

Wild Chimpanzees Produce Group-Specific Calls: a Case for Vocal Learning?

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Abstract

Vocal learning, where animals can modify the structure of their vocalizations as a result of experience, has been found in a range of birds and mammals. Although vocal learning is a fundamental aspect of developing spoken language, there is as yet little evidence that vocal learning occurs in primates. Here we examine whether vocal learning may occur in chimpanzees. We analysed whether wild male chimpanzees, *Pan troglodytes verus*, of four communities living in a similar habitat in the Taï Forest, Côte d'Ivoire, developed community specific pant hoots. If so, we expected males of three contiguous communities to have distinct pant hoots, while pant hoots of males from a fourth, distant community, located 70 km away, should only differ from those of the contiguous communities by chance. Our analysis confirmed these expectations. In addition, the acoustic distances between the pant hoots of pairs of individuals did not correlate with the genetic relatedness of those pairs, where genetic relatedness was determined using nuclear DNA analysis. Thus, neither habitat nor genetic differences accounted for the observation that there were acoustic differences in the pant hoot structure of males living in neighbouring communities, but not in those of males from a distant community. This suggests that chimpanzees may actively modify pant hoots to be different from their neighbours, providing support for the vocal learning hypothesis.

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Introduction

Vocal learning has sparked considerable interest, as it is required to develop spoken language. Vocal learning has been documented across a range of bird and mammal taxa, and is defined as the modification of the acoustic structure of a vocalization as a result of experience (Janik & Slater 2000). Versatile vocal

learners, those able to mimic the vocalizations of other members of their own and of other species, include some oscine birds (for review see Baylis 1982), psittaciformes such as parrots (Todt 1975), marine mammals and humans (for review see Janik & Slater 1997). Other species such as rhesus monkeys (Sutton et al. 1973) and cats (Molliver 1963) can be trained to modify the amplitude and duration of their calls through learning, although it is not clear whether this also occurs naturally. However, to incorporate new sounds into a repertoire, the ability to actively modify pitch or other frequency characteristics of vocalizations through learning is also required (Janik & Slater 2000). To date there is limited evidence that non-human primates are able to actively modify the pitch or other frequency parameters of their calls in spite of a range of studies addressing vocal learning (for reviews see Janik & Slater 1997, 2000; Fischer 2003). This implies that the extraordinarily flexible vocal learning abilities of humans must have evolved since humans last shared a common ancestor with chimpanzees, some 4–6 million years ago.

In mammals and psittaciforme birds, the striking similarity between diverse taxa that are vocal learners is that they live in large, socially complex and often fission–fusion groups (where individuals can be separated for hours or days at a time). They often communicate across long distances and in noisy environments, like tropical forest or aquatic habitats (parrots: e.g. Vehrencamp et al. 2003; marine mammals: e.g. Tyack & Sayigh 1997; bats: Jones & Ransome 1993; humans: Nettle 1999). Such species typically have individual and group specific calls, so that individuals or groups can be identified by their call alone (Bradbury & Vehrencamp 1998). While group specific calls can result from genetic differences between groups (prairie dogs: Travis et al. 1997, squirrel monkeys: Lieblich et al. 1980), they may also result from learning, so that an individual's call converges with those of others (humpback whales: Payne & Payne 1985, yellow-naped amazon parrot: Wright & Wilkinson 2001).

Learning of group specific calls is suggested to permit quicker recognition of group members (Nowicki 1983), help maintain social bonds (Tyack & Sayigh 1997; Vehrencamp et al. 2003) and signal group identity in cooperative defence (Brown & Farabaugh 1997; Nettle 1999, Wright & Wilkinson 2001). The advantages of vocal learning include both accentuating individual or group differences beyond the differences that arise from vocal tract morphology in order to minimize caller ambiguity (Janik & Slater 1997), and a more flexible ability to emphasize affiliations, such as being able to match the call characteristics of a new group after dispersal (Wright & Wilkinson 2001), or during temporary associations (Tyack 1997; Janik & Slater 1998). We suggest that amongst primates, chimpanzees are likely to exhibit vocal learning, as they live in socially complex fission–fusion groups in tropical forest habitats and communicate over long distances (Goodall 1986; Boesch & Boesch-Achermann 2000).

Two studies have suggested that chimpanzees may be able to modify their vocalizations as a result of auditory and social experience. Both studies examined the pant hoot, a long-distance call used during both within and between group interactions. Two male chimpanzee dyads in Mahale, Tanzania, demonstrated

call convergence, meaning that their calls became acoustically more similar to their chorus partner's than when calling alone (Mitani & Gros-Louis 1998). Mitani & Gros-Louis concluded that the chimpanzees were actively modifying their calls. While the results are promising, replicating this study would be important as sample size only permitted rigorous analysis of one dyad. A second study found that pant hoots of males from two different captive chimpanzee groups showed group level acoustic differences (Marshall et al. 1999). Because chimpanzees of each group probably came from several different regions, suggesting limited within group genetic relatedness, it seemed that their individual pant hoot structures must have converged over time. In addition, a pant hoot that ended with a raspberry sound was introduced into one group by a new chimpanzee and this pant hoot variation was subsequently adopted by others. Although the raspberry sound was already present in the repertoire of the other chimpanzees, they had not previously combined it with a pant hoot. Marshall et al.'s work (1999) demonstrates that male chimpanzees living together in a group may have a tendency to converge the structure of their pant hoots.

Furthermore, it is known that pant hoots encode individual differences (Marler & Hobbett 1975) and that pant hoot structure differs for geographically separated chimpanzee populations (Mitani et al. 1992, 1999). However, it is not clear whether this is because of environmental or genetic differences, or due to vocal learning. Similarly, for other primate studies that show either call convergence (pygmy marmosets: Elowson & Snowdon 1994) or regional dialects (red-chested moustached tamarins: Maeda & Masataka 1987, Japanese macaques: Sugiura 1998, barbary macaques: Fischer et al. 1998), the mechanism by which these have arisen remains debated (Janik & Slater 2000; Fischer 2003).

In order to determine if group-specific calls are indicative of vocal learning, acoustic variation resulting from genetic differences must first be ruled out. In frogs, for example, which are not known for having extensive learning abilities, dialects across populations vary according to the genetic distances between populations (Ryan et al. 1996; Wycherley et al. 2002). Conversely, in oscine birds, where songs are learned, a strong association between vocal and genetic variation is not usually found (Catchpole & Slater 1995). In the current absence of knowledge of specific genes involved in the production and structure of vocalizations, these studies have relied on a comparison of genetic and acoustic similarity between individuals and groups. Measurement of genetic similarity currently acts as the best available approximation of individuals sharing either a predisposition to produce a particular vocalization or of sharing genetically determined physical characteristics. As vocal characteristics are to some extent determined by physical structures, such as size of the lungs and length and shape of the vocal tract (Lieberman 1984), physically similar individuals are likely to have similar vocal characteristics.

In this study we examined whether vocal learning may occur in chimpanzees. We examined whether adult males from four communities, living in similar habitats in the Taï National Park, Côte d'Ivoire, had pant hoots with community specific structures, which could not be explained by genetic differences.

