

Social Change Affects Vocal Structure in a Callitrichid Primate (*Callithrix kuhlii*)

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Abstract

Vocal plasticity in the face of changing social context is well-documented in passerine birds, but the degree to which changes in social environment affect the vocal structure of non-human primates is a topic which has remained largely unexplored. We assessed whether modification of social environments, in this case the presence of marmosets in neighboring cages, influenced the vocal morphology of phee calls, which possess ‘signature’-like features, in Wied’s black tufted-ear marmosets (*Callithrix kuhlii*). Individual phee calls were obtained over a period of 8 wk from 11 animals maintained in rooms with stable social environments. After this baseline phase, seven marmosets were housed for an additional 8 wk in rooms that contained cages with unfamiliar marmosets, while four marmosets maintained the same neighbors as the first phase. Calls were digitized and both frequency and temporal parameters were measured. Multivariate discriminant function analyses (DFA) generated from vocalizations collected in the first phase produced functions that accurately classified calls to the correct individual, showing that calls had significant individual distinctiveness. DFAs generated from vocalizations in the first phase of the study continued to show high classification accuracy for marmosets in a stable social environment, but DFAs from the first phase were significantly less likely to correctly classify vocalizations in marmosets that were housed next to novel conspecifics. These data show that phee calls, which have signature-like properties in marmosets, can be modified by changes in social context. The results suggest a degree of plasticity in vocal signals that is rare among non-human primates.

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Introduction

One of the most fundamental questions regarding the development of any communication signal is the extent to which its structure and ultimate usage are

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relatively fixed and static throughout the signaler's life span, or the degree to which these features are modified by experience. The study of non-human primate communication is no exception. Indeed, one of the most important, and yet unanswered, questions is the extent to which non-human primate vocal behavior is innate, learned or involves a combination of the two (Newman & Symmes 1982; Symmes & Biben 1992). In spite of the remarkable plasticity in human vocal communication, early investigations into the development of non-human primate vocal signals concluded that vocal structure was relatively stable at birth and underwent little modification during development (Lieblich et al. 1980; Newman & Symmes 1982). Given the long period of development that characterizes most primates, it would seem counterintuitive that the ontogeny of primate vocal communication would be so fixed and invariant.

In contrast to these earlier findings, recent studies have suggested that vocal structure in primates is not necessarily fixed at birth, but undergoes a certain amount of change during development. For instance, infant pygmy marmoset (*Cebuella pygmaea*) vocalizations undergo clear developmental changes, becoming more adult like and less variable over time (Elowson et al. 1998). Likewise, the grunt vocalizations of young vervet monkeys (*Cercopithecus aethiops*) are highly erratic, taking several years to stabilize to an adult form (Cheney & Seyfarth 1986). A similar phenomenon has also been reported in macaques. The 'coo' vocalizations of young rhesus macaques (*Macaca mulatta*) undergo significant developmental changes in acoustic structure (Hammerschmidt et al. 2000). While these studies may provide evidence that vocal structure and the mechanisms underlying vocal production are not entirely fixed at birth, the results could simply reflect maturational effects (e.g. changes in the size or shape of the morphological structures that shape vocal parameters), and may not represent flexibility in the production mechanisms that regulate vocal structure.

In studies of avian vocal communication, there have been several clear demonstrations of non-maturational variability in vocal structure that is produced in response to modifications of the signaler's social environment. For example, adult male budgerigars modify call structure to resemble those of unfamiliar conspecifics when placed in a common social environment (Hile et al. 2000). Similarly, newly-formed groups of black-capped chickadees acoustically converge on the D-note of their 'chickadee' call during flock formation (Nowicki 1989). These examples of signal modification occur in the context of a social unit (pair or flock), and the changes in vocal structure among interacting partners may serve to mediate or facilitate the formation of social bonds.

Individual bottle nose dolphins (*Tursiops truncatus*) possess distinct whistle calls known to function in group cohesion and individual recognition (Janik & Slater 1998; Sayigh et al. 1998). Recent studies of modification in these highly conserved vocal signals have revealed that during certain social encounters individual dolphins are able to produce the distinct whistle of another individual (Janik 2000). Known as 'whistle matching', this ability to emit the distinct whistle of another individual has been hypothesized to act in the context of alliance formation and to signal group membership to third parties (Janik 2000). Similar

to avian species, signal modification in bottle nose dolphins seems to occur in the context of the maintenance of social bonds. Therefore, changes in the social environment of animals may constitute one of the most critical features that influence vocal plasticity.

