more dispersed in that function.

Results of phylogenetic analyses

Heuristic search

The resulting clades of the heuristic search with all OTU data are represented in Figures 3.6 and 3.7 (tree length = 333; CI = 0.2643; RI = 0.5496). The orangutan taxa are

perfectly grouped into its two islands. Furthermore, the Batang Ai (NW Borneo) *OTU*'s are clustered together and separated from the remaining Borneo (SW, NE, and E Borneo) *OTU*'s. Looking at the branch lengths of the two *phylograms*, a clear splitting may be found between the single Ranun *OTU* and all other Sumatra *OTU*'s (Figure 3.6).



Figure 3.6. *Maximum parsimony-phylograms* of complete *OTU* data matrix as a result of the heuristic search (tree length = 333; *CI* = 0.2643; *RI* = 0.5496)



Figure 3.7. *Maximum parsimony-cladograms* of complete *OTU* data matrix (a) as a consensus of 2 trees by the heuristic search (tree length = 333; CI = 0.2643; RI = 0.5496) and (b) as a consensus of 1000 replicates by the bootstrap analysis with *50% majority-rule* (tree length = 469; CI = 0.1876; RI = 0.2996)

The resulting dendrograms of the heuristic search with reduced OTU data are portrayed in Figures 3.8 and 3.9 (tree length = 278; CI = 0.3165; RI = 0.5476). Here, the *Pongo* taxa are split into 4 clades: NW Borneo, SW-NE Borneo, Ranun (Sumatra), and Ketambe-Suaq Balimbing (Sumatra). Within the Ketambe-Suaq Balimbing bush, the Ketambe OTU's are clustered apart from the remaining Suaq Balimbing OTU's. Although Figure 3.8 presents just two *phylograms* as a sample of the twenty most parsimonious trees, the described pattern can be found in all dendrograms.

In all phylogenetic trees, the *Pan* data is separated from the *Pongo* taxa (Figures 3.6-3.9).



Figure 3.8. *Maximum parsimony-phylograms* of 20 resulting trees of the reduced *OTU* data matrix by the heuristic search (tree length = 278; *CI* = 0.3165; *RI* = 0.5476)

Bootstrap 50% majority-rule

The dendrograms of the bootstrap analysis with complete *OTU* data (tree length = 469; CI = 0.1876; RI = 0.2996) are presented in Figure 3.7, whereas those with reduced *OTU* data (tree length = 392; CI = 0.2245; RI = 0.2762) may be found in Figure 3.9.

Although both phylogenetic trees vary somewhat in their numerical values, they have a similar topology. Hereby, three monophyletic clades appear in more than 70% of the pseudoreplicates: Batang Ai 1-4, Ulu Segama-Kutai, and Ketambe 1-3. Whereas the value ranges caused by different *OTU* data never exceeds 4% for the Batang Ai 1-4 (72-73%) and for the Ketambe 1-3 (74-78%) cluster, the value range equals 12% (73% with complete *OTU* data; 85% with reduced *OTU* data) for the Ulu Segama-Kutai cluster.

Besides the three monophyletic clades, a fourth group with 67% support results from the data with complete OTU's: Tanjung Puting 1-2. Since the Tanjung Puting 2 OTU is excluded from the reduced version, such cluster is bound to be missing here.



Figure 3.9. *Maximum parsimony-cladograms* of the reduced *OTU* data matrix (a) as a consensus of 20 trees by the heuristic search (tree length = 278; CI = 0.3165; RI = 0.5476) and (b) as a consensus of 1000 replicates by the bootstrap analysis with 50% majority-rule (tree length = 392; CI = 0.2245; RI = 0.2762)
4. Discussion

Call rates and temporal dispersion

With 4.3 calls a day, Batang Ai data depict a vocal rate of 290% more than the highest measured values reported (Table 1.2) (Galdikas, 1983: Tanjung Puting, SW Borneo). It may be the case, however, that previous authors recorded less calls because they concentrated more on behavioral contexts than on monitoring sounds (Galdikas, 1983; MacKinnon, 1974; Mitani, 1985).

Based on the high acoustic rate, on numerous orangutan appearances and visible nests, as well as on home range estimates, the orangutan population in Batang Ai is presumably of high density. This is possibly effected by the profusion of ripe empili (*Lithocarpus* sp.) fruit which appear to play an important part in their diet. Thus, easy access to food, among other factors, may stimulate orangutan accumulation and vocal rate (Delgado & van Schaik, 2000; MacKinnon, 1971).

Results from Batang Ai show a similar bimodal temporal *long call* dispersion as Tanjung Puting data (Galdikas, 1983), however, in Ulu Segama, Kutai, and Ranun, vocal preferences varied much with time (MacKinnon, 1974; Mitani, 1985). This confirms MacKinnon's (1974) generalization of Borneo and Sumatra based on two locations unsuitable. Notably, differences in calculated circadian spectra as well as in call rates may be accounted by environmental and methodical factors.

The fact that orangutans occasionally call during the night (Davila Ross, this study; Galdikas, 1983; MacKinnon, 1974; Mitani, 1985) is not in accordance with the behavior of diurnal primates. Nocturnal vocalizing is even more surprising since orangutans compete acoustically during this time with other species (crickets, cicadas, other insects) producing the loudest sounds (Davila Ross, this study). However, *long calls* produced at night are probably the result of competition among males with different social status. I presume that less dominant males prefer nocturnal calling because of the delay and decrease in non-vocal reactions of dominant individuals. Lower ranking orangutans get hereby the chance to vocally compete without expecting enraged dominant males to leave the sleeping nest and approach them. This way, night offers an acoustic opportunity for lower ranking males.

Call structure

Orangutan *long calls* are more diverse and complex than previously thought. The *long call* sequence does not strictly consist of an introduction, a climax, and a tail-off, as described

by MacKinnon (1974). Although this seems to be the regular pattern, some variations occur in their presence and temporal sequence.