Methods

Study Site, Individuals and Data Collection

We recorded pant hoot vocalizations from adult male chimpanzees of three contiguous habituated communities, North, Middle and South, from Apr. 1998 through to May 2000 in the Taï National Park, Côte d'Ivoire, West Africa (see Boesch & Boesch-Achermann (2000) and Herbinger et al. (2001) for more details). The South community was 4 km to the south of the North community, with the Middle community being sandwiched between the two. In addition, we recorded vocalizations from the Guiroutou community, a semi-habituated community 70 km to the south of the other three communities. In this study, we only included pant hoots from adult males as they pant hoot considerably more than females (Marler & Tenaza 1977, own data). All adult males of the North, Middle and South communities were included as well as three well-habituated males of Guiroutou. We used continuous focal animal sampling, with dawn to dusk follows for the contiguous communities and ad libitum sampling (Altmann 1974) for the Guiroutou community. C.C. collected 1044 h of data from North and Middle community males and I. H. collected 178 h of data from the South and 80 h from the Guiroutou community. Table 1 presents the numbers of males, their known and estimated ages. Males alternated as focal animals and were observed from a distance of 3–15 m. All vocalizations were recorded using a Sennheisser ME65/K6 (Wennebostal, Germany) directional microphone and windshield (frequency response: 50–15,000 Hz \pm 2.5 dB re 20 μ Pa) and a Sony WMD6C Professional Walkman or Marantz PMD 222 portable cassette recorder (Tokyo, Japan).

From 1999 onward, fresh faecal samples for genetic analysis were collected from all members of the North, Middle and South community. Samples were preserved by desiccation using silica gel beads as previously described (Bradley et al. 2000).

Table 1: Number of pant hoots per individual per community used in the analyses for travel and food contexts, and ages of individuals

Age and Pant hoot context	Community												Total
	North			Middle			South			Guiroutou			
	*Mac	Mar	Nin	Urs	Leo	Bob	Zyo	Mku	Kao	Dal	Zad	Soe	
Age (yr)	34 ^a	18	12	31 ^a	20 ^a	16 ^a	34 ^a	39 ^a	21 ^a	>30 ^a	approx. 20 ^a	approx. 20 ^a	
Travel	11	22	3	17	4	5	3	3	4	18	4	3	97
Food	6	17	5	6	3	3	5	3	4	4	4	4	64

Ages are taken from the beginning of the study. ^aEstimated ages. *Individuals.

Description of Pant Hoots

A pant hoot is a species typical long distance call, comprised of up to four phases (Fig. 1) (Marler & Hobbett 1975; Mitani et al. 1999, own data). Although any phase may be absent, when the phases are present, they occur in a relatively fixed order, as follows: (i) the introduction has one or several tonal elements, with a level fundamental frequency of 300–600 Hz and harmonics rarely visible; (ii) the build-up generally has up to 25 shorter tonal exhaled elements inter-dispersed with broad-band, noisy inhaled elements of similar duration, giving the phase a rapid, rhythmic quality. The fundamental frequency is between 200–500 Hz, which may gradually rise towards the end of the phase; (iii) the climax usually contains one or several screams, with a high fundamental frequency of 800–2000 Hz, many harmonics, and high variability in the degree of noisy or tonal quality. The duration of a single climax scream is between 0.2–1.0 s. As well as screams, hoo and bark vocalizations may also be produced in the climax phase. All elements are inter-dispersed with low frequency voiced inhaled elements; (iv) finally the let-down is similar to the build-up but with fewer elements and with decreasing, rather than a rising pitch, or fundamental frequency. It is the most frequently omitted phase, occurring in about 40% of pant hoots in Tai.

Pant hoots are produced in multiple contexts, including both between and within community activities. Between community activities include territory border patrolling and neighbour encounters. Within community activities include travelling, approaching or meeting chimpanzees in other parties, arriving at food or feeding, nesting and occasionally during conflicts.

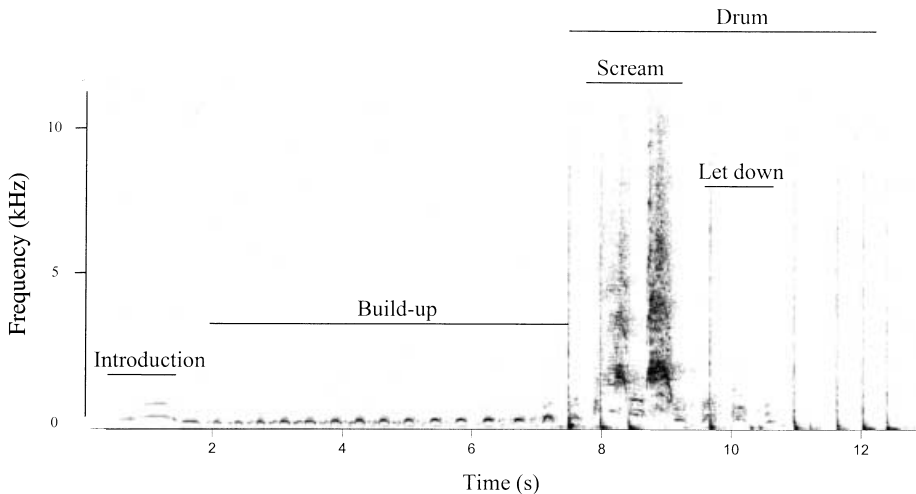


Fig. 1: Spectrogram of a pant hoot showing its four pant hoot phases, produced in association with a tree-drumming

Another common long-distance signal produced by chimpanzees is tree-buttress drumming, where chimpanzees pound on tall buttress roots of trees with their hands and feet, producing an impressive sound that can carry over 1 km. Because drumming is often produced in association with pant hoots during travel contexts, we also analysed whether drumming characteristics differ between communities.

Analysis

Acoustic analysis of pant hoots and drums

Only pant hoots and drums that met the following criteria were selected for the analysis: certainty of signaller, unambiguous context, without overlap with other signallers or masking background noise. Overlapping, or chorused, pant hoots were excluded as an individual's call characteristics may change during chorusing (Mitani & Gros-Louis 1998). To limit pseudo-replication, only one pant hoot and drum per signaller was included for the duration of an uninterrupted activity, such as travelling or feeding. Furthermore, because pant hoots produced in different contexts may be acoustically different (Uhlenbroek 1996) we included only pant hoots produced in travel and food contexts and conducted separate analyses for each respectively. Following these criteria, 364 pant hoots were selected for testing whether the presence or absence of pant hoot phases were influenced by community identity. To test the acoustic characteristics of all phases simultaneously, however, only 161 pant hoots, those with all phases present, were analysed (Table 1).

For the acoustic analysis, we digitized pant hoots using Canary 1.2.4 with sampling frequencies of either 22.05 kHz/16 bits or 44.1 kHz/16 bits (Charif et al. 1995). Down sampling using an anti-aliasing filter and fast Fourier transforms were conducted using SIGNAL sound analysis system (Engineering Design, Belmont, MA; Beeman 1996) (1024-pt FFT; time resolution: 5 ms; frequency range: 8820 Hz; frequency resolution: approx. 22 Hz). Presence and absence of the four pant hoot phases as well as of drummings were documented. Then a suite of variables from each phase were measured (Appendix), either by hand using Canary 1.2.4 (with a filter bandwidth: 174.9 Hz; time resolution: 0.73 ms; frequency resolution: 23.22 Hz) or using an acoustic software programme, LMA, developed and customized by Hammerschmidt (1990), where values were calculated at 5 ms intervals throughout each call.

Statistical analysis

Determining variables influenced by community identity As acoustic discrimination of calls by humans and animals is rarely dependent on a single acoustic variable, we tested whether continuous and categorical variables were influenced by community identity, using a simultaneous discriminant function

analysis (DFA) (Tabachnick & Fidell 2001). The variables are combined into $n-1$ discriminant functions (where n is the number of groups in the grouping variable). The discriminant functions are selected so that the ratio of the between to the within group variances is maximized. Based on the discriminant functions, calls are assigned to their appropriate community or to another community, producing a percentage of correct classification.

