

Patterns of Vocal Sharing and Social Dynamics in a Captive Group of Campbell's Monkeys (*Cercopithecus campbelli campbelli*)

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Although vocal sharing is widespread at several phylogenetic levels, few descriptions concerned primates. The present study involved the dynamics of vocal structures and social organization in a captive group of Campbell's monkeys (*Cercopithecus campbelli campbelli*) at 3-year periods, using precise sound recording and comparison. The authors focused on combined harmonic 6 calls, often involved in vocal exchanges and associated with approaches. Each female produced 1 to 4 variants, shared, or not, between individuals. Changes appeared between years in the form of disappearance, appearance, or transformation of variants. There was a decrease in the global degree of sharing over the years. Greater changes were observed after social disturbance. Sharing would be more important in disturbed than stable groups to advertise bonds.

Call or song sharing within groups reflects social affinities in several species of birds (Brown & Farabaugh, 1997; Brown, Farabaugh, & Veltman, 1988; Feeke, 1982; Griessmann & Naguib, 2002; Hausberger, 1997; Hausberger, Richard-Yris, Henry, Lepage, & Schmidt, 1995; Hile & Striedter, 2000; Nowicki, 1989; Payne & Payne, 1997), frog (Gerhardt, Roberts, Bee, & Schwartz, 2000), and mammals (bats: Boughman, 1998; Jones & Ransome, 1993; dolphins: McCowan & Reiss, 1997; Smolker & Pepper, 1999; Tyack, 1993; Tyack & Sayigh, 1997; whales: Ford, 1991; P. J. O. Miller & Bain, 2000; Weilgart & Whitehead, 1997; Yurk, Barrett-Lennard, Ford, & Matkin, 2002). Given the generality of this phenomenon at very different phylogenetic levels, one can wonder why vocal convergence has been described for primates only in callitrichids (Elowson & Snowdon, 1994; Rukstalis, Fite, & French, 2003; Snowdon, Elowson, & Roush, 1997; Snowdon & Elowson, 1999), Japanese monkeys (Sugiura, 1998), and chimpanzees (Marshall, Wrangham, & Clark-arcadi, 1999; Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998).

Several primate species have been shown to actively modify the acoustic structure of their calls in specific social contexts (squirrel monkey: Biben, 1993; Biben, Symmes, & Masataka, 1986; capped gibbons: Geissmann, 1983; Japanese macaques: Masataka, 1992),

and geographical dialects have been described (Japanese macaque: Green, 1975; tamarin: Maeda & Masataka, 1987; chimpanzee: Mitani, Hasegawa, Gros-Louis, Marler, & Byrne, 1992; Barbary macaque: Fischer, Hammerschmidt, & Todt, 1998). Vocal sharing also requires that vocal communication plays an important role in social life. Words like *conversation* and *dialogue* have found their way into published investigations of vocal behavior (Maurus, Kuehlhorn, Wiesner, Braclay, & Streit, 1985; Snowdon & Cleveland, 1984; Symmes & Biben, 1988).

Why, then, is there so little evidence of vocal sharing in primates? Different reasons have been evoked: call type studied (e.g., alarm calls vs. affiliative calls), methods of measurement, and species studied (Snowdon et al., 1997).

In the present study, we investigated the possibility of vocal sharing by studying social calls (Gautier, 1988) in a monkey species living in multifemale groups: the Campbell's monkeys (*Cercopithecus campbelli*). Previous studies in the same captive group had revealed that each female produces one to several variants of the combined harmonic (CH) 6, a call type most often produced while approaching a group member, and that some of these variants can be produced by different females (Lemasson, Gautier, & Hausberger, 2003).

Here we looked at the way the CH6 variants are distributed between females and whether this can be related to social affinities. In order to make sure that this possible sharing is indeed related to social relations, we followed both the social and vocal dynamics over a 2-year period while changes (birth, male replacement) occurred within the group. We ensured the detection of fine structural variations by using telemetric recordings, and we analyzed vocal data with an index of similarity, which has proved useful in similar studies on birds (Adret-Hausberger, 1983; Farabaugh, Linzenbold, & Dooling, 1994; Hile, Plummer, & Striedter, 2000; E. H. Miller, 1982) and cetaceans (P. J. O. Miller & Bain, 2000). We finally tested the generality of the phenomenon by comparing the data to those obtained in two other captive groups that had no relation with our main study group or between each other.

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Method

Subjects and Housing Conditions

Our study focused mainly on one large group of Campbell's monkeys (Group 1: *Cercopithecus c. campbelli*) composed of 1 adult male (Gavroche, 12.5 years old) and two matriline: Matriline 1 (mother Lisa, 14.5; daughters Plume, 6.5; Lowina, 5.5; Maricopa, 4; and Chilula, 3) and Matriline 2 (sisters Shawnee, 5.5; Tilamook, 3; and Bela, 1.5). The composition of the group changed during the study (see Figure 1): the replacement of the present adult male (Sirano: 9 years old at Year 2) and the birth of 2 males (Pikachu, Lisa's son and Togepi, Lowina's son). The monkeys were housed in an indoor (21 m² × 3 m)–outdoor (21 m² × 4 m) enclosure at the Station Biologique de Paimpont (Paimpont, France).

In order to look for generality in the observations, we observed two additional groups over shorter periods: a small group of Campbell's monkeys (Group 2: *Cercopithecus c. campbelli*) composed of 3 nonrelated adult females (Doreen, 13.5; Olive, 15; and Putsu, 14) and 2 of Doreen's sons (Infant 1, Juvenile 2), and a small group of Lowe's monkeys (Group 3: *Cercopithecus c. lowei*) composed of 1 adult male (Willy 9), 2 nonrelated adult females (Lome, 8.5; Female X, 14.5) and a hybrid *C. c. campbelli* × *C. c. lowei* male (Hybrid 4, Female X's son).

Those two last groups were housed in a similar-sized indoor–outdoor enclosure as the first group, at Beauval Zooparc (France). They were separated by 20 m and were in visual and vocal contact in their outdoor enclosures. The founder individuals of the three groups were not related and had been caught wild in different locations. In the three groups, the monkeys were kept in the indoor part during the observations of social behavior in order to ensure identification of partners more easily, but the recording of calls was made in the whole enclosure.

Data Collection and Analysis

Calls were recorded at three time periods: Year 1, Year 2, and Year 3 for Group 1 (Figure 1). Each sound recording period was preceded (during the month before) by an observation of social interactions within the group. For Groups 2 and 3, observations and sound recordings were performed at the same time, in Year 3.

Social Interactions

Observations were made with a voice recorder (AIWA TP-560) to collect information on social relationships. Focal monkey sampling was used for Group 1 (Altmann, 1974): 1 monkey was followed for 5 min and every dyadic interaction was recorded. Observations (Years 2 and 3) covered a period of 10 continuous days, with three sessions a day (at feeding time in the morning; at midday; and late in the afternoon, 1 hr after feeding). Equal observation time was performed for each focal monkey (150 min). Scan sampling was used to collect information on social relationships in Groups 2 and 3. Totals of 209 scans per individual (Group 2) and 186 scans per individual (Group 3) were thus obtained.

Interactions were divided into several categories: *affiliative interactions* (approach: e.g., run to, follow; contact: e.g., grasp gently, place hand on; sniffing), *social play* (e.g., pursue, hang on tail of), *avoidance* (e.g., flee, deviate), *aggression* (e.g., threaten, fight with), and *vocal exchange of cohesion–contact calls*. Vocal exchange was previously defined as a succession of calls in less than 1 s (Lemasson et al., 2003). Whereas in exchanges involving only 2 monkeys, it was easy to determine who responded to whom, this was more difficult when several monkeys called successively. In this case, we considered all possible dyads: For example, if successive calls belonged to the Monkeys A, B, C, and D, we considered the dyads AB, AC, AD, BC, BD, and CD.