Seven note types of exhalation and one of inhalation were identified in the present study. Most of these show exceptions in the temporal position they usually occupy. In addition, rare occurrences of other sounds were found in the sonagrams.

Making *long call* analysis even more complex, male orangutans are able to utter synchronic sounds of occasionally alternating intensities. The stereo production of call units is unique in the study of non-human primates (Geissmann, pers. comm.). Even gibbons (family Hylobatidae), which are known to vocalize extraordinary *great calls* with impressive acoustic features, solely emit one sound at a time (Geissmann, pers. comm.).

Presumably, the production of synchronic sounds together with their changing intensity are made possible by the tremendous throat pouches of orangutans, which inflate and vibrate during calling (e.g. Davila Ross, pers. obs.; MacKinnon, 1971; Rodman, 1973). Their orangutan air sac system is most impressive of all primates (cited in Brown & Ward, 1988). Furthermore, possessing the ability to regulate pressures, air sacs may acoustically function to amplify, resonate, and prolong sounds as well as lower their harmonic frequencies (Brown & Ward, 1988; cited in Hewitt & MacLarnon, 2001; Rodman, 1973; Starck & Schneider, 1960).

The complexity of the *long call* structure has never been thoroughly investigated. Any detailed work with such focus would be of most interest, especially if variation in acoustic structure is considered together with ethological contexts and geographical variables.

Orangutan phylogeny

Inter-island comparison

The phylogenetic outcome of this study (Figures 3.6-3.9) does not support a Borneo-Sumatra dichotomy as proposed by most authors (e.g. Janczewski et al., 1990; Meera Khan et al., 1982; Xu & Arnason, 1996) nor rejects more complex orangutan classifications as found by Groves et al. (1992), Muir et al. (2000), and Uchida (1998). The bootstrap analyses of vocal characteristics produced highly polytomous trees (Figures 3.7 & 3.9), which do not confirm either of the alternate views mentioned above. The heuristic search of the complete OTU data matrix indicates an island separation (Figure 3.7a). The same analysis used for the reduced OTU's, however, presents a polytomy of four main clades and, therefore, does not support an island bifurcation (Figure 3.9a). Notably, results of the heuristic search devaluate to some degree when compared with those of the bootstrap analyses by its less stable arrangements.

Furthermore, the MDS *long call* graph shows no strong difference (43% of the data overlapping) between Bornean and Sumatran vocalizations (Figure 3.4c). Although MDS *OTU* diagrams indicate more vocal discrepancies (17-21% of the data overlapping) between the islands, the polygons of the three Bornean groups appear to be quite distinct from each other (Figures 3.4a & b). As a matter of fact, in the MDS *OTU* (Figures 3.4a & b) and discriminant (Figure 3.5) scatterplots, inter-island distances are equal to or smaller than some intra-island ranges of Borneo, much like the morphological findings by Groves et al. (1992) and Uchida (1998). However, multivariate analysis merely shows similarity (or dissimilarity) among taxa. Although similarity is often correlated with phylogenetic relationship, it can also be completely misleading (Geissmann, 2003). Results of multivariate studies should not be mistaken with phylogenetic, although they may be of an assistance in phylogenetic evaluations. Therefore, phylogenetic conclusions based on the analysis of similarity (e.g. Groves, 1986, 2001; Groves et al., 1992; Röhrer-Ertl, 1984; Uchida, 1998) should be regarded with caution.

Considering solely phylogenetic studies when comparing Bornean and Sumatran data, only one work firmly supports the idea of a more complex classification (Muir et al., 2000) and a somewhat contradictory back-up comes from a "dichotomous" cladogram in which 6 of 58 individuals "lacked expectations" (Ryder & Chemnick, 1993). Yet, five phylogenetic analyses supporting an island dichotomy (Warren et al., 2001; Zhang et al., 2001; Zhi et al., 1996) contradict and outnumber the former two. Thus, a Borneo-Sumatra bifurcation seems to be more likely, although possible answers for diverse outcomes need to be encountered.

More solid findings of this study were found by focusing on specific orangutan populations. A total of three monophyletic groups resulted from bootstrap analyses:

Ketambe, NW Borneo, and NE-E Borneo (Figures 3.7 & 3.9). These clades indicate stronger vocal differences between demes within the islands than between Bornean and Sumatran orangutans. Notably, the resulting trees should be looked at with caution because neither ecological factors nor behavioral contexts of the vocalizations were examined thoroughly. In addition, *long calls* may differ depending on the individuality of the caller.

Ketambe

Of all Sumatran data, the bootstrap trees solely indicate Ketambe (74-78%) to form a monophyletic clade (Figures 3.7 & 3.9). Although the proposed occurrence of two sympatric orangutan populations and their intermediates (Rijksen, 1978; Rijksen & Meijaard, 1999) elucidated the results of more than one Sumatran lineages in previous studies (e.g. Karesh et al., 1997; Muir et al., 2000; Ryder & Chemnick, 1993; Zhi et al., 1996), it is unlikely to explain the findings of the present work.

With two sympatric taxa in Sumatra, one would expect two main clades, each including individuals from every representatively sampled locality. Using this study, the two main clusters might both include *OTU*'s from Ketambe and Suaq Balimbing. However, such outcome was not derived from *long call* data. Instead, the two to three Ketambe individuals form a fairly well supported monophyletic cluster, whereas the Suaq Balimbing orangutans and single samples from other Sumatran localities exhibit a more ladder-like topology in the shortest trees and virtually no resolution in the bootstrap cladograms.

The tight clustering of the Ketambe samples may have various causes. North Sumatran orangutans – once most likely a single deme – live these days in fragmented areas due to habitat destruction (Rijksen & Meijaard, 1999). As a result, Ketambe individuals may also be more closely related to each other than average males in other orangutan localities.