We conducted discriminant function analysis on two sets of data: pant hoots produced in travel contexts and pant hoots produced in food contexts. For each set of data we conducted two DFAs, the first included pant hoots from the three contiguous communities whilst the second also included pant hoots from the distant community. This enabled us to determine how well the pant hoots of the contiguous communities classified as groups compared with those of the distant community. As we had differing numbers of pant hoots per individual, we randomly selected balanced data sets for each analysis (using three calls per individual per community), to avoid over representation of any individual. The balanced data sets were used to create the discriminant functions, producing the original classification score. To test the robustness of the discriminant functions, all the remaining calls (60% of the total data) were then classified according to the functions, producing the external classification score. We entered all variables into the DFA. For each DFA, more than half of the variables used were strongly correlated with other variables. Of these, all but those variables which correlated most strongly to the discriminant functions were automatically removed by the DFA. Additionally, more than half of the remainder were only weakly correlated to the discriminant functions and were also removed.

In order to determine if any community differences found reflected actual community differences or were just a chance by-product of individual differences, we conducted a permuted DFA (programmed by Roger Mundry) for each of the four DFAs. The permuted DFA also controlled for the effects of using replicates (R. Mundry & C. Sommer, pers. comm.). Each individual was randomly assigned to one of either the three or four groups respectively, with a DFA being conducted for every possible permutation for the three group analysis (1680 permutations). For the four group analysis, as the number of possible permutations exceeded permutation power, the DFA was repeated 1000 times. If the observed external classification score lay outside of the 95% confidence interval of the permuted distribution of classification scores, the result was deemed significantly different from chance.

In addition to looking at the overall observed classification scores in the four community analyses, we looked at the classification scores per community to determine whether the pant hoots of some communities were classified better than others. We tested if the observed external classification result of the distant community was significantly lower than that of the three contiguous communities using one-tailed Chi-squared tests with subdivision (Zar 1999). Communities that were not significantly different from each other were tested together against the distant community. For communities where the number of pant hoots was too small to determine classification scores from the DFA external classification

result, we used the jack knife classification, which formed the discriminant functions using each case except for the case being classified (Tabachnick & Fidell 2001).

To determine how well pant hoots could be attributed to individual signallers, a non-permuted DFA procedure was conducted for the nine individuals from the three contiguous communities for both travel and food data sets (as with only one independent variable permutation is not required). As in the community level analysis, three pant hoots per individual were used to create the discriminant functions and the remaining pant hoots were used to produce the external classification score.

Testing acoustic vs. genetic distances

To compare acoustic and genetic differences, we calculated first the acoustic distance between each pair of chimpanzees as follows: we took the centroids (the mean discriminant scores) of all calls for each individual for both contexts and then calculated a distance matrix using Euclidean distances.

A total of 114 individuals from the North, Middle and South communities were analysed by microsatellite genotyping, including the previously published data from 108 individuals (Vigilant et al. 2001). For the genotyping we used nine highly variable microsatellite markers, and the ability of this set of markers to discriminate individuals is supported by the high (> 0.999) average probability of paternity exclusion provided by these markers in this population (Bradley et al. 2000). Details of the genotyping process have been presented elsewhere, but it is worth noting that we employed several measures to ensure accuracy of genotypes, as is necessary when using DNA from non-invasive samples (Bradley et al. 2000; Morin et al. 2001; Vigilant et al. 2001). Genetic relatedness was estimated for each pair of chimpanzees within and between the three contiguous communities. Symmetrical estimates of pairwise relatedness (R) were produced using the Queller and Goodnight index (Queller & Goodnight 1989) implemented in the program RELATEDNESS 5.0, with standard errors estimated by jackknifing over loci. However, the non-independence of the pairwise comparisons complicates assessment of the significance of the relatedness estimates obtained. Thus, in order to determine whether a given pair of individuals should be considered 'related', we used the program Kinship, which uses simulations in order to determine the significance of the likelihood ratio of a suggested relationship category vs. the null hypothesis of no relationship (Goodnight & Queller 1999). The set of microsatellite loci used has previously been shown to provide estimates of R consistent with known familial relationships in these communities (Vigilant et al. 2001). The ability of the set of nine loci to provide reliable estimates of genetic relatedness of individuals was further evaluated by means of a rarefaction analysis (described in: Altmann et al. 1996). This analysis, in which pairwise relatedness is estimated using information from a single locus and re-estimated after sequential addition of the remaining loci, revealed that the variance in estimates using our data diminished after the addition of the seventh locus (data not shown). In order

to reduce the tendency to underestimate relatedness values as a consequence of using allele frequencies from related individuals, the relatedness estimates were calculated using allele frequencies derived from genotypes of 45 individuals of no known relatedness, selected proportionally from the three communities and both sexes.

In order to compare average relatedness estimates obtained for groups of males, permutation tests, in which the nine males of interest were randomly resorted into three groups of three individuals 5000 times, were used to assess whether the average observed male relatedness within and between communities was different from chance. Acoustic distances and genetic relatedness of chimpanzee pairs were correlated using a permuted Rowwise matrix K_r correlation test (Hemelrijk 1990) to determine the correlation significance, using the programme MatMan (Noldus 1998). The data were permuted 5000 times.

Results

Effect of Community Identity on Pant Hoot Structure

Community differences in pant hoot structure could be identified for the three contiguous communities, with external classification at 81% for pant hoots in travel and 84% for pant hoots in food contexts (Fig. 2). In each case the classification scores were significantly higher than for those achieved by random assignment of individuals (permuted DFA: travel $p = 0.01$, food $p = 0.005$). The 1680 permuted classification scores for travel ranged from 16 to 91% with a mean of 60%, and for food ranged from 8 to 84% with a mean of 45%). Both temporal and frequency variables, from the first three pant hoot phases, distinguished the pant hoots of different communities (Table 2 and Appendix). Presence or absence of pant hoot phases and drum variables showed no differences between communities.

The discriminant functions included six and five variables for pant hoots produced in travel and food contexts respectively (Fig. 2). In Fig. 2a, function one correlated with the dominant frequency band (DFB) of the exhaled build-up element and the maximum peak frequency of the climax, while function two correlated with DFB of the inhaled build-up element, the number of introduction elements, the acceleration of the build-up and duration of climax scream. In Fig. 2b, function one correlated with the DFB of inhaled and exhaled build-up elements as well as the total number of build-up elements, the minimum fundamental frequency, maximum peak frequency and duration of climax scream. Function two correlated with the number of introduction elements, acceleration of the build-up and the mean tonality of the climax scream.

For travel, a typical South community pant hoot was characterized by having higher pitched exhaled build-up elements with the energy in the climax scream being distributed over a lower range than a typical Middle or North community pant hoot (Figs 2 and 3). A typical Middle community pant hoot was characterized by having more introduction elements, higher pitched inhaled