Two indices were calculated on the basis of these observations in order to assess the social position of each female within the group in terms of hierarchical dominance rank and level of social integration:

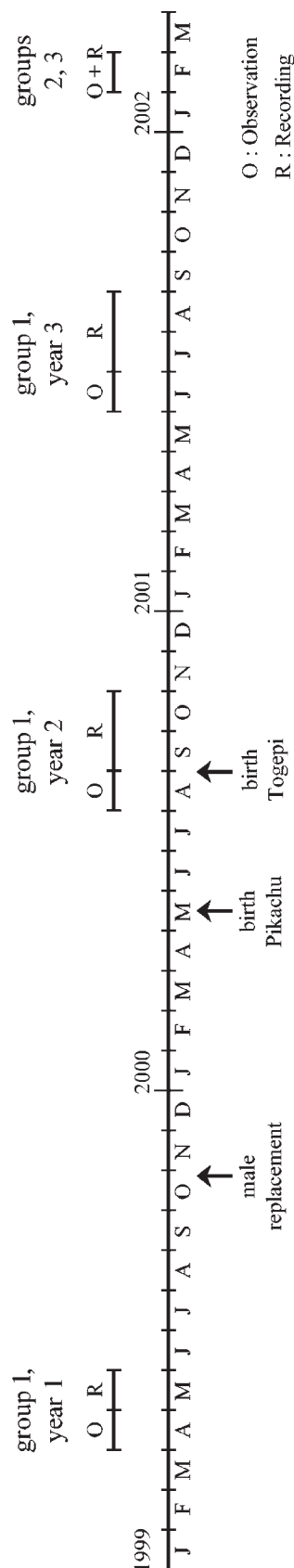


Figure 1. Observation and recording periods. Social observations of call recordings were performed at three year periods for Group 1 and only one period for Groups 2 and 3. During this study the group composition changed (male replacement and births). J–D = January–December.

Dominance index. We used the index developed by Zumpe and Michael (1986): For each pair of monkeys, (a) the number of aggressive acts produced by one monkey toward the other is expressed as a percentage of the total number of aggressive acts produced by both monkeys toward each other, (b) the number of occurrences of avoidance behavior received was calculated with the same method, and (c) the two precedent scores were averaged for each monkey. Then, for each monkey, the dominance index was calculated by averaging the scores obtained in (c) with all the other monkeys in the group. Campbell's monkeys seem to rely more on a monitor-adjust type of social organization (Rowell, 1988) than on aggressive interactions. Therefore, a low number of such interactions was observed (0–15), and the index gives the general trends in terms of hierarchy, rather than a precise evaluation of dominance. It was calculated independently for each year.

Social integration index. We developed an index to assess the investment of each female in the three networks (on the basis of the frequency of occurrences of behavior and the number of partners): affiliative interaction, social play, and vocal exchange for behaviors both received and given. The social integration index was calculated as $(n/N) \times (p/P) \times 100$, where n = number of occurrences of a behavioral category initiated (or received) by a given individual (i), N = number of occurrences of that behavioral category initiated (or received) by all group members, p = number of group members with whom the individual (i) interacted for the given behavioral category, and P = number of individuals in the group – 1.

Nonparametric statistics (binomial tests with Bonferroni correction) were used to construct the sociograms.

Sound Recordings

Calls were recorded with two systems: telemetric and ordinary microphone recording. The telemetry was developed only for Years 2 and 3 (Group 1) and could not be used for Groups 2 and 3 because of the zoo's constraints. We also used ordinary microphone recordings to record calls from females of Group 1 that were still carrying an infant, as we did not want to disturb them by catching them, which was necessary in order to install telemetric equipment.

Telemetric recording. The telemetric system was based on a technique developed by Gautier (1979, 1983) and was transformed to avoid the attenuation of high frequencies, often emitted by our species. It was composed of a transmitter, a receiver, and a numeric stereophonic digital audio tape recorder (Tascam DA-P1). The transmitter was composed of a microphone (LEM EM123T) positioned over the larynx area in a rubber collar; an oscillator that emitted from 90 to 130 Mhz, assembled on a circular printed circuit board; and a lithium battery (3 V). All these

elements were fixed on a leather harness with two straps crossing the chest and the back of the monkey and passing over the shoulders, adjusted by two buckles. This technique enabled us to have better recordings but may have led to a lower number of recordings per time period, because only 2 females could be recorded at the same time, due to limitations of the receiver. Recording times for the different pairs changed in a rotating way.

Ordinary microphone recording. We recorded calls with a unidirectional microphone (Sennheiser MKH815) linked to the aforementioned digital audio recorder. Recordings were obtained in a similar array of circumstances as those obtained with telemetry.

A total of 242 hr and 20 min of recording was performed leading to the analysis of 632 calls (see Table 1). Some females did not produce the CH6 calls in some periods. This could be explained by the globally low level of vocal production in some females (Maricopa, Plume, Lisa) or by physiological changes (e.g., Bela was pregnant in Year 3). Of course, in all cases (telemetry or ordinary recording), observations were made simultaneously, ensuring additional information about context.

Sound Analysis

The female vocal repertoire has been described previously and is composed of 10 call types. In the present study, we concentrated on CH calls, which are preferentially produced in the food context or during social interactions. Using an original method for analyzing the context of call production (Lemasson, Richard, & Hausberger, 2004), we found that the different subtypes were used in different contexts. We could differentiate, on the basis of both their acoustic structure and their context of production, six subtypes of CH calls. In particular, the CH6 subtype was associated with affiliative interactions (approach and contact). CH6 calls are composed of two subunits: one low-pitched trill, and one high-pitched frequency-modulated arch element (Figure 2). This arch was shown to support the highest level of intra- and interindividual variability on different parameters. For these reasons, we focused our analysis on the high-pitched second part of CH6 calls.

Sonograms were computed on an Amiga microcomputer program for sound analysis and synthesis (Richard, 1991). The calls used for spectrographic analysis were digitized at a 24-kHz sampling rate with an 8-bit sample size. The spectrographic analysis was done with fast Fourier transformations (FFT) with sizes of 256 points for each analyzed time window. Resulting spectrograms had a time resolution of 2.49 ms and frequency resolution of 100 Hz.

Given the duration and patterns of variation of these calls, it appeared that comparisons of sonograms required a more integrative method than the simple measurements of frequency or duration parameters that are classi-

Table 1
Number of CH6 Calls Recorded for Each Female

Group and year	Subject								Recording time (no. of days recorded)
	Be	Ti	Sh	Ch	Ma	Lo	Pl	Li	
Group 1									
Year 1	16*	27*	18*	13*	7*	21*	0*	0*	8 hr 30 min* (6 days)
Year 2	40	25	23	47	0	5*	7	0*	92 hr 20 min + 4 hr 30 min* (37 days)
Year 3	0	61	72	39*	0	104	6*	10	101 hr + 18 hr* (24 days)
Total	56	113	113	99	7	130	13	10	
Group 2	Do	Ol	Pu						12 hr* (7 days)
	4*	6*	47*						
Group 3	Fx	Me							6 hr* (7 days)
	4*	30*							

Note. Asterisks indicate ordinary microphone recording; all other calls and recording times are from telemetric recording. CH = combined harmonic; Be = Bela; Ti = Tilamook; Sh = Shawnee; Ch = Chilula; Ma = Maricopa; Lo = Lowina; Pl = Plume; Li = Lisa; Do = Doreen; Ol = Olive; Pu = Putsu; Fx = Female X; Me = Lome.

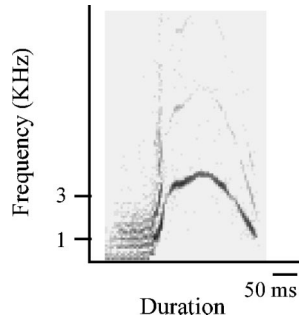


Figure 2. Example of sonogram of a combined harmonic 6 call.

cally used in primates (Elowson & Snowdon, 1994; Mitani & Brandt, 1994; Sugiura, 1998). Similarity indices have been used successfully for such long whistled structures in various species of birds and cetaceans (Farabaugh et al., 1994; Hile et al., 2000; E. H. Miller, 1982; P. J. O. Miller & Bain, 2000). The index software used here is described in Adret-Hausberger (1983) and was adapted by means of a customized software. The similarity index was calculated by comparing the frequency contours of each pair of sonograms. The program automatically looked for the best superposition of two given sonograms by transposing one sonogram above the other along the duration axis and frequency axis, because some frequency parameters decreased with age. We then calculated an index value for each comparison. Comparisons were made both at the intra- and the interindividual levels within the period of a year and between years; each call was compared to all other calls. Other methods, like cross-correlations, were tested but were unable to give clear evaluations of similarities and/or dissimilarities between calls.

We used the UPGMA clustering algorithm, as in several studies in songbirds (Baptista & Gaunt, 1997; Cicero & Benowitz-Fredericks, 2000; Farabaugh et al., 1994; Hile & Striedter, 2000; Williams, 1990), to classify the structures produced by each individual at each period, based on similarity indices (software NTSYS-pc, SAHN clustering program, Rohlf, 1992). Groups of calls within a female repertoire emerged, defining variants to the CH6 call (see also Lemasson, Gautier, & Hausberger, 2003). The cluster analysis revealed that a threshold $i = 0.30$ appeared, which differentiated variants. Two examples are illustrated in Figure 3: Tilamook produced two stable variants of calls corresponding to two groups of calls (1 and 2) and two additional variants that were only recorded once. Similarly, Chilula presented three variants corresponding to three groups of calls produced (1, 2, and 3), plus two additional occasional variants.