Since orangutans have very flexible behavior (e.g. Delgado & van Schaik, 2000; MacKinnon, 1974; Rijksen & Meijaard, 1999), Ketambe *long calls* may be directly influenced by numerous local factors, e.g. sound environment, population density, social system, and habitat structure. A work in progress dealing with ecological effects on orangutan *long calls* (Delgado, pers. comm.) may give valuable background to the phylogeographic approach in this study. Why the four to five Suaq Balimbing individuals do not exhibit any clustering is unknown.

With the Ketambe clade, the question arises whether the association of sympatric Sumatran orangutans and statistically derived Sumatran lineages of other studies is always appropriate. Thus far, regional details on Sumatran samples were never effectively analyzed in any phylogenetic study on orangutans. Although Röhrer-Ertl (1984) and Zhi et al. (1996) included samples from two different sites, they formatted their data and made it uninformative for biogeographic purposes. Röhrer-Ertl (1984) grouped his cranial collection into solely two taxonomic units. Zhi et al. (1996) commented in their publication no further on the sites and

worked with haplotypes rather than individuals or *OTU*'s, making it impossible to trace the samples. Therefore, future studies should include data from specific Sumatran localities and morphs in their analyses. This way, results may be better suited to answer questions regarding orangutan phylogeny and paleo-migration.

NW Borneo

Another monophyletic group was found for NW Borneo (72-73%) (Figures 3.7 & 3.9). Thus far, thrice NW Bornean data were found to be distinct from those of other areas (Groves, 2001; Uchida, 1998; Warren, 2001), once they were intermixed with SW Bornean orangutans (Röhrer-Ertl, 1984), and thrice they resulted in no separate clade (Zhi et al., 1996). Surprisingly, the cranial study by Groves et al. (1992) produced opposing results for both sexes. Whereas one outcome clearly indicated discrepancies between NW Bornean and other males, data on females depicted much aggregation with those from NE Borneo.

The Batang Ai calls included in the present analyses were recorded from two different sites with clearly different infrastructures (Appendix 1; see Methods: Field study in Batang Ai National Park). This monophyly of four to six Batang Ai callers diminishes to some degree habitat structure to be the primary cause of possible local call adjustments, as suggested for Ketambe (see Discussion: Sumatran lineages).

NE-E Borneo

The strongest vocal evidence of a phylogenetic distinction within the genus *Pongo* lineage concerns the NE-E Bornean clade with bootstrap values of 73-85% for the reduced *OTU* matrix (Figures 3.7 & 3.9). This supports the idea of NE and E Bornean orangutans to have shared, at least recently, the same gene influx. As already suggested by others (Rijksen, 1978; Rijksen & Meijaard, 1999), the Kayan River (Figure 1.1) may not be an effective barrier for the migration of orangutans. Additional support comes from Groves (2001) who found a similar regional association.

The NE-E Bornean monophyly demonstrates that a phylogenetic approach on *long calls* is an appropriate method for orangutan systematics. Because Ulu Segama (NE Borneo) and Kutai (E Borneo) are unlikely to offer identical ecological surroundings (e.g. Delgado & van Schaik, 2000; MacKinnon, 1974; Rodman, 1973, 1988), the common clade of these areas should have low bootstrap values if numerous environmental factors influence these vocalizations. This is not the case. However, the small sample size (*OTU*'s: n = 2) and the problem of identifying the callers of all 5 collected *long calls* need to be noted.

Other studies with information on both NE and E Borneo clearly indicate two distinct orangutan demes (Röhrer-Ertl, 1984; Warren et al., 2001). Therefore, the relationship of NE and E Bornean orangutans and their taxon management should be dealt with cautiously

(Andayani et al., 1998). Hopefully, in the future, more phylogeographic studies will include data of these areas.

Centers of dispersion

Of all Bornean taxa, discriminant analysis shows that SW Bornean *long calls* most closely resemble sounds emitted by Sumatran orangutans (Figure 3.5). Groves et al. (1992) came up with similar results on crania, especially for males. Also, Muir et al. (1998b) mentioned unpublished mitochondrial DNA tests showing Sumatran samples closest to SW Bornean data. All three studies corroborate the primary orangutan migration route between South Sumatra and SW Borneo during the alternating glacial epochs (e.g. Courtenay et al., 1988; Röhrer-Ertl, 1984; Warren et al., 2001).

Before dispersing orangutan populations may have merged from either one or both directions of this land bridge (e.g. Courtenay et al., 1988; Muir et al., 2000; Warren et al., 2001), the extinct Sumatran *Pongo pygmaeus palaeosumatrensis* ostensibly entered SW Borneo and migrated from there to other parts of the island (Courtenay et al., 1988; Rijksen & Meijaard, 1999; Röhrer-Ertl, 1984). With focus on the heuristic search of this study, it may also explain why SW Bornean (Figures 3.6-3.9) *long calls* are intermediaries of those from Sumatra and NE-E Borneo.

In addition, MDS analysis showed both NW and SW Bornean calls to have more in common with Sumatran than with NE-E Bornean vocal data (Figure 3.4). Similarly, Uchida (1998) found NW Bornean samples to mostly resemble those of Sumatra. These results support that a more northern dispersal route between Sumatra and NW Borneo was also used (Courtenay et al., 1988). Nonetheless, the northern land bridge was evidently more difficult to pass and for much longer periods submerged than the southern course of traveling (Courtenay et al., 1988; Muir et al., 1998b).

Contrarily, Röhrer-Ertl (1984) and Warren et al. (2001) found no particular Bornean taxa closest to the Sumatran clade.