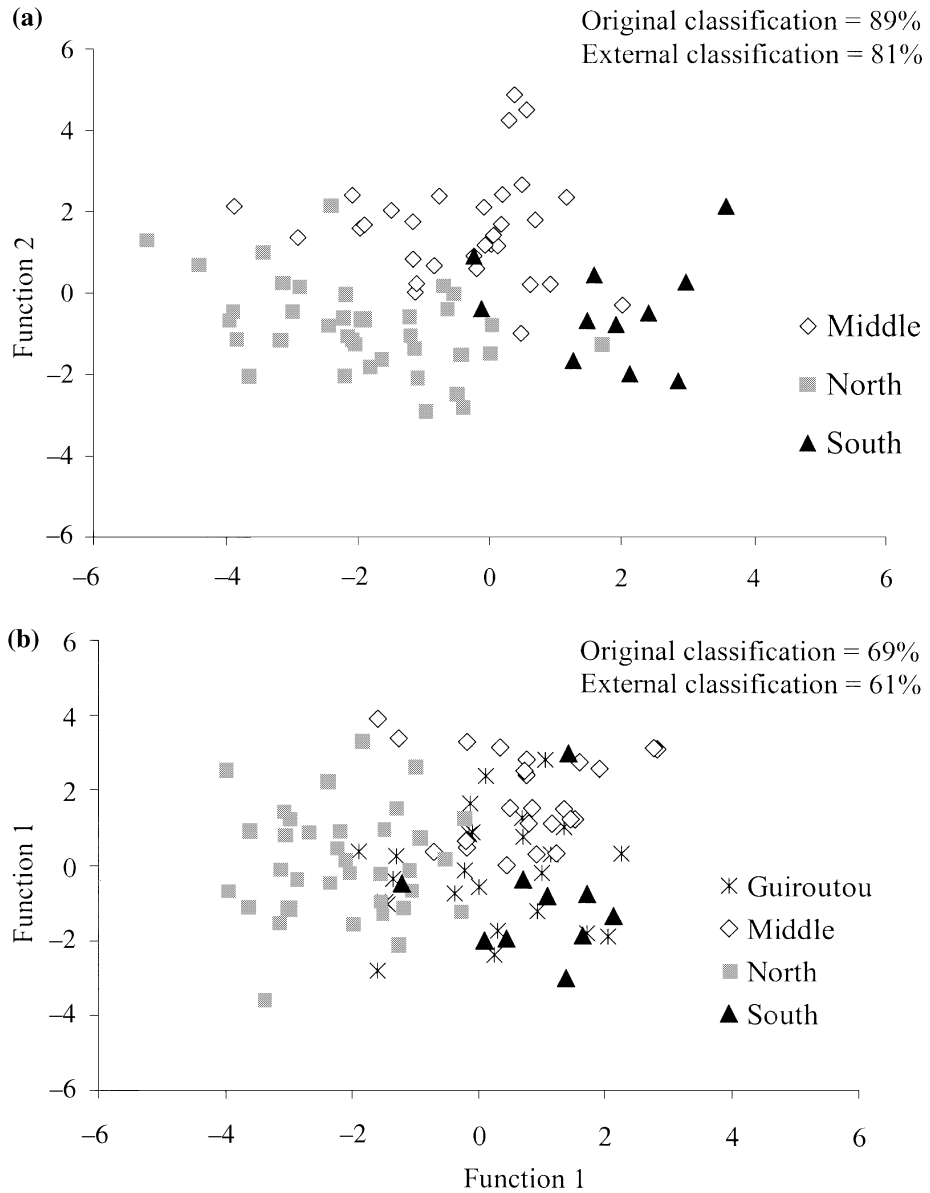


Fig. 2: Community differences in pant hoot structure, demonstrated with pant hoots produced in travel contexts, for (a) three contiguous communities and (b) three contiguous communities and the distant community. See text for the variables, which correlated with functions one and two

build-up elements with a faster rate of acceleration and a longer climax stream than a typical North or South community pant hoot (Figs 2 and 3). For food, the North community pant hoots were characterized by having lower pitched exhaled

Table 2: Variables ($\bar{x} \pm SD$) showing community differences in pant hoot structure in the discriminant function analyses (DFA), for all four chimpanzee communities, in travel and food contexts, using the same number of pant hoots per individual

Acoustic variable	Context of pant hoot	Community			
		North	Middle	South	Guiroutou
Introduction: number of elements	Travel ^{a,b,c}	2.67 ± 1.65	3.56 ± 1.81	1.44 ± 1.42	2.33 ± 1.8
	Food ^{a,b,c}	1.67 ± 1.0	2.89 ± 1.6	1.67 ± 1.11	2.4 ± 0.88
Build-up: DFB of exhaled element	Travel ^{a,b,c}	266 ± 36	311 ± 38	331 ± 22	312 ± 42
	Food ^{a,b}	296 ± 76	336 ± 50	343 ± 39	305 ± 43
Climax: scream duration	Travel ^{a,b,c}	371 ± 102	563 ± 153	479 ± 142	486 ± 187
	Food ^{b,c}	421 ± 69	611 ± 244	553 ± 177	540 ± 241
Climax: maximum peak frequency	Travel ^{a,b,c}	4811 ± 1837	3619 ± 1012	2408 ± 1707	2837 ± 1606
	Food ^{b,c}	5127 ± 1557	5966 ± 1682	2942 ± 2527	2575 ± 2180
Climax: minimum peak frequency	Food ^{a,b,c}	934 ± 221	746 ± 166	684 ± 155	799 ± 235
Climax: mean tonal quality	Travel ^b	26.3 ± 14.5	25.4 ± 14.4	16.7 ± 8.3	14.8 ± 4.4
Climax: maximum tonal quality	Food ^{a,b,c}	150 ± 64	230 ± 115	77 ± 43	93 ± 45
Build-up: rate of first half	Food ^{a,c}	3.1 ± 0.63	3.4 ± 0.74	2.6 ± 0.71	3.14 ± 1.1
Build-up: DFB of inhaled element	Travel ^{a,b,c}	326 ± 67	425 ± 51	361 ± 50	368 ± 70
Build-up: acceleration rate	Travel ^{a,b,c}	-0.12 ± 0.5	-0.3 ± 0.38	0.3 ± 0.35	0.11 ± 0.76
Build-up: number of elements	Travel ^{b,c}	15.3 ± 7.2	8.89 ± 5.15	9.78 ± 5.14	8.55 ± 3.08
Climax: minimum F0	Travel ^b	943 ± 171	791 ± 58	839 ± 128	775 ± 107
Drum: proportion of beats before climax phase	Travel ^b	0.6 ± 0.33	0.38 ± 0.39	0.74 ± 0.32	0.15 ± 0.18

Variables used for three^a and four^b community analyses. F0, fundamental frequency; DFB, dominant frequency band. See appendix for more detailed explanations of the acoustic variables. Variables used for the DFA of individual^c differences, but not for the three communities DFA, in travel contexts were: rate of first half of build-up and total number of build-up elements; in food contexts were: DFB of inhaled – DFB of exhaled build-up element, total number of build-up elements, maximum F0 of climax scream, as well as the number of barks in climax phase.