Marmosets and tamarins (Primates; Family Callitrichidae) are small neotropical primates that possess rich vocal repertoires (Cleveland & Snowdon 1982). Among the vocal signals in these repertoires are vocalizations referred to as long calls. These calls are used in a variety of social contexts, including intragroup cohesion and intergroup spacing (Snowdon 1993). There is considerable variability among species in the acoustic morphology of these signals, and they may serve as important taxonomic characters (Snowdon 1993). In addition to differences among species, there is also high variability in call structure among individuals of the same species. There have been several demonstrations that these calls possess signature-like properties, with high variability in call structure between individuals, and low variability in call structure within an individual signaler (Snowdon & Cleveland 1980; Jones et al. 1993; Snowdon 1993; Jorgensen & French 1998). Several recent studies have suggested that the acoustic structure of these vocalizations is highly flexible, even in adult signalers. For instance, placing common marmosets in isolation from their home group is associated with modification in the acoustic structure of the phee call (Norcross & Newman 1993; Schrader & Todt 1993). Further, pygmy marmosets housed in the presence of novel conspecifics exhibited a significant reduction in variation in the vocal structure of individual-specific trill calls over a 10-wk period (Elowson & Snowdon 1994). Finally, individual black tufted-ear marmosets (*Callithrix kuhlii*) displayed significant changes in the acoustic structure of phee calls over a 3- to 4-yr period of time (Jorgensen & French 1998). Thus, these signature-like calls in callitrichids may be a useful model for assessing vocal plasticity in non-human primates.

Marmosets and tamarins live in highly social groups, usually consisting of a reproductive male–female pair and several non-reproductive offspring of varying ages (Moynihan 1970; Stevenson & Poole 1976; Hubrecht 1985). Although these groups are extremely social and cooperative, they are by no means completely stable. Emigration from one group to another, or the formation of new pair bonds, may occur several times over the lifetime of an individual (Digby & Barretta 1993). These changes in intragroup demography constitute significant sources of social variability. Further, the modification of territorial boundaries, dispersal processes, and group turnover can change the identity of intergroup social contacts (Rylands 1989). The multiple functions of the phee call (defense of territory, location of separated group members, and mate attraction) demonstrates its integral role in the complex social lives of marmosets and tamarins, and suggests that the acoustic parameters of the phee call might be particularly sensitive to changes in social environments.

The purpose of our present experiment was to test whether changes in intergroup social environments were associated with modifications in the vocal structure of phee calls in marmosets. We recorded baseline information on phee calls in 11 marmosets housed in stable social environments, and used discriminant

function analysis (DFA) to differentiate and predict individual callers. After this baseline period, seven marmosets were exposed to new neighbors, while four remained with long-term neighbors, and phee calls were again recorded. To the extent that phee calls are modified by social context, we predicted that our ability to correctly classify calls by DFA in this second phase of the study would decrease significantly in marmosets with new neighbors, relative to the calls collected from marmosets in stable social environments.

Methods

Subjects and Housing

Subjects for this study were 11 Wied's black tufted-ear marmosets (*C. kuhlii*) maintained in five social groups at the Callitrichid Research Center at the University of Nebraska at Omaha. Wire mesh enclosures for each group measured approximately $1.2 \times 0.9 \times 2.4$ m. All enclosures were equipped with branches, nest boxes, and various enrichment devices. Marmosets were fed a mixture of Zupreem marmoset diet (Hills Brothers), Mazuri primate fiber sticks, various fresh fruit and vegetables, and dairy products. Marmosets were also given free access to fresh water. The three colony rooms involved in this study were maintained at a constant temperature of 20–22°C and were subject to a 12:12 light/dark cycle. Visual access between groups housed in the same colony room was eliminated, but animals had both auditory and olfactory contact with other marmoset groups housed in enclosures in the same colony room. Table 1 presents demographic information for all marmosets in the experiment.

Table 1: Demographic information for marmosets in the experiment

Experimental conditions	Sex	Age (yr)
Social constant		
Jin	F	6.5
Nic	M	2.0
Vol	F	3.0
Pam	F	1.5
Social change		
Ana ^a	M	4.5
The ^a	F	6.0
Sti ^a	F	8.5
Can ^a	M	3.0
Pix ^b	F	9.0
Hea ^b	M	9.5
Pal ^b	M	3.0

^aSocial change, new physical environment; ^bSocial change, same physical environment.