Future studies

Loud call analyses should become a more common tool to reconstruct primate phylogeny. Although this study does not lead to a firm statement on inter-island comparisons, *long call* analysis is a useful approach to investigate orangutan phylogeny as it presents reasonable monophyletic clades. Its results successfully give an insight to the systematics of orangutans, similar to numerous vocal analyses on other primate taxa. Furthermore, works on vocalizations are less invasive ways to collect data than most efforts on anatomy, morphology, genetics, or molecular biology because there is no need to trace nor intervene with the focal animal.

Since *long calls* may differ depending on social and habitat factors, a study with such focus is currently in progress (Delgado, pers. comm.). Additionally, differences in life stages (transitional, flanged, past-prime) and phenotypic features (e.g. body sizes, throat pouches, flanges) can give interesting insights to the phylogenetic evaluations of this work. If ontogenetical and ecological factors exist and if they can be excluded from the database, a phylogenetic study of orangutan *long calls* could be improved.

All systematic efforts need specific frameworks of inter- and intra-individual data carried out by appropriate statistical methods. Although such an approach may help evaluate relationships between populations, studies on individuality of primates are rare (Geissmann, pers. comm.).

As compared data on temporal call dispersions and acoustic measures show (Davila Ross, this study; MacKinnon, 1974), generalizations for Borneo and Sumatra should not be attempted based solely on two orangutan populations. Because such misleading information may even turn out to be a scaffold for other works, cautiousness in its interpretation is here commendable. Therefore, systematic studies on orangutans would benefit from including various, geographically dispersed populations. Localities of samples should be traceable throughout the analytical process or, better yet, be worked with separately.

More phylogenetic works with numerous dispersed orangutan populations are needed for improved knowledge on orangutan systematics and conservation management. Most effective would be studies including diverse data (e.g. vocal, genetic, and morphological) to reconstruct phylogenetic trees.

Conservation

Conservationists agree on the importance of avoiding hybridization of any orangutan taxa based on the devastating effects it could have on reproduction, viability, and biological diversity. Although, in the case of captive orangutans, hybrid fertility does not seem to exhibit any reduction (e.g. Becker, 2000; cited in de Boer & Seuánez, 1982), it is unknown at this point whether defects appear after several generations. Moreover, pre- and post-mating mechanisms (see discussion of the biological species concepts in Groves, 2001) that may immensely decrease the fitness of wild living hybrids, have not been investigated.

These days, Bornean and Sumatran orangutans are being managed as two separate conservation units, but the possibility still exists of mixing up genetic material of orangutan taxa within the islands by displacement. Considering all phylogeographic studies, orangutans from Northwest Borneo, Northeast Borneo, East Borneo, Southwest Borneo, and North Sumatra (and the few remaining individuals from the more "southern" parts of Sumatra) should be dealt with separately, as proposed by the Orangutan Action Plan (Andayani et al., 1998). Although *long call* data of this work, together with the cranial study of Groves (2001),

depict Northeast and East Bornean orangutans as one deme, it would be prudent to use utmost caution in conservation procedures.

5. Conclusions

- 1. Orangutans may emit synchronic sounds as part of their *long calls*.
- 2. *Long call* analysis is a useful approach to study orangutan phylogeny.
- 3. This work provides no support nor rejection for island-specific clades but strongly indicates monophyletic groups for Ketambe (Sumatra), Northwest Borneo, and Northeast-East Borneo respectively.
- 4. More phylogenetic works with numerous dispersed orangutan populations are needed. Hereby, special treatment should be applied when handling exact sites of samples from Borneo as well as Sumatra.
- 5. As a precaution, orangutans from Northwest Borneo, Northeast Borneo, East Borneo, Southwest Borneo, North Sumatra, and South Sumatra should be dealt with as separate management units.

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8. Appendices

Appendix 1: Recording collection

List of orangutan *long calls* and chimpanzee *pant hoots* included with information on site, number of calls, date, recordist, equipment (no.= number)

Area	Site	OTU no.*	No. of calls	Date	Recordist	Equipment
NW Borneo	Bukit Spantu, Batang Ai National Park	4	2	09.02	Davila Ross , M.	Sony WM D6C tape recorder, Sennheiser ME 60 directional microphone
	Kota Enggam, Batang Ai National Park	1-3	9	08.02	Davila Ross , M.	Sony WM D6C tape recorder, Sennheiser ME 60 directional microphone
NE Borneo	Segama River, Ulu Segama Reserve	5	2	12.69	MacKinnon, J.	Uher tape recorder with parabolic reflector, Philips tape recorder
E Borneo	Mentoko River, Kutai Reserve	6	3	07.81- 11.82	Mitani, J.	Uher 4400 IC tape recorder, Gibson P650 directional microphone
SW Borneo	Cabang Panti, Gunung Palung National Park	7	4	11.99	Peters, H.	Sony TCS-430 tape recorder, Sony ECM T140 microphone
		8	12	06.89	Mitani, J.	Sony TCD-D10, TC-D5M, WM-D6C tape recorders, Sennheiser ME 80, ME 88, MKH 816 directional microphones
	Sekonyer River, Tanjung Puting Reserve	9-10	4	2001	Singleton, I.	Aiwa tape recorder, simple microphone
		11	5	08.85	Barbeau, P.	unknown
		12	1	1992	Krause, B.	unknown
Sumatra	Ketambe River, Gunung Leuser Reserve	13-15	15	summer 2000	Delgado, R.	Marantz PMD 221 tape recorder, Sennheiser ME 67 directional microphone
	Ranun River, North Sumatra	16	3	0411.71	MacKinnon, J.	Uher tape recorder with parabolic reflector, Philips tape recorder
	Sikundur Area, West Langkat Reserve	17	1	summer 2000	Wich, S.	Sony WM D6C tape recorder, Sony ECM T140 microphone
	Soraya Research Area, Gunung Leuser Reserve	18	1	08.99	Assink, P.	Sony WM D6C tape recorder, Sony ECM T140 microphone
	Suaq Balimbing, Gunung Leuser Reserve	19-23	13	summer 1999	Delgado, R.	Marantz PMD 221 tape recorder, Sennheiser ME 67 directional microphone
Gambia**	Baboon Island, River Gambia National Park,	24	1	02.86	de Maximy, A.	Nagra IV-S tape recorder, Schoepes microphone
Tanzania**	Kasoje, Mahale Mountains National Park	25	2	08.90	Mitani, J.	Sony TCD-D10, TC-D5M, WM-D6C tape recorders, Sennheiser ME 80, ME 88, MKH 816 directional microphones
Uganda**	Budongo Forest, Masindi District	26	5	07.95	Wong, J.	Marantz PMD 201 tape recorder, Sennheiser ME 66 directional microphone

