Zoological Studies **44**(2): 275-294 (2005)

Zoological Studies

The Vocal Repertoire of Formosan Macaques, *Macaca cyclopis*: Acoustic Structure and Behavioral Context

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(Accepted January 31, 2005)

Minna J. Hsu, Li-Ming Chen, and Govindasamy Agoramoorthy (2005) The vocal repertoire of Formosan macaques, *Macaca cyclopis*: acoustic structure and behavioral context. *Zoological Studies* **44**(2): 275-294. In this paper, we present data on the physical structure of vocalizations for the 1st time recorded from wild Formosan macaques, *Macaca cyclopis*, at Mt. Longevity, Taiwan. Field observations and spectrographic analysis of sound recordings of Formosan macaques revealed 25 basic patterns with 35 repertoires. Formosan macaques employ a complex vocal system composed of well-separated sound classes as well as acoustic categories connected by intermediate gradations. Comparisons of the vocal repertoire of Formosan macaques with those of other species in the genus *Macaca* indicate some similarities in composition and structural design. http://www.sinica.edu.tw/zool/zoolstud/44.2/275.pdf

Key words: *Macaca cyclopis*, Vocal repertoire, Social behavior, Taiwan.

Social behavior typically relies on communication, and an understanding of a species' social organization therefore requires an integrated knowledge of its communication system, including vocalizations (Cheney and Seyfarth 1990). Despite the fact that studies of vocal communication have been conducted on a variety of primate species ranging from lemurs to chimpanzees, the macaques represent the most-comprehensively investigated, both in terms of the number of species studied and the breadth of topics covered (Green 1975, Deputte and Goustard 1980, Bauers and de Waal 1991, Hauser 1991, Hohmann 1991, Bauers 1993, Hauser and Marler 1993, Rendall et al. 1996, Wheatley 1999, Fischer and Hammerschmidt 2002, Ceugniet and Izumi 2003). However, only a few studies in the past analyzed vocal repertoires, both qualitatively and quantitatively, in species such as lion-tail macaques (Hohmann and Herzog 1985), bonnet macaques (Hohmann 1989), and long-tail macaques (Palombit 1992). Thus our understanding of vocal communication in the genus *Macaca* is still inadequate, especially for lesser-known species such as the Formosan macaque, *Macaca cyclopis*.

Formosan macaques are endemic to the island of Taiwan. The majority live in social groups and use visual and acoustic signals to regulate intra- and inter-group social actions. However, the propagation of visual signals may be restricted to short distances since their habitat is dominated by forest vegetation with undulating hillocks or steep uplifted coral reef hills. It can be expected that environmental conditions play a key role in shaping systems of vocal communication. Therefore, the social environment, such as the group size and composition, can also have a strong influence on the structure of vocal patterns as well as the general vocal repertoire (Marler 1976).

This paper for the 1st time describes the physical structures of vocal patterns obtained from wild Formosan macaques. In total 25 classes of vocal patterns were distinguished, and their sonograms analyzed. The frequency of use of each

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vocal pattern is illustrated. Data on social behavior were also collected to highlight the context in which each vocalization was given. Finally, we have compared the vocal repertoire of Formosan macaques with those of other species in the genus *Macaca*.

MATERIALS AND METHODS

A long-term field study to investigate the demographic parameters and social behavior of Formosan macaques at Mt. Longevity, Kaohsiung, southern Taiwan, (22°9'N, 120°15'E) began in July 1993 (see Hsu et al. 2000 2001 2002, Hsu and Lin 2001 for study site details). Investigations of vocal behaviors were conducted on selected groups (C, B, D, E, F, G, and Ia) from Oct. 1999 to Oct. 2000. Field recordings were conducted 1~2 d/wk from dawn to dusk. All study animals mentioned in this paper are individually identifiable due to the availability of long-term demographic data and genealogical information (Hsu and Lin 2001). We followed the broad age classification as: (1) infant I (< 7 mo); (2) infant II (≥7 mo and < 14 mo); (3) juveniles (14 mo~3 yr); (4) subadults (female, SAF: 4 yr; male, SAM: 4~5 yr); and (5) adults (female, AF: primiparous females or females ≥ 5 yr old; male, AM: ≥ 6 yr old). Infants were separated according to the stage of weaning which approximately occurs at 7 mo of age. Group C was the major focal group (accounting for 88.5% of the observation time) which was followed for 1~2 d/wk from dawn to dusk whenever possible. This group contained 63 individuals (as of Aug. 2000), and its composition included 8 AM, 19 AF, 6 SAM, 2 SAF, 9 juvenile males (JM), 4 juvenile females (JF), 5 infant I, and 10 infant II. The sizes of the other 6 groups ranged from 37 to 75. All were multi-male, multi-female social groups.

Behavioral data and sound recordings were simultaneously collected from all study groups for a total of 375 h, using scan sampling (55 h), and all-occurrence and focal animal sampling (320 h) methods (Lehner 1996). Sound recordings were mainly obtained (332 h, 88.5%) from the habituated group C. Data collection commenced when the appearance of the observer no longer caused any obvious change in the group's activities. In addition to the recordings of vocalizations, the age and sex of the vocalizer and behavioral data on social interactions were recorded. The distance between the observer and the animal varied from 1 to 10 m.

Sound recordings were made using a Sony professional cassette recorder (TC-D5 PRO II) and a directional microphone (Sennheiser MKH 460). Spectrographic analyses were carried out on a Macintosh computer (G3/350KHz) using the Canary software package (vers. 1.2.4). Sounds were digitized with 16-bit accuracy from audio tapes at a sampling rate of 44.1 kHz, using a 1024-p fast Fourier transformation (FFT, with a Hamming window); this setting provided a frequency resolution of 43 Hz and a temporal resolution of 3 ms. Classification of the repertoire was based on measurement of the physical parameters of time, frequency, and energy distribution following Hohmann (1989) and Moody et al. (1990). In addition, the age and sex of the vocalizing individuals and the context of the utterance were also considered.

We followed the terminology of Struhsaker (1967) for describing the acoustic properties of the basic patterns, which contain the following elements: units (tonal, non-tonal, compound, and mixed), phrases, and bouts. The unit is the basic element of a monkey sound or call, and is represented as a continuous tracing along the temporal (horizontal) axis of a sonogram. The phrase is a group of units separated from other similar groups by a time interval greater than any time interval separating the units within a phrase. A bout is a grouping of 1 or more phrases separated from other similar groupings by a time interval greater than that separating any phrases within a bout

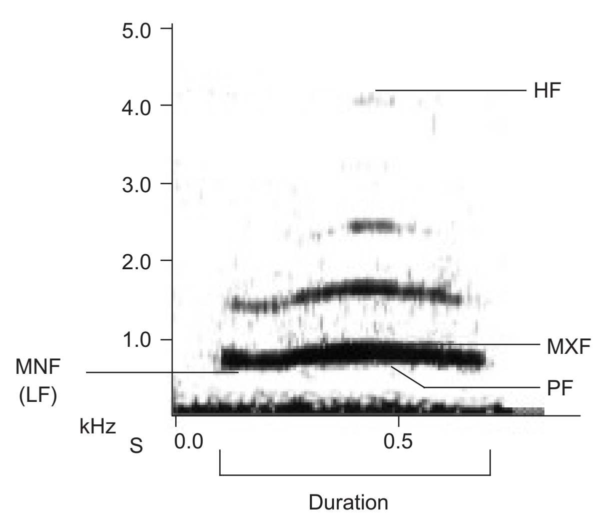

Fig. 1. Spectrogram of a typical unit of isolation coo from an infant to show the spectral parameters measured in this study: Maximal fundamental frequency (MXF), Minimal fundamental frequency (MNF), Highest frequency (HF), Lowest frequency (LF), Peak frequency (PF) and duration of each unit.

(Struhsaker 1967). The acoustic parameters, the context of the emission, and a comparison with previous references were used to classify the vocal repertoire in Formosan macaques (Table 1). In addition, the age and sex of the vocalizing individuals and the context of the utterance were also considered.

Previous qualitative studies of vocal repertoires (Green 1975, Hohmann and Herzog 1985, Hohmann 1989) indicated that from the perspective of both production and perception, fundamental frequency is typically the most-salient acoustic feature (Moody et al. 1990). Therefore, a suite of acoustic features was selected for analysis. The spectral measurements included the maximal fundamental frequency (MXF), minimal fundamental frequency (MNF), highest frequency (HF), lowest frequency (LF), peak frequency (PF), and duration of each unit (Fig. 1). The peak frequency was the frequency which had the highest amplitude in a unit, and some physical parameters below were obtained by extrapolation, including the median fundamental frequency (FF = (MXF + MNF)/2), modulation of the fundamental frequency (MFF =

Table 1. Vocal patterns of species in the Genus *Macaca* homologous to the repertoires of *M. cyclopis*

Vocal patterns of	Equivalent call type in other species				
M. cyclopis	species	call-type label	Context	Acoustic structure	References
1-1. Contact coo	*M. fuscata*	Short low coo; Long low coo; Smooth early high	*fu*: smooth early high mostly used during young alone.	*fu*: smooth early high with higher FF (≥0.52 kHz)	Green 1975
	M. mulatta	Clear call Coo call	similar	*mu*: longer duration (0.46 s)	Rowell and Hinde 1962 Hauser 1991
	M. fascicularis	Coo call	similar	*fa*: narrow RF (max to 1.5 kHz)	Palombit 1992; Wheatley 1999
	M. radiata	Contact whoo	similar	*ra*: higher FF (0.57 kHz), narrow RF (2.63 kHz)	Hohmann 1989
	M. silenus	Whoo call	similar	*sil*: narrow MFF (0.1-0.2 kHz)	Hohmann and Herzog 1985
	M. sinica	Hum	*si*: following an alarm	similar	Dittus 1988
	M. arctoides	Coo call	similar	*ar*: shorter duration (0.13 s)	Bauers and de Waal 1991
1-2. Isolation coo	*M. fuscata*	Dip early high	similar	similar	Green 1975
	M. radiata	Isolation whoo	similar	*ra*: higher FF (1.04 kHz), longer duration (0.72 s)	Hohmann 1989
	M. fascicularis	Coo call	similar	*fa*: higher PF (up to 5 kHz)	Wheatley 1999
	M. sinica	Infant separated call-2	similar	*si*: higher FF (0.7-1.0 kHz), longer duration (0.8-1.1 s)	Dittus 1988
	M. mulatta	Clear call	similar	similar	Rowell and Hinde 1962
1-3. Long distance coo	*M. radiata*	Long distance whoo	similar	*ra*: longer FF (1.34kHz), wider MFF (1.47 kHz), narrow RF (5.6 kHz), high PF(1.8 kHz)	Hohmann 1989
	M. fuscata	Dip late high; Smooth late high	*fu*: subordinate at dominant; estrus female	similar	Green 1975
1-4. Cohesion coo	*M. fuscata*	Double	*cy*: dispersal, appearance of feeder etc.	similar	Green 1975
2-1. Atonal greeting	*M. fuscata*	Atonal girney	similar	*fu*: high HF (3-4 kHz)	Green 1975
2-2. Tonal greeting	*M. radiata*	Greeting	similar	*ra*: lower FF (0.18 kHz), narrow MFF(0.24 kHz), lower RF (1.99 kHz), higher PF (0.62kHz)	Hohmann 1989
	M. fuscata	Musical	*fu*: young toward their mothers	similar	Green 1975
2-3. Girney	*M. fuscata*	Girney	similar	similar	Green 1975
	M. silenus	Greeting	similar	similar	Hohmann and Herzog 1985
3. Female copulation call	*M. fascicularis*	Copulation call	similar	*fa*: narrow RF (5.2 kHz)	Depputte and Goustard 1980
	M. silenus	Female copulation call	similar	*sil*: narrow RF (4-7 kHz)	Hohmann and Herzog 1985
	M. sylvanus	oestrus call	similar	*sy*: narrow RF (8 kHz), lower *HF* (8 kHz)	Fischer and Hammerschmidt 2002

Table 1. (Cont.)