Pairwise indices were then averaged to obtain a mean similarity value for intra- and interindividual comparisons, and several levels could be discriminated:

1. Intraindividual comparisons revealed that each individual had clearly separated variants whatever the year period (mean index within variants = 0.34 ± 0.02 , mean index between variants = 0.25 ± 0.03).
2. Interindividual comparisons confirmed that variants could be shared by more than one individual (mean index within variants = 0.31 ± 0.01 [vary from 0.30 to 0.33]), and that different variants were clearly divergent (mean index between variants = 0.20 ± 0.05 [vary from 0.09 to 0.29]).

Contextual analyses showed that there were no differential use of variants according to circumstances.

Nonparametric statistical tests were used in order to look for correlations (Spearman test) and comparisons of groups (Mann-Whitney test).

Results

Individual Repertoire of Variants in Each Session

The number of calls recorded varied between years, with a higher proportion in Year 1. This may be due to recording methods (see the Method section) and/or stability of the group. However, one to four different variants were found per individual at each year period (see Figure 4), and this number was not correlated with the number of calls recorded (e.g., three variants for Lowina in Year 1 – $N[\text{calls}] = 21$ and Year 3 – $N[\text{calls}] = 104$, one variant for Tilamook in Year 1 with 27 calls recorded, two in Year 1 with 25 recorded). Thus, the lower number of recordings in Year 1 does not explain the lower variation observed for some individuals. At that time, Bela presented three variants for 16 calls recorded, whereas Tilamook had only one, with 27 calls recorded. Large variations between individuals were observed, some only unshared; others, like Bela, shared almost all their variants.

Variants were shared by 2–4 individuals in all three periods (Figure 4): Year 1 (Variants A, B, C, and D), Year 2 (Variants B', G, H, and I) and Year 3 (Variants G and H). Other variants appeared restricted to 1 individual, although we cannot exclude that they may have been shared with the individuals that were silent at that time.

From one year to the next, we observed that individuals could clearly maintain a given variant (interyear index ≥ 0.30), lose it, or gain a new one (interyear index ≤ 0.25). But we also observed that variants with an intermediary index ($0.26 \leq \text{interyear index} \leq 0.30$), presented a quite similar, but not exactly identical, shape; thus, we concluded that there had been a gradual transformation of a given variant to a new version (see example of Chilula's changes in Figure 5).

Variations Over Years

Numerous changes were observed, especially between Years 1 and 2 (Figure 4). The six variants observed in Year 1 disappeared and were never observed again. Some structures in Year 2 seemed, however, to derive (e.g., B', D', F') from some of them, but these derived structures were not necessarily shared by the same individuals. More similarities were observed between Year 2 and Year 3, as six variants were common to both periods.

It is interesting that the number of variants recorded increased over time (6 in Year 1, 9 in Year 2, and 12 in Year 3). This is not related to the fact that 2 monkeys (Plume and Lisa) called only on Sessions 2 and 3, as they appeared to share an existing variant with another individual.

Differences between monkeys appeared in their degree of sharing, both within and between recording periods. Thus, Bela shared all her calls (excepted D') in the 2 years when she could be recorded, whereas Lowina showed no (Year 2) or little (Year 1 and 3) sharing over the whole time. Others, like Shawnee, who shared most of her variants in Year 1, showed a clear decrease of sharing over time, with no sharing in Year 3.

In fact, we observed a clear increase in the tendency to have individual-specific variants over time: 2 out of 6 variants were not shared in Year 1, 5 of the 9 in Year 2, and 10 of the 12 in Year 3. Thus, the increase of the number of variants seems to be related to an increase in the nonshared variants.

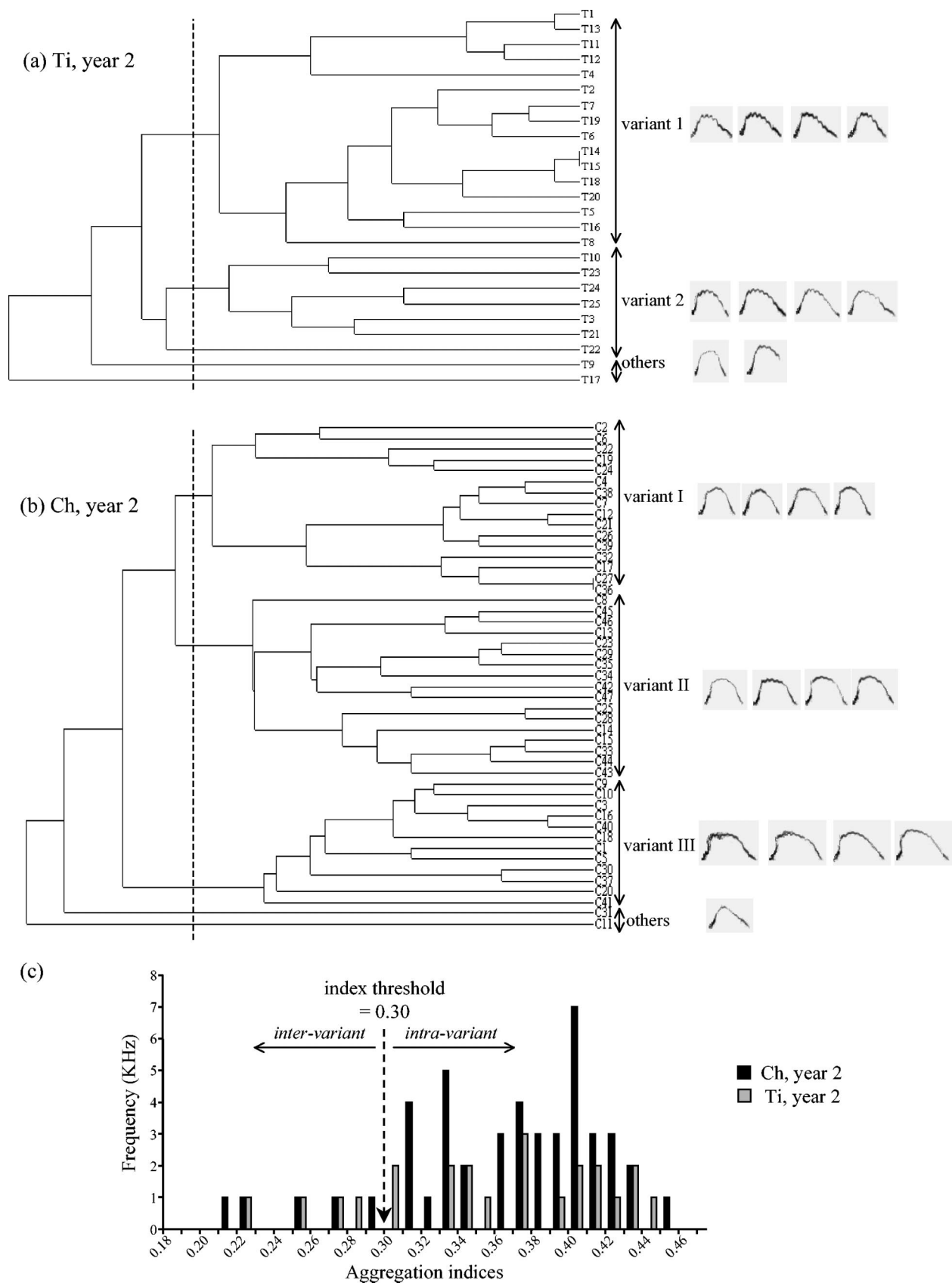


Figure 3. Dendrograms showing the results of cluster analysis. Two examples of dendrograms in Year 2. Examples of sonograms are illustrated on the right side of dendrograms. a: Tilamook (Ti) presented two variants. b: Chilula (Ch) presented three variants. c: The histograms represent the frequency of the indices, resulting from the cluster analysis, at each aggregation level, for both females. A common threshold of 0.30 emerged (which delimited dotted lines in dendrograms) enabling us to classify the structures emitted by each individual.