Recording

5 Vocalizations were collected with a Marantz (model PMD 201) portable
6,7 analog cassette recorder on Maxell UR tape cassettes. We used a Sennheiser ME
80 directional microphone (frequency range: 50–15 000 Hz). All recordings were
made between 07.30 and 15.00 hours with all 11 marmosets recorded for 30 min,
three times per week. Prior to each recording session animals were allowed to
8 habituate in the presence of an observer, approx. 1.5 m from the enclosures.
Individual marmosets were identified by speaking the name of the vocalizing
animal directly into the microphone immediately following the end of the call
(Jorgensen & French 1998). Colony room doors were left slightly ajar in order to
stimulate calling bouts from focal animals (McConnell & Snowdon 1986).
Vocalizations were collected for a total of 16 wk. The documentation of baseline
acoustic structure occurred during the first 8 wk of the study (phase I). During
this phase, recordings of spontaneously produced phee calls were collected from
marmosets in colony rooms where they had resided for at least 4 mo, and into
which no unfamiliar conspecifics had been introduced for a period of at least
10 wk prior to the beginning of the study.

At the end of phase I, experimental animals were housed in the presence of a
group of novel conspecifics (social change, $n = 7$). Of these seven individuals, four
were moved into a different colony room containing a group of novel conspecifics,
while three remained in the same room but neighboring cages contained
unfamiliar, novel marmosets. The purpose of these two experimental conditions
was to determine if changes in the social environment, rather than or in addition
to changes in the physical environment, were responsible for any change in an
individual's vocal structure. In the control condition, marmosets were maintained
in the same social environment (social constant, $n = 4$). Calls were recorded
during the 8-wk-long phase II period in a manner identical to phase I.

Acoustic Analysis

Phee calls were analyzed by sound spectrograms generated with Canary 1.2.4
bioacoustics workstation software (Cornell Laboratory of Ornithology, Ithaca,
NY, USA) on a Macintosh G3 computer. Each spectrogram was measured for a
total of nine acoustic and temporal features: total call duration (Call Dur),
syllable duration (Syl Dur), inter-syllable interval (ISI), peak frequency (High
Freq), minimum frequency (Low Freq), frequency range (Δ Freq), start frequency
(Start Freq), stop frequency (Stop Freq), and total number of syllables per call
(Num Syl). Duration measures were accurate to the nearest ms, and frequency
measures were accurate to the nearest Hz. The nine parameters chosen for this
study are similar to those used in earlier studies of callitrichid vocal behavior
9 (Jones et al. 1993; Norcross & Newman 1993; Elowson & Snowdon 1994;
Jorgensen & French 1998), and are known to exhibit significant variation among
individuals in *C. kuhlii* (Jorgensen & French 1998). To ensure an equal
contribution of individual marmosets to the data set, 10 calls recorded from

each individual in each phase of the study were included for final analysis (Norcross et al. 1999).

Data Analysis

Prior investigations have successfully used DFA to investigate both temporal stability and social context effects in primate vocalizations. Using DFA, Jorgensen & French (1998) revealed a lack of stability in the vocal structure of phee calls in marmosets over an extended period of time. Norcross et al. (1999) demonstrated that marmoset phee calls are clearly discernible based on context (i.e. home cage vs. isolation). In this particular study, we used predictive DFA as a means of determining whether marmosets alter the acoustic structure of their phee call when placed in the presence of novel conspecifics. Predictive DFA allows for the classification of subjects into groups on the basis of several different measurements (Stevens 1996). In this case, we used predictive DFA to classify marmoset phee calls to individual marmosets. Discriminant functions for classifying calls to specific individuals were generated (SPSS 10.1 for Windows) using acoustic and temporal parameters from calls collected prior to introducing marmosets to unfamiliar conspecifics. To enhance the validity and accuracy of these classifications, we used a 'jack-knifed' or 'leave-one-out' procedure. In this test, the phee call to be classified is not used in the creation of the classification function. These same functions were then used to classify calls recorded after the introduction of unfamiliar animals. We then analyzed the changes in the percentage of correctly classified calls between marmosets in the social constant and social change groups with a two-factor mixed design ANOVA. We expected that significant changes in acoustic structure would be reflected in lower classification accuracy for marmosets in the social change vs. the social constant group.