Vocal patterns of *M. cyclopis*	Equivalent call type in other species				
	species	call-type label	Context	Acoustic structure	References
4. Male copulation call	*M. radiata*	Male copulation call	similar, but *M. radiata* have higher rate of utterances during copulation	*ra*: low FF(1.18 kHz), narrow RF (6.9 kHz), low PF (1.3 kHz)	Hohmann 1989
	M. silenus	Male copulation call	similar	*sil*: highly MFF (1-3 kHz)	Hohmann and Herzog 1985
5. Mounting grunt	*M. radiata*	Mounting grunt	similar	*ra*: higher PF (1.3 kHz)	Hohmann 1989
6. Alarm call	*M. fuscata*	Late-high-alarm, Early-high-alarm	similar	*fu*: Harmonic in the first part	Masataka 1983
	M. radiata	Alarm call	similar, but different stimulus	*ra*: more segments, tonality	Hohmann 1989
	M. fascicularis	Kra	similar, but different stimulus	*fa*: narrow RF (6.8 kHz)	Palombit 1992; Wheatley 1999
7. Grunt	*M. mulatta*	Grunt	similar	similar	Hauser and Marler 1993
	M. sinica	Grunt	similar	*si*: longer duration (up to 0.5 s)	Dittus 1988
	M. fascicularis	Grunt	similar	*fa*: narrow RF (4.2 kHz)	Palombit 1992; Wheatley 1999
	M. radiata	Contact rattle	similar	*ra*: lower RF (1.7 kHz), longer duration (0.23 s)	Hohmann 1989
	M. arctoides	Staccato grunt	similar	similar	Basuer 1993
8. Threat rattle	*M. radiata*	Threat rattle	similar	*ra*: narrow RF (3.8 kHz), longer duration (0.44 s)	Hohmann 1989
	M. fuscata	Gruff	similar	*fu*: narrow RF (6-7 kHz)	Green 1975
	M. fascicularis	Threat rattle	similar	*fa*: narrow RF (6.5 kHz), longer duration (0.35 s)	Palombit 1992; Wheatley 1999
	M. silenus	Rattle	*sil*: toward intergroup members or other species	*sil*: harsh, non-tonal quality	Hohmann and Herzog 1985
	M. mulatta	Trilled bark	similar	*mu*: narrow RF (6-7 kHz)	Hauser and Marler 1993
9. Growl	*M. fuscata*	Growl	similar	*fu*: narrow RF (7-8 kHz)	Green 1975
	M. silenus	Grunt	similar	similar	Hohmann and Herzog 1985
10. Vibrato growl	*M. radiata*	Vibrato growl	similar	*ra*: lower FF(0.22 kHz), narrow RF (5.5 kHz), longer duration (0.4 s)	Hohmann 1989
	M. silenus	Warning call	*sil*: toward potential predator, as alarm calls	similar	Hohmann and Herzog 1985
11. Roar	*M. fuscata*	Roar	fu: mostly used during sexual solicitation	*fu*: narrow RF (6-7 kHz)	Green 1975
12. Bark	*M. radiata*	Bark	*cy*: interspecies encounters (i.e. birds)	similar	Hohmann 1989
	M. fuscata	Class VII scream and shriek	similar	*fu*: lack of narrow beam which frequency range from baseline	Green 1975
	M. silenus	Noise scream	similar	*sil*: lack of undulated scream	Hohmann and Herzog 1985
	M. fascicularis	Noisy and undulated scream	similar	*fa*: narrow RF (7.5 kHz)	Wheatley 1999
13. Squeal	*M. radiata*	Squeal	similar	*ra*: lower FF (2.6 kHz)	Hohmann 1989
	M. silenus	Shriek	similar	similar	Hohmann and Herzog 1985
	M. fuscata	Class VI squeal and screech	similar	*fu*: tonality	Green 1975
14. Noise and undulated scream	*M. mulatta*	Noise and undulated scream	similar	*mu*: lack of narrow beam which frequency range from baseline	Gouzoules et al. 1984 1998
	M. radiata	Noise and undulated scream	similar	similar	Hohmann 1989
	M. nemestrina	Contact aggressive scream	similar	*ne*: lack of narrow beam which frequency range from baseline; narrow RF (6.6-7.6 kHz)	Gouzoules et al. 1984 1998

Table 1. (Cont.)

Vocal patterns of	Equivalent call type in other species				
M. cyclopis	species	call-type label	Context	Acoustic structure	References
15. Tonal scream	*M. mulatta*	Tonal scream	similar	*mu*: lower FF (2.4 kHz), narrow RF(5.1 kHz)	Gouzoules et al. 1984 1998
	M. radiata	Tonal scream	similar	*ra*: higher FF (10.4 kHz), high MFF (4.4 kHz), narrow RF (4.7 kHz)	Hohmann 1989
	M. fascicularis	Tonal scream	similar	similar	Wheatley 1999
16-1. Tonal squeak	*M. radiata*	Tonal squeak	similar	*ra*: low FF (2.1 kHz), low PF (2.5 kHz)	Hohmann 1989
	M. fuscata	Class IV squeak; class V chirp	similar	similar	Green 1975
16-2. Compound squeak	*M. mulatta*	Pulse scream	similar	*fu*: non-tonal unit, lower HF (up to 10 kHz)	Gouzoules et al. 1984 1998
	M. fascicularis	Pulse scream	similar	*fa*: lower HF (9 kHz), longer duration (0.35 s)	Wheatley 1999
17. Chuckle	*M. radiata*	Chuckle	similar	*ra*: shorter duration (0.08 s)	Hohmann 1989
18-1. Food yell	*M. sinica*	Food call	similar	*cy*: superimposed by noisy portion	Dittus 1988
18-2. Oui	*M. fuscata*	Class Ⅲ Oui	similar	*cy*: superimposed by slight noisy portion	Green 1975
18-3. Harmonic arch	*M. mulatta*	Harmonic arch	*cy*: also during reunite	*cy*: superimposed by slight noisy portion	Hauser and Marler 1993
19-1. Tonal hack	*M. fuscata*	Class Ⅳ low squawk, ech	similar	similar	Green 1975
	M. radiata	Tonal hack	similar	*ra*: wider RF (8.6 kHz), higher PF (3.0 kHz)	Hohmann 1989
19-2. Compound hack	*M. mulatta*	Pulse scream	similar	*mu*: higher PF (4.3 kHz)	Gouzoules et al. 1984 1998
	M. radiata	Compound hack	similar	*ra*: lower FF (0.16 kHz), higher PF (3.4 kHz)	Hohmann 1989
	M. sylvanus	Shrill bark	*sy*: interspecies disturbance	similar	Fischer et al. 1995
20. Squawk	*M. fuscata*	Class Ⅳ	high squawk	similar	similar Green 1975
21. Cluck	*M. radiata*	Cluck	*cy*: while infants were ignored	similar	Hohmann 1989
22. Gecker	*M. sylvanus*	Gecker	similar	*sy*: narrow RF	Fischer and Hammerschmidt 2002
	M. radiata	Sneeze	similar	*ra*: higher PF (1.9 kHz)	Hohmann 1989
	M. silenus	Sneeze	similar	similar	Hohmann and Herzog 1985
23. Whine	*M. fuscata*	Whine	similar	*fu*: higher LF (1.8 kHz), higher HF (7-8 kHz)	Green 1975
	M. silenus	Milk grumble	*sil*: during sucking, a lack of milk	*cy*: higher FF (0.5 kHz)	Hohmann and Herzog 1985
24. Weeping	*M. radiata*	Pulse whoo	similar	*ra*: higher FF (1.3 kHz), wider RF (5.8 kHz)	Hohmann 1989
	M. silenus	Weeping	similar	*sil*: lower FF (0.3-0.5 kHz)	Hohmann and Herzog 1985
	M. sinica	Infant separation call	similar	*si*: longer duration (0.8-1.1s)	Dittus 1988
25. Babble	*M. radiata*	Babble	similar	similar	Hohmann 1989

cy: *M. cyclopis*; *fa*: *M. fascicularis*; *fu*: *M. fuscata*; *mu*: *M. mulatta*; *ra*: *M. radiata*; *ar*: *M. arctoides*; *sil*: *M. silenus*; *si*: *M. sinica; sy: M. sylvanus* and *ne*: *M. nemestrina*. Highest frequency (HF), lowest frequency (LF), peak frequency (PF), median fundamental frequency (FF), modulation of fundamental frequency (MFF) and total range of frequency (RF) were acoustic parameters.

MXF - MNF), and the total frequency range (RF = HF - LF).