** = recordings of chimpanzees

* = see Table 2.2

Appendix 2: Sonagrams

Appendix 2.1. Chimpanzee *pant hoot* from Chimpanzee 2 *OTU* (Chimp 3G) using manual scaling (a) 1.5 s/cm and 0.4 kHz/cm and (b) 0.5 s/cm and 0.4 kHz/cm









Appendix 2.3. Orangutan *long call* from Ulu Segama *OTU* (US 1A) (manual scaling with1.5 s/cm and 0.4 kHz/cm)



Appendix 2.4. Orangutan *long call* from Kutai *OTU* (KU 1A) (manual scaling with1.5 s/cm and 0.4 kHz/cm)







Appendix 2.5. Orangutan *long call* from Tanjung Puting 3 *OTU* (TP 2B) (manual scaling with1.5 s/cm and 0.4 kHz/cm)



Appendix 2.6. Orangutan *long call* from Gunung Palung 1 *OTU* (GP 1D) (manual scaling with1.5 s/cm and 0.4 kHz/cm)



Appendix 2.7. Orangutan *long call* from Ketambe 1 *OTU* (KE 1B) (manual scaling with1.5 s/cm and 0.4 kHz/cm)

Appendix 2.8. Orangutan *long call* from Ranun *OTU* (RR1A) (manual scaling with1.5 s/cm and 0.4 kHz/cm)







Appendix 3: Definition of variables

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Abbreviations: Comp. = comparison, dB = decibel, hz = hertz, max. = maximum, min. = minimum, s = seconds, no. = number, n.u. = no unit, pos. = position, pres. = presence, % = percentage
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No.	Qualitative variable	Unit	Definition
	Call		
1	Transition of sounds	N.u.	Type of sound transition
2	Pres. connected sounds	N.u.	Presence of different note types without interval interference
3	Pres. echo-like sounds	N.u.	Presence of same note type without interval interference
4	Pres. note type H	N.u.	Presence of huitu (H) note type
	Numerical variable		
	Call		
5	No. of sound levels	N.u.	Number of sound levels
6	No. of sounds	N.u.	Number of sounds
7	Quantity segment B	N.u.	Number ratio of segments B to sounds
8	% Ascending sounds	N.u.	Percentage of ascending sounds in number of sounds
9	% Descending sounds	N.u.	Percentage of descending sounds in number of sounds
10	% Central sounds	N.u.	Percentage of central sounds in number of sounds
11	% Nonmodulation	N.u.	Percentage of nonmodulated sounds in number of sounds
12	% Modulation	N.u.	Percentage of modulated sounds in number of sounds
13	% Multimodulation	N.u.	Percentage of multimodulated sounds in number of sounds
14	% Note type R	N.u.	Percentage of note types R in number of sounds
15	% Note type S	N.u.	Percentage of note types S in number of sounds
16	% Note type I	N.u.	Percentage of note types I in number of sounds
17	Pos. max. frequency	N.u.	Position of sound with highest frequency
18	Pos. min. frequency	N.u.	Position of sound with lowest frequency
19	Pos. max. bandwidth	N.u.	Position of sound with longest frequency range
20	Pos. min. bandwidth	N.u.	Position of sound with shortest frequency range
21	Pos. max. peak frequency	N.u.	Position of sound with highest peak frequency
22	Pos. min. peak frequency	N.u.	Position of sound with lowest peak frequency
23	Pos. max. duration	N.u.	Position of sound with longest time range
24	Pos. min. duration	N.u.	Position of sound with shortest time range
25	Pos. max. peak intensity	N.u.	Position of sound with highest peak intensity
26	Pos. min. peak intensity	N.u.	Position of sound with lowest peak intensity
27	Side of hook	N.u.	Number ratio of lower left hook to lower right hook
28	Side of tail	N.u.	Number ratio of lower left tail to lower right tail
	Sound		
29	No. of harmonics	N.u.	Number of harmonic frequencies dominantly visible
30	Pos. harmonic level	N.u.	Position of harmonic frequency dominantly visible

Appendix 3. (continued)

