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RESEARCH ARTICLE

Call Diversity of Wild Male Orangutans: A Phylogenetic Approach

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Over the past 20 years several studies have attempted to clarify orangutan systematics based on DNA sequences and karyological and morphological data; however, the systematic and phylogenetic relationships among orangutan taxa remain controversial. Surprisingly, few systematic studies have used data from wild-living orangutans of exactly known provenance. Furthermore, most of these studies pooled data from huge geographic areas in their analyses, thus ignoring possibly distinct subpopulations. This study represents a new approach to orangutan systematics that uses orangutan long calls. Long calls are species-specific vocalizations used by many nonhuman primates, and data on their acoustical and temporal structures have been used to assess the relationships among, and phylogenies of, several primate taxa. Altogether, 78 long calls from wild-living orangutans from five populations in Borneo and five in Sumatra were included in the analyses. Aside from the chiefly paraphyletic topology of cladistic results, which neither support nor reject a Borneo-Sumatra dichotomy, bootstrap values support three monophyletic clades (northwest Borneo, northeast-east Borneo, and Ketambe) that corroborate geographic groups. The shortest trees and multivariate analyses provide some support for a closer relationship between Sumatran and specific Bornean demes than between particular Bornean demes themselves, indicating that conservation management

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should be based on orangutans from different populations rather than on just the two island-specific groups. Am. J. Primatol. 69:305–324, 2007.

Key words: orangutans (*Pongo* spp.); long call; call diversity; phylogeny; population differences; conservation

INTRODUCTION

Today wild orangutans live solely in the rainforests of Borneo and Sumatra, two islands in southeast Asia. On Sumatra, their distribution is limited largely to its northern region [Rijksen, 1995; Rijksen & Meijaard, 1999]. Bornean orangutans are more widely distributed throughout their island, with the exceptions of southeast and north central Borneo [Bennett, 1998; Rijksen & Meijaard, 1999]. In Borneo, central mountain ranges and the rivers Kapuas, Mahakam, Barito [e.g., MacKinnon et al., 1997; Muir et al., 1998; Zhi et al., 1996], and possibly Kayan [Rijksen, 1978; Rijksen & Meijaard, 1999] split the orangutans into three to four geographically isolated demes corresponding to southwest, northwest, and northeast-east Borneo (the latter may consist of two isolated demes living in northeast and east Borneo, respectively) [Warren et al., 2001; Yeager, 1999].

There is much controversy concerning systematic relationships among orangutan taxa. Some authors propose that Bornean and Sumatran orangutans should be classified as two species/subspecies [e.g., Janczewski et al., 1990; Xu & Arnason, 1996], whereas others favor a more complex classification [e.g., Courtenay et al., 1988; Delgado & van Schaik, 2000]. More studies appear to support an island dichotomy [de Boer & Seuánez 1982; Dugoujon et al., 1984; Meera Khan et al., 1982; Röhrer-Ertl, 1984; Ryder & Chemnick, 1993; Warren et al., 2001; Wijnen et al., 1982; Zhang et al., 2001; Zhi et al., 1996] than to contradict it [Groves et al., 1992; Muir et al., 2000; Uchida, 1998]. However, a critical review of these studies reveals that they differ greatly in the strength of their methodologies. For instance, only five of these reports (three in favor of the island dichotomy [Röhrer-Ertl, 1984; Warren et al., 2001; Zhi et al., 1996], and two in favor of another classification [Groves et al., 1992; Uchida, 1998]) included precise information on the apes' provenance. Such information is essential in order to properly investigate relationships among orangutan taxa–particularly since studies that compare only the two islands will fail to consider the strong impact that orangutan paleo-migration may have had on the present populations. In addition, with the exceptions of a few reports [Groves, 1986, 2001; Groves et al., 1992; Röhrer-Ertl, 1984; Uchida, 1998; Warren et al., 2001; Zhi et al., 1996], studies on orangutan systematics have evaluated data from zoos, laboratories, and rehabilitated individuals rather than from wild orangutans. Such a sample choice can easily lead to errors because the natal areas of these orangutans can rarely be reliably determined.

Although four studies found evidence for the distinctiveness of certain geographically separate groups of Bornean orangutans [Groves et al., 1992; Röhrer-Ertl, 1984; Uchida, 1998; Warren et al., 2001], two did not [Warren et al., 2000; Zhi et al., 1996]. Moreover, even when we compare the only two phylogenetic studies that focused on wild-living orangutans [Warren et al., 2001; Zhi et al., 1996], it is still not possible to understand the phylogenetic relationships among Bornean populations because the resulting cladograms exhibit no obvious similarities in topology, and three cladograms of the same orangutans produced by Zhi et al. [1996] differed strongly depending on the sequence that was used to calculate the trees (see Fig. 1). In addition, several studies found more than one lineage in Sumatran orangutans [Karesh et al., 1997; Muir et al., 2000; Ryder & Chemnick, 1993; Zhang et al., 2001; Zhi et al., 1996]. These topologies are often explained in terms of the occurrence of two sympatric orangutan taxa in north Sumatra [Rijksen, 1978].

Figure 1 shows previously published ''phylogenetic trees'' based on cluster analysis [Röhrer-Ertl, 1984] and cladistic methods [Muir et al., 2000; Ryder & Chemnick, 1993; Warren et al., 2001; Zhang et al., 2001; Zhi et al., 1996]. Studies that use cluster analysis or multivariate methods instead of cladistic methods basically compare similarities and differences of traits–not phylogenetic relationships [Geissmann, 2003]. Although similarities may correlate with relationships, this is not always the case, and phylogenetic conclusions based on the analysis of similarity alone should be regarded with caution.

Habitat loss and degradation caused by human activities and natural disasters have forced orangutan populations into disjointed forest pockets that are unsuitable for their continued survival. As a part of conservation efforts, orangutans from such threatened fragment populations are often relocated into other, more suitable areas where conspecifics already reside [Yeager, 1999]. These conservation activities can create a new and serious problem: the hybridization of orangutan demes. Hybridization often cannot be avoided because of inadequate knowledge about orangutan systematics. Because taxonomists strongly disagree on the validity of ''potential'' orangutan taxa within Borneo and Sumatra [e.g., Muir et al., 2000; Röhrer-Ertl, 1984; Ryder & Chemnick, 1993; Xu & Arnason, 1996], it is difficult from the point of view of conservation management to decide how to deal with fragmented populations that are declining in size. Therefore, it is a high priority to achieve a better understanding of orangutan systematics, taxon identification, and boundary demarcations.