All statistical analyses were conducted using Statistical Analysis System software (SAS Institute 2000). All mean values are presented as ± 1 standard deviation. Duncan's multiple range tests were used to test the similarity among 4 vocal types of coos and of 5 acoustic variables (FF, MFF, RF, PF, and duration) among alarm calls, grunts, and threat rattles followed by analysis of variance (ANOVA) of each parameter. In addition, significant differences of some acoustic parameters between different vocal types were tested using Wilcoxon rank tests. Canonical discriminant analy-

Table 2. Vocal types of 25 basic patterns of the vocal repertoire of Formosan macaques: mean values of physical parameters and mean variation (± S.D., only for sample size more than 10) in parentheses

Vocal types [No. of unit analyzed]	Basic feature	Median fundamental frequency (kHz)	Modulation of fundamental frequency (kHz)	Range of unit (kHz)	Total range of frequency (kHz)	Peak frequency (kHz)	Duration of unit (sec)
1-1. Contact coo [249]	tonal	0.41 (0.13) [b*]	0.20 (0.09) [a]	0.11~11.8	3.42 (2.61) [b]	0.44 (0.17) [a]	0.26 (0.11) [a]
1-2. Isolation coo [73]	tonal or compound	0.64 (0.11) [c]	0.25 (0.09) [a]	0.23~11.1	2.30 (1.65) [a]	0.74 (0.18) [b]	0.32 (0.13) [b]
1-3. Long distance coo [204]	tonal	0.69 (0.17) [d]	0.33 (0.13) [b]	0.23~16.2	8.26 (3.21) [c]	0.80 (0.31) [b]	0.43 (0.11) [c]
1-4. Cohesion coo [56]	compound or mixed	0.34 (0.14) [a]	0.21 (0.10) [a]	0.04~15.4	8.45 (3.04) [c]	0.72 (0.38) [b]	0.33 (0.10) [b]
2-1. Atonal greeting [65]	non-tonal	Baseline	-	baseline~6.1	1.79 (1.34)	0.26 (0.13)	0.10 (0.09)
2-2. Tonal greeting [29]	tonal	0.26 (0.06)	0.35 (0.18)	0.18~9.85	2.90 (2.63)	0.41 (0.21)	0.28 (0.10)
2-3. Girney [84]	tonal, compound or mixed	0.27 (0.08)	0.13 (0.06)	0.05~11.6	3.17 (2.40)	0.40 (0.35)	0.22 (0.12)
3. Female copulation call [556]	non-tonal	Baseline	-	baseline~21.9	10.14 (3.04)	0.79 (1.13)	0.06 (0.02)
4. Male copulation call [42]	tonal	2.26 (0.98)	0.85 (0.50)	0.8~22.0	12.98 (4.31)	3.43 (1.60)	0.14 (0.07)
5. Mounting grunt [14]	non-tonal	Baseline	-	baseline~8.3	7.15 (1.59)	0.16 (0.07)	0.28 (0.06)
6. Alarm call [77]	tonal, compound or mixed	0.30 (0.15) [c]	0.24 (0.15) [c]	baseline~21.8	10.71 (3.20) [b]	0.89 (0.70) [c]	0.21 (0.07) [c]
7. Grunt [430]	non-tonal or mixed	0.23 (0.10) [b]	0.18 (0.08) [b]	baseline~16.8	8.94 (3.02) [a]	0.34 (0.32) [a]	0.13 (0.05) [a]
8. Threat rattle [148]	non-tonal or mixed	0.14 (0.04) [a]	0.14 (0.05) [a]	baseline~18.6	10.25 (2.49) [b]	0.59 (0.96) [b]	0.16 (0.03) [b]
9. Growl [169]	non-tonal	Baseline	-	baseline~16.6	10.02 (2.66)	0.55 (1.07)	0.19 (0.08)
10. Vibrato growl [56]	mixed	0.31 (0.09)	0.18 (0.07)	0.06~16.5	9.27 (3.82)	0.60 (0.41)	0.13 (0.09)
11. Roar [29]	non-tonal	Baseline	-	baseline~16.9	9.89 (3.14)	0.63 (0.92)	0.21 (0.07)
12. Bark [20]	non-tonal	Baseline	-	baseline~19.0	8.70 (4.66)	1.18 (0.37)	0.21 (0.07)
13. Squeal [103]	tonal, compound or mixed	4.07 (1.16)	2.41 (1.36)	0.8~21.2	13.95 (2.57)	4.98 (1.75)	0.44 (0.18)
14-1. Noise scream [129]	non-tonal	Baseline	-	baseline~22.0	16.17 (4.12)	4.05 (1.89)	0.38 (0.16)
14-2. Undulated scream [61]	mixed	0.37 (0.17)	0.24 (0.10)	baseline~21.6	15.23 (1.72)	3.80 (1.43)	0.60 (0.22)
15. Tonal scream [20]	tonal	5.61 (1.37)	1.72 (1.34)	0.9~21.6	9.38 (2.96)	6.07 (1.23)	0.39 (0.09)
16-1. Tonal squeak [151]	tonal	4.58 (1.43)	1.29 (0.82)	1.2~22.0	10.20 (3.65)	5.93 (2.33)	0.14 (0.06)
16-2. Compound squeak [194]	compound or mixed	3.39 (1.31)	1.22 (0.76)	0.9~21.8	13.92 (2.64)	6.49 (2.43)	0.16 (0.06)
17. Chuckle [20]	mixed	1.20 (0.30)	1.19 (0.52)	0.2~15.8	10.00 (3.84)	2.11 (0.75)	0.22 (0.08)
18-1. Food yell [13]	tonal or mixed	2.35 (1.12)	1.72 (0.76)	0.09~13.5	11.91 (2.43)	3.20 (1.88)	0.31 (0.06)
18-2. Oui [12]	tonal or mixed	2.22 (0.87)	2.29 (1.31)	0.5~21.6	15.65 (2.84)	4.59 (1.56)	0.43 (0.13)
18-3. Harmonic arch [7]	tonal or compound	0.73	0.95	0.09~13.5	7.97	0.82	0.33
19-1. Tonal hack [197]	tonal	1.13 (0.43)	0.47 (0.41)	0.4~20.4	6.43 (3.92)	1.45 (0.93)	0.03 (0.01)
19-2. Compound hack [288]	compound or mixed	0.97 (0.76)	0.51 (0.49)	baseline~21.8	11.98 (3.65)	1.96 (1.21)	0.09 (0.04)
20. Squawk [96]	tonal	1.33 (0.36)	0.74 (0.34)	0.4~21.8	12.09 (3.63)	1.67 (0.75)	0.09 (0.05)
21. Cluck [83]	tonal	0.95 (0.27)	0.31 (0.10)	0.3~9.5	2.91 (1.73)	1.18 (0.80)	0.04 (0.02)
22. Gecker [116]	tonal or mixed	0.37 (0.12)	0.19 (0.09)	0.1~17.1	5.45 (4.70)	0.52 (0.45)	0.03 (0.01)
23. Whine [11]	tonal, compound or mixed	0.52 (0.05)	0.21 (0.05)	0.2~4.4	2.16 (1.11)	0.76 (0.40)	0.58 (0.38)
24. Weeping[24]	tonal	0.70 (0.11)	0.22 (0.04)	0.37~7.2	2.06 (1.28)	0.74 (0.11)	0.34 (0.08)
25. Babble [15]	tonal	0.45 (0.14)	0.18 (0.05)	0.2~3.6	1.86 (0.57)	0.77 (0.39)	0.07 (0.02)

*: [a, b, c, d] were from Duncan's multiple range tests for five variables. Different letters indicated significant differences existed ($p < 0.05$) within four types of coos or among alarm call, grunt and threat rattle.

sis was used to measure the squared distances between the 4 types of coos. Chi-square test was used to test differences in the occurrence of male and female copulation calls.

RESULTS

In total, 25 vocal patterns with 35 repertoires and behavioral contexts of vocalizations were distinguished (Table 1), and their sonograms were analyzed from 7997 units recorded from focal animal sampling (320.4 h). Basic features including structure, range of units, FF, MFF, RF, PF, and duration of the 35 vocal repertoires are described in Table 2. Among all vocal repertoires of Formosan macaques, coo calls were the most common vocalization (with a relative frequency of 18.59%), followed by hacks (17.78%) and grunts (11.85%).

Coo calls

These were the most commonly uttered calls in the vocal repertoire. According to the structural features and behavioral contexts of the utterances, at least 4 types were recognized.

(i) Contact coo. Adult females and both sexes of subadults, juveniles, and infants emitted contact coos (Fig. 2A-D) in 3 different contexts. (a) When infants were exploring alone, they emitted this call apparently in order to maintain contact with their mother. (b) They were associated with initiation of group procession: usually 1 animal initiated the call and some of its peers responded with contact coo calls, which resulted in troop movement. (c) When monkeys heard or saw a familiar person who usually provides fruit or bread to them, troop members would join together and excitedly emit this type of call, followed by grunts and/or food yells.

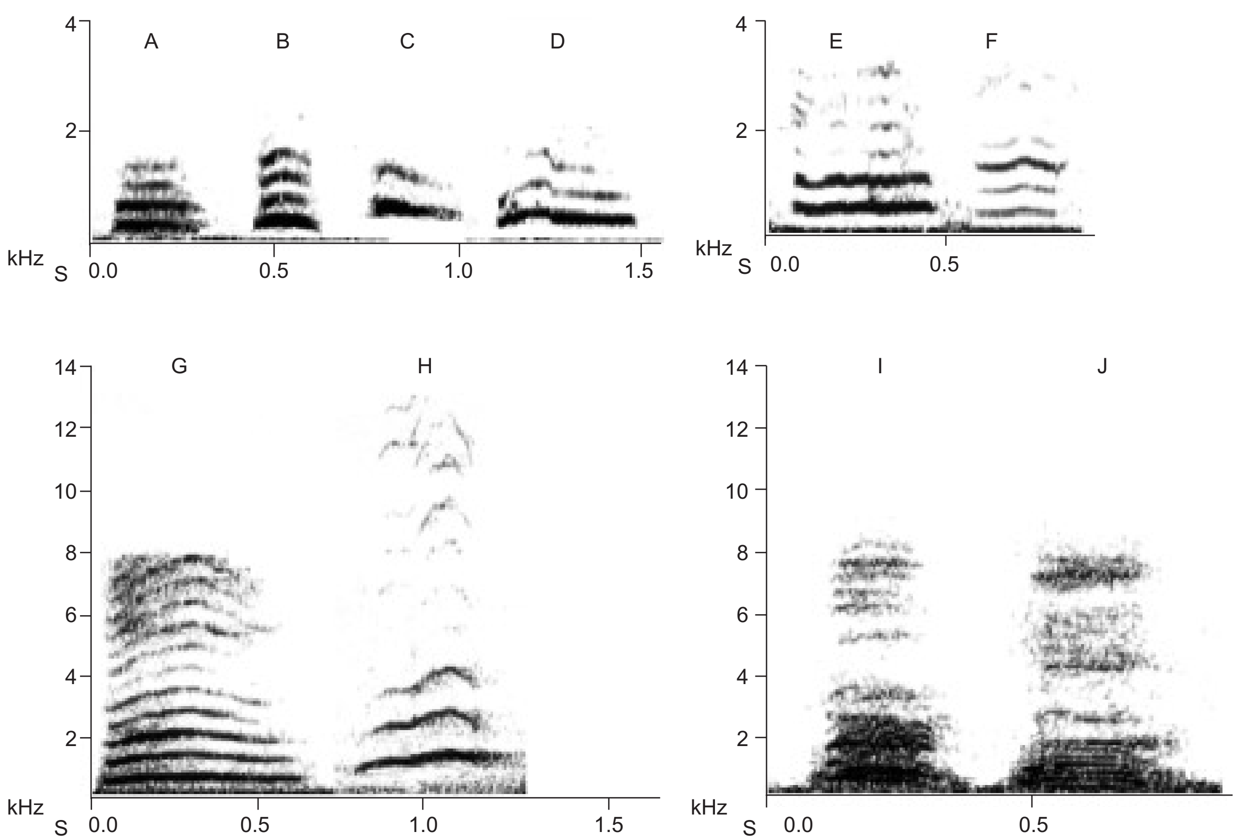

Fig. 2. A-D: Contact coos. A: a contact coo with low modulation from an adult female before her movement; B: frequency modulated contact coo of an adult female directed towards her infant; C: a juvenile male during affiliative approach. D: adult female before group movement. E-F: Isolation coos. E: infant (age class II) ignored while its mother fell asleep; F: isolated infant (age class I) during agonistic interaction; G-H: Long distance coos. G and H: a juvenile male and an infant (age class II) while isolation from the main group; I-J: Cohesion coos. I: a juvenile female in response to human calls. J: an adult female helping an infant to look for its mother.