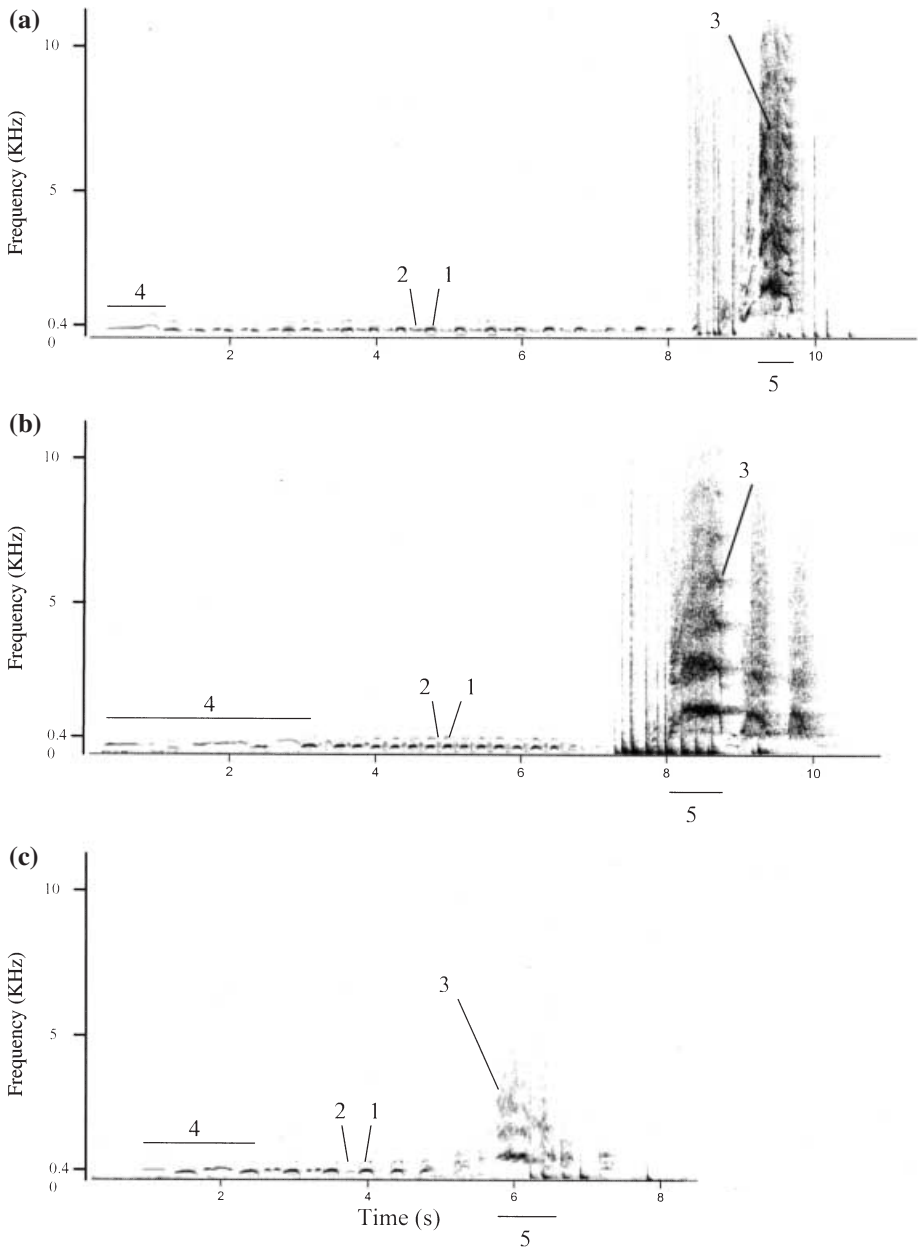


Fig. 3: The typical pant hoot of each community: (a) North, (b) Middle and (c) South. A pant hoot closest to the mean discriminant score is shown for each community. The distinguishing variables are 1, dominant frequency band (DBF) of exhaled; 2, inhaled build-up elements; 3, maximum peak frequency of the climax scream; 4, number of introduction elements; 5, duration of climax scream; 6, acceleration rate of build-up

build-up elements and energy in the climax scream starting from a higher frequency than the Middle and South communities. The Middle community pant hoots were characterized by the climax screams having a less tonal quality, more introduction elements and a slower rate of production of build-up elements than the North and South communities (Table 2 and Appendix).

When the distant community was added, the external classification of pant hoots dropped to 61% in travel and 64% in food contexts (Fig. 2b). This was not significantly different from the external classification scores achieved by random assignment of individuals (permuted DFA: travel $p = 0.5$, food $p = 0.1$. The 1000 permuted classification scores for travel ranged from 22 to 93% with a mean of 60%, and for food ranged from 7 to 100%, with a mean of 46%). The first two discriminant functions of the DFA explained 77 and 94% of the overall variance for travel and food contexts respectively and correlated with both temporal and frequency variables (Fig. 2b; Table 2). The third discriminant function for travel contexts, which explained the remaining 23% of the variance, correlated with the proportion of drums occurring before the climax. In addition, we looked more closely at the DFA classification scores in order to determine if pant hoots from particular communities tended to be more often misclassified than others. Significantly more of the distant community pant hoots were misclassified in both travel and food contexts as compared with those of the other three communities (Table 3).

In sum, we were able to confirm that the community differences were not a chance clustering of individual differences, by using the random assignment DFA procedure, run on two parallel analyses – pant hoots produced in travel and food contexts respectively, even though we only had three males per community.

Table 3: Percentage of pant hoots of each community that correctly classified in the four community discriminant function analyses (DFA), and cross-community comparisons

Community	Percentage of correct classification				Compared with distant community			
	Travel		Food		Travel		Food	
	Travel	n	Food	n	χ^2	p	χ^2	p
Guiroutou (distant)	31	16	33 ^a	12	9.5	0.01	6	0.02
Middle	65	17	50 ^a	12				
North	78	27	68	19				
South	78 ^b	9	72 ^a	12				

Brackets indicate communities tested together against the distant community in the subdivision chi-squared test. $df = 1$ for each test. Percentage of correct classification in the DFA is taken as the external classification, the mean of the jack knife and external classifications scores^a, or just the jack knife classification^b due to sample sizes. p-Values are corrected for multiple testing using Bonferroni.

Effect of Individual Identity on Pant Hoot Structure

We tested whether individual differences in pant hoots could be characterized using different acoustic components from those which were required to show community differences in pant hoots. Individual differences were identified. External classification was 67% for travel and 68% for food context pant hoots, both of which were significantly above chance levels (chance classification for nine individuals = 11.1%, travel: Exact $\chi_1^2 = 65.9$, $p < 0.001$, food: Exact $\chi_1^2 = 68$, $p < 0.001$). The first two discriminant functions of the DFA included 83 and 71% of the overall variance for travel and food contexts respectively. Eight variables were used to determine individual differences in travel contexts. Although six variables were the same as those used to determine community differences between the three contiguous communities, two additional build-up variables were needed to determine individual differences (Table 2). This suggests that group specificity was characterized by a particular combination of variables. Although these variables were also used to determine individual differences, they alone were not sufficient. To determine individual differences two additional variables were needed, which were independent from the group variables. The same was observed for the pant hoots in food contexts, as ten variables were required to determine individual differences, only four of which were the same as those used to determine community differences (Table 2). Furthermore, one variable needed for determining community differences was not needed for determining individual differences.

Comparing Acoustic Distances with Genetic Relatedness

Two of nine pairs of within community males and four of 27 pairs of males from different communities had an estimated R exceeding 0.195, the average relatedness previously estimated for known paternal half-siblings in this population (Vigilant et al. 2001) (Table 4). However, analysis using Kinship showed that only three of these dyads were significantly likely to represent half-siblings. The average relatedness of all three males in the South community, $R = 0.1311$, was significantly different from zero, the level for random relatedness ($p < 0.05$), mainly because one of the South community pairs was highly related ($R = 0.44$), but were not father and son. The average relatedness for the other two communities and for all between community comparisons, however, were not significantly different from 0 ($p = 0.18$). It is worth noting that although the South community males were generally more related than the males of the other two communities, their pant hoots did not classify better than those of the other communities (Table 3).

Acoustic similarity of pant hoots between individuals was not a function of genetic relatedness (Table 4) (permuted Rowwise matrix correlation test: travel: Kendall's tau = -0.06, $n = 36$ dyads, $p = 0.75$; food: Kendall's tau = 0.04, $n = 36$ dyads, $p = 0.43$). Furthermore, the acoustic distances did not differ between related ($n = 3$ dyads) and unrelated pairs of individuals (permuted

Table 4: (a) Pairwise genetic relatedness values between chimpanzees in the three contiguous communities and the acoustic distances of pant hoots between the same pairs in (b) travel contexts and (c) food contexts