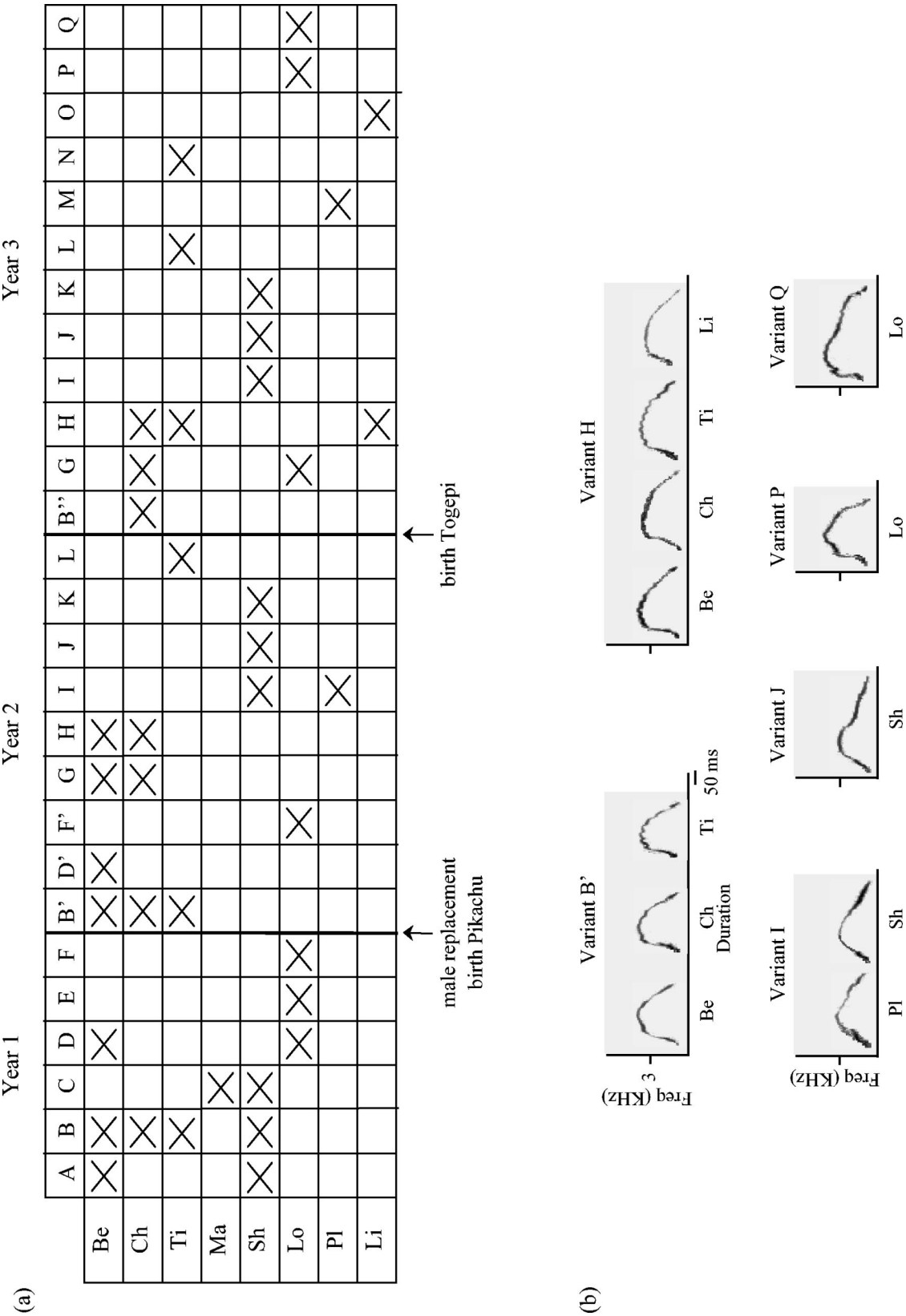


Figure 4. Dynamics of individual repertoires and variant sharing. a: The variants (A–Q) present in all three periods are illustrated in columns and the females of Group 1 in lines (ranked according to their age, the youngest in the first line). An X indicates that a female possessed a given variant in her repertoire. For example, Variant B was present in the repertoires of Bela (Be), Tilamook (Ti), Shawnee (Sh), and Chilula (Ch), but not in the repertoires of Maricopa (Ma), Lowina (Lo), Plume (Pl), and Lisa (Li). Changes in group composition between years were also noticed. b: Some examples of sonograms of shared and nonshared variants are illustrated. The name of the female that produced the given call is indicated under each sonogram.

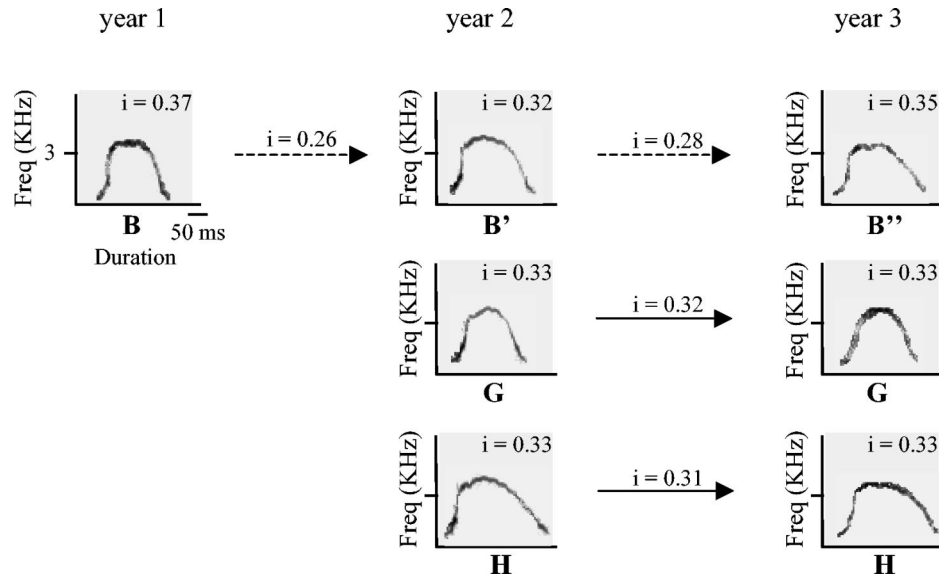


Figure 5. Gradual changes of variant. The figure illustrates an example of variant changes over years. Chilula displayed one Variant B in Year 1; three variants, including two new variants (G and H) and a new version of the B variant (B') in Year 2; and three variants, including one new version of the B' variant (B'') and the same G and H variants in Year 3. Mean intrayear index is presented in the upper left corner of each sonogram, and interyear index above each arrow. Names of variants are indicated under each sonogram.

Social Influence on Call Flexibility

The degree of sharing (number of variants shared by an individual over a 1-year period ÷ number of variants produced by this individual at the same period) was not explained by the matriline (Mann–Whitney test, Matriline 1 vs. Matriline 2, $U = 123$, $n_1 = 9$, $n_2 = 13$, $p = .53$), or by the status (Spearman correlation, dominance index calculated for each female per year: $n = 24$, $r = .01$, $p = .95$) of the emitter (Table 2). But a significant negative correlation between the degree of sharing and the age of the emitter was observed (Spearman correlation, $r_s = -.45$, $n = 24$, $p < .05$). Because young animals play and vocally exchange more than older animals, a positive correlation was also observed between the degree of sharing and the social integration indices for

social play, both initiated (Spearman correlation, $r_s = .53$, $n = 24$, $p < .05$) and received ($r_s = .42$, $n = 24$, $p < .05$), and for vocal exchange, both initiated ($r_s = .43$, $n = 24$, $p < .05$) and received ($r_s = .42$, $n = 24$, $p < .05$; see Table 3). This was not observed for the social investment in affiliative interactions (initiated: $r_s = .17$, $n = 24$, $p = .43$, received: $r_s = -.25$, $n = 24$, $p = .23$). Thus, the females exhibiting more vocal sharing were also those more involved in social exchanges like play or vocal interactions. For example, Bela and Chilula, who shared almost all their variants in Years 1 and 2, had the higher indices within the group for social integration in play and vocal exchanges, contrary to Lowina. This could also explain changes over the years. For example, Shawnee was highly integrated in vocal exchanges, both initiated and received, in Year 1, when she shared all her variants, as compared with Years 2 and 3, when she only shared one of her six variants.

We observed that more variant changes were observed between Years 1 and 2 than between Years 2 and 3. This corresponded to the replacement of the adult male.