(ii) Isolation coo. Only infants and juveniles uttered this type of call when they had lost physical contact with their kin. The youngest individual recorded making this call was a 5-wk-old infant. Infants and juveniles emitted this call when they were ignored or when being weaned by their mothers. It was usually accompanied by hacks, clucks, and weeping.

(iii) Long-distance coo. This call is tonal or composed of compound units characterized by a high, rising, well-modulated fundamental frequency, and high sound pressure (Fig. 2G, H). All age and sex classes with the exception of adults uttered this call. This call was uttered when an immature animal had lost visual contact with its mother or the main group. It was usually accompanied by visual orientation and locomotive activity.

(iv) Cohesion coo. This call is composed of mixed units characterized by low, extremely close harmonic frequency bands superimposed on a noisy portion (Fig. 2I, J). All age and sex classes with the exception of infants uttered this call, mainly during arousal states such as the appearance of an expected feeder, during an inter-group agonistic encounter, when an isolated infant was searching for its mother, and when contact with group members had been lost. During group dispersal, dominant females emitted this call, apparently to increase group cohesion.

According to the univariate test statistics, the acoustic features of these 4 types of coos significantly differed ($p < 0.001$) in FF ($F_{3,578} = 198.48$), MFF ($F_{3,578} = 64.67$), RF ($F_{3,578} = 165.32$), PF ($F_{3,578} = 84.87$), and duration ($F_{3, 578} = 87.49$). The average PF of a contact coo was 0.44 kHz (± 0.17), significantly lower than that of the other 3 types (0.72~0.80 kHz, Table 2). Modulation of the fundamental frequency of the long-distance coo (0.33 ± 0.13 kHz) was significantly higher than for the other types of coo calls (Duncan's multiple range test, $p < 0.05$, Table 2). The mean RF of the long-distance coo (8.26 ± 3.21 kHz) and that of the cohesion coo (8.45 ± 3.04 kHz) were similar (Duncan's multiple range test, $p > 0.05$), but both were larger than that those of the contact and isolation coos ($p < 0.05$). The average duration of the contact coo was the shortest (0.26 ± 0.11 s), while that of the long-distance coo was the longest (0.43 ± 0.11 s). However, there was no difference between the average durations of the isolation coo (0.32 ± 0.13 s) and cohesion coo (0.33 ± 0.10 s, $p > 0.05$).

Canonical discriminant analysis of the remaining principal components indicated 3 functions differentiating the 4 types of coos. The 1st 2 canonical functions accounted for 95.5% of the eigenvalue cumulative proportion. The plot of the 1st 2 canonical functions indicated that although all types of coos presented statistically significant differences, this could not be ascribed to a simple pattern of 1 function (plots of the remaining functions followed the same general pattern as in Fig. 3). The squared Mahalanobis distance betweens any 2 types varied from 11.82 (isolation coo and cohesion coo) to 3.88 (contact coo and isolation coo); all distances significantly differed ($p < 0.001$). The squared distances between the cohesion coo and 2 other types (isolation coo and long-distance coo) were relatively far away, respectively, at 11.82 and 7.71.

Greeting call

All age and sex classes uttered this type of call. Three types of greeting calls were distinguished. An atonal greeting was given by a

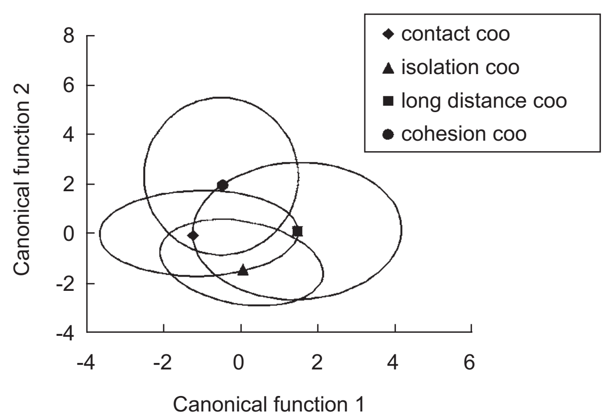

Fig. 3. Scores of first two canonical functions obtained from the canonical discriminant analysis of four types of coo calls. Each circle indicated 95% confidence ellipse of a mean of each type of coo calls obtained from the analysis.

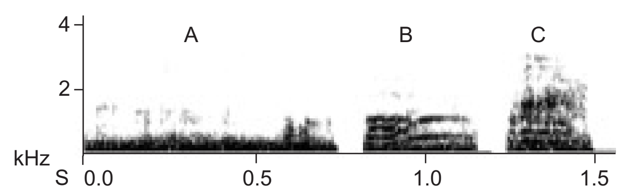

Fig. 4. Greeting calls. A: a series of atonal greeting from an adult female who join a subgroup in which infant present. The noise background at approximately 0.33 kHz should be ignored. B: juvenile male during affiliative approach while troop was reuniting. C: infant male during affiliative approach before mounting.

female approaching other females with infants (Fig. 4A). A tonal greeting was uttered by all age and sex classes except infants (Fig. 4B). A subordinate individual would emit a tonal greeting when approaching dominant peers for interactions such as playing, moving, and foraging. A Girney greeting is a variable, but predominantly tonal sound of low frequency (< 2 kHz) that is superimposed on short, atonal segments resulting from tongue or lip movements (Fig. 4C). This call was uttered when a monkey approached a dominant individual. It was followed by submissive behaviors such as huddling, embracing, grooming, mounting, eyebrow flashing, or lip smacking.

Female copulation call

This call is a rapid succession of phrases, composed of from 4 to 69 units (24.5 ± 17.5 units, n = 23), which was exclusively emitted by adult and subadult females during copulation. Each unit consisted of a narrow noise beam (the structure of a non-tonal vertical striation) in which energy was emphasized at the baseline as well as at 3.47 ± 0.58 kHz (n = 556, Fig. 5A). The typical temporal organization of the phrasestarted quietly and was separated by greater intervals and then became louder and rhythmically pulsed in rapid succession.

Not all females emitted this type of call during copulation. During 1999, 73 copulations were observed, among which this call occurred in 51 cases. The emission rate was close to 70%. They often emitted this call in the last part of the copulation, and it usually continued even after the physical contact with the male companion had been broken.

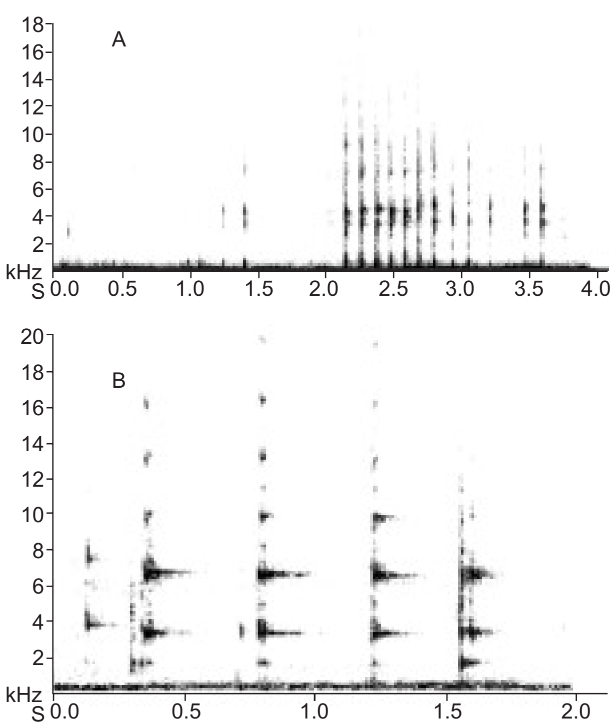

Fig. 5. A: Female copulation calls, a phrase of female copulation calls given by an adult female irregularly started in the last part of the copulation and more rhythmically lasted longer than the physical contact with the male. B: Male copulation calls, produced by an adult male with 5 compound units. The noise background on the base should be ignored.

Male copulation call

Male copulation calls with tonal units were seldom uttered, but were unique to adult males during copulation. Whistle-like sounds were uttered in irregular trains or well-structured phrases containing up to 4 pulses. The units consisted of 4~7 discrete frequency bands (from 1.5 to 19.5 kHz) with low degrees of modulation (Fig. 5B). In contrast to females, males emitted copulation calls significantly less frequently (X^2 = 54.36, df = 1, p < 0.001); the emission rate was 6.8% (n = 73). During mating, the head of the male was held forward with its face towards the female. At this stage, the female often turned upward and/or pulled the shoulder of the male by exposing her teeth. The male's face occasionally was so close to the female that its mouth would touch her face. During emission, the lips of the male were parted, but its jaws were always closed.

Mounting grunt

These grunts were irregular trains of short

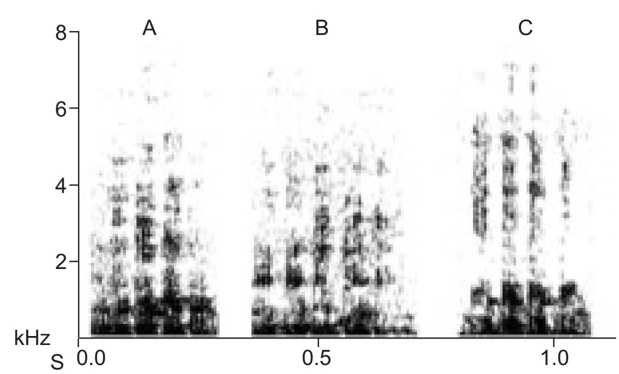

Fig. 6. Mounting grunts. A and B: given by alpha and beta male respectively while they attempted to mount. C: given by an adult male while being mounted by a sub-adult male.

and noisy pulses, with an additional frequency band at approximately 1.2 and/or 3 kHz (Fig. 6). Only adult males produced these calls in connection with affinitive mounting of another adult or subadult male. Typically, after a dominant male revealed an affiliative expression (i.e., gave a grunt or lip smacking) toward a subordinate male, it would induce the production of atonal greeting calls from the subordinate and the occurrence of affiliative mounting of the male peer. At this time, a train of mounting grunts was uttered.

Alarm call

A single unit of the alarm call is composed of 2~3 narrow non-tonal segments. The segmental structure contained discrete, irregularly modulated frequency bands and was preceded by a comparatively short non-tonal element (Fig. 7). The alarm call was produced by all age classes; the youngest animal seen to produce it was a 3-mo-old male infant. This call is highly intensive, consisting of plosive utterances with a wide noise-like frequency range.