Loud calls are relatively stereotyped, species-specific vocalizations that are produced by many nonhuman primates [Geissmann, 2000]. Data on loud-call structure have been used successfully to reconstruct phylogenies of, and to assess relationships among, various groups of primates, including lemurs [Macedonia & Stanger, 1994; Stanger, 1995], galagos [Zimmermann, 1990], callitrichids [Snowdon, 1993; Wittiger, 2002], black and white colobus monkeys [Oates & Trocco, 1983; Oates et al., 2000], langurs [Stünkel, 2003], guenons [Gautier, 1988, 1989], and gibbons [Geissmann, 1993, 2002a,b; Haimoff et al., 1982, 1984; Konrad & Geissmann, in press]. Often these results corroborate those obtained in molecular works [Takacs et al., in press]. Species-specific characteristics of loud calls are genetically determined in gibbons [Brockelman & Schilling, 1984; Geissmann, 1984, 1993, 2000; Tenaza, 1985] and guenons [Gautier & Gautier, 1977], and possibly also in other primates, including orangutans (zookeepers of Zoo Osnabrück, personal communication). Although loud-call morphology may also be influenced by factors other than genetics, such as social influences (e.g., in chimpanzees [Crockford et al., 2004; Marshall et al., 1999]), and therefore cannot be viewed as an equivalent marker to DNA in investigations of phylogenies, loud-call data can be easily and noninvasively collected from nonhabituated subjects of wild populations, and sonographic analysis of calls is certainly more economical than DNA sequencing.

Thus, loud-call analysis can be a very interesting alternative approach to shed light on the phylogenetic relationships of wild orangutan populations. Preliminary results already suggest that orangutan long calls differ among populations [Galdikas, 1983; Galdikas & Insley, 1988; MacKinnon, 1971, 1974;

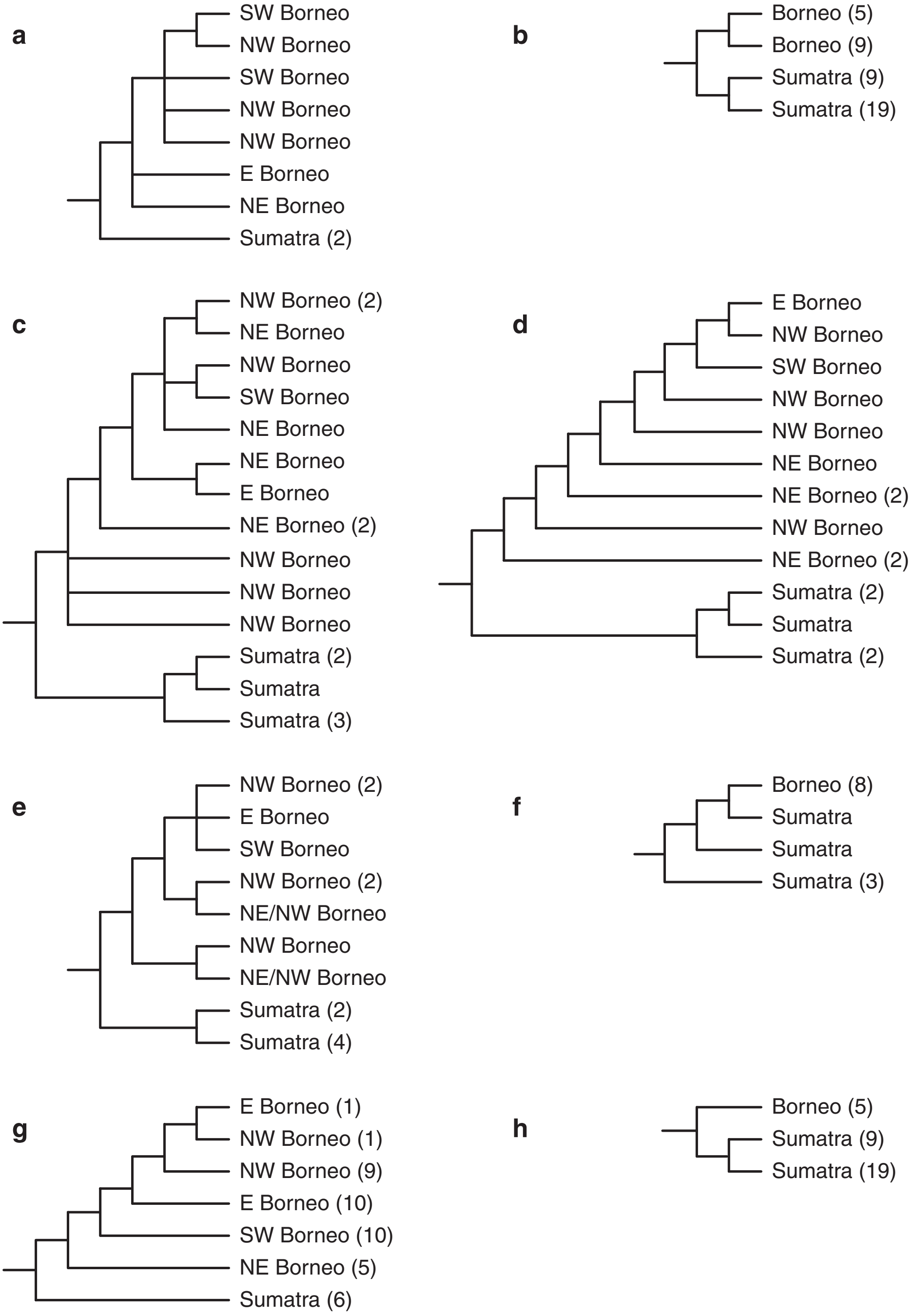

Fig. 1. Systematic trees of one morphological study derived by cluster analysis (**a**) and of seven phylogenetic analyses (**b–h**): (**a**) Röhrer-Ertl [1984]: craniometry; (**b**) Ryder and Chemnick [1993]: mtDNA restriction endonuclease cleavage site; (**c**) Zhi et al. [1996]: mt 16S rRNA; (**d**) Zhi et al. [1996]: minisatellite data; (**e**) Zhi et al. [1996]: mtDNA restriction fragment length polymorphisms (RFLPs); (**f**) Muir et al. [2000]: mtDNA sequences of NADH subunit 3 and cytochrome B; (**g**) Warren et al. [2001]: control region mtDNA; and (**h**) Zhang et al. [2001]: ND5 mtDNA. Numbers in parentheses indicate the number of individuals.