(a)		Pairwise r values								
Community Individual		North			Middle			South		
		Mac	Mar	Nin	Urs	Leo	Bob	Zyo	Mku	Kao
North	Mac	–								
	Mar	0.01	–							
	Nin	–0.24	–0.14	–						
Middle	Urs	0.09	–0.06	0.18						
	Leo	–0.05	–0.17	0.21	0.33	–				
	Bob	0.22	0.1	–0.13	–0.24	–0.34	–			
South	Zyo	0.09	–0.2	–0.37	–0.23	–0.34	–0.04	–		
	Mku	0.05	0.15	0.16	–0.17	–0.12	0.14	0.15	–	
	Kao	0.21	0.23	–0.23	–0.11	–0.2	0.16	0.04	0.44	–
(b)		Acoustic distances between pairs								
Community Individual		North			Middle			South		
		Mac	Mar	Nin	Urs	Leo	Bob	Zyo	Mku	Kao
North	Mac	–								
	Mar	3.98	–							
	Nin	7.74	4.33	–						
Middle	Urs	5.83	4.12	3.24	–					
	Leo	9.62	6.20	1.90	4.67	–				
	Bob	10.93	7.15	3.44	6.61	2.15	–			
South	Zyo	12.65	8.79	5.25	8.40	3.83	1.80	–		
	Mku	12.78	8.89	5.48	8.67	4.15	2.06	0.39	–	
	Kao	5.98	2.31	4.56	5.78	6.10	6.32	7.68	7.70	–
(c)		Acoustic distances between pairs								
Community Individual		North			Middle			South		
		Mac	Mar	Nin	Urs	Leo	Bob	Zyo	Mku	Kao
North	Mac	–								
	Mar	1.79	–							
	Nin	4.62	1.79	–						
Middle	Urs	2.16	1.42	2.53	–					
	Leo	3.32	1.07	1.31	1.22	–				
	Bob	6.11	2.97	1.51	3.99	2.80	–			

Table 4: (continued)

South	Zyo	5.18	5.43	4.52	4.72	0.23	5.43	–		
	Mku	7.43	6.47	4.93	6.31	0.15	5.08	2.71	–	
	Kao	1.77	1.75	2.98	0.45	0.20	4.43	4.93	6.65	–

Numbers in bold: pairs of chimpanzees significantly likely to be related at least at the level of half-siblings ($p < 0.05$). Negative R-values signified individuals that were less related than the average pair in the population. Estimates of pairwise genetic relatedness for all possible pairs of individuals ranged from $R = -0.34$ to $R = 0.44$, with the expected value for half-siblings being $R = 0.25$.

Rowwise matrix correlation test: travel: Kendall's tau = -0.06 , $n = 36$ dyads, $p = 0.68$; food: Kendall's tau = 0.02 , $n = 36$ dyads, $p = 0.47$). As a conservative measure, we repeated this test including all pairs of chimpanzees with higher relatedness value than those showing a significant likelihood of being related, using the programme Kinship. The results were still non-significant (permuted Rowwise matrix correlation test: travel: Kendall's tau = -0.19 , $n = 36$ dyads, $p = 0.89$; food: Kendall's tau = -0.07 , $n = 36$ dyads, $p = 0.72$).

Discussion

We found that male chimpanzee pant hoots from three contiguous communities encode community as well as individual differences. Acoustic differences between pairs of chimpanzees were not correlated to the genetic relatedness of those pairs. Furthermore, testing the pant hoots of a distant community with those of the contiguous communities showed that the distant community pant hoots discriminated poorly from those of the three contiguous groups. These results support the hypothesis that acoustic differences in pant hoots between individuals were learned rather than genetically determined.

Pant hoots of adult male chimpanzees in the Taï forest were structurally different between neighbouring communities, suggesting that individuals hearing a neighbouring male chimpanzee pant hoot are likely to recognize to which neighbouring community the signaller belongs. These results suggest a mechanism for chimpanzee's discrimination between community member and neighbour pant hoots, demonstrated via playback experiments on the same three communities, by I. Herbinger and C. Boesch (unpubl. data). In 39 experimental trials where male pant-hoots of community members and neighbours were played back to the males of the three study communities, the latter showed differences in vocal, behavioural and spatial response patterns according to whether the simulated signaller was a community member or neighbour.

We found that the pant hoots of a distant community were not acoustically different from the three neighbouring communities, which was consistent with our expectation that distant community pant hoots differ randomly from the pant hoots of the contiguous communities. This suggests that on hearing a pant hoot from a stranger that the listener has never heard before, the listener may be unsure

of the signaller's identity, either perceiving the signaller as a community member or a neighbour. This would explain the observations of Herbinger and Boesch (own data), who found that after playing back a pant hoot from a strange male (from the same distant community, in 21 experimental trials), average responses of males from the three study communities lay between those elicited for playbacks of community member and neighbour pant hoots.

We did not find support for the hypothesis that vocal differences were principally attributable to genetic differences. There was no correlation between the genetic relatedness within pairs of chimpanzees within and between the three contiguous communities and the acoustic differences in the pant hoots of the same pairs. An absence of such a correlation is consistent with results found in species known to be vocal learners (e.g. Catchpole & Slater 1995). In addition, the genetic relatedness between males within and between communities was generally at chance levels, a similar pattern to that found when comparing the relatedness of all 42 males across the three Tai communities (Vigilant et al. 2001). Gene flow between the distant community and the contiguous communities over 70 km away was likely to be even smaller than that found between neighbouring communities, suggesting that genetic differences do not explain the phenomenon that chimpanzees have distinct pant hoots from their neighbours but not from strangers.

Similarly, habitat differences seem unlikely to account for these results. Habitat differences, such as forested compared with open areas, affect sound transmission properties and therefore animals living in different habitats may adapt their vocalizations accordingly (Wiley & Richards 1982). The distant community has higher rainfall and more variable altitude (Menzies 2000) than the contiguous communities, whereas the habitat of the three contiguous communities is relatively homogenous. If environmental differences account for differences in pant hoot structure we would expect the distant community pant hoots to differ more relative to the contiguous communities. However, we found exactly the opposite as acoustic differences in pant hoot structure were the largest for the contiguous communities. As neither genetic nor environmental differences seem to explain the observation that chimpanzees have distinct pant hoots from their neighbours but not from strangers, the alternative explanation is that Tai chimpanzees learn their community pant hoot.

Other possible confounding factors that might explain community level differences in the pant hoot structure include age, size and physical condition. As all three communities had both young and old males (Table 1), age was unlikely to account for community level differences in pant hoots. Likewise, given the limited evidence of community specific genetic or habitat variation, we suggest that body size, weight or other measures of the males' physical condition were likely to show greater within than between community variation, although we did not have specific measures for these.

Our results, then, support the learning hypothesis, as the existence of community specific pant hoots between neighbours, but not strangers, suggests that chimpanzees are actively modifying their pant hoots to diverge among neighbours. Although the results support the hypothesis that pant hoot differences

are learned, the type and mechanism of learning is not clear. Chimpanzees must be modifying their pant hoot structure so that it converges with other community members' pant hoots, thus social influence is inherent. Janik & Slater (2000) have suggested two types of social learning in animal communication, firstly when an existing vocalization is simply produced in a new context (contextual learning), or secondly, when a new call type is produced by active modification of call parameters, including frequency parameters (production learning). The second requires vocal learning while the first does not. In this study we cannot rule out contextual learning as an explanation for community differences in pant hoot structure as no new call types were identified. Rather, pant hoots showed acoustic variability and graded, rather than discrete, differences within and between individuals and communities (Fig. 2) (Mitani 1994). Therefore, in using a community specific pant hoot, chimpanzees may be selecting a narrow range from a wide range of possible graded pant hoot types in their repertoire.

Furthermore, community differences were encoded in both temporal and frequency variables. The frequency variables were not restricted to those of pitch change, where pitch changes can occur simply as an artefact of increasing respiratory pressure (Hsiao et al. 1994). We therefore suggest that fine-tuned control of temporal and frequency parameters across different pant hoot phases may be possible. As fine-tuned control of frequency parameters is unlikely to be achieved through respiratory control alone, we suggest that chimpanzees may have a degree of active control over both their respiratory system and parts of their vocal tract, and therefore may be capable of production learning. However, further research is needed to verify this.