The alarm call was given for various reasons such as (1) while being chased or attacked by stray dogs, (2) when solders in military uniform approached (parts of the study site is still a restricted military base, and solders occasionally disturb the monkeys), (3) when visitors approached with walking sticks, slingshots, and stones (people occasionally harass the monkeys by chasing them, throwing stones, or using slingshots), (4) when people carried large objects such as bicycles, construction materials, etc., and (5) when monkeys sighted raptors in the area. As soon as the alarm call was produced, the group reacted by fleeing or stopping all activities. They scanned the area and in the direction of the alarm call to locate the possible source of the threat. Alarm calls were also produced during inter-group conflicts, especially when intruder males were seen near social groups.

Grunt

All age/sex classes commonly produced these calls. Each unit was composed of 2~4 non-tonal or mixed segments with energy concentrated at the base (< 600 Hz). Due to different contexts, modulation of the frequency range in each segments was from the baseline of the sonogram to 2~16 kHz. These calls were used in 4 contexts. (1) When groups began to move, monkeys exchanged these calls while visually scanning the area and group members (Fig. 8A). (2) This call was given while approaching or being approached by an unrelated group member. Also, high-ranking individuals emitted this call to gain physical contact, mainly grooming, from low-ranking peers; the low-ranking individuals responded with grunts or greeting calls and rushed to initiate physical contact. (3) This call was given during female-infant (non-mother) interactions. When a female attempted to reach an infant in order to groom, hold, and care for it, she would produce this type of call toward the infant who was in close contact with its mother (Fig. 8B, C, E). (4) This call was given when being fed by humans.

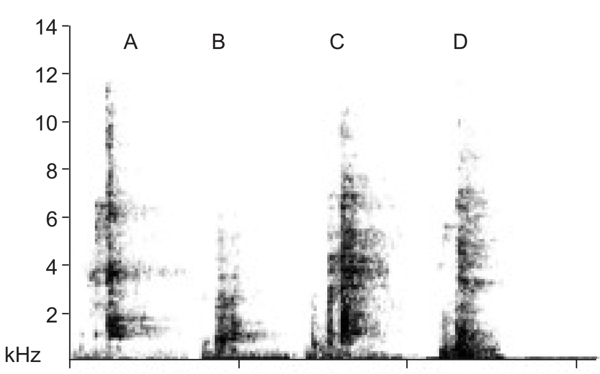

Fig. 7. Alarm calls. A: infant (age class II) towards visitors near their resting area. B and C: sub-adult female and male, respectively, towards dogs. D: adult female while human harasses.

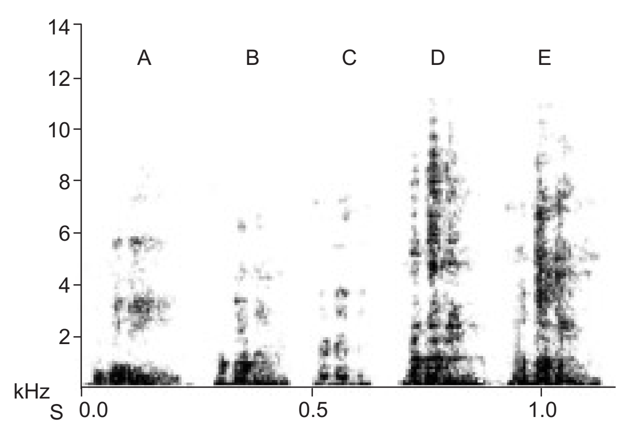

Fig. 8. Grunts. A: an adult female during group movement. B: an adult female while approaching another female with infant. C: sub-adult female emitted toward the mother while the mother of the isolated infant appeared. D: juvenile male while reunited with the group. E: juvenile female while attempting to approach a female with infant.

Threat rattle

These rattles consist of temporally segmented 3~6 non-tonal or mixed units with longer-period amplitude modulation, which appear as bursts or pulses (Fig. 9). The frequency range of each segment was from the baseline of the sonogram to 8~16 kHz and had a duration of 0.4~0.45 s (Fig. 9). Moreover, some contained discrete, irregularly modulated frequency bands whose energy was concentrated at approximately 2.82 kHz (± 0.7, n = 21) and showed little baseline energy. All age and sex classes except infants younger than 7 mo uttered this type of call during intra- and inter-group agonistic interactions as well as during inter-species interactions involving people and birds. The calls were accompanied by facial expressions of open-mouth threats. With increasing intensity, the spectrogram changed in that the microscopic pulsation was lost and the proportion of energy at the baseline increased. When the intensity and probability of an attack increased, the fine segmentations diminished and the energy at the baseline predominated, forming a growl.

In contrast to grunts, threat rattles are characterized by their longer duration, wider frequency range, and higher PF. There were statistically significant differences in FF, MFF, PF, and duration among the alarm calls of grunts and threat rattles (Duncan's multiple range test, df = 2, 652, p < 0.05), whereas no difference in the RF between alarm calls and threat rattles was noted (p > 0.05, Table 2).

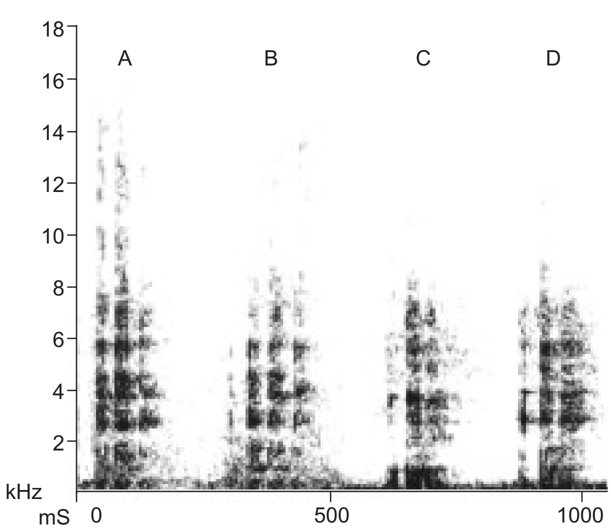

Fig. 9. Threat rattles. A-D: recorded from two adult females emitted respectively while visitors near their resting area.

Growl

Growls consist of non-tonal or mixed units predominantly uttered by high-ranking females and males during agonistic inter- and intra-group encounters. In some cases, the calls were uttered in rapid succession, forming a phrase. This call is characterized by its predominant baseline energy. Modulation of the frequency range of each unit was from 1 to 16 kHz, and the duration was 0.1~0.2 s (Fig. 10). This vocalization was never recorded in infants younger than 7 mo. Whereas threat rattles were given during mild and moderate threats and within standoffs, growls were usually produced during intense threats or attacks. Dominant individuals emitted growls when lunging or chasing. The opponents involved were chased and mauled when caught. These even lasted until an attack was finished: dominant individuals were seen staring and producing growls and/or rattles towards the subordinate individuals on occasion.

Vibrato growl

The vibrato growl is composed of several close, narrow frequency bands superimposed on a noisy overlay (in a frequency range of from 1 to 16 kHz) with a duration of 0.04~0.52 s (Fig. 11). This call was uttered by all age and sex classes during agonistic intra- and inter-group and interspecies encounters. When tourists harassed the monkeys or when other monkeys (of the same or a neighboring group) harassed them, these calls were produced and were accompanied by open-mouth

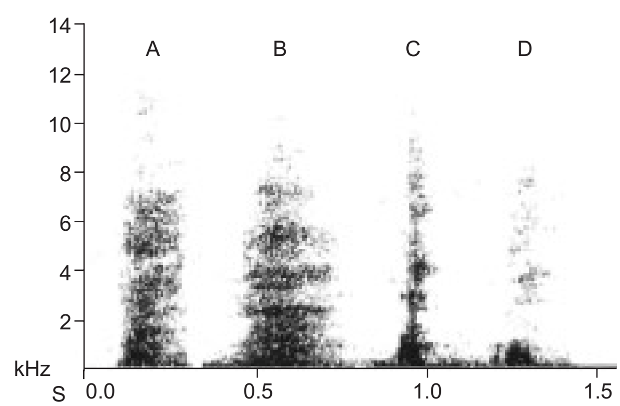

Fig. 10. Growls. A: produced by an adult male towards an invading male. B: given by an adult female towards a juvenile male within the same group. C and D: given by a juvenile and a sub-adult female respectively towards dogs.

threats. Growls and/or threat rattles preceded these calls, and the spectrogram revealed transitional forms betweens these 3 basic patterns. Therefore, the vibrato growl was used in the beginning when the animal that produced the call approached its target (a human or monkey) in order to attack it. The duration of the bout of calls depended on the reaction of the receivers.

Roar

Units of roars were similar to growls, but roars were given in a series with sequentially decreasing intensity and intervening sounds of inspiration of air (Fig. 12). Adult and subadult males and adult females roared in agonistic threats in both intra-or inter-group encounters. Roaring accompanied by the tree-shaking display was typical of an adult male who was engaged in a fight, or who had been disturbed or interrupted during sexual solicitations.

Bark

Barks are intense, plosive, non-tonal units with prolonged energy emphasis at a relatively low 1.18 kHz (±0.37, n = 20, Fig. 13). Adult and subadults of both sexes barked during interspecies aggressive conflicts with dogs or birds and also during inter and intra-group agonistic encounters. They were uttered separately or in short phrases predominantly by adult and subadult males and females. The bark was uttered during interspecies aggressive conflicts (i.e., with dogs and birds) and during inter and intra-group agonistic encounters. On 5 occasions when monkeys saw a Gray Treepie (*Dendrocitta formosae*) near the resting or feeding area, adult females emitted barks and growls toward the birds, and as a result, the birds flew away. However, the average peak frequency of the bark was significantly higher than that of the growl (Wilcoxon rank test, $p < 0.005$).

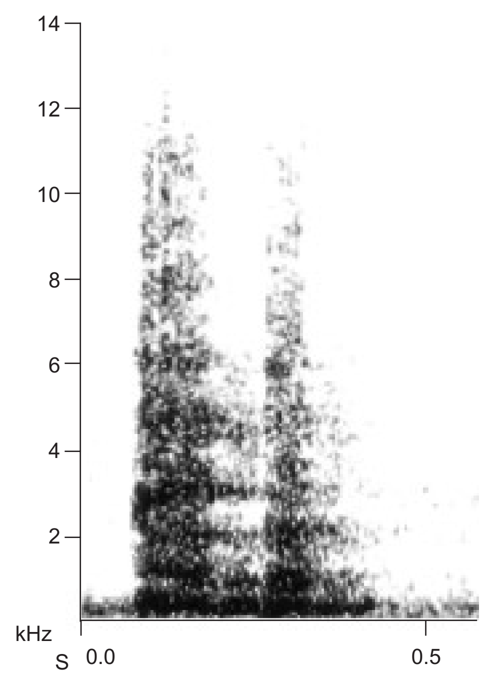

Fig. 12. Roar. Two units of decreasing intensity and two intervening loud inspirations, given by adult male during intra-group agonistic interactions.