We observed some associations between preferential partners and vocal sharing (see Figure 6). Individuals that shared variants never avoided one another, whereas individuals with no shared variant could. We also observed that Bela, Tilamook, and Chilula—who often played together in Year 1—shared Variant B and still shared a new version of this variant (B') and often played together in Year 2. This variant was present in Chilula's repertoire (B'') only in Year 3, when the level of social play greatly decreased. Shawnee, who shared all her variants with Bela in Year 1, also initiated play with her. Some sharing dyads were also often preferential partners for vocal exchanges (Bela–Shawnee–Tilamook: Year 1; Bela–Chilula and Chilula–Tilamook: Year 2). Surprisingly, we observed a sharing between Plume, the highest

Table 2
Dominance Index

Subject	Year 1	Year 2	Year 3
Bela	11.9	16.7	10.0
Chilula	54.8	44.4	25.0
Lisa	26.9	33.3	25.0
Lome	43.8	33.3	23.8
Maricopa	18.1	44.4	20.0
Plume	86.9	60.8	40.0
Shawnee	8.33	6.9	0.0
Tilamook	9.38	16.1	5.0
Male	40.9	66.7	85.0

Note. The hierarchical rank of dominance is calculated for all individuals in Group 1 on the basis of the number of aggressive acts produced and avoidance received. The higher the dominance index value, the higher ranking the individual. When the male was replaced between Years 1 and 2, we observed that the rank of the two males varied.

Table 3
Social Integration Indices

Subject	Year 1			Year 2			Year 3		
	Affiliative	Play	Vocal exchange	Affiliative	Play	Vocal exchange	Affiliative	Play	Vocal exchange
Behavior initiated									
Bela	20.6	15.1	17.6	9.5	22.2	16.2	3.8	1.8	10.8
Chilula	16.0	22.2	13.7	9.2	12.3	14.4	12.2	0.4	8.4
Lisa	8.5	1.3	9.6	8.3	0.1	14.2	2.3	0.0	22.1
Lome	6.5	0.0	1.7	2.8	0.1	1.2	85.0	0.3	2.6
Maricopa	11.7	12.6	12.0	11.5	0.3	3.7	6.7	0.1	2.6
Plume	15.2	0.0	6.2	7.7	0.5	5.8	11.4	0.1	0.2
Shawnee	11.9	0.5	9.6	9.5	6.8	4.4	8.4	0.0	1.4
Tilamook	5.4	7.8	13.1	12.6	12.3	3.3	2.0	0.0	4.6
Male	3.3	0.0	0.0	6.8	0.5	0.1	10.6	0.0	0.2
Behavior received									
Bela	6.6	26.8	15.1	7.5	19	27.3	5.7	1	9.2
Chilula	10.6	10.4	12.4	6.4	11.1	7.9	9.2	0.3	7.3
Lisa	18	3.1	9.6	25	1.7	6.2	16	0.4	7.7
Lome	5	0.1	5.2	4	0	0	12	1.1	5
Maricopa	8.7	5.1	10.4	10.3	5.3	7.2	8.9	0.1	3.4
Plume	13.7	0	5.9	11.5	1.5	1.5	7.5	0.1	0.1
Shawnee	7.2	0.1	10.3	7.5	1.4	1.9	9	0.5	3.7
Tilamook	8.6	6.7	10.8	8.2	8.5	7.6	3.5	0	8.1
Male	20.4	0.2	0	6.5	0.6	0		0	0.1

Note. The social integration indices are calculated for all individuals in Group 1 on the basis of the number of interactions (affiliative, play, vocal) initiated or received and the number of partners within the group. The higher the social integration index value, the more socially active the individual.

ranking female, and Shawnee, the lowest ranking female in Year 2 (Table 2).

Vocal Structures in Groups 2 and 3

We also observed one or two variants per individual in Groups 2 and 3 (see Figure 7). One variant was shared by 2 females in Group 2 who were involved in affiliative interactions (Putsu-Olive: mean index = 0.39). The same variant was also present in Female X of Group 2 (Putsu-Female X: mean index = 0.30). Although the two groups were physically isolated, they could interact visually and vocally.

Moreover, we observed that all Group 2 and 3 calls diverged with Group 1 calls, in terms of frequency modulation (similarity index < 0.30). Therefore, these complementary data, although obtained from different types of groups, confirmed the trend to show variants of the CH6 calls and demonstrated some vocal sharing between individuals.

Discussion

The recording of variations of 632 calls over years in a captive group of Campbell's monkeys confirmed the existence of variants that could or could not be shared between individuals. Vocal sharing was not explained by kinship relations. We observed that structures shared in two other groups had very different frequency modulation from those recorded in Group 1. The pattern of sharing to some extent reflected social affinities, and more sharing was observed in younger females who were better integrated socially, as measured by a social integration index, particularly in play and

vocal exchanges. Changes appeared between years, with disappearance, appearance, or transformation of variants, and a general decrease in the degree of sharing was observed.

Studies on primates revealed that animals are able to produce the species' vocal repertoire without an adult model (Gautier & Gautier-Hion, 1977; Geissmann, 1984; Leiblich, Symmes, Newman, & Shapiro, 1980; Masataka & Fujita, 1989; Owren, Dieter, Seyfarth, & Cheney, 1992; Seyfarth & Cheney, 1986). The strongest evidence comes from isolation-reared (Winter, Handley, Ploog, & Schott, 1973) and deafened (Talmage-Riggs, Winter, Ploog, & Mayer, 1972) squirrel monkeys showing normal development. Despite a strong innate vocal production, vocal flexibility capacities under social influence manifestly exist in primates. Several studies in primates revealed evidence for strong social influence on call usage (Boinski & Mitchell, 1992; Gautier & Gautier, 1982; Hauser, 1989; McCowan & Reiss, 2001; Roush & Snowdon, 1994, 1999; Seyfarth & Cheney, 1997) and the capacity of primates to actively modify vocal structures under social influences. Squirrel monkeys produce "answer" and "question" chucks within a given vocal exchange differing in the peak frequency of several acoustic features. They also respond more often to prerecorded question chucks than answer ones (Biben et al., 1986). Female capped gibbons, in the absence of males, produce the male's as well as their own contribution to duets (Geissmann, 1983). Human caregivers succeeded in conditioning Japanese macaques to modify their vocalizations in a feeding context (Masataka, 1992). Even in the calls of Group 1, which show a high level of flexibility, some acoustic features (e.g., the duration of oscillation quavering) seemed to be species specific. Similarly,