Mitani, 1985; Rijksen, 1978] and individuals [Galdikas, 1983; Mitani, 1985; Rijksen, 1978] (Davila Ross, personal observation).

Orangutan loud calls (usually termed long calls) are emitted solely by adult flanged males [Galdikas & Insley, 1988; MacKinnon, 1971; Mitani, 1985]. They are the loudest orangutan vocalizations [e.g., Galdikas, 1983; MacKinnon, 1971, 1974; Mitani, 1985] and can last up to 3 min (Davila Ross, personal observation). MacKinnon [1971, 1974] described their acoustic structure and distinguished among three successive parts of this vocalization. Orangutan long calls have been proposed to function over far distances as a spacing device among males [Galdikas, 1983; Mitani, 1985; MacKinnon, 1971, 1974; Rijksen, 1978] or to attract females [Galdikas, 1983; Horr, 1972, 1975; MacKinnon, 1969; Rodman, 1973].

The objectives of this study were to 1) describe the structure of orangutan long calls, 2) compare long calls between different orangutan populations, 3) assess the phylogenetic relationships among populations based on vocal characteristics, and 4) discuss the relevance of the results for orangutan systematics and taxon management in conservation.

MATERIALS AND METHODS

Recording Collection

Samples were obtained from field researchers as detailed in Table I. A total of 78 orangutan long calls from 10 wild-living populations in Borneo and Sumatra (Fig. 2), and eight pant-hoots from male chimpanzees (*Pan troglodytes*) from three populations in central Africa were included in the analyses. The long calls were grouped in accordance with geographic barriers into five areas: northwest (NW) Borneo, northeast (NE) Borneo, east (E) Borneo, southwest (SW) Borneo, and north Sumatra. Additional information on orangutan recording sites can be found in earlier publications (Batang Ai [Meredith, 1993], Kutai [Mitani, 1985; Rodman, 1973], Ulu Segama [MacKinnon, 1973; Newbery et al., 1999], Gunung Palung [Knott, 1998], Tanjung Puting [Galdikas, 1979, 1985a,b], Ketambe [Rijksen, 1978], Ranun [MacKinnon, 1973, 1974], Sikundur [MacKinnon, 1973], and Suaq Balimbing [Singleton & van Schaik, 2001].

Sonograms and Measurements

The sound recordings were digitized with a sample rate of 11.025 kHz and a sample size of 16 bit. Time vs. frequency displays (sonograms) of the sound material were generated using the software Canary 1.2.4 on a Power Macintosh G3 [Charif et al., 1995], with the following parameter adjustments: filter bandwidth = 87.42 Hz; frame length = 512 points; grid resolution time = 128 points; grid resolution frequency = 21.53 Hz; fast Fourier transform [FFT] size = 512 points; clipping level = –80 dB. Figure 3 shows a sonogram of an orangutan long call.

Altogether, 64 variables were measured, as listed in Table AI in Appendix A. Five note types (bubbling (B), huitus (H), roars (R), intermediaries (I), and sighs (S)) are usually present in an orangutan long call (Fig. 3). However, because of the wide variety of call elements that do not belong to any of these note types, call elements were also grouped in accordance to their lateral tendencies (variables 11–13 and 27–28) to describe ascending, descending, or symmetrical sound structures, and to their fundamental frequency modulations (variables 14–16) to

TABLE I. List of Samples With Information on Sites and Recordings, Name of Operational Taxonomic Unit (OTU), Number of Calls and Apes, and Individual Identification Status, Respectively

Area	Site	Recorder, recording date, and recording equipment	OTU name	No. calls	No. apes	ID
NW B	Kota Enggam, Batang Ai NP	Davila Ross, M. (2002); TR: Sony WM-D6C, d-mic: Sennheiser ME 60	Batang Ai 1	5	1	+
			Batang Ai 2	2	1–2	–
			Batang Ai 3	2	1	+
	Bukit Spantu, Batang Ai NP	Davila Ross, M. (2002); TR: Sony WM-D6C, d-mic: Sennheiser ME 60	Batang Ai 4	2	1–2	–
NE B	Danum Valley Conservation Area, Ulu Segama Forest R	Davila Ross, M. (2003); TR: Sony WM-D6C, d-mic: Sennheiser ME 60	Ulu Segama 1	3	1	+
	Segama River, Ulu Segama Forest R	MacKinnon, J. (1969); TRs: Uher, parabolic reflector, Philips	Ulu Segama 2	2	1–2	–
E B	Mentoko River, Kutai R	Mitani, J. (1981–82); TR: Uher 4400 IC, d-mic: Gibson P650	Kutai	3	1–3	–
SW B	Cabang Panti, Gunung Palung NP	Peters, H. (1999); TR: Sony TCS-430, mic: Sony ECM T140	Gunung Palung 1	4	1	+
		Mitani, J. (1989); TRs: Sony TCD-D10, TC-D5M, WM-D6C, d-mics: Sennheiser ME 80, ME 88, MKH 816	Gunung Palung 2	12	1	+
	Sekonyer River, Tanjung Puting R	Singleton, I. (2001); TR: Aiwa, simple mic	Tanjung Puting 1	3	1	+
			Tanjung Puting 2	1	1	+
		Barbeau, P. (1985); equipment unknown	Tanjung Puting 3	5	1	+
		Krause, B. (1992); equipment unknown	Tanjung Puting 4	1	1	–