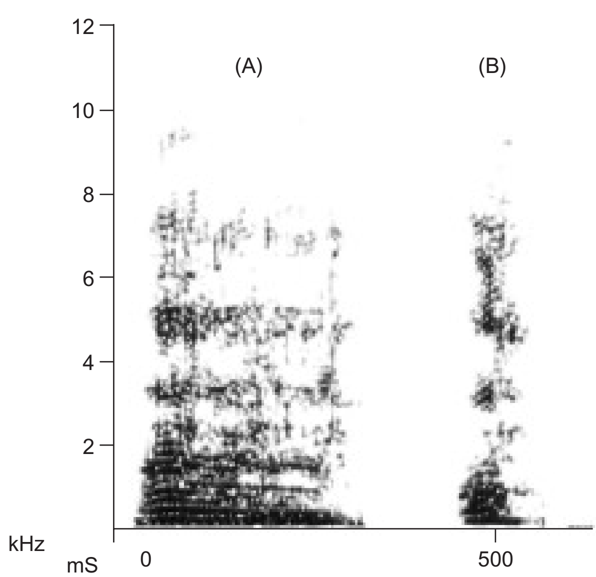

Fig. 11. Vibrato growls: given by a sub-adult female (A) and a juvenile female (B) when disturbed by a visitor.

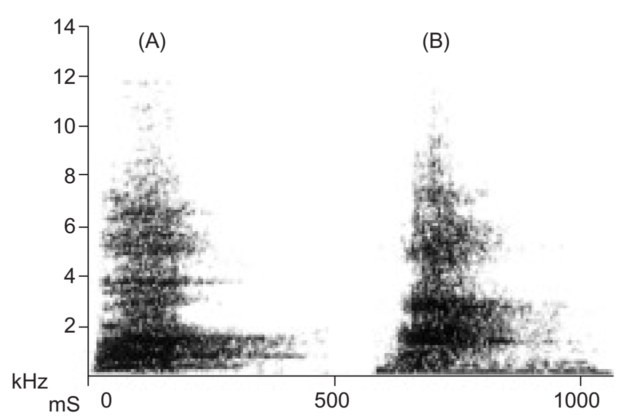

Fig. 13. Barks: given by an adult male (A) and adult female (B) toward a possible bird-of- prey.

Squeal

Squeals are tonal, compound or mixed units with well-modulated, harmonic frequency bands (Fig. 14). The unit of a squeal is composed of well-modulated, harmonic frequency bands with a range of 4~16 kHz and superimposed on or attached to noise beams during long-duration ranges of from 0.2 to 1.1 s (Fig. 14). All age and sex classes produced this call during intra and inter-group and interspecies agonistic interactions, i.e., in response to threats from high-ranking peers, monkeys from other groups, and dogs. In addition, infants would emit this call accompanied by violent spasmodic motions and then run to their mother for protection. Moreover, infants and young juveniles gave this call when they had lost contact with their mother and/or the main group. It was frequently combined with several coo calls and sometimes changed into a scream.

Noisy and undulating screams

These calls were recorded from individuals in all sex and age classes in response to threats, attacks, or maltreatment by dominant or older individuals. The energy distribution and duration of noisy screams varied considerably, ranging from narrow beams with plosive onsets to prolonged segments with gradually increasing energy (Fig. 15A, B). The main energy was often concentrated in a medium frequency range (4.04 ± 1.89 kHz, n = 129).

The units of undulating screams were characterized by discrete, irregular, and slightly modulated harmonics (with the mean modulation of harmonics of 0.24 kHz). As in noisy screams, the duration and energy distribution varied to a large degree (Fig. 15C, D). In a number of recordings, the tonal arrangement was marginal, the discrete harmonics were fading, and frequencies were more-evenly distributed. Usually, the sound lasted until the victim fled the area. The transition gradually emerged (frequently between the onset and cessation of a single unit), leading from the noisy

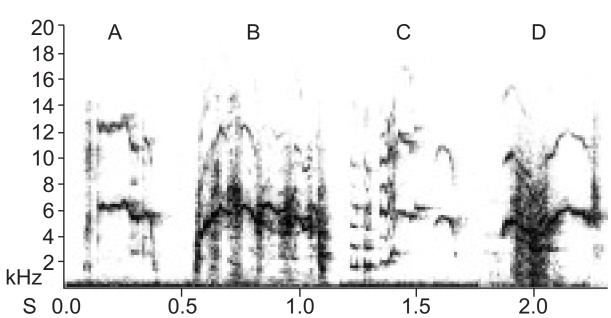

Fig. 14. Squeal. A: produced by juvenile female when she was attacked by an adult female. B: produced by an adult female during group encounter. C: given by an infant when the group was near dogs. D: given by an infant female when she lost contact with her mother.

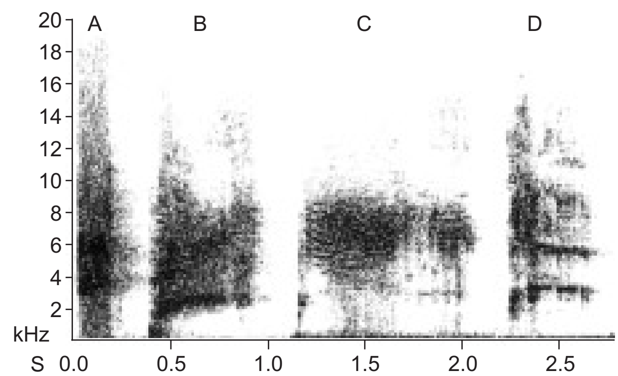

Fig. 15. Noise and undulated screams. A and B: Noise screams given by an infant male and an adult female when they were chased, attacked and threatened by other members. C and D: undulated screams. C: given by a juvenile female when she was bitten by an adult female. D: given by infant female while weaning and physically abused.

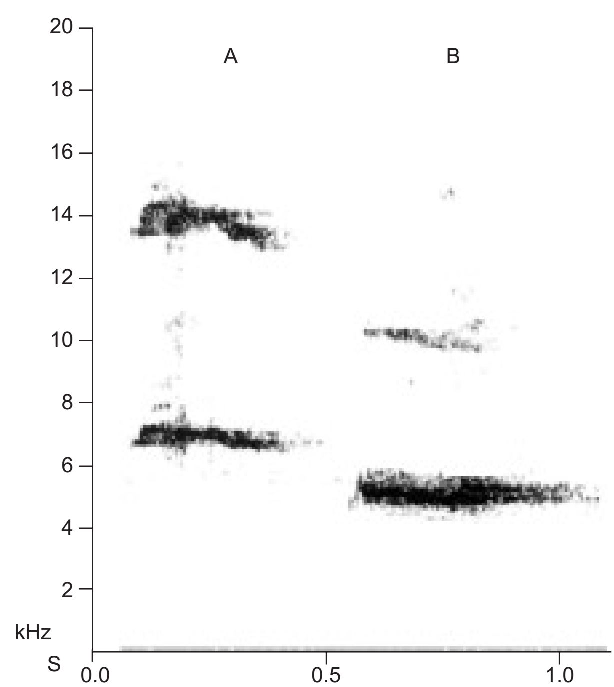

Fig. 16. Tonal screams. A: given by an infant when trying to locate its mother. B: by a juvenile male when he was threatened by an adult female.

scream to the more-tonal undulating scream.

Tonal scream

Tonal screams exhibited intergradations between squeals and tonal squeaks. In contrast to squeals, tonal screams consisted of 2~3 harmonic frequency bands with rarely a noisy portion (Fig. 16), and of a comparatively longer duration (from 0.3~0.6 s) than tonal squeaks. Sometimes, one was composed of 2 or 3 tonal squeaks that were combined with a short gap or a collapse. All age and sex groups except adult males uttered this call during inter- and intra-group agonistic encounters as well as when one had lost contact with its mother or the main group. However, these calls were also uttered when peers reunited or sighted a feeder.

Squeak

Squeaks are plosive, tonal or compound sounds of a high pitch (> 4 kHz) and short duration (< 0.3 s), emitted during social arousal and in defensive withdrawal (Fig. 17). Two types of squeaks were distinguished: tonal squeaks are composed of discrete, well-modulated frequency bands that follow a noisy burst (Fig. 17A-C), while compound squeaks have discrete, well-modulated frequency bands and are superimposed on or attached to a noisy portion (Fig. 17D-F). All age and sex classes emitted these 2 types of squeaks, except no tonal squeak was recorded from adult males. During agonistic interactions, victims would usually withdraw by producing a phrase of a compound squeak and/or a compound hack, and this might be followed by tonal squeaks. When subordinate monkeys were supplanted by dominant ones or by approaching people, they would utter a squeak, accompanied by showing their teeth and crouching on the ground or moving away. In the mating season, adult females produced squeak calls when dominant males directly approached them for mating. An infant would also utter this call when separated from its mother, or when it approached its mother who was preoccupied with its mate; the male would either push or threaten the infant to shoo it away.

The acoustic structures and utilization of these submissive calls (including noisy and undulating screams, squeals, tonal screams, and squeaks) depended on the existence of physical contact during aggressive interactions. Noisy and undulating screams were mostly given in physically aggressive interactions (68%, 36 of 53 cases) whereas squeals, tonal screams, and squeaks were mostly given in non-physically aggressive interactions (76%, 123 of 163 cases).

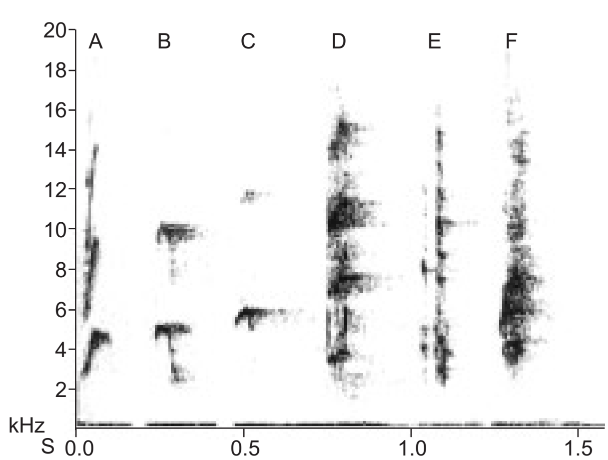

Fig. 17. Squeaks. A-C: tonal squeaks. A: produced by an infant who it didn't get food. B: given by an adult female when she was chased by others. C: given by an infant while ignored by mother. D-F: compound squeaks. D and E: given by 2-years-old juvenile female and an infant male respectively when they were attacked (the peak frequency of 'E' at 10.25 kHz). F: given by an infant when ignored by its mother.