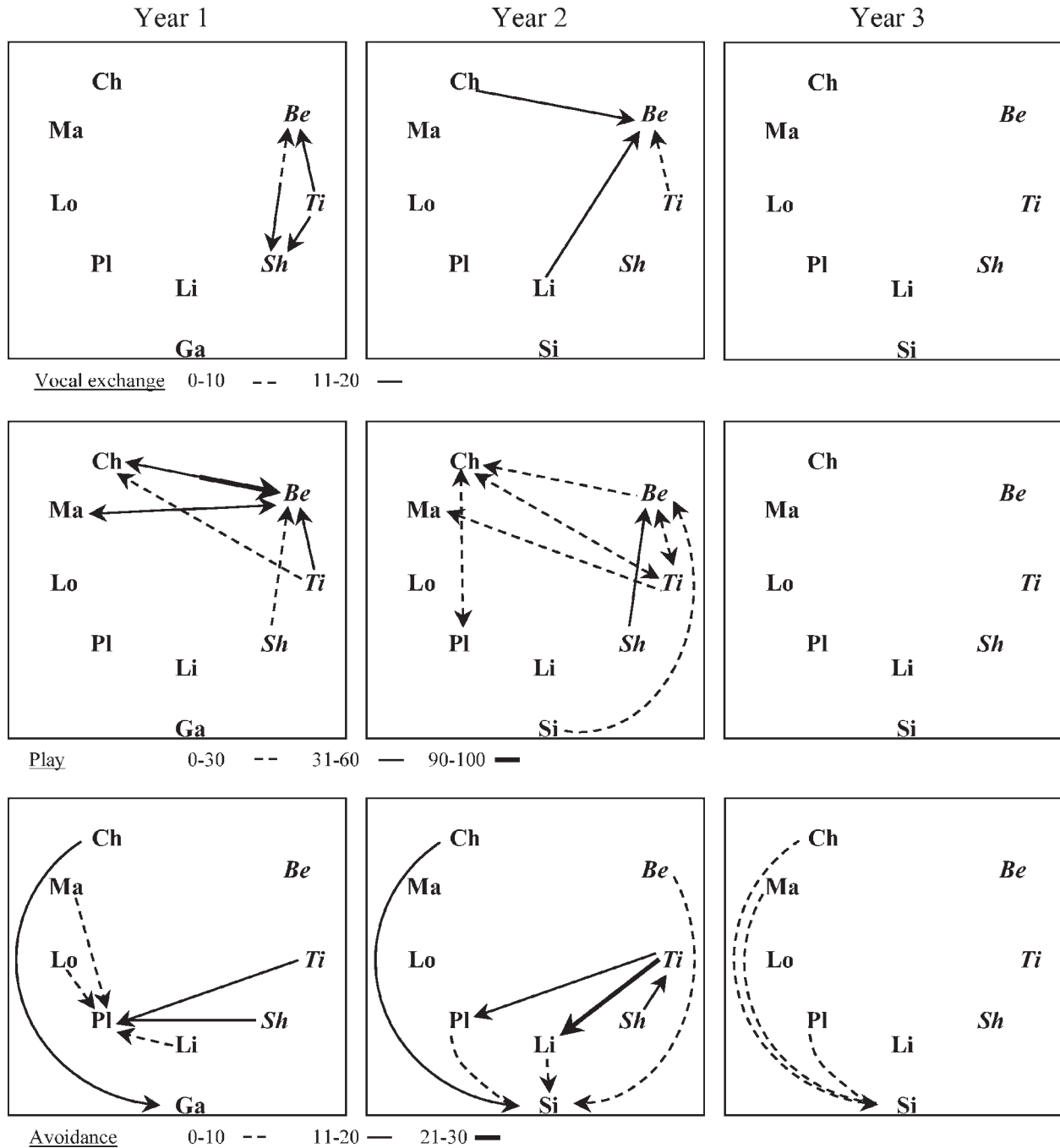


Figure 6. Sociograms. Matriline 1 monkeys are on the left of each sociogram, Matriline 2 are on the right. The arrows are directed from the emitter to the receiver of a behavior; their thickness is correlated to the frequency of the interaction. Only interactions occurring more often than expected by chance (excluding infants) for a given emitter are represented (binomial tests, $\alpha = .05$ with Bonferroni correction). The sociograms represent the results for vocal exchange, social play, and avoidance at each period. No significant interactions were observed for vocal exchange and social play in Year 3. Ga = Gavroche; Si = Sirano; Li = Lisa; Pl = Plume; Lo = Lowina; Ma = Maricopa; Ch = Chilula; Sh = Shawnee; Ti = Tilamook; Be = Bela.

European starlings produce universal whistle themes that can show fine variations leading to particular dialectal variants (Hausberger, 1997).

Vocal sharing is widespread in several species of birds (yellow-

rumped cacique: Feekes, 1982; chickadees: Nowicki, 1989; Australian magpie: Brown et al., 1988; Brown & Farabaugh, 1997; indigo buntings: Payne & Payne, 1997; nightingales: Griessmann & Naguib, 2002), quacking frog (Gerhardt et al., 2000) and mam-

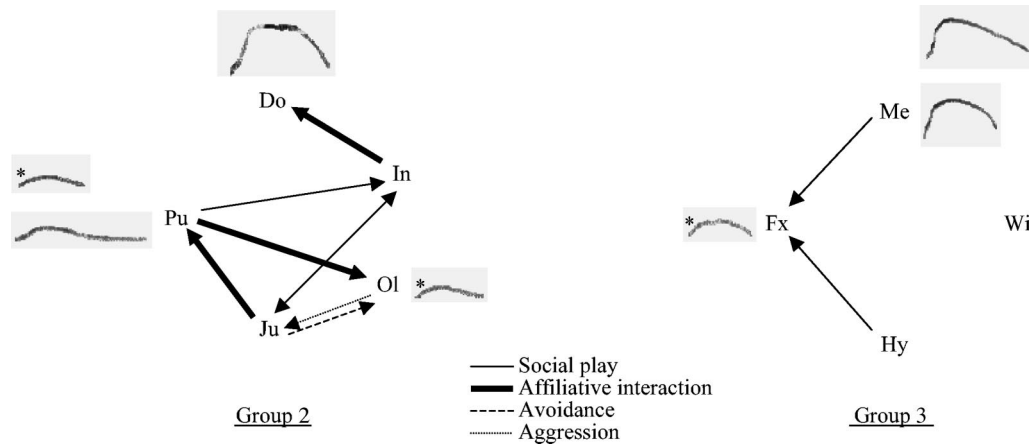


Figure 7. Sociograms and vocal sharing in Groups 2 and 3. This figure illustrates social interactions within Groups 2 (left) and 3 (right; same tests as described in Figure 4) and vocal variants in all adult females. Asterisks indicate variant sharing between individuals (mean index [Pu-Ol] = 0.42, [Pu-Fx] = 0.30). Do = Doreen; Me = Lome; In = Infant 1; Pu = Putsu; Fx = Female X; Wi = Willy; Ol = Olive; Ju = Juvenile 2; Hy = Hybrid 4.

mals (bats: Jones & Ransome, 1993; bottlenose dolphins: McCowan & Reiss, 1997; Tyack, 1993; killer whales: Ford, 1991; P. J. O. Miller & Bain, 2000; Yurk, Barrett-Lennard, Ford, & Matkin, 2002; sperm whales: Weilgart & Whitehead, 1997), and some recent studies demonstrated such a phenomenon in primates (Elowson & Snowdon, 1994; Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998; Rukstalis et al., 2003; Snowdon et al., 1997). Vocal sharing observed at a given time can be the result of several factors, including response to a common eliciting stimulus or to a common emotional state ("motivational-structural" rules, Morton, 1977). It can also be the result of a convergence/divergence dynamic phenomena. This was observed in chickadees (Mammen & Nowicki, 1981; Nowicki, 1989), Australian magpie (Brown & Farabaugh, 1997), greater spear-nosed bats (Boughman, 1998), and bottlenose dolphins (Smolker & Pepper, 1999). The most detailed studies in primates, which support our present results, concern captive callitrichids, which changed their vocal structures when a new group was introduced in their neighborhood (Elowson & Snowdon, 1994; Rukstalis et al., 2003; Snowdon et al., 1997) and after pairing (Snowdon & Elowson, 1999).

Several factors can be involved in the production of shared vocalizations. Cultural transmission within maternal lineages are illustrated in vocal clans in killer whales (Ford, 1991; Yurk et al., 2002), and son-mother acoustic similarities in bottlenose dolphins (Sayigh, Tyack, Wells, & Scott, 1990). In primates, similarities in closely related animals have been described in rhesus macaques' coo calls (Hauser, 1992) and pigtailed macaques' screams (Gouzoules & Gouzoules, 1990). Here we found that vocal sharing was not related to kinship relations. This was confirmed by some observations in two other groups: Some vocal sharing occurred between nonrelated females. Although the data from the two additional groups are not really comparable, given the differences in social composition, they seem to indicate (a) that the variations observed in Group 1 were not just reflecting a species-typical range of variation, (b) that the existence of variants within the CH6 calls and some sharing may be a general trend for the species, and (c) that kin relations may not be necessary for sharing to occur.

Social learning based on familiarity between individuals has been shown in primate species as in Snowdon's studies in pygmy marmosets. Marshall et al. (1999) illustrated a limited example of propagation of a novel pant-hoot variant after introduction of a new male in a group.

Chimpanzees matching pant hoots spent more time together than others, and the degree of within-individual variation in calls was correlated to the frequency of chorusing (Mitani & Brandt, 1994). In dolphins, creation of alliances between males are associated with vocal convergence (Sayigh et al., 1990; Smolker & Pepper, 1999; Tyack, 1997; Tyack & Sayigh, 1997). Several studies in birds (Brown & Farabaugh, 1997; Hile & Striedter, 2000), including European starlings (Hausberger, 1997; Hausberger et al., 1995), revealed that vocal sharing occurred mostly among preferential partners within groups. An influence of hierarchical dominance rank has been described in chimpanzees. The higher ranking member of a dyad gave long-distance calls that converged on those produced by their chorus partner (Mitani & Gros-Louis, 1998).

The function of vocal sharing is still unclear. Dolphins, for example, in contexts of isolation, use a predominant and shared whistle type rather than individually distinctive signature whistles (McCowan & Reiss, 2001). Vocal sharing could enable the identification of the caller as a member of a social affiliative unit, by means of a vocal "social badge" (Brown & Farabaugh, 1997). This implies that all members of a group are able to recognize those signatures. Primates are able to discriminate kin from nonkin (Rendall, Rodman, & Edmond, 1996), familiar individuals from strangers (Biben & Symmes, 1991), and individual identity (Cheney & Seyfarth, 1982; Rendall et al., 1996) on the basis of vocal cues alone. A hypothetical function of vocal sharing would be not only to initiate and maintain social bonds within those units, but also to signal alliance to compete against other units (Smolker & Pepper, 1999).