S	Ketambe River, Gunung Leuser R	Delgado, R. (2000); TR: Marantz PMD 221, d-mic: Sennheiser ME 67	Ketambe 1	5	1	+
			Ketambe 2	5	1	+
			Ketambe 3	5	1	–
	Ranun River	MacKinnon, J. (1971); TRs: Uher, parabolic reflector, Philips	Ranun	3	1–3	–
	Sikundur Area, West Langkat R	Wich, S. (2000); TR: Sony WM-D6C, mic: Sony ECM T140	Sikundur	1	1	–
	Soraya Research Area, Gunung Leuser R	Assink, P. (1999); TR: Sony WM-D6C, mic: Sony ECM T140	Soraya	1	1	–
	Suaq Balimbing, Gunung Leuser R	Delgado, R. (1999); TR: Marantz PMD 221, d-mic: Sennheiser ME 67	Suaq Balimbing 1	3	1	+
			Suaq Balimbing 2	3	1	+
			Suaq Balimbing 3	2	1	+
			Suaq Balimbing 4	3	1	+
			Suaq Balimbing 5	2	1	–
A[a]	Baboon Island, River Gambia NP, Gambia	De Maximy, A. (1986); TR: Nagra IV-S, mic: Schoepes	Chimpanzee 1	1	1	–
	Kasoje, Mahale Mountains NP, Tanzania	Mitani, J. (1990); TR: Sony TCD-D10, TC-D5M, WM-D6C, d-mics: Sennheiser ME 80, ME 88, MKH 816	Chimpanzee 2	2	1	+
	Budongo Forest, Masindi District, Uganda	Wong, J. (1995); TR: Marantz PMD 201, d-mic: Sennheiser ME 66	Chimpanzee 3	5	1–5	–

[a] Recordings of chimpanzees used as outgroup in phylogenetic analysis.

A = Africa, B = Borneo, d- = directional, ID = ape identification status, mic = microphone, No. = number of, TR = tape-recorder, TRs = tape-recorders, NP = National Park, R = Reserve, S = Sumatra.

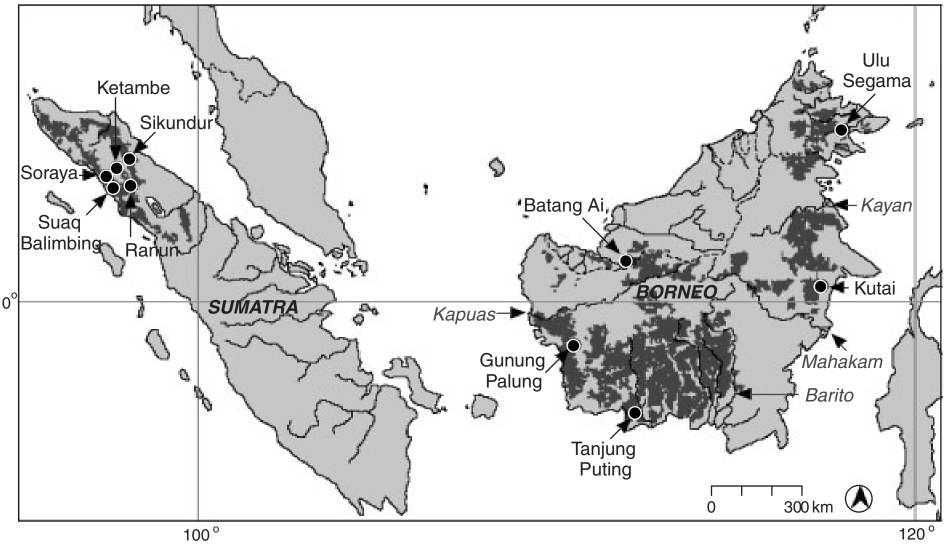

Fig. 2. Recording sites (dots) on Borneo and Sumatra with current orangutan distribution (dark shaded areas) and main rivers (map adapted from Rijksen and Meijaard [1999]).

describe nonmodulated, modulated, or multimodulated sound structures (see Appendix).

The following terms used to describe variables in the Appendix can be explained as follows (variable numbers in parentheses): ‘‘bubbling (B)-like element’’ (42 and 43): acoustic structures that resemble those of note type B, but differ in that they are either attached directly before or after a sound (Fig. 3); ‘‘comparison’’ (32–35, 48, 54, and 63): difference between two consecutive call elements; ‘‘curve’’ of note type I (56 and 57): second-highest peak and its connected ascending and descending slopes (Fig. 3); ‘‘dominant’’ fundamental or other harmonic frequency (29 and 30): fundamental or other harmonic frequency of highest dB-value for the first and second halves of the sound duration; ‘‘frequency line’’ of note type S (58): frequency that takes up the longest horizontal line in note type S (Fig. 3); ‘‘hook’’ (27): short ascending or descending hook-like feature in the sonogram at the beginning or end of a symmetrical sound, respectively; ‘‘tail’’ (28): tail-like segment of the lowest frequency at the left or right side of a symmetrical sound (Fig. 3).

To avoid differences in results due to differences in recording qualities and circumstances, we did not measure the variables of a single dB-value. Variables with data on amplitudes were only included when two such dB-values were measured and their difference was compared.

Multivariate Analysis

In addition to a phylogenetic approach, a multivariate analysis was conducted. Multidimensional scaling (MDS) is a method that is able to plot multivariate similarity or dissimilarity data on a two-dimensional scatterplot with a minimum of distortion (SYSTAT; SYSTAT, Inc., Evanston, IL). For the purposes of the present analysis, Euclidian distance and the Kruskal Monotonic method were adopted [Sneath & Sokal, 1973] (SYSTAT).