Chuckle

The structure of chuckles was similar to that of food yells, but with a lower pitch (Fig. 18). The units of chuckles consist of discrete, ascending, modulated frequency bands that are superimposed on noisy segments of low energy. All age and sex classes uttered this call in connection with agonistic intra- and inter-group interactions. The behavioral sequences involving chuckles were characterized by the regular alternation of agonistic signals (vocal and visual), directed against an opponent,

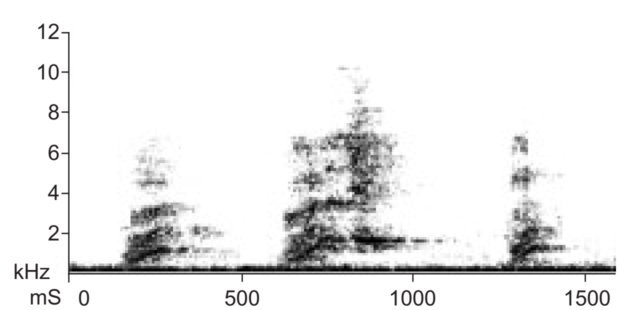

Fig. 18. Chuckle: three units of "chuckles" given by an adult female when she confronted an invading male.

with submissive signals of chuckles toward high-ranking group members, similar to the protect threat described by Kummer (1967). Chuckles often occurred in combination with noisy and undulating screams.

Harmonic arch

Based on the acoustic structure and context of the emission, 3 types could be identified. (1) Food yells (Fig. 19A-D), consisted of harmonic frequency bands of with an arched shape, which was superimposed on the noisy portion. These calls only occurred during the appearance of a feeder. (2) The oui (Fig. 19E), type showed such an abrupt upward shift of pitch that the tracing is vertically displaced with an apparent discontinuity. In some cases, it was superimposed on a noisy segment. These calls were heard at the appearance of feeders as well as when reuniting with the main group or with a mother. In addition, it was also heard from a 1-yr-old female rushing to reach its mother in response to the contact coo of mother during group movement. (3) The harmonic arch (Fig. 19F) exhibits a rising pitch. The additional energy is evidenced either as a burst of noise crossing the tonal band or sudden enrichment of the overtone structure. This call occurred not only when monkeys reunited as well as at the appearance of feeders, but also during inter- and intra-group agnostic interactions.

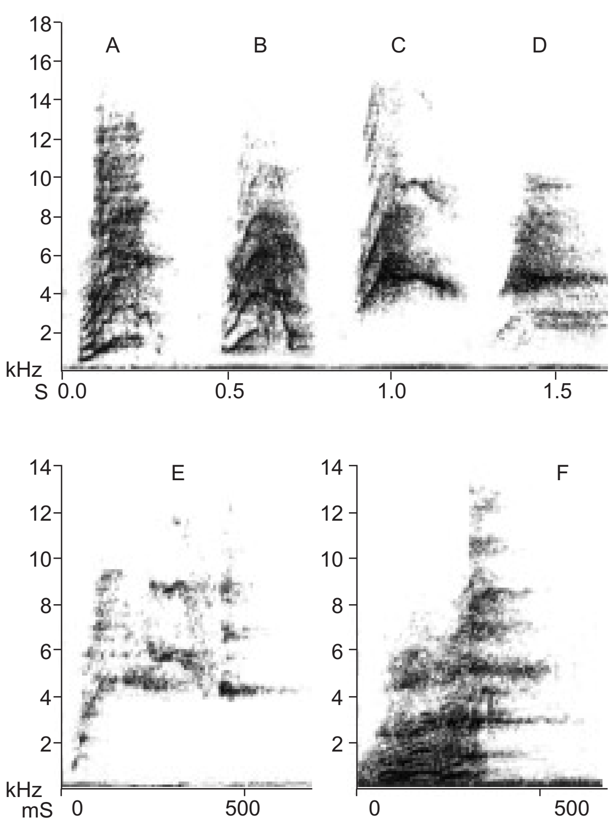

Fig. 19. Harmonic arch. A-D: food yells given by adult females when feeder appeared. E: Oui, given by a juvenile male when feeder appeared. F: Harmonic arch, given by a sub-adult male when reunited with the group.

Hack

Based on the structural features, 2 types of hacks were recognized. The tonal hack consists of discrete frequency bands with a sharp negative slope (Fig. 20A-D). The fundamental frequency was characteristically at 0.7~1.3 kHz and had an extremely short duration (of approximately 0.03 s). The compound hack is a tonal element superimposed on, attached to, or masked by noise. In some samples, a narrow noise beam preceded the compound unit (Fig. 20E-H).

Hacks were produced by all age/sex classes, but mostly by infants. When mothers rejected them, infants produced this call in an effort to resume physical contact. Subordinate individuals produced these calls in response to rejection attempts to achieve physical contact, or maltreatment from dominant peers. In states of high arousal, it was accompanied by spasmodic motions and specific facial expressions (i.e., the bared-teeth gecker face). Tonal and compound hacks were mostly used in the contexts of young

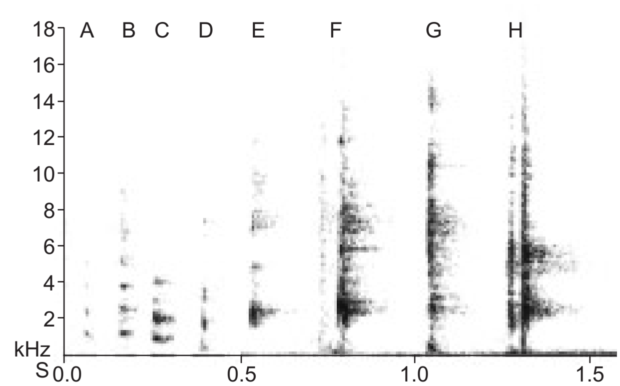

Fig. 20. Hacks. A-D: tonal hacks. A, B and D: given by infant (age class I) who were alone, ignored. C: given by infant (age class II) while being rejected. E-H: compound hacks. E and F: given by the same infant male (age class II) while being threatening (peak frequency 2.45 kHz). G: given by infant female (age class II) while weaning (peak frequency at 2.75 kHz). H: given by infant female (age class I) while being ignored (peak frequency at 2.45 kHz).

being weaned, rejected, isolated, or ignored by their mother (48.3%, 85 of 176 cases), followed by intra-group physically aggressive interactions (12.5%) and non-physically aggressive interactions (11.4%).

Squawk

Squawks contain a predominance of harmonic frequency bands, and are a plosive, bark-like vocalization, but with a higher fundamental frequency range of 0.8~1.5 kHz (Fig. 21). These calls were used during defense, i.e., when an animal had been supplanted or had withdrawn from the approach of a dominant monkey or which was cringing at its approach. Also, these calls were emitted when macaques were ignored during food begging. This call was emitted predominantly by infants, followed by juveniles, and was occasionally heard from adult females.

Cluck

Clucks are short-duration (0.04~0.06 s) tonal or compound units composed of 1~4 slightly modulated harmonic frequency bands ranging from 0.5 to 5.8 kHz (Fig. 22). Clucks were predominantly emitted by infants (85.7%), with a few from juveniles, when isolated from the group, or ignored or rejected by their mother. Clucks were also recorded during group movements since infants often had difficulties in keeping up with the movement of the troop. A motherwould sit in proximity to her infant but would disregard it until the infant had emitted a gecker and scream, and then the mother would rush to carry the infant. Clucks were emitted when food begging was ignored, and ceased after monkeys received some food. Moreover, in some cases, they were combined with noise screams or coo calls.

Gecker

The units of the gecker call were of poor tonal quality, uttered in staccato-like phrases and exclusively by infants with 1 exception from juveniles. A unit of the gecker call consists of 2~4 modulated frequency bands with a descending tendency (Fig. 23). In contrast to the tonal hack, the lower fundamental frequency of a gecker is characteristically at 0.45~0.6 kHz. Gecker calls were predominantly emitted by infants (90.1%), and a few by juveniles.

An infant would usually utter gecker calls when its mother neglected or rejected its attempts to gain physical contact. It was also a response to a mother’s sudden locomotive activities, when she did not hold her infant, resulting in the infant seemingly about to lose physical contact with its mother. At that time, the infant would produce the gecker call, with the result that its mother would immediately grasp it firmly. The gecker call usually stopped after the mother resumed physical con-

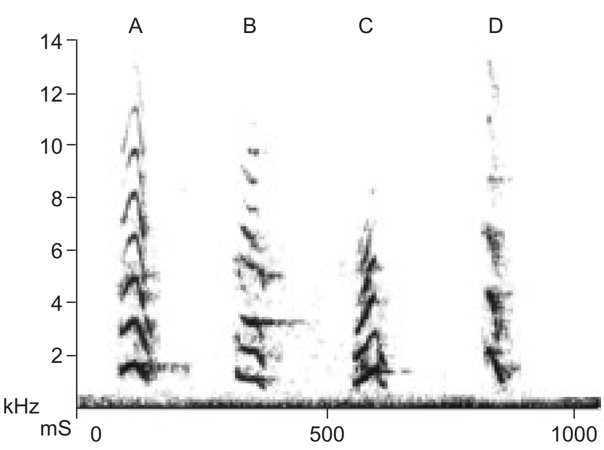

Fig. 21. Squawks. A and B: given by infants (age class I) while didn't get food. C: given by a juvenile male while being threatened. D: given by an infant (age class I) while mother ignored.

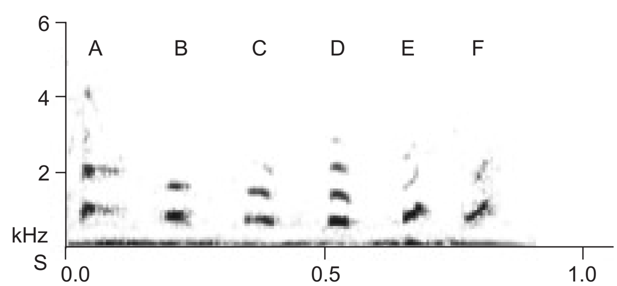

Fig. 22. Clucks. A-F: given by infants (age class II) while being rejected, weaned, and ignored respectively.

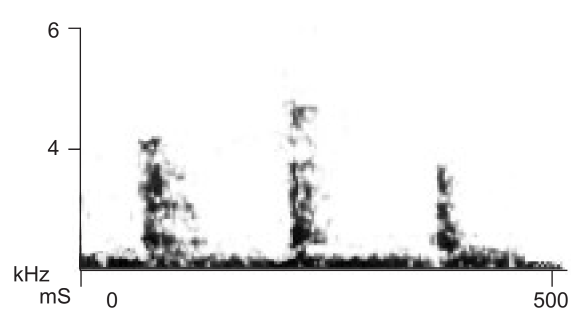

Fig. 23. Three units of “Gecker” given by an infant (age class I) during distress because its mother and another female embracing.

tact. Moreover, infants also gave the call in response to a rough pull from other females or other unspecific disturbances. In addition, this vocalization was accompanied by violent spasmodic motions and a submissive facial expression (e.g., bared teeth).

Whine

Each unit of a whine is composed of several warbled harmonic frequency bands of rich modulation and was occasionally superimposed on or attached to noisy segments (Fig. 24). The duration range of a unit is from 0.12 to 0.7 s, and the maximal frequency band is approximately from 2 to 4 kHz (Fig. 24).