The encoding of community identity in pant hoots might be driven by both within and between community functions. Although chimpanzees behave highly territorially, with violent and sometimes lethal encounters between neighbouring males (Nishida et al. 1985; Goodall 1986), the overlap zone between neighbouring communities encompasses a large percentage of their home range (90% of the home range in Taï, Herbinger et al. 2001). Encounters with neighbours occur about twice per month (Boesch & Boesch-Achermann 2000), often involving an element of surprise as the dense forest habitat only enables visual identification of approaching individuals within a range of 20–30 m. For chimpanzees living in a fission–fusion social system, an individual relying on visual identification can only determine if an approaching individual is a community member or neighbour at close range. Reciprocal vocal advertizing of identity by community members should minimize uncertainty of whether approaching chimpanzees are community members or neighbours. While this could be achieved by acoustic signalling of individual differences (a possibility we cannot exclude), individuals also need to ensure that their pant hoot does not sound like a neighbour's. One efficient possibility is to encode community differences in the pant hoot. Signalling community identity may also indicate a readiness to collaborate in territorial defence (Brown & Farabaugh 1997; Nettle 1999, Wright & Wilkinson 2001) or may act as territory marking. Chimpanzees' use of community specific pant hoots may thus serve both affiliative within group and aggressive between group

functions, following the pattern suggested for known vocal learning species living in territorial, fission–fusion groups (Australian magpies: Brown & Farabaugh 1997, humans: Nettle 1999).

Our results have shown that chimpanzee pant hoots are both individually and community specific. Community specificity pant hoots could not be attributed to genetic or environmental factors, suggesting that the structure of chimpanzee calls was influenced by experience. This is consistent with Marshall et al.'s (1999) findings with captive chimpanzees, that pant hoots of chimpanzees living in a group show structural convergence, and Mitani & Gros-Louis' (1998) findings, that pant hoot convergence occurs between chimpanzees during chorusing. Our results show that chimpanzees modify temporal characteristics and may also actively modify certain frequency characteristics of their vocalizations, an ability that can potentially increase communication complexity (Janik & Slater 2000). Further research, such as longitudinal studies documenting acoustic convergence of individuals' pant hoots over time, is needed to verify this. The current study adds to the results of others (Maeda & Masataka 1987; Mitani et al. 1992, 1999; Elowson & Snowdon 1994; Fischer et al. 1998; Mitani & Gros-Louis 1998; Marshall et al. 1999; Rukstalis et al. 2003) in suggesting that non-human primates may learn to modify frequency components of their vocalizations, a prerequisite for the evolution of spoken language.

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Literature Cited

- Altmann, J. 1974: Observational study of behavior: sampling methods. *Behaviour* **49**, 227–267.
- Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D. J., Mututua, R. S., Saiyalel, S. N., Wayne, R. K., Lacy, R. C. & Bruford, M. W. 1996: Behavior predicts genetic structure in a wild primate group. *Proc. Natl. Acad. Sci. U. S. A.* **93**, 5797–5801.
- Baylis, J. R. 1982: Avian vocal mimicry: its function and evolution. In: *Acoustic Communication in Birds*, Vol. 2 (Kroodsma, D. E. & Miller, E. H., eds). Academic Press, New York, pp. 51–84.
- Beeman, K. 1996: *SIGNAL Operation Manual*. Engineering Design, Belmont, MA.
- Boesch, C. & Boesch-Achermann, H. 2000: *The Chimpanzees of the Taï Forest*. Oxford Univ. Press, Oxford.
- Bradbury, J. W. & Vehrencamp, S. L. 1998: *Principles of Animal Communication*. Sinauer Associates, Sunderland, MA.

- Bradley, B. J., Boesch, C. & Vigilant, L. 2000: Identification and redesign of human microsatellite markers for genotyping wild chimpanzee (*Pan troglodytes verus*) and gorilla (*Gorilla gorilla gorilla*) DNA from faeces. *Cons. Genet.* **1**, 289–292.
- 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: *Social Influences on Vocal Development* (Snowdon, C. T. & Hauserberger, M., eds), Cambridge Univ. Press, Cambridge, pp. 98–127.
- Catchpole, C. K. & Slater, P. J. 1995: *Bird song*. Cambridge Univ. Press, Cambridge.
- Charif, R. A., Mitchell, S. & Clark, C. W. 1995: *Canary 1.2 User's manual*. Cornell Laboratory of Ornithology, Ithaca, New York.
- Elowson, A. M. & Snowdon, C. T. 1994: Pygmy marmosets, *Cebuella pygmaea*, modify vocal structure in response to changed social environment. *Anim. Behav.* **47**, 1267–1277.
- Fischer, J. 2003: Developmental modifications in the vocal behavior of non-human primates. In: *Primate Audition: Ethology and Neurobiology* (Ghazanfar, A. A., ed.), CRC Press, New York, pp. 109–126.
- Fischer, J., Hammerschmidt, K. & Todt, D. 1998: Local variation in Barbary macaque shrill barks. *Anim. Behav.* **56**, 623–629.
- Goodall, J. 1986: *The Chimpanzees of Gombe – Patterns of Behaviour*. The Belknap Press of Harvard Univ. Press, Cambridge, MA.
- Goodnight, K. F. & Queller, D. C. (1999) Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Mol. Ecol.* **8**, 1231–1234.
- Hammerschmidt, K. 1990: Individuelle Lautmuster bei Berber-affen (*Macaca sylvanus*): ein Ansatz zum Verständnis ihrer vokalen Kommunikation. PhD thesis, Freie Universität Berlin, Berlin.
- Hemelrijk, C. K. 1990: A matrix correlation test used in investigations of reciprocity and other social interaction patterns at group level. *J. Theor. Biol.* **143**, 405–420.
- Herbinger, I., Boesch, C. & Rothe, H. 2001: Territory characteristics among three neighbouring chimpanzee communities in the Taï National Park, Côte d'Ivoire. *Int. J. Primatol.* **22**, 143–167.
- Hsiao, M. D., Solomon, N. P., Luschei, E. S. & Titze, I. R. 1994: Effect of subglottic pressure in fundamental frequency of the canine larynx with active muscle tension. *Ann. Otol. Rhinol. Laryngol.* **103**, 817–821.
- Janik, V. M. & Slater, P. J. B. 1997: Vocal learning in mammals. *Adv. Stud. Behav.* **26**, 59–99.
- Janik, V. M. & Slater, P. J. B. 1998: Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim. Behav.* **56**, 829–838.
- Janik, V. M. & Slater, P. J. B. 2000: The different roles of social learning in vocal communication. *Anim. Behav.* **60**, 1–11.
- Jones, G. & Ransome, R. D. 1993: Echolocation calls of bats are influenced by maternal effects and change over a lifetime. *Proc. R. Soc. Lond. B Biol. Sci.* **252**, 125–128.
- Lieberman, P. 1984: *The Biology and Evolution of Language*. Harvard Univ. Press, Cambridge, MA.
- Lieblisch, A. K., Symmes, D., Newman, J. D. & Shapiro, M. 1980: Development of the isolation peep in laboratory-bred squirrel monkeys. *Anim. Behav.* **28**, 1–9.
- Maeda, T. & Mastataka, N. 1987: Locale-specific vocal behaviour of the tamarin (*Saguinus I. Labiatus*). *Ethology* **75**, 25–30.
- Marler, P. & Hobbett, L. 1975: Individuality in a long-range vocalization of wild chimpanzees. *Z. Tierpsychol.* **38**, 97–109.
- Marler, P. & Tenaza, R. 1977: Communication in apes with special references to vocalizations. In: *How Animals Communicate* (Sebeok, T. A., ed.). Indiana Univ. Press, Bloomington, pp. 965–1033.
- Marshall, A. J., Wrangham, R. W. & Arcadi, A. C. 1999: Does learning affect the structure of vocalizations in chimpanzees? *Anim. Behav.* **58**, 825–830.
- Menzies, A. 2000. Structure et composition floristique de la zone Ouest du Parc National de Taï (Côte d'Ivoire) Masters thesis, Université de Genève.
- Mitani, J. 1994: Social factors influencing the acoustic variability in 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 three hypotheses. *Behaviour* **135**, 1041–1064.
- Mitani, J., Hasegawa, T., Gros-Louis, J., Marler, P. & Byrne, R. 1992: Dialects in wild chimpanzees? *Am. J. Primatol.* **27**, 233–243.