We observed over the 3 years a decrease in the overall degree of sharing and an increase of individual-specific structures in the females' repertoires. This could be explained by the increase of

age, as we observed a negative correlation between the degree of sharing and age. Animals getting older and acquiring more social experience share less. Moreover, greater changes were observed between Years 1 and 2, which corresponded to the replacement of the adult male, than between Years 2 and 3. We could thus think that vocal sharing would be more important in disturbed groups as a means of advertising affiliative bonds than in stable groups, in which the social network is known by individuals and conveying individual identity may be enough. Seyfarth and Cheney (1997) demonstrated in vervets that a social experience is needed before knowing, for example, which members of their group rank above and below them. This raises a new hypothesis that could explain the rareness of sharing in primates given the high stability of primate groups. This would also suggest possible higher capacities in social cognition, enabling, after the group has become stable, each member to have an assessment of social bonds, without the need for social markers.

The necessity to possess individual specific elements in the repertoires has not been studied in depth in animals. Banner-tailed kangaroo rats adjust their foot-drumming signatures to differ from those of their new neighbors after they change their territory (Randall, 1995). Daughters diverged more than sons from their mother's signature whistle in bottlenose dolphins in order to avoid inbreeding (Tyack & Sayigh, 1997). Even in groups displaying convergence phenomenon, individuals always retain unique notes, syllables, or specific structure characteristics in birds (Brown & Farabaugh, 1997; Hausberger et al., 1995), dolphins (McCowan & Reiss, 1997) or monkeys (Jorgensen & French, 1998; Snowdon et al., 1997). Snowdon and Hausberger (1997) proposed the notion of "optimal vocal sharing" (p. 5) for this phenomenon: The vocal system should provide not only group identity (social markers), but also individual identity. This balance may be different in different species and may depend on social stability and cognitive abilities. In Campbell's monkeys (and maybe other nonhuman primates), it may be hypothesized that fewer social markers are needed when groups are stable and are oriented toward less sharing and more individual identity.

References

- Adret-Hausberger, M. (1983). Variations dialectales des sifflements de l'étourneau sansonnet sédentaire en Bretagne [Dialectal variations in the whistles of sedentary European starlings in Brittany]. *Zeitschrift für Tierpsychologie*, 62, 55–71.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–267.
- Baptista, L. F., & Gaunt, S. L. L. (1997). Social interaction and vocal development in birds. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 23–40). Cambridge, England: Cambridge University Press.
- Biben, M. (1993). Recognition of order effects in squirrel monkey antiphonal call sequences. *American Journal of Primatology*, 29, 109–124.
- Biben, M., & Symmes, D. (1991). Playback studies of affiliative vocalizing in captive squirrel monkeys: Familiarity as a cue to response. *Behaviour*, 117, 1–19.
- Biben, M., Symmes, D., & Masataka, N. (1986). Temporal and structural analysis of affiliative vocal exchanges in squirrel monkeys (*Saimiri sciureus*). *Behaviour*, 29, 259–273.
- Boinski, S., & Mitchell, C. M. (1992). Ecological and social factors affecting the vocal behavior of adult female squirrel monkeys. *Ethology*, 92, 316–330.
- Boughman, J. W. (1998). Vocal learning by greater spear-nosed bats. *Proceedings of the Royal Society of London Series B*, 265, 227–233.
- Brown, E. D., & Farabaugh, S. M. (1997). What birds with complex social relationships can tell us about vocal learning: Vocal sharing in avian groups. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 98–127). Cambridge, England: Cambridge University Press.
- Brown, E. D., Farabaugh, S. M., & Veltman, C. J. (1988). Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*. I. Vocal sharing within and among groups. *Behaviour*, 104, 1–28.
- Cheney, D. L., & Seyfarth, R. M. (1982). Recognition of individuals within and between groups of free-ranging vervet monkeys. *American Zoologist*, 22, 519–529.
- Cicero, C., & Benowitz-Fredericks, Z. M. (2000). Song types and variation in insular populations of Lincoln's sparrow (*Melospiza lincolnii*) and comparisons with other *Melospiza*. *The Auk*, 117, 52–64.
- Elowson, A. M., & Snowdon, C. T. (1994). Pygmy marmosets (*Cebuella pyraea*) modify vocal structure in response to changed social environment. *Animal Behaviour*, 47, 1267–1277.
- Farabaugh, S. M., Linzenbold, A., & Dooling, R. J. (1994). Vocal plasticity in budgerigars (*Melopsittacus undulatus*): Evidence for social factors in the learning of contact calls. *Journal of Comparative Psychology*, 108, 81–92.
- Feeles, F. (1982). Song mimesis within colonies of *Cacicus c. cela* (Icteridae, Aves). A colonial password? *Zeitschrift für Tierpsychologie*, 58, 119–152.
- Fischer, J., Hammerschmidt, K., & Todt, D. (1998). Local variation in Barbary macaque shrill barks. *Animal Behaviour*, 56, 623–629.
- Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal water of British Columbia. *Canadian Journal of Zoology*, 69, 1454–1483.
- Gautier, J.-P. (1979). Biotelemetry of the vocalizations of a group of monkeys. In C. J. Amlaner & D. W. Macdonald (Eds.), *A handbook on biotelemetry and radiotracking* (pp. 535–544). Oxford, England: Pergamon Press.
- Gautier, J.-P. (1983). Qualities and drawbacks of radiotransmitted vocalizations of monkey through laryngophones; New perspectives in analysis. *Folia Primatologica*, 41, 218–230.
- Gautier, J.-P. (1988). Interspecific affinities among guenons as deduced from vocalizations. In A. Gautier-Hion, F. Bourlière, J.-P. Gautier, & J. Kingdon (Eds.), *A primate radiation evolutionary biology of the African guenons* (pp. 194–226). Cambridge, England: Cambridge University Press.
- Gautier, J.-P., & Gautier, A. (1982). Vocal communication within a group of monkeys: An analysis by biotelemetry. In C. T. Snowdon, C. H. Brown, & M. R. Petersen (Eds.), *Primate communication* (pp. 5–39). Cambridge, England: Cambridge University Press.
- Gautier, J.-P., & Gautier-Hion, A. (1977). Communication in Old World monkeys. In T. Sebeok (Ed.), *How animals communicate* (pp. 890–964). Bloomington: Indiana University Press.
- Geissmann, T. (1983). Female capped gibbon sings male song. *Journal of Human Evolution*, 12, 667–671.
- Geissmann, T. (1984). Inheritance of song parameters in the gibbon song, analysed in 2 hybrid gibbons (*Hylobates pileatus* × *H. lar*). *Folia Primatologica*, 42, 216–235.
- Gerhardt, H. C., Roberts, J. D., Bee, M. A., & Schwartz, J. J. (2000). Call matching in the quacking frog (*Crinia georgiana*). *Behavioral Ecology and Sociobiology*, 48, 243–251.
- Gouzoules, H., & Gouzoules, S. (1990). Matrilineal signatures in the recruitment screams of pigtailed macaques *Macaca nemestrina*. *Behaviour*, 115, 327–347.
- Green, S. (1975). Dialects in Japanese monkeys: Vocal learning and cultural transmission of local-specificity behavior? *Zeitschrift für Tierpsychologie*, 38, 304–314.