These calls were recorded from infants II when aroused and agitated, particularly after weaning, or from female juveniles who were lost or had been abandoned by their mother. It was given as an infant once again came into affiliative contact with its mother, i.e., at the mother's chest.

Weeping

The isolation coo was segmented by lapses of vocal output which formed a weeping call. Only infants and juveniles uttered this type of call. The number of segments ranges from 2 to 5. Each unit has a range of 0.6~1.2 kHz during 0.4~0.6 s (Fig. 25A). The tonal units of weeping were emitted by infants (classes I and II) to get attention or physical contact as is typical of the stage of weaning. It was often followed by isolation coos, hacks, and/or squeaks in this period. Frequently, a cluck or tonal hack was combined with a weeping call.

A 6-mo-old female infant wept and looked towards its mother when the mother continued sleeping and rejected several of its approaches. In addition, she also produced gecker calls, squeaks, and squeals together with the weeping. That induced another adult female to approach.

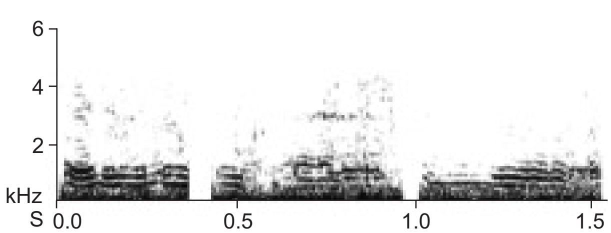

Fig. 24. Whine. A series of "whines" given by an older infant female (age class II) after a wean tantrum. The noise background at the base should be ignored.

Babble

Babbles are soft, mild tonal units occasionally uttered exclusively by infants of both sexes (Fig. 25B). This call was connected with the process of independent exploration. It was also directed towards the mothers or another member when it was attempting to leave an infant, or when infants saw an adult male appear in the area.

DISCUSSION

Formosan macaques use 25 basic patterns of vocalizations in different contexts, and these are comparable to the reported vocal patterns of other species in the genus *Macaca* (Green 1975, Gouzoules et al. 1984 1998, Hohmann and Herzog 1985, Dittus 1988, Hohmann 1989, Bauers and de Waal 1991, Hauser 1991, Palombit 1992, Fisher et al. 1998). Assessment of the vocalizations of Formosan macaques demonstrates a high symmetry early in life. Except for the sex-specific copulation calls and mounting grunts, male and female Formosan macaques shared almost the entire repertoire.

Communication systems can be distinguished on the basis of whether signals within the repertoire are discrete or graded (Marler 1977, Hammerschmidt and Fischer 1998, Fischer and

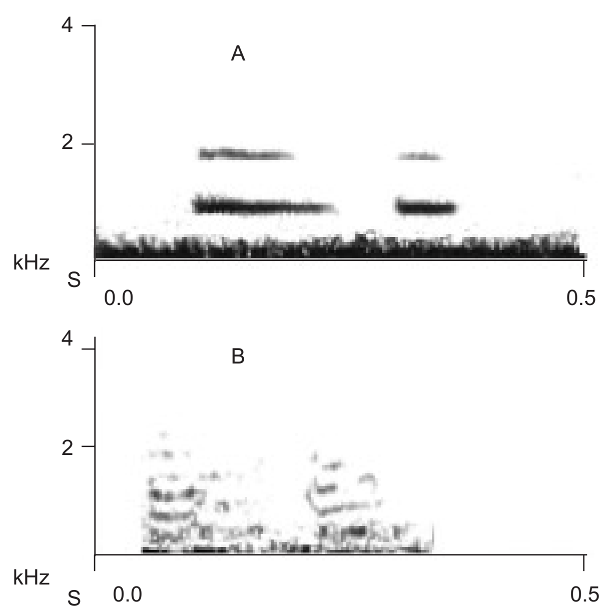

Fig. 25. A: weeping, consists of two tonal segments, given by an infant (age class I) as ignored by its mother. B: two babbles of a female infant (age class I).

Hammerschmidt 2002). The discrete signals of Formosan macaques include calls such as coos, greetings, grunts, mounting grunts, male and female copulation calls, weeping, whines, and babbles, for which alternations of the structural features were restricted and transitional forms between call types were rare or absent. The graded signals were aggressive calls (threat rattles, growls, barks, and alarms), submissive calls (screams, squeals, and squeaks), and distress calls (squawks, hacks, clucks, and gecker calls). Green (1981) reported a vocal repertoire composed of discrete and intergraded patterns for lion-tailed macaques. Similarly, in bonnet macaques, Hohmann (1989) recorded vocalizations with variations in physical parameters on a large scale that led to structural intergradations between different elements of the repertoire.

Vocal repertories composed of intergraded signals may be expected to have evolved among those species with ready visual access to each other (Marler 1976 1977). Intergradations are supposed to be more frequent in species less dependent on audible signals for their social regulation (Fischer et al 1995, Fischer and Hammerschmidt 2002). However, most primate repertoires are neither completely graded nor consist completely of discrete signals, but are characterized by mixtures of graded and discrete signal structures (Green and Marler 1979). Therefore, structural criteria alone are insufficient to comprehensively assess and characterize the vocal repertoire. Earlier studies of primate vocalizations showed minor differences in certain parameters (Green 1975, Snowdon and Pola 1978, Masataka 1983, Dittus 1984 1988) which may serve to transmit different types of information, either about the internal state of the vocalizer or external factors such as the presence of food or a predator (Hohmann 1985).

Looking at the correlations between acoustic signals and the behavioral contexts, some of the calls, namely copulation calls and alarm calls, were clearly related to particular interactions or specific external stimuli. Concerning the context of emission, coo calls, greetings, and grunts, can be summarized as affinitive contact calls for reduction of distance and/or maintenance of close proximity among group members. The growls, threat rattles, and vibrato growls were uttered by dominant animals to intimidate sub-dominate group mates, and members of other groups or other species.

In spite of the significant structural differences in the submissive calls, correlations between the acoustic structure and social context were less clear. Playback studies of rhesus macaques revealed that distinctively structured screams reflect the level of arousal of the caller and have been significantly associated with specific social factors (Gouzoules et al. 1984 1998). In the present study, the noisy screams and undulating screams were given during severe agonistic interactions leading to physical aggression, while squeals, tonal screams, and squeaks were given during agonistic interactions without physical aggression.

When infant and juvenile Formosan macaques are in trouble, they produce screams, squeals, squeaks, and alarm calls that attract the attention of kin-related individuals. In many species of primates, mothers can identify their offspring using vocal cues, and vocal recognition of infants and juveniles, especially their distress calls, is advantageous in primate groups when mothers can reduce the risk their offspring face (Maestripieri 1994, Cheney and Seyfarth 1990). In Formosan macaques, screams and squeals appeared to acquire or gain support from group mates to form an agonistic alliance, and distinct structural submission calls may function in ally recruitment as a key element of social tactics rather than in indicating the emotional state of the vocalizer as reported among rhesus macaques (Gouzoules et al. 1984).

On the other hand, the acoustic structure was obviously influenced by the context of emission. The fundamental frequency of the call used in submissive contexts was generally low, and in aggressive contexts, the fearful individual produced a significantly higher fundamental frequency than did the aggressive individual. The data support the motivation-structure rule suggested by Morton (1977) using published materials on birds and mammals.

Alarm calls were emitted mostly by subadult males and females. Interestingly, alpha males never gave the alarm call. Conspicuous usage differences in both sexes also occurred in relation to the appearance of a feeder. Adult females and juveniles usually produced tonal screams, food yells, coo calls, and grunts in response to a feeder, whereas adult males exclusively gave grunts. On the other hand, adult males did not use tonal screams, tonal squeaks, or contact coos, but adult females gave these calls. Moreover, certain sounds associated with appeasement and/or submission (e.g., screams, squeals, and squeaks) were not produced by adult males.

Age-specific patterns of utterances of vocalizations are distinct in Formosan macaques. Some calls were produced initially by infants, but later vanished from individuals' repertoires, including the cluck, weeping, gecker call, and babble. Although weeping and gecker calls were heard from young juveniles whose mothers did not have dependent infants, this might have been due to the juveniles' relapse into infancy. Although they were given in the same agonistic context, the tonal vibrato growl used by infants differed from both the harsher, noisy call (i.e., growl) of older individuals, as well as the threat rattle also given by infants. These differences might be associated with the ontogeny of physical development and vocal usage (Hauser 1993).

The most-noticeable differences can be found in coo calls. Barbary macaques appear to lack the coo call but produce structurally different calls in the same context. In Formosan as well as Japanese macaques, there is extensive variation within coo calls depending on changes in the socio-ecological environment. On the other hand, male Formosan macaques do not produce loud calls that are common in arboreal primates such as lion-tail macaques (Hohmann and Herzog 1985), Sulawesi macaques (Muroyama and Thierry 1998), long-tail macaques (van Schaik and van Noordwijk 1985), gibbons (Mitani 1985), mangabeys (Waser 1977), and langurs (Vogel 1973, Hohmann 1991). There appear to be similarities in the vocal repertoire among Formosan, Japanese, and rhesus macaques, and these species are known to be closely related (Cronie et al. 1980, Fooden 1980, Melnik and Kidd 1985). Both Formosan and Japanese macaques inhabit similar habitats with less visual restrictions, which may promote structural variations in vocal patterns by allowing clear visual and vocal communications. Vegetation, humidity, and temperature variations as well as other bioacoustical phenomena were reported to have a decisive influence on the transmission and intelligibility of vocalizations including causing the degradation of acoustic patterns (Wiley and Richards 1978).

This study indicates that Formosan macaques employ a complex vocal system composed of discrete sound classes as well as acoustic categories connected by intermediate gradations. Age-specific differences in their vocal behaviors are more pronounced than are asymmetries between sexes. Certain vocalizations were produced or ceased to be produced by certain sex or age classes, and these differences might be associated with social organization, sexual selection, social suppression, and experience. The vocal repertoire of Formosan macaques reveals similarities to other species within the genus *Macaca*, especially to the closely related Japanese and rhesus macaques suggesting the influence of phylogeny, habitat distribution, and social organization in the evolution of vocal communication. The data presented in this paper on the vocal communication by Formosan macaques can serve as a valuable tool for a further understanding of not only the evolutionary function of vocal communication but also the complex social behavior in this lesser-known primate species.

Acknowledgments: The field study on Formosan macaques at Mt. Longevity was partially funded by the Republic of China's National Science Council through a research grant (NSC 88-2313-B-020-023) awarded to G. Agoramoorthy and M. J. Hsu. We are grateful to Drs. D. Rendall, S. Semple, F. Burton, S. Green and anonymous reviewers for their critical comments on earlier versions of the manuscript. The vocal communication research was basically inspired by S. Gaunt and A. Thompson of the Borror Laboratory of Bioacoustics, the Ohio State University. We appreciate their encouragement and support.

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