Although we predicted that a change in social environment would ultimately lead to a significant change in the acoustic structure of phee calls, we had no a priori predictions regarding the direction of change in vocal parameters (e.g. whether call duration would increase or decrease in the presence of new social neighbors). To test whether call parameters were modified in a consistent fashion, we performed sign tests on the direction of change for each parameter for marmosets in the social change condition. Finally, we evaluated whether the magnitude of change in each vocal parameter was greater for marmosets in the social change than in the social constant condition by comparing the absolute change across phases of the experiment for each parameter using an independent-sample t test.

Results

Marmoset phee calls collected during phase I of the study demonstrated individually distinct, or 'signature' properties. The discriminant functions correctly assigned calls to individuals with high accuracy, ranging from 60 to

100% correct classification. The first three discriminant functions accounted for 90.9% of the variance (54.2%, 25.2%, and 11.5% for functions 1, 2, and 3, respectively). The standardized canonical discriminant function coefficients for these functions are presented in Table 2. Call Dur and Num Syl were important variables in differentiating individual calls in the first two functions, and Δ Freq, High Freq, Syl Dur, and ISI had high values in function 3. The ability of the discriminant functions to correctly assign vocalizations in the two groups was the same (social constant: $85.0 \pm 8.3\%$; social change: $84.3 \pm 6.3\%$). Table 3 presents the classification matrix from the discriminant functions generated for all marmosets in phase I.

Table 2: Standardized canonical discriminant function coefficients for the first three functions

Parameter	Function 1	Function 2	Function 3
Call Dur	-1.85	0.88	0.47
Δ Freq	0.22	0.44	0.74
High Freq	-0.10	0.22	-0.61
Low Freq	0.64	0.26	0.19
Start Freq	-0.24	0.14	-0.27
Stop Freq	0.08	0.40	0.22
Num Syl	2.04	-0.82	-0.16
Syl Dur	-1.5	0.09	-0.61
ISI	-0.06	0.43	0.56

See text for definition of acoustic parameters.

Table 3: Discriminant function analyses (DFA) classification matrix generated from vocalizations recorded during phase I of the study. Values indicate percentage of calls assigned to individuals by the DFA

ID	Predicted caller identity										
	Ana	The	Pix	Hea	Sti	Can	Pal	Jin	Nic	Vol	Pam
Ana ^a	90	0	0	0	0	0	0	0	0	10	0
The ^a	10	80	0	0	0	0	0	0	10	0	0
Pix ^a	0	0	90	0	0	0	0	0	10	0	0
Hea ^a	0	0	0	100	0	0	0	0	0	0	0
Sti ^a	0	0	0	10	60	0	0	10	10	10	0
Can ^a	0	0	0	0	0	100	0	0	0	0	0
Pal ^a	20	10	0	0	0	0	70	0	0	0	0
Jin ^b	0	0	0	0	0	0	0	100	0	0	0
Nic ^b	0	0	0	0	0	0	0	0	80	10	10
Vol ^b	0	0	0	0	10	0	0	0	30	60	0
Pam ^b	0	0	0	0	0	0	0	0	0	0	100

^aSocial constant; ^bSocial change.

Table 4: Phase II reclassification matrix, using DFA generated from vocalizations recorded during phase I of the study. Values indicate percentage of calls assigned to individuals by the DFA

ID	Predicted caller identity										
	Ana	The	Pix	Hea	Sti	Can	Pal	Jin	Nic	Vol	Pam
Ana ^a	20	10	0	0	20	0	30	10	0	10	0
The ^a	0	20	0	0	0	0	30	20	0	10	20
Pix ^a	0	0	0	0	0	0	0	70	0	0	30
Hea ^a	0	0	20	50	20	0	10	0	0	0	0
Sti ^a	0	0	0	20	70	0	0	0	0	10	0
Can ^a	0	0	0	30	30	30	0	10	0	0	0
Pal ^a	0	0	0	50	40	0	0	10	0	0	0
Jin ^b	0	0	10	0	20	0	0	80	0	0	0
Nic ^b	0	0	0	0	0	0	0	0	70	0	20
Vol ^b	10	0	0	0	10	0	0	0	0	70	10
Pam ^b	0	0	0	0	0	0	0	0	0	0	100

^aSocial change; ^bSocial constant.