- Griessmann, B., & Naguib, M. (2002). Song sharing in neighboring and non-neighboring thrush nightingales (*Luscia lusciana*) and its implications for communication. *Ethology*, 108, 377–387.
- Hausberger, M. (1997). Social influences on song acquisition and sharing in the European starling (*Sturnus vulgaris*). In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 128–156). Cambridge, England: Cambridge University Press.
- Hausberger, M., Richard-Yris, M.-A., Henry, L., Lepage, L., & Schmidt, I. (1995). Song sharing reflects the social organization in a captive group of European starling (*Sturnus vulgaris*). *Journal of Comparative Psychology*, 109, 222–241.
- Hauser, M. D. (1989). Ontogenetic changes in the comprehension and production of vervet monkeys (*Cercopithecus aethiops*) vocalizations. *Journal of Comparative Psychology*, 103, 149–158.
- Hauser, M. D. (1992). Articulatory and social factors influence the acoustic structure of rhesus macaque vocalizations: A learned mode of production? *Journal of the Acoustical Society of America*, 91, 2175–2179.
- Hile, A. G., Plummer, T. K., & Striedter, G. F. (2000). Male vocal imitation produces call convergence during pair bonding in budgerigars *Melopsittacus undulatus*. *Animal Behaviour*, 59, 1209–1218.
- Hile, A. G., & Striedter, G. F. (2000). Call convergence within groups of female budgerigars (*Melopsittacus undulatus*). *Ethology*, 106, 1105–1114.
- Jones, G., & Ransome, R. (1993). Echolocation of bats are influenced by maternal effects and change over a lifetime. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 252, 125–128.
- Jorgensen, D. D., & French, J. A. (1998). Individuality but not stability in marmoset long calls. *Ethology*, 104, 729–742.
- Leiblich, A. K., Symmes, D., Newman, J. D., & Shapiro, M. (1980). Development of the isolation peep in laboratory bred squirrel monkeys. *Animal Behaviour*, 28, 1–9.
- Lemasson, A., Gautier, J. P., & Hausberger, M. (2003). Vocal similarities and social bonds in Campbell's monkey (*Cercopithecus campbelli*). *Comptes Rendus Biologies*, 326, 1185–1193.
- Lemasson, A., Richard, J. P., & Hausberger, M. (2004). A new methodological approach to context analysis of call production. *Bioacoustics*, 14, 111–125.
- Maeda, T., & Masataka, N. (1987). Local-specific vocal behavior of the tamarin (*Sanguinus labiatus*). *Ethology*, 75, 25–30.
- Mammen, D. L., & Nowicki, S. (1981). Individual differences and within-flock convergence in chickadee calls. *Behavioral Ecology and Sociobiology*, 9, 179–186.
- Marshall, A. J., Wrangham, R. W., & Clarkacadi, A. (1999). Does learning affect the structure of vocalizations in chimpanzees? *Animal Behaviour*, 58, 825–830.
- Masataka, N. (1992). Attempts by animal caretakers to condition Japanese macaque vocalization result inadvertently in individual-specific calls. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. B. M. De Waal (Eds.), *Topics in primatology, Vol. 1: Human origins* (pp. 271–278). Tokyo: University of Tokyo Press.
- Masataka, N., & Fujita, K. (1989). Vocal learning of Japanese and rhesus monkeys. *Behaviour*, 168, 191–199.
- Maurus, M., Kuehlmorgan, E., Wiesner, E., Barclay, D., & Streit, K. M. (1985). Dialogues between squirrel monkeys. *Language & Communication*, 5, 185–191.
- McCowan, B., & Reiss, D. (1997). Vocal learning in captive bottlenose dolphins: A comparison with humans and nonhuman animals. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 178–207). Cambridge, England: Cambridge University Press.
- McCowan, B., & Reiss, D. (2001). The fallacy of 'signature whistles' in bottlenose dolphins: A comparative perspective of 'signature information' in animal vocalizations. *Animal Behaviour*, 62, 1151–1162.
- Miller, E. H. (1982). Character and variance shift in acoustic signals of birds. In D. E. Kroodsma & E. H. Miller (Eds.), *Acoustic communication in birds* (Vol. 1, pp. 253–295). New York: Academic Press.
- Miller, P. J. O., & Bain, D. E. (2000). Within-pod variation in the sound production of a pod of killer whales *Orcinus orca*. *Animal Behaviour*, 60, 617–628.
- Mitani, J. C., & Brandt, K. L. (1994). Social factors influence the acoustic variability in the long-distance calls of male chimpanzees. *Ethology*, 96, 233–252.
- Mitani, J. C., & Gros-Louis, J. (1998). Chorusing and call convergence in chimpanzees: Tests of 3 hypotheses. *Behaviour*, 135, 1041–1064.
- Mitani, J. C., Hasegawa, T., Gros-Louis, J., Marler, P., & Byrne, R. (1992). Dialects in wild chimpanzees? *American Journal of Primatology*, 27, 233–243.
- Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, 111, 855–869.
- Nowicki, S. (1989). Vocal plasticity in captive black-capped chickadees: The acoustic basis and rate of call convergence. *Animal Behaviour*, 37, 64–73.
- Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1992). Evidence of limited modification in the vocalizations of cross-fostered rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. B. M. De Waal (Eds.), *Topics in primatology, Vol. 1: Human origins* (pp. 257–270). Tokyo: University of Tokyo Press.
- Payne, R. B., & Payne, L. L. (1997). Field observations, experimental design, and the time and place of learning bird songs. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 57–84). Cambridge, England: Cambridge University Press.
- Randall, J. A. (1995). Modification of foot-drumming signatures by kangaroo rats: Changing territories and gaining new neighbours. *Animal Behaviour*, 49, 1227–1237.
- Rendall, D., Rodman, P. S., & Edmond, R. E. (1996). Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, 51, 1007–1015.
- Richard, J. P. (1991). Sound analysis and synthesis using an Amiga micro-computer. *Bioacoustics*, 3, 45–60.
- Rohlf, F. J. (1992). NTSYS-pc: Numerical taxonomy and multivariate analysis system (Version 1.70) [Computer software]. New York: Exeter Software.
- Roush, R. S., & Snowdon, C. T. (1994). Ontogeny of food-associated calls in cotton-top tamarins. *Animal Behaviour*, 47, 263–273.
- Roush, R. S., & Snowdon, C. T. (1999). The effects of social status on food-associated calling behaviour in captive cotton-top tamarins. *Animal Behaviour*, 58, 1299–1305.
- Rowell, T. E. (1988). The social system of guenons, compared with baboons, macaques and mangabey. In A. Gautier-Hion, F. Bourlière, J.-P. Gautier, & J. Kingdon (Eds.), *A primate radiation evolutionary biology of the African guenons* (pp. 439–451). Cambridge, England: Cambridge University Press.
- Rukstalis, M., Fite, J. E., & French, J. A. (2003). Social change affects vocal structure in a callitrichid primate (*Callithrix kuhlii*). *Ethology*, 109, 327–340.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., & Scott, M. D. (1990). Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: Stability and mother-offspring comparisons. *Behavioral Ecology and Sociobiology*, 26, 247–260.
- Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, 34, 1640–1658.
- Seyfarth, R. M., & Cheney, D. L. (1997). Some general features of vocal development in nonhuman primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 249–273). Cambridge, England: Cambridge University Press.
- Smolker, R., & Pepper, J. W. (1999). Whistle convergence among allied

- male bottlenose dolphins (Delphinidae, *Tursiops* sp.). *Ethology*, 105, 595–617.
- Snowdon, C. T., & Cleveland, J. (1984). "Conversations" among pygmy marmosets. *American Journal of Primatology*, 7, 15–20.
- Snowdon, D. T., & Elowson, A. M. (1999). Pygmy marmosets modify call structure when paired. *Ethology*, 105, 893–908.
- Snowdon, C. T., Elowson, A. M., & Roush, R. S. (1997). Social influences on vocal development in New World primates. In S. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 234–248). Cambridge, England: Cambridge University Press.
- Snowdon, C. T., & Hausberger, M. (Eds.). (1997). *Social influences on vocal development*. Cambridge, England: Cambridge University Press.
- Sugiura, H. (1998). Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. *Animal Behaviour*, 55, 673–687.
- Symmes, D., & Biben, M. (1988). Conversational vocal exchanges in squirrel monkeys. In D. Todt, P. Goedeeking, & D. Symmes (Eds.), *Primate vocal communication* (pp. 123–132). New York: Springer-Verlag.
- Talmage-Riggs, G., Winter, P., Ploog, D., & Mayer, W. (1972). Effect of deafening on the vocal behaviour of the squirrel monkey (*Saimiri sciureus*). *Folia Primatologica*, 17, 404–420.
- Tyack, P. L. (1993). Animal language research needs a broader comparative and evolutionary framework. In H. L. Roitblat, L. M. Herman, & P. Nachtigall (Eds.), *Language and communication: Comparative perspectives* (pp. 115–152). Hillsdale, NJ: Erlbaum.
- Tyack, P. L. (1997). Development and social functions of signature whistles in bottlenose dolphins *Tursiops truncatus*. *Bioacoustics*, 8, 21–46.
- Tyack, P. L., & Sayigh, L. S. (1997). Vocal learning in cetaceans. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 208–233). Cambridge, England: Cambridge University Press.
- Weilgart, L., & Whitehead, H. (1997). Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology*, 40, 277–285.
- Williams, H. (1990). Models for song learning in the zebra finch: Fathers or others? *Animal Behaviour*, 39, 745–757.
- Winter, P., Handley, P., Ploog, D., & Schott, D. (1973). Ontogeny of squirrel monkey calls under natural conditions and under acoustic isolation. *Behaviour*, 47, 230–239.
- Yurk, H., Barrett-Lennard, L., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, 63, 1103–1119.
- Zumpe, D., & Michael, R. P. (1986). Dominance index: A simple measure of relative dominance status in primates. *American Journal of Primatology*, 10, 291–300.

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