No.	Metrical variable	Unit	Definition
	Call		
31	Duration of call	S	Time range from beginning to end of call
32	Duration of segment B	S	Time range from beginning to end of segment B
	Sound		
33	Duration of sound	S	Time range from beginning to end of sound
34	Duration of interval	S	Time range from beginning to end of interval
35	Ratio sound interval	N.u.	Ratio of duration of sound to duration of interval
36	Maximum frequency	Hz	Highest frequency
37	Minimum frequency	Hz	Lowest frequency
38	Comp. max. frequencies	Hz	Comparison of maximum frequencies
39	Comp. min. frequencies	Hz	Comparison of minimum frequencies
40	Comp. bandwidths	Hz	Comparison of bandwidths
41	Comp. sound rates	S	Comparison of sound rates
42	Appendix prior	S	Time span of atonal elements attached before sound
43	Appendix past	S	Time span of atonal elements attached after sound
	Note type R		
44	Bandwidth	Hz	Range of frequency
45	Peak frequency	Hz	Frequency with highest peak intensity
46	Pos. peak frequency	N.u.	Position of peak frequency within bandwidth
47	Pos. peak time	N.u.	Position of peak time within duration
48	Comp. peak intensity	dB	Comparison of peak intensities
49	Shape	Hz/s	Bandwidth divided by duration
	Note type S		
50	Dominant frequency line	Hz	Frequency line with longest duration
51	Bandwidth	Hz	See note type R
52	Peak frequency	Hz	See note type R
53	Peak frequency position	N.u.	See note type R
54	Peak time position	N.u.	See note type R
55	Comp. peak intensity	dB	See note type R
56	Shape	Hz/s	See note type R
	Note type I		
57	Bandwidth	Hz	See note type R
58	Peak frequency	Hz	See note type R
59	Pos. peak frequency	N.u.	See note type R
60	Pos. peak time	N.u.	See note type R
61	Comp. peak intensity	dB	See note type R
62	Shape	Hz/s	See note type R
63	Hook frequency	Hz	Frequency of hook tip
64	Hook length	N.u.	Ratio of hook length to bandwidth

Appendix 4: Character state names and symbols

Abbreviations: Comp. = comparison, max. = maximum, min. = minimum, no. = number, pos. = position, pres. = presence, % = percentage

No.	Qualitative variable	Character state name and symbol
	Call	
1	Transition of sounds	0 = abrupt 1 = gradual
2	Pres. connected sounds	0 = absent, 1 = present
3	Pres. echo-like sounds	0 = absent, 1 = present
4	Pres. note type H	0 = absent, 1 = present
	Numerical variable	
	Call	
5	No. of sound levels	0 = < 1.100, 1 = 1.100-1.329, 2 = ≥ 1.330
6	No. of sounds	$0 = < 17.000, 1 = 17.000-42.999, 2 = \ge 43.000$
7	Quantity segment B	$0 = < 0.015, 1 = 0.015 - 0.059, 2 = \ge 0.060$
8	% Ascending sounds	$0 = < 14.000, 1 = 14.000-27.999, 2 = \ge 28.000$
9	% Descending sounds	0 = < 32.700, 1 = ≥ 32.700
10	% Central sounds	$0 = < 42.000, 1 = 42.000-54.999, 2 = 55.000-67.999, 3 = \ge 68.000$
11	% Nonmodulation	0 = < 31.000, 1 = 31.000-50.999, 2 = ≥ 51.000
12	% Modulation	$0 = < 40.000, 1 = 40.000-59.999, 2 = 60.000-72.499, 3 = \ge 72.500$
13	% Multimodulation	$0 = < 4.500, 1 = \ge 4.500$
14	% Note type R	$0 = < 50.000, 1 = \ge 50.000$
15	% Note type S	0 = < 21.000, 1 = 21.000-41.999, 2 = ≥ 42.000
16	% Note type I	0 = < 2.700, 1 = ≥ 2.700
17	Pos. max. frequency	0 = beginning, 1 = middle, 2 = end
18	Pos. min. frequency	0 = beginning, 1 = middle, 2 = end
19	Pos. max. bandwidth	0 = beginning, 1 = middle, 2 = end
20	Pos. min. bandwidth	0 = beginning, 1 = end
21	Pos. max. peak frequency	0 = beginning, 1 = middle, 2 = end
22	Pos. min. peak frequency	0 = beginning, 1 = end
23	Pos. max. duration	0 = beginning, 1 = middle
24	Pos. min. duration	0 = beginning, 1 = end
25	Pos. max. peak intensity	0 = beginning, 1 = end
26	Pos. min. peak intensity	0 = beginning, 1 = end
27	Side of hook	$0 = < 1.000, 1 = \ge 1.000$
28	Side of tail	0 = < 1.383 1 = 1.383-11.999, 2 = ≥ 12.000
	Sound	
29	No. of harmonics	0 = < 1.000, 1 = 1.000-1.749, 2 = ≥ 1.750
30	Pos. harmonic level	0 = < 2.000, 1 = 2.000-2.199, 2 = ≥ 2.200

No.	Metrical variable	Character state name and symbol
	Call	
31	Duration of call	0 = < 10.000, 1 = 10.000-44.999, 2 = ≥ 45.000
32	Duration of segment B	0 = < 7.500, 1 = ≥ 7.500
	Sound	
33	Duration of sound	0 = < 0.500, 1 = 0.500-0.724, 2 = ≥ 0.725
34	Duration of interval	0 = < 0.535, 1 = 0.535-1.199, 2 = ≥ 1.200
35	Ratio sound interval	$0 = < 6.400, 1 = \ge 6.400$
36	Maximum frequency	$0 = < 641.000, 1 = \ge 641.000$
37	Minimum frequency	0 = < 115.000 1 = 115.000-119.999, 2 = ≥ 120.000
38	Comp. max. frequencies	0 = < (-23.000), 1 = (-23.000)-2.499, 2 = 2.500-44.999, 3 = ≥ 45.000
39	Comp. min. frequencies	0 = < (-3.400), 1 = (-3.400)-3.399, 2 = ≥ 3.400
40	Comp. bandwidths	0 = < (-10.000), 1 = ≥ (-10.000)
41	Comp. sound rates	0 = < (-0.021), 1 = (-0.021)-(-0.001), 2 = ≥ 0.000
42	Appendix prior	0 = < 0.078, 1 = 0.078-0.104, 2 = ≥ 0.105
43	Appendix past	$0 = < 0.290, 1 = \ge 0.290$
	Note type R	
44	Bandwidth	$0 = < 600.000, 1 = \ge 600.000$
45	Peak frequency	$0 = < 370.000, 1 = \ge 370.000$
46	Pos. peak frequency	0 = < 0.530, 1 = ≥ 0.530
47	Pos. peak time	$0 = < 0.690, 1 = \ge 0.690$
48	Comp. peak intensity	0 = < (-0.015), 1 ≥ (-0.015)
49	Shape	0 = < 700.000, 1 = 700.000-1049.999, 2 = ≥ 1050.000
	Note type S	
50	Dominant frequency line	$0 = < 160.000, 1 = \ge 160.000$
51	Bandwidth	$0 = < 250.000, 1 \ge 250.000$
52	Peak frequency	0 = < 211.000, 1 = 211.000-279.999, 2 = ≥ 280.000
53	Peak frequency position	$0 = < 0.520, 1 = \ge 0.520$
54	Peak time position	$0 = < 0.200, 1 = \ge 0.200$
55	Comp. peak intensity	0 = < (-0.200), 1 = ≥ (-0.200)
56	Shape	$0 = < 600.000, 1 = \ge 600.000$
	Note type I	
57	Bandwidth	0 = < 250.000, 1 = ≥ 250.000
58	Peak frequency	0 = < 255.000, 1 = ≥ 255.000
59	Pos. peak frequency	0 = < 0.525, 1 = ≥ 0.525
60	Pos. peak time	$0 = < 0.670, 1 = \ge 0.670$
61	Comp. peak intensity	0 = < (-0.500), 1 = ≥ (-0.500)
62	Shape	$0 = < 500.000, 1 = \ge 500.000$
63	Hook frequency	$0 = < 410.000, 1 = \ge 410.000$
64	Hook length	0 = < 0.382, 1 = ≥ 0.382