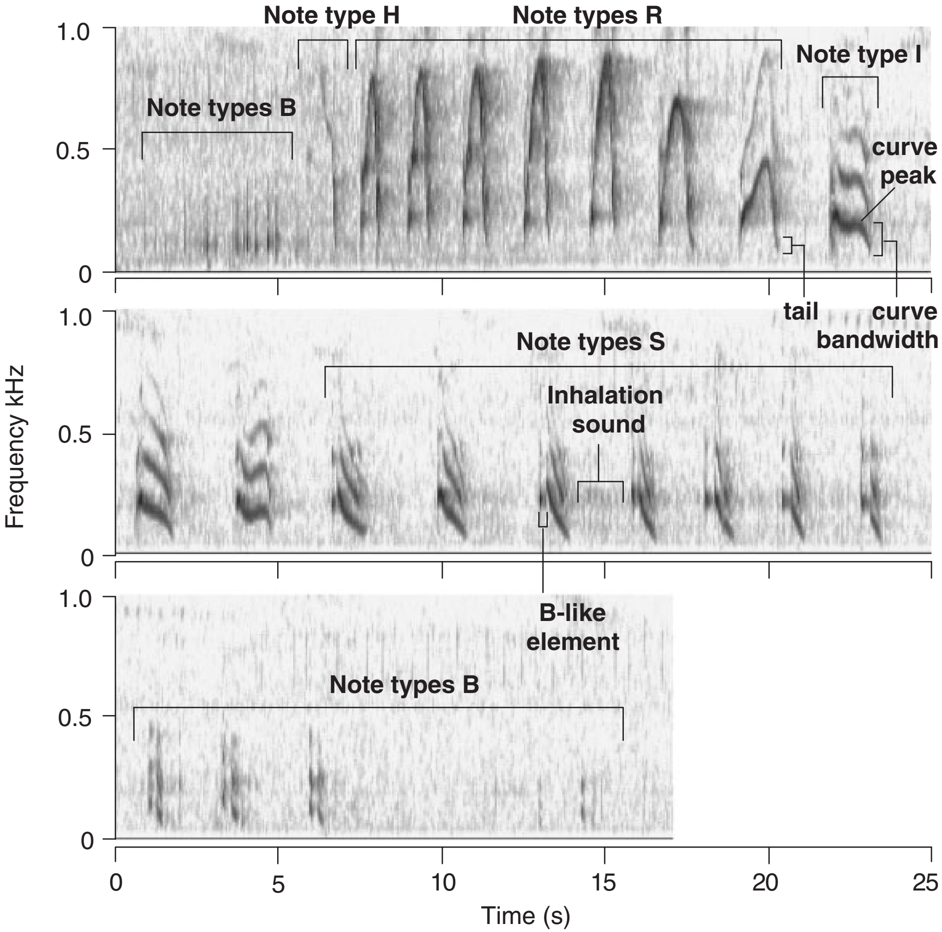

Fig. 3. Sonogram of a complete but relatively short orangutan long call from the Danum Valley Conservation Area (Ulu Segama 1) showing various note types, including B, H, R, I, and S, and inhalation sounds.

Phylogenetic Analyses

The data matrix consisted of 64 variables and 27 operational taxonomic units (OTUs). An OTU is defined as either one identified or all unidentified individual(s) within one population (Table I). Vocal data were coded for each variable, resulting in a set of conditions known as character states [Maddison & Maddison, 2000]. A list of all variables and their character states is provided in the Appendix. Using the MacClade 4.0 software [Maddison & Maddison, 2000], variables were labeled as ‘‘ordered,’’ character states were termed to have ‘‘equal weight,’’ and data inapplicable to certain OTUs were recorded as ‘‘missing.’’ Cladograms were calculated using the PAUP* 4.0b10 (PPC) software [Swofford, 1999]. All cladograms are based on the maximum parsimony procedure, which minimizes the number of character states that are interpreted as synapomorphies [Sudhaus & Rehfeld, 1992; Swofford & Olsen, 1990]. The shortest trees were determined using the heuristic method implemented in PAUP. If the shortest-tree analysis revealed more than one topology, a strict consensus tree of alternative topologies representing polytomies was constructed. In addition, we calculated trees with the bootstrap procedure of PAUP in order to assess the stability of the various groupings within the phylogeny [Maddison & Maddison, 2000]. Bootstrap values were determined based on 1000 replications; values below 50% were ignored [Kitching et al., 1998]. To produce ‘‘rooted trees,’’ we used the pant-hoots of chimpanzees (*Pan troglodytes*) as the outgroup.

RESULTS

Call Structure

Deviations from the three-part structure of the long call (described by MacKinnon [1974] as consisting of an introduction, a climax, and a tail-off) are common. In our samples, any of these segments may repeat, differ in its sequential position, or be absent. Callers produce exhalation as well as inhalation sounds. The most common note types of exhalation are bubbling (B), huitus (H), roars (R), intermediaries (I), and sighs (S) [Davila Ross, 2002] (Fig. 3). Orangutans often purr during inhalation, and the sound is sonographically similar to bubbling but with more regular pulses (Fig. 3). Interestingly, some long calls have biphonal call elements [Davila Ross & Geissmann, 2004].

Multivariate Analysis

Figure 4 shows MDS plotting for all OTUs with minimum contour polygons identifying samples from NW Borneo, NE-E Borneo, SW Borneo, and Sumatra, respectively. Because of the small sample size available, samples from NE and E Borneo (Ulu Segama: two OTUs; Kutai: one OTU) were tentatively grouped

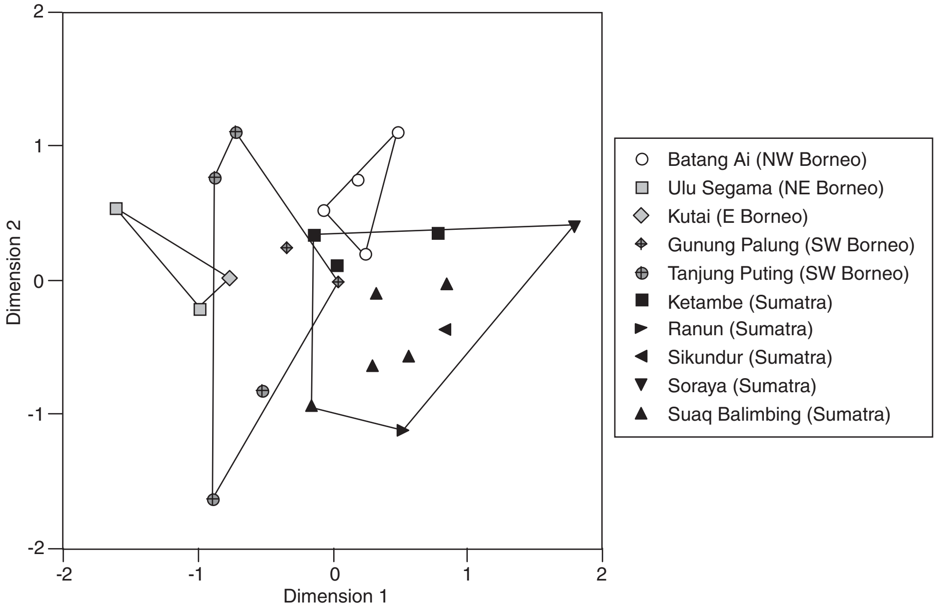

Fig. 4. Multidimensional scaling plot for all OTUs with minimum contour polygons identifying samples from NW Borneo, NE-E Borneo, SW Borneo, and Sumatra, respectively. The sample sizes (number of individuals and calls) are shown in Table I.

together, although it is possible that the Kayan River may split this group into distinct demes.