- Mitani, J. C., Hunley, K. L. & Murdoch M. E. 1999: Geographic variation in the calls of wild chimpanzees: a reassessment. *Am. J. Primatol.* **47**, 133—151.
- Molliver, M. E. 1963: Operant control of vocal behavior in the cat. *J. Exp. Anal. Behav.* **135**, 1041—1064.
- Morin, P. A., Chambers, K. E., Boesch, C. & Vigilant, L. 2001: Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). *Mol. Ecol.* **10**, 18435—18444.
- Nettle, D. 1999: Linguistic Diversity. Oxford Univ. Press, New York.
- Nishida, T., Hiraiwa-Hasegawa, M., Hasegawa, T. & Takahata, Y. 1985: Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. *Z. Tierpsychol.* **67**, 284—301.
- Noldus 1998: Matman 1.0. Noldus Information Technology b.v., Wageningen.
- Nowicki, S. 1983: Flock-specific recognition of chickadee calls. *Behav. Ecol. Sociobiol.* **12**, 317—320.
- Payne, K. & Payne, R. 1985: Large scale changes over 19 years in songs of humpback whales in Bermuda. *Z. Tierpsychol.* **68**, 89—114.
- Queller, D. C. & Goodnight, K. F. 1989: Evolution (Lawrence, Kans) **43**, 258—275.
- Rukstalis, M., Fite, J. E. & French, J. A. 2003: Social change affects vocal structure in a callitrichid primate (*Callithrix kuhlii*). *Ethology* **109**, 327—340.
- Ryan, M. J., Rand, A. S. & Weigt, L. A. 1996: Allozyme and advertisement call variation in the Tungara frog, *Physalaemus putulosus*. *Evolution* **50**, 2435—2453.
- Sugiura, H. 1998: Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. *Anim. Behav.* **55**, 673—687.
- Sutton, D., Larson, C., Taylor, E. M. & Lindeman, R. C. 1973: Vocalization in rhesus monkeys: conditionality. *Brain. Res.* **52**, 225—231.
- Tabachnick, B. G. & Fidell, L. S. 2001: Using Multivariate Statistics, 4th edn. Allyn & Bacon, London.
- Todt, D. 1975: Social learning of vocal patterns and modes of their application in grey parrots (*Psittacus erithacus*). *Z. Tierpsychol.* **39**, 178—188.
- Travis, S., Slobodchikoff, C. N. & Keim, P. 1997: DNA fingerprinting reveals low genetic diversity in Gunnison's prairie dog (*Cynomys gunnisoni*). *J. Mammal.* **78**, 725—732.
- Tyack, P. L. 1997: Development and social function of signature whistles in bottlenose dolphins, *Tursiops truncatus*. *Bioacoustics* **8**, 21—46.
- Tyack, P. L. & Sayigh, L. S. 1997: Vocal learning in cetaceans. In: Social Influences on Vocal Development (Snowdon, C. T. & Hauserberger, M., eds). Cambridge Univ. Press, Cambridge, pp. 208—233.
- Uhlenbroek, C. 1996: The Structure and Function of the Long-Distance Calls Given by Male Chimpanzees in Gombe National Park. PhD thesis, Univ. of Bristol.
- Vehrencamp, S. L., Ritter, A. F., Keever, M. & Bradbury, J. W. 2003: Responses to playback of local vs. distant contact calls in the orange-fronted conure, *Aratinga canicularis*. *Ethology* **109**, 37—54.
- Vigilant, L., Hofreiter, M., Siedel, H. & Boesch, C. 2001: Paternity and relatedness in wild chimpanzee communities. *Proc. Natl. Acad. Sci. U. S. A.* **98**, 12890—12895.
- Wiley, R. H. & Richards, D. 1982: Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Acoustic Communication in Birds, Vol. 1 (Kroodsma, D. E. & Miller, E. H., eds). Academic Press, New York, pp. 131—181.
- Wright, T. F. & Wilkinson, G. S. 2001: Population genetic structure and vocal dialects in an amazon parrot. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 609—616.
- Wycherley, J., Doran, S. & Beebee, T. J. C. 2002: Frog calls echo microsatellite phylogeography in the European pool frog (*Rana lessonae*). *J. Zool. Lond.* **258**, 479—484.
- Zar, J. H. 1999: Biostatistical Analysis, 3rd edn. Prentice Hall, Engelwood Cliffs, New Jersey.

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Appendix: All acoustic variables from the four pant hoot phases and associated tree-drummings, considered in the analyses

(a) Pant hoot phases and drums: variables measured using Canary 1.2.4
Presence/absence of introduction phase Number of introduction elements ^{a,b,c,d,e,f} F0 at midpoint of first introduction element (Hz) Presence/absence of build-up phase Total number of build-up elements ^{c,e} Number of elements in first half of build-up Number of elements in second half of build-up Total duration of build-up (ms) Rate of first half of build-up ^{b,e,f} Rate of second half of build-up Rate of second half-rate of first half of build-up (acceleration rate) ^{a,c,e} DFB at midpoint of inhaled elements (Hz) ^{a,c,e} DFB at midpoint of exhaled elements (Hz) ^{a,b,c,d,e} DFB of inhaled-DFB of exhaled elements (Hz) ^f Presence/absence of climax phase Number of screams in climax phase Number of barks in climax phase ^f Number of hoos in climax phase Total number of climax elements Proportion of screams vs. other elements in climax phase Proportion of barks vs. other elements in climax phase Proportion of hoos vs. other elements in climax phase Presence/absence of letdown phase Number of elements in letdown phase Presence/absence of drumming Number of drum beats Total duration of drumming phase Rate of drum beats Proportion of beats produced before the climax phase ^c Proportion of beats produced during the climax phase Proportion of beats produced after the climax phase
(b) First climax scream: variables measured using LMA
Minimum ^c , maximum ^f , start, end and mean of Fundamental frequency (F0) across all time segments (Hz) Climax scream duration (ms) ^{a,c,d,e,f} measured from start to end of the scream Location of maximum F0 as a proportion of call length Maximum ^{b,d,f} and mean ^c measures of 'tonality' of the F0 (Hz), (the number of times the original curve of the F0 crosses the average, approximates noisy vs. pure tonality) Factor of the linear trend of the F0 across the call (whether the call is rising, falling or flat), and Maximum and mean difference between the trend line and the F0 (Hz) Maximum frequency of all peak frequencies across the call (Hz) ^{a,c,d,e,f} Minimum frequency of all peak frequencies across the call (Hz) ^{b,d,f} Peak frequencies with maximum and minimum amplitudes across whole call (Hz) Maximum difference in peak frequency in successive time segments (Hz)

Appendix: (continued)

Slope of F0 from start to maximum (Hz/ms)
Slope of peak frequency from start to maximum (Hz/ms)
Maximum F0 start F0 (Hz) and Maximum F0 minimum F0 (Hz)

DFB = dominant frequency band. Variables showing differences in the discriminant function analyses between the three contiguous communities in travel^a and food^b contexts, between the four communities in travel^c and food^d contexts, and between individuals in the three contiguous communities in travel^e and in food^f contexts. Correlated climax scream variables are listed together.