Using the discriminant functions generated from calls collected in phase I, we then classified calls recorded during phase II. Our results show that new social contexts are associated with significant modifications in the acoustic parameters of phee calls in marmosets. The classification matrix for calls recorded during phase II but classified by the DFA generated from calls collected in phase I is presented in Table 4. In correctly assigning phee calls to individuals in the social constant condition, the classification accuracy remained relatively high, but the ability of the DFA to correctly classify calls to individuals in the social change condition was considerably reduced after the introduction of novel conspecifics (Fig. 1). A two-way mixed design ANOVA revealed a significant interaction between time and social condition on the percentage of correct classification [$F(1,9) = 9.38, p = 0.014$]. Post-hoc *t* tests showed that classification accuracy for vocalizations collected from marmosets after a change in social context was significantly reduced [$t(6) = 4.72, p = 0.003$], while classification accuracy was unaltered if no social change occurred [$t(3) = 0.77, ns$]. Although sample sizes were not sufficient for statistical evaluation, we compared classification accuracies for animals in the social change condition for two subsets of this group: (1) marmosets that were housed in both novel rooms and in the presence of novel social partners ($n = 3$), vs. (2) marmosets that remained in their familiar room but were housed with new neighbors beginning at week 9 ($n = 4$). Our results show that the reduction in classification accuracy from phase I to phase II for marmosets that received an environmental and social change (82.5 ± 8.5 – $35.0 \pm 11.9\%$) was similar to the reduction in classification accuracy associated with a simple social change (86.7 ± 8.8 – $16.7 \pm 16.0\%$).

Changes in the immediate social environment of marmosets are associated with dramatic changes in the acoustic properties of phee calls. The magnitude and

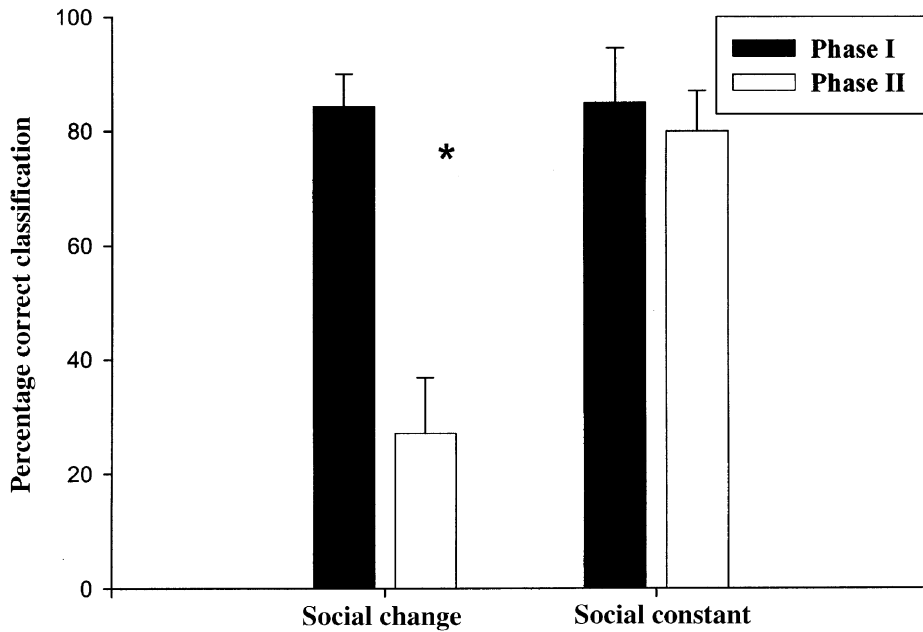


Fig. 1: Percentage of correctly classified marmoset phee calls for both the social constant and social change groups, phase I (weeks 1–8) vs. phase II (weeks 9–6)

direction of change for each vocal parameter in individual marmosets are shown in Table 5. We used sign tests to determine if there was any consistency to the directionality of change in the calls produced by marmosets in the social change condition. Results revealed no reliable direction of modification for any of the nine parameters included in this study ($p > 0.05$). Finally, independent sample t tests revealed that the absolute change of the vocal parameters was significantly greater for marmosets in the social change than in the social constant condition for two of the nine acoustic parameters [start frequency $t(9) = 3.51$, $p = 0.007$ and number of syllables per call $t(9) = 4.82$, $p = 0.001$].