The polygons slightly overlap three times. SW Bornean data take up an intermediary position between the polygons of NE-E Borneo and Sumatra. Furthermore, data of NW Borneo overlap with those of Sumatra (particularly those of Ketambe) and are farthest away from the NE-E polygon.

Phylogenetic Analyses

The resulting phylogenetic trees, including all long-call data, are presented in Fig. 5. The following four monophyletic clades appear in more than 60% of the replicates of the bootstrap analysis: 1) all four samples from NW Borneo (Batang

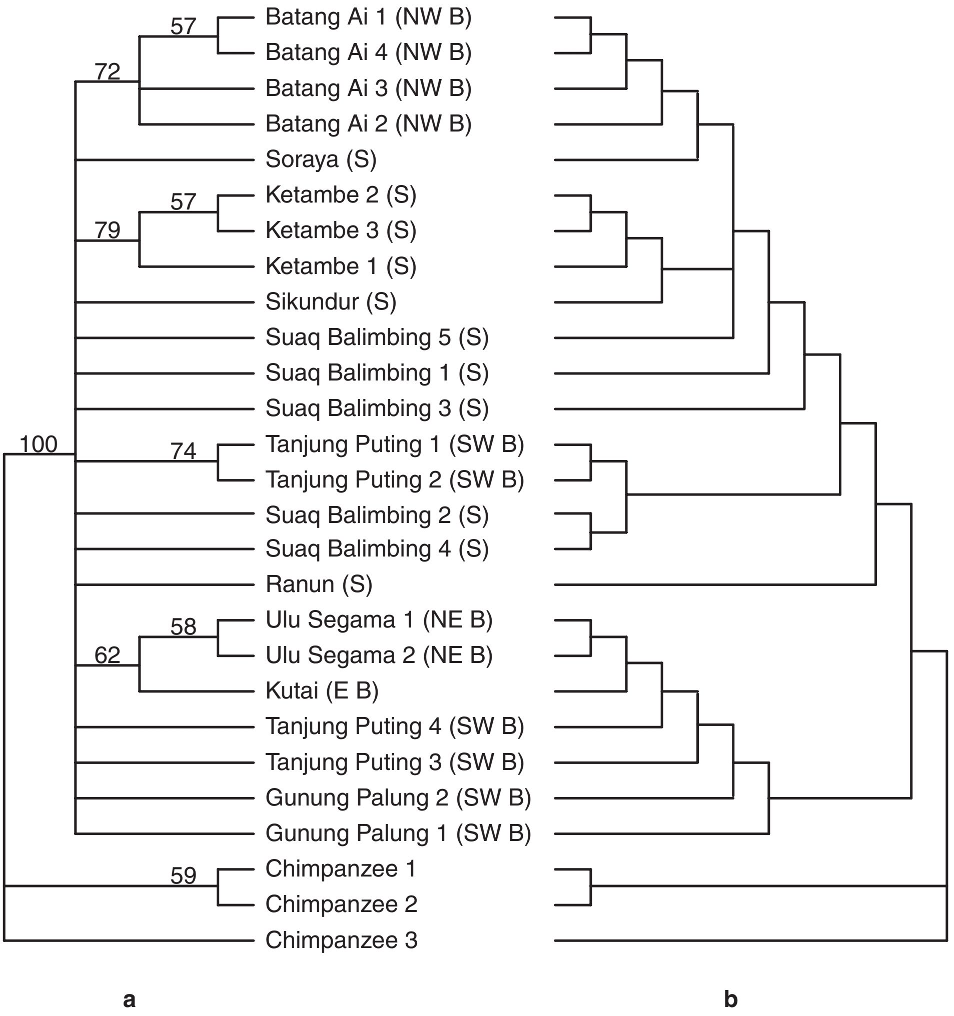

Fig. 5. Maximum parsimony cladograms of all samples (27 OTUs, 64 variables). **a:** Bootstrap 50% majority-rule consensus tree. The bootstrap values for 1000 replications are noted above the branches (tree length = 479; CI = 0.184; RI = 0.314). **b:** Strict consensus of the three shortest trees found in a heuristic search (tree length = 340, CI = 0.259, RI = 0.558).

Ai), 2) all three samples from NE-E Borneo (Ulu Segama, Kutai), 3) all three samples from Ketambe in Sumatra, and 4) two of four samples from Tanjung Puting in SW Borneo. The remaining OTUs all contribute to the chiefly paraphyletic structure of the bootstrap cladogram. The shortest trees determined using a heuristic search exhibit a basal bifurcation into a purely Bornean clade (all NE-E and four SW OTUs) and a clade including samples from both islands (two SW Bornean and all NW Bornean and Sumatran OTUs).

To test whether samples consisting of only one long call negatively affected the resolution of the calculated phylogenies, we repeated a bootstrap analysis after those samples were excluded (n = 5; Table I). The resulting tree supports the same first three monophylies (NW Borneo: 71%; NE-E Borneo: 75%; Ketambe in Sumatra: 75%) as the bootstrap cladogram with the complete data set. The clade consisting of two samples from Tanjung Puting in SW Borneo is absent in the reduced version because one of the two clade members was excluded.

Character state names and symbols that show taxon-specificity for Sumatra, Borneo, NW Borneo, NE-E Borneo, SW Borneo, or Ketambe long calls are marked in the Appendix.

DISCUSSION

Orangutan long calls are more diverse and complex than previously thought. The long-call sequence does not consist strictly of an introduction, a climax, and a tail-off, as described by MacKinnon [1974]. Although this seems to be the typical pattern, variations in the presence and temporal sequence of segments are common.

The five most frequently occurring note types of exhalation and one of inhalation were identified in typical orangutan long calls (Fig. 3). In addition, other sounds and biphonal call elements may occasionally occur [Davila Ross, 2002; Davila Ross & Geissmann, 2004].

Three monophyletic groups (NW Borneo, NE-E Borneo, and Ketambe in Sumatra) of the bootstrap analyses are in accordance with geographic barriers between and within the islands (Figs. 2 and 5). Notably, these clades are present despite orangutan long-call idiosyncrasies [Galdikas, 1983; Mitani, 1985; Rijksen, 1978] (Davila Ross, personal observation), uneven sample sizes, and variations in recording equipment (Table I).