Appendix 4. (continued)

Appendix 5: Coded OTU data matrix

	Variable															
ΟΤU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Batang Ai 1	0	0	1	0	0	1	1	0	1	2	1	2	0	0	1	0
Batang Ai 2	0	0	1	1	0	1	2	2	0	2	1	2	0	0	1	0
Batang Ai 3	0	0	0	1	0	2	2	2	1	2	1	2	0	0	1	0
Batang Ai 4	1	0	1	0	0	1	1	0	1	2	0	2	0	0	1	1
Gunung Palung 1	1	1	0	1	0	1	2	2	0	3	0	3	0	0	0	1
Gunung Palung 2	1	0	0	0	0	1	2	1	0	1	1	2	1	0	1	1
Tanjung Puting 1	1	0	0	0	0	1	1	1	0	1	1	1	1	0	1	1
Tanjung Puting 2	1	0	0	0	1	2	1	0	0	0	1	1	1	0	0	1
Tanjung Puting 3	1	0	0	0	0	1	2	1	0	1	1	1	1	0	1	1
Tanjung Puting 4	1	0	0	0	0	1	1	1	0	0	1	1	0	0	1	1
Ulu Segama	1	0	0	0	1	1	2	0	0	0	1	0	0	0	2	1
Kutai	1	0	1	0	1	1	2	0	0	0	1	0	0	0	2	1
Ketambe 1	1	1	0	0	1	2	1	2	0	3	0	3	0	1	0	0
Ketambe 2	1	1	0	0	1	2	1	2	1	3	0	3	0	1	0	1
Ketambe 3	1	0	0	0	1	2	1	0	1	2	0	3	0	1	1	1
Ranun	1	0	0	0	1	1	1	2	0	2	1	2	1	1	0	0
Sikundur	1	1	1	0	1	2	1	2	1	3	0	3	0	1	0	1
Soraya	0	0	0	1	0	1	1	2	0	3	0	3	0	0	0	0
Suaq Balimbing 1	1	0	0	0	1	1	1	2	0	3	0	3	0	1	0	1
Suaq Balimbing 2	1	0	0	0	1	2	1	2	0	3	0	2	1	1	0	1
Suaq Balimbing 3	1	1	0	0	1	2	2	2	0	3	0	3	0	1	0	1
Suaq Balimbing 4	1	1	0	0	1	2	2	2	0	2	1	2	0	1	1	1
Suaq Balimbing 5	1	0	0	0	1	2	1	2	0	3	0	3	0	1	0	1
Chimpanzee 1	0	0	0	0	0	0	0	2	0	2	1	2	0	1	0	0
Chimpanzee 2	0	0	0	0	0	0	0	2	0	3	0	2	0	1	1	0
Chimpanzee 3	0	0	0	0	0	0	0	2	0	2	1	1	1	0	0	0

List of codes for each variable of all OTU's

	Variable															
ΟΤυ	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Batang Ai 1	1	2	1	1	1	1	0	0	0	1	1	0	1	1	2	0
Batang Ai 2	1	2	1	0	1	1	1	1	0	1	1	1	1	1	2	0
Batang Ai 3	1	2	1	0	1	1	1	1	1	1	1	0	1	1	2	0
Batang Ai 4	1	2	0	0	1	1	1	1	0	1	1	0	1	1	2	0
Gunung Palung 1	1	1	1	1	0	1	0	0	1	0	1	1	1	2	1	1
Gunung Palung 2	1	1	1	0	0	1	0	0	0	0	1	0	1	1	1	1
Tanjung Puting 1	0	1	1	0	0	1	0	1	0	1	1	0	2	2	2	1
Tanjung Puting 2	0	1	1	0	0	1	0	0	0	1	1	0	2	2	2	0
Tanjung Puting 3	1	1	1	1	1	1	0	0	0	0	1	0	1	1	2	1
Tanjung Puting 4	1	2	1	0	1	1	1	1	0	1	1	1	2	1	1	1
Ulu Segama	0	1	0	0	0	1	0	1	0	1	1	0	1	2	2	1
Kutai	0	2	1	0	1	1	0	1	0	1	1	0	2	1	2	1
Ketambe 1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	2	0
Ketambe 2	0	1	0	0	1	1	1	1	1	0	1	0	1	2	2	1
Ketambe 3	0	2	0	0	0	1	1	0	1	0	1	0	1	1	1	1
Ranun	1	1	1	0	1	1	1	1	0	1	1	1	2	2	1	1
Sikundur	1	2	1	0	0	1	1	1	0	1	1	1	2	2	2	0
Soraya	2	2	1	1	0	1	1	0	0	1	1	1	2	2	2	1
Suaq Balimbing 1	1	1	1	1	1	1	1	0	1	0	1	1	2	2	2	1
Suaq Balimbing 2	0	1	0	1	0	1	1	0	1	1	1	1	2	2	2	0
Suaq Balimbing 3	1	1	1	0	0	1	1	1	0	1	1	1	2	2	2	1
Suaq Balimbing 4	0	1	0	1	0	1	1	1	1	1	1	1	2	2	2	0
Suaq Balimbing 5	0	2	0	0	1	1	1	1	0	1	1	1	2	2	2	1
Chimpanzee 1	2	0	2	0	2	0	1	0	1	0	0	1	0	0	0	?
Chimpanzee 2	2	1	2	0	2	0	1	1	1	1	0	1	0	0	0	?
Chimpanzee 3	2	0	2	0	1	0	0	1	0	1	1	1	0	0	0	?