Discussion

The phee call in Wied's black tufted-ear marmosets (*C. kuhlii*) possesses characteristics associated with a signature vocalization: high within-individual consistency and high between-individual variability. However, marmosets modified the structure of their phee call in response to changing social conditions. As predicted, marmosets exposed to novel conspecifics significantly altered the acoustic structure of the phee call, while marmosets maintained in a stable social environment did not experience significant fluctuations in vocal structure. Analysis of the nine vocal parameters examined in this study indicated no consistency in direction of change in the acoustic structure of marmosets exposed

Table 5: Change in individual acoustic parameters (phase II – phase I) for marmosets in social change and social constant conditions. Mean values for each group represent the average of the absolute change for each parameter

Condition	ID	Call Dur (s)	Δ Freq (kHz)	Peak Freq (kHz)	Low Freq (kHz)	Start Freq (kHz)	Stop Freq (kHz)	Num Syl	Syl Dur (ms)	ISI (ms)
Social change	Ana	-0.81	-0.20	-0.15	-0.31	-0.21	-0.29	-1.3	125.28	-8.38
	The	-0.33	-0.002	-0.24	-0.13	-0.19	0.15	-1.0	123.95	83.10
	Pix	-0.84	-0.29	-0.41	-0.10	-0.15	-0.28	-1.5	17.69	37.75
	Hea	0.83	0.11	0.54	0.43	0.47	0.40	1.4	21.69	-13.72
	Sti	-0.66	0.08	-0.12	-0.21	-0.27	-0.12	-0.8	106.64	-35.30
	Can	0.29	-0.16	0.30	0.45	0.39	0.23	1.5	-71.15	-58.89
	Pal	-0.31	-0.06	-0.06	-0.20	-0.20	-0.41	-1.5	286.19	-10.81
Mean (abs)		0.58	0.13	0.26	0.27	0.27	0.27	1.29	107.51	35.42
	SEM	0.10	0.04	0.07	0.05	0.04	0.04	0.11	34.25	10.51
Social constant	Jin	0.12	0.07	0.06	-0.04	0.02	-0.10	0.5	-3.48	-7.38
	Nic	-0.74	0.14	-0.11	-0.25	-0.07	-0.07	-0.8	27.12	-16.26
	Vol	-0.27	-0.24	-0.16	-0.17	-0.10	-0.08	-0.4	21.43	10.93
	Pam	0.22	-0.08	-0.19	-0.11	-0.01	-0.37	0.3	10.23	2.41
Mean (abs)		0.34	0.13	0.13	0.14	0.05	0.15	0.5	15.56	9.24
	SEM	0.14	0.04	0.03	0.04	0.02	0.07	0.11	5.34	2.92
t (df = 9)		ns	ns	ns	ns	3.51	ns	4.82	ns	ns
p		ns	ns	ns	ns	0.007	ns	0.001	ns	ns

to unfamiliar neighbors. Additionally, the absolute magnitude of change was significantly greater for marmosets in the social change group in only two of nine measured parameters (start frequency and number of syllables per call).

In their discussion on primate vocal communication, Snowdon & Elowson (1992) identified four basic mechanisms by which the fundamental acoustic structure of vocal signals arise: ontogeny is limited (vocal structure is fixed at birth), vocal structure is affected by physical maturation, vocal learning occurs only during a limited time period, or individuals maintain vocal plasticity throughout life (open learning system). Early investigations of squirrel monkey communication suggested that the fundamental mechanism affecting vocal structure is a limited ontogeny (Lieblich et al. 1980; Newman & Symmes 1982). More recently, physiologic changes during maturation have also been shown to significantly impact the vocal structure of a variety of non-human primates (vervet monkeys, *C. aethiops*: Cheney & Seyfarth 1986 pygmy marmosets, *C. pygmaea*: Elowson et al. 1998; rhesus macaques, *M. mulatta*: Hammerschmidt et al. 2000). However, in contrast to these earlier findings, we present evidence of vocal plasticity in the marmoset. Unlike squirrel monkeys, whose vocal structures are generally fixed at birth, black tufted-eared marmosets maintain the ability to alter vocal structure well into adulthood (Lieblich et al. 1980; Newman & Symmes 1982). Similarly, variation in vocal parameters that occur as a result of physiologic changes during development generally produce stereotypical patterns of modification, such as decreasing pitch with increasing body size (Hammerschmidt et al. 2000). In the present study no such patterns of modification emerged from the data. More importantly, all of the marmosets included in the data analysis were considered adults (>18 mo of age) prior to the beginning of the study. Therefore, any modification of vocal parameters due to maturational effects would have occurred before the onset of the experiment. The results of this investigation suggest that some non-human primates may maintain vocal plasticity throughout life, and are not constrained by physical maturation or a limited ontogeny.