The vocal phylogenies determined in this study were highly polytomous (Fig. 5). They support neither the Borneo-Sumatra dichotomy that was found in several previous studies [e.g., Warren et al., 2001; Zhang et al., 2001; Zhi et al., 1996] nor the more-complex orangutan classifications proposed by Groves et al. [1992], Muir et al. [2000], and Uchida [1998].

At least in tendency, the shortest trees (heuristic method) and MDS plots of this study support a more complex topology than an island dichotomy (Figs. 4 and 5b). They suggest that some intra-island vocal differences are stronger than inter-island ones, in that the NW Bornean calls appear to be more similar to Sumatran calls than to any other Bornean calls. This interpretation is at least partly supported by earlier multivariate studies of cranial and dental characteristics, and suggests that Sumatran and Bornean orangutans cannot be classified simply in accordance with their islands [Groves et al., 1992; Uchida, 1998]. Although multivariate analyses merely show similarity/dissimilarity, their results often correlate with phylogenetic relationships.

Our multivariate analysis of vocal data suggests that both SW and NW Bornean calls are very close to Sumatran calls (Fig. 4). A close relationship between Sumatran and SW Bornean orangutans was also found by Groves et al. [1992] based on cranial data (especially for males) and by Muir et al. [1998] based on unpublished mitochondrial DNA data. These studies, in combination with ours, appear to corroborate the notion that a primary orangutan migration route was established between south Sumatra and SW Borneo in the course of alternating glacial epochs [e.g., Courtenay et al., 1988; Röhrer-Ertl, 1984; Warren et al., 2001]. In contrast to this view, DNA data obtained by Warren et al. [2001] suggest that NE Bornean orangutans are closest to Sumatran taxa, while Zhi et al. [1996] in their second analysis and Röhrer-Ertl [1984] found that no particular Bornean taxon was closest to the Sumatran clade (Figs. 1a and d). From SW Borneo, as suggested by vocal data, orangutans may once have migrated to NE-E Borneo (Figs. 4 and 5). A close relationship between Sumatran and NW Bornean orangutans supports the hypothesis that a northern dispersal route between Sumatra and NW Borneo also was in use [Courtenay et al., 1988], and both orangutan taxa were found to be very similar in tooth morphology [Uchida, 1998]. Nevertheless, the northern land bridge appears to have been more difficult to pass and was submerged for longer periods than the southern course [Courtenay et al., 1988; Muir et al., 1998].

Long-call variables that account for taxon specificity in Sumatra and Borneo (variables 5, 8, and 33) and SW Borneo (variables 11 and 13) mirror differences in call morphology; NW (variables 1 and 43) and NE-E Borneo (variables 13, 15, and 42) long calls differ from those of other taxa in call and sound morphology; and Ketambe (variables 53 and 56) long calls are distinct in note type I morphology (see Appendix). Furthermore, Ketambe long calls differ from those of other orangutan taxa in that their biphonal character is more prominent [Davila Ross & Geissmann, 2004].

The possibility remains that long-call data may be the result not only of genetics, but also of external influences. Social learning, which affects chimpanzee loud-call (pant-hoot) morphology [Crockford et al., 2004; Marshall et al., 1999], may cause similarities across long calls of orangutans within the same deme that reflect cultural affiliation, and our results could mirror a more recent form of orangutan migration rather than paleo-migration. However, even if orangutan males did adjust their long-call morphology according to a social tutor living in the same forest, social influences cannot fully explain our results. For instance, Suaq Balimbing orangutans have been reported to be much more sociable than any other orangutan population studied so far in Borneo or Sumatra [e.g., van Schaik, 2005], yet long calls do not exhibit a corresponding outlier position of Suaq Balimbing orangutans when compared to other orangutan populations.

Although our approach may not be equivalent to phylogenetic approaches based on purely genetic material, research on vocal phylogenies can reveal interesting results and should be strongly considered in studies of nonhabituated individuals from wild and endangered populations, since such data can be easily and noninvasively obtained.

Conservationists agree on the importance of avoiding hybridization of any orangutan taxa, because of the deleterious effects it could have on reproduction, viability, and/or biological diversity [Templeton, 1989]. Bornean and Sumatran orangutans are currently being managed as two separate conservation units, but the possibility still exists (due to displacement) that genetic material from distinct orangutan taxa on the islands will become mixed. As a precaution, orangutans from NW, NE, E, and SW Borneo may need to be dealt with separately, as proposed by the Orangutan Action Plan [Yeager, 1999]. A division into four

Bornean taxa would also coincide more or less with the distribution of the four Bornean gibbon taxa (*Hylobates agilis albibarbis*, *H. muelleri abbotti*, *H. m. funerus*, and *H. m. muelleri*) [Marshall & Sugardjito, 1986] and the patchy distribution areas of some Asian colobines of the genus *Presbytis* (*P. femoralis*, *P. frontata*, *P. hosei*, and *P. rubicunda*) [Brandon-Jones et al., 2004].

Too little is known about the phylogenetic relationships of orangutan populations within Sumatra. Interestingly, the topologies of Ketambe and the remaining Sumatran OTUs of our bootstrap analyses contradict the proposed occurrence of two sympatric Sumatran orangutan populations [Rijksen, 1978; Rijksen & Meijaard, 1999]. For Sumatran orangutans, more phylogeographic research including subjects of reliably known provenance is urgently needed to improve our knowledge of their systematics and strategies for conservation management.