Appendix 5. (continued)

	Variable															
OTU	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Batang Ai 1	1	2	0	0	1	2	1	1	0	0	0	1	0	0	1	1
Batang Ai 2	2	2	0	0	0	2	2	1	2	0	1	1	0	0	0	1
Batang Ai 3	2	2	0	0	1	2	2	1	0	0	1	1	0	0	1	1
Batang Ai 4	1	2	0	0	1	2	2	1	2	0	1	1	0	1	1	1
Gunung Palung 1	1	1	1	1	1	2	2	1	1	0	0	1	1	1	0	0
Gunung Palung 2	1	1	1	0	1	2	2	1	1	0	0	1	1	1	1	0
Tanjung Puting 1	2	1	1	0	0	2	1	1	2	1	0	0	0	1	0	0
Tanjung Puting 2	2	1	1	0	0	2	1	1	1	1	0	0	0	1	0	0
Tanjung Puting 3	2	2	1	1	1	2	2	1	2	1	0	1	1	1	0	0
Tanjung Puting 4	2	2	0	0	1	2	2	1	1	0	0	0	1	1	0	0
Ulu Segama	2	2	1	0	1	2	2	1	2	2	0	1	1	1	1	0
Kutai	2	2	0	0	1	1	1	1	1	2	0	0	1	1	0	0
Ketambe 1	1	1	1	1	1	2	1	1	1	0	0	1	0	0	0	0
Ketambe 2	1	1	1	0	1	2	1	1	0	0	0	1	0	1	0	0
Ketambe 3	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0
Ranun	1	1	0	0	1	2	1	1	0	0	0	0	0	1	0	1
Sikundur	1	1	0	0	1	2	1	1	1	0	0	1	0	1	0	1
Soraya	1	1	0	0	0	1	2	0	1	0	1	1	0	1	0	0
Suaq Balimbing 1	1	1	1	0	0	1	1	1	0	0	0	0	0	1	0	1
Suaq Balimbing 2	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	1
Suaq Balimbing 3	1	1	1	0	0	2	1	1	1	0	0	0	0	1	0	1
Suaq Balimbing 4	1	2	0	0	0	2	1	1	0	0	0	0	0	1	0	1
Suaq Balimbing 5	1	1	1	0	0	1	1	1	0	0	0	1	0	1	0	1
Chimpanzee 1	0	0	1	0	2	1	1	0	0	0	0	0	0	1	0	0
Chimpanzee 2	0	0	1	0	2	0	0	0	0	0	0	1	1	1	0	1
Chimpanzee 3	0	0	0	0	2	0	0	0	2	0	0	0	1	1	0	1

Appendix 5. (continued)
	Vari	iable														
OTU	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Batang Ai 1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Batang Ai 2	0	0	0	0	1	1	0	0	0	0	0	0	?	0	0	1
Batang Ai 3	1	0	1	0	1	1	1	0	0	0	1	0	1	0	0	1
Batang Ai 4	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	1
Gunung Palung 1	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0	1
Gunung Palung 2	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	1
Tanjung Puting 1	0	0	0	0	1	0	1	0	1	1	1	0	1	0	0	0
Tanjung Puting 2	0	1	0	1	1	0	?	0	1	1	1	0	1	0	0	0
Tanjung Puting 3	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0
Tanjung Puting 4	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1
Ulu Segama	1	1	1	1	0	1	0	0	1	1	1	0	1	0	0	1
Kutai	1	1	1	1	1	1	0	0	1	1	1	0	0	1	0	0
Ketambe 1	1	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0
Ketambe 2	1	1	0	1	0	1	0	0	0	1	0	1	0	1	1	0
Ketambe 3	1	1	0	1	0	1	1	0	1	1	0	1	0	1	1	0
Ranun	0	1	0	1	1	0	1	0	1	1	1	0	0	0	0	0
Sikundur	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0
Soraya	1	?	?	?	?	?	?	?	0	0	1	0	0	0	0	1
Suaq Balimbing 1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1
Suaq Balimbing 2	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	1
Suaq Balimbing 3	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0
Suaq Balimbing 4	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0
Suaq Balimbing 5	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0
Chimpanzee 1	2	?	?	?	?	?	?	?	1	1		0	1	0	1	0
Chimpanzee 2	2	1	1	2	1	1	0	1	?	?	?	?	?	?	?	?
Chimpanzee 3	2	1	0	2	1	1	0	1	1	0	0	0	0	1	0	1

Appendix 5. (continued)

Appendix 6: Sonagrams of note types

Most common note types of orangutan long calls (manual scaling with 0.7 s/cm and 0.2 kHz/cm)