Previous investigations of marmoset vocal stability have produced discrepancies in their results. Jones et al. (1993) reported that the acoustic structure of common marmoset phee calls remained highly stable over long periods of time. This result is not consistent with the results presented in this study, nor with several previous examinations of marmoset vocal structure (Elowson & Snowdon 1994; Jorgensen & French 1998; Snowdon & Elowson 1999). The disparities in these results may be accounted for by differences in the methodology used to obtain them. Jones et al. (1993) collected calls from marmosets separated from their social groups and placed in isolation. However, in the present study as well as in the previous studies mentioned, vocalizations were collected from individuals residing in their normal social groups. The presence or absence of social partners has previously been shown to have a significant effect on the acoustic structure of phee calls (Norcross & Newman 1993; Schrader & Todt 1993; Norcross et al. 1999). This difference in procedures could account for the possible differences in these studies. Removing individual marmosets from their

social groups could produce differences in affective arousal states. In fact, an insignificant amount of variation in call structure observed by Jones et al. (1993) was attributed to this source. In our study, all individuals remained in their pre-existing groups throughout the experiment. Therefore, differences in affective arousal states are not likely to have caused the large variation in acoustic structure we have reported here.

A fundamental characteristic of callitrichid vocalizations is the existence of an individual signature system encoded within the phee call. A signature system is the production of individually distinctive calls and the recognition of individual callers based on these individual differences in acoustic parameters (McCowan & Reiss 2001). The use of the phee call in intergroup communication and cohesion may obscure the adaptive value of vocal flexibility in changing social conditions. Marmosets that alter the acoustic structure of their phee call may do so for two possible reasons. On one hand, marmosets may alter the acoustic structure of their vocalizations in order to maximize differences in phee calls to avoid possible overlap with novel conspecifics. In order to maintain a signature system, individuals must be recognizable on the basis of their individual acoustic profile. Individuals may actively modify the structure of their phee calls in order to ensure they retain acoustic individuality during times of social change, in a manner analogous to the 'jamming avoidance response' in the frequency of electric organ discharge in weakly electric fish (e.g. Zakon et al. 1999). On the other hand, marmosets may alter the acoustic structure of vocalizations by reducing individual distinctiveness to converge on a more common or shared vocal signal. These changes could arise to facilitate the formation of new social bonds, a process that may be seen in certain avian and cetacean species (e.g. Nowicki 1989; Janik 2000). When unfamiliar pygmy marmosets (*C. pygmaea*) are placed in a common social environment, levels of individual variability in call structure are reduced, and vocal convergence has been proposed as an explanation of this result (Elowson & Snowdon 1994; Snowdon & Elowson 1999). While these notions of vocal divergence and convergence represent intriguing questions, the limitations of our design do not allow us to directly test these alternatives.

The alteration of a vocal signal that contains individual signature information represents a potential obstacle to the process of recognition of individual callers by group mates and other conspecifics. This results in several implications for the mechanisms that underlie recognition systems. First, individuality may be maintained if the acoustic parameters that are modified are not important to individual recognition on the part of receivers. Secondly, individuality could be maintained if the degree of modification of the acoustic properties of the calls was within tolerance limits for the neural mechanisms underlying recognition of individuality. Finally, a signature system could be maintained in the face of plasticity in the signature signals if receivers actively update the stored representations of others' call structures. According to Wang (2000), the cortical representation of vocalizations or sounds stored in the auditory cortex of an individual is shaped by what that individual hears on a day-to-day basis. This

system would, therefore, allow the maintenance of an accurate, up-to-date 'picture' of individual vocalizations in order to maintain a vocal recognition system. Further research is needed to determine exactly what mechanisms serve to maintain recognition in the face of vocal plasticity.

From the results presented here we can conclude that not only do marmosets maintain vocal plasticity throughout life, but the social environment of the caller also has a significant impact on the ultimate structure of its vocalizations. The results presented in this study have added to a small but growing body of evidence suggesting that the basic mechanisms controlling and influencing the acoustic structure of non-human primate vocalizations go beyond a limited ontogeny and simple maturation effects. By demonstrating that acoustic structure is not necessarily fixed at birth and that social environment has a significant impact on acoustic parameters, we have added to a much needed framework for future research concerning vocal plasticity in social species.

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