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APPENDIX A

TABLE AI. Variable Names and Character States With Taxon-Specificity Marked for Sumatra (1), Borneo (2), NW Borneo (3), NE-E Borneo (4), SW Borneo (5), and Ketambe (6) Long Calls

No.	Qualitative variable	Character state name and symbol
	Call	
1	Sound transition throughout entire call	0 = abrupt, 1 = gradual
2	Pres. of different note types without interval interference	0 = absent, 1 = present
3	Pres. of same note type without interval interference	0 = absent, 1 = present
	Numerical variable	
	Call	
4	No. of sound levels (i.e., distinct between-notes changes in dominant frequency in a call)	0 = <1.330, 1 = ≥1.330
5	No. of sounds	0 = <17.000, 1 = 17.000–42.9991, 2 = ≥43.000^{2}
6	Rel. no. of bubblings (B)	0 = <0.015, 1 = 0.015–0.049, 2 = ≥0.050
7	Rel. no. of huitus (H)	0 = <27.000, 1 = ≥27.000
8	Rel. no. of roars (R)	0 = <50.000^{1}, 1 = ≥50.000^{2}
9	Rel. no. of intermediaries (I)	0 = <2.700, 1 = ≥2.700
10	Rel. no. of sighs (S)	0 = <21.000, 1 = 21.000–41.999, 2 = ≥42.000
11	Rel. no. of ascending sounds	0 = <14.000, 1 = 14.000–27.9995, 2 = ≥28.000
12	Rel. no. of descending sounds	0 = <32.700, 1 = ≥32.700
13	Rel. no. of symmetrical sounds	0 = <42.000^{4}, 1 = 42.000–54.9995, 2 = 55.000–67.999, 3 = ≥68.000
14	Rel. no. of nonmodulated sounds	0 = <24.000, 1 = ≥24.000
15	Rel. no. of modulated sounds	0 = <40.000^{4}, 1 = 40.000–59.999, 2 = 60.000–72.499, 3 = ≥72.500
16	Rel. no. of multimodulated sounds	0 = <4.500, 1 = ≥4.500
17	Pos. of sound with highest frequency	0 = beginning, 1 = middle, 2 = end
18	Pos. of sound with lowest frequency	0 = beginning, 1 = middle, 2 = end
19	Pos. of sound with longest bandwidth	0 = beginning, 1 = middle, 2 = end
20	Pos. of sound with shortest bandwidth	0 = beginning, 1 = end
21	Pos. of sound with highest peak frequency	0 = beginning, 1 = middle, 2 = end
22	Pos. of sound with lowest peak frequency	0 = beginning, 1 = end
23	Pos. of sound with longest duration	0 = beginning, 1 = middle
24	Pos. of sound with shortest duration	0 = beginning, 1 = end

25	Pos. of sound with highest peak intensity	0 = beginning, 1 = end
26	Pos. of sound with lowest peak intensity	0 = beginning, 1 = end
27	No. ratio of left- to right-sided hooks of sounds	0 = <1.000, 1 = ≥1.000
28	No. ratio of left- to right-sided tails of sounds	0 = <1.500, 1 = ≥1.500
29	No. of dominant harmonic frequencies per sound	0 = <1.000, 1 = 1.000–1.749, 2 = ≥1.750
	Sound	
30	Pres. of dominant fundamental frequency	0 = present, 1 = infrequently present, 2 = absent
	Metrical variable	
	Call	
31	Call duration [s]	0 = <10.000, 1 = 10.000–44.999, 2 = ≥45.000
32	Comparison of maximum frequencies [Hz]	0 = <(−23.000), 1 = (−23.000)–2.499, 2 = ≥2.500
33	Comparison of minimum frequencies [Hz]	0 = <(−3.400), 1 = (−3.400)–3.3992, 2 = ≥3.400[1]
34	Comparison of bandwidths [Hz]	0 = <(−10.000), 1 = ≥(−10.000)
35	Comparison of sound rates [s]	0 = <(−0.021), 1 = (−0.021)–;(−0.001), 2 = ≥0.000
36	Bubbling (B) duration [s]	0 = <7.500, 1 = ≥7.500
	Sound	
37	Sound duration [s]	0 = <0.500, 1 = 0.500–0.724, 2 = ≥0.725
38	Interval duration [s]	0 = <0.500, 1 = 0.500–1.199, 2 = ≥1.200
39	Sound duration per interval duration	0 = <6.400, 1 = ≥6.400
40	Highest frequency [Hz]	0 = <650.000, 1 = ≥650.000
41	Lowest frequency [Hz]	0 = <115.000 1 = 115.000–119.999, 2 = ≥120.000
42	Duration of bubbling(B)-like elements before sound [s]	0 = <0.078, 1 = 0.078–0.104, 2 = ≥0.105[4]
43	Duration of bubbling(B)-like elements after sound [s]	0 = <0.290, 1 = ≥0.290[3]
	Note type R (roar)	
44	Frequency range [Hz]	0 = <600.000, 1 = ≥600.000
45	Peak frequency [Hz]	0 = <370.000, 1 = ≥370.000
46	Pos. of peak frequency within bandwidth	0 = <0.530, 1 = ≥0.530
47	Pos. of peak time within duration	0 = <0.690, 1 = ≥0.690
48	Comparison of peak intensities [dB]	0 = <(−0.015), 1 ≥(−0.015)
49	Bandwidth divided by duration [Hz/s]	0 = <700.000, 1 = 700.000–1049.999, 2 = ≥1050.000
	Note type I (intermediary)	
50	Bandwidth [Hz]	0 = <250.000, 1 = ≥250.000
51	Peak frequency [Hz]	0 = <255.000, 1 = ≥255.000
52	Pos. of peak frequency within bandwidth	0 = <0.525, 1 = ≥0.525

53	Pos. of peak time within duration	$0 = <0.670$, $1 = \geq 0.670^{6}$
54	Comparison of peak intensities [dB]	$0 = <(-0.500)$, $1 = \geq(-0.500)$
55	Bandwidth divided by duration [Hz/s]	$0 = <500.000$, $1 = \geq 500.000$
56	Frequency of curve peak [Hz]	$0 = <410.000$, $1 = \geq 410.000^{6}$
57	Curve bandwidth (see Fig. 3) divided by note type I bandwidth	$0 = <0.382$, $1 = \geq 0.382$
	Note type S (sigh)	
58	Frequency line of longest duration [Hz]	$0 = <160.000$, $1 = \geq 160.000$
59	Bandwidth [Hz]	$0 = <250.000$, $1 \geq 250.000$
60	Peak frequency [Hz]	$0 = <211.000$, $1 = 211.000$–279.999, $2 = \geq 280.000$
61	Pos. of peak frequency within bandwidth	$0 = <0.520$, $1 = \geq 0.520$
62	Pos. of peak time within duration	$0 = <0.200$, $1 = \geq 0.200$
63	Comparison of peak intensities [dB]	$0 = <(-0.200)$, $1 = \geq(-0.200)$
64	Bandwidth divided by duration [Hz/s]	$0 = <600.000$, $1 = \geq 600.000$

dB, decibel; Hz, Hertz; s, seconds; no., number; pos., position; pres., presence; rel., relative.