

RESEARCH ARTICLES

Dialects in Wild Chimpanzees?

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Chimpanzees emit a loud, species-typical long distance call known as the pant hoot. Geographic variation between the pant hoots of chimpanzees living in two neighboring populations, the Mahale Mountains and Gombe Stream National Parks, Tanzania, was examined. Analysis of six acoustic features revealed subtle differences in the way chimpanzees from the two populations called. Individuals from the Mahale study site uttered one section of their pant hoots at a faster rate and with shorter elements than animals from Gombe Stream. In addition, individuals at Mahale delivered broader-band, higher pitched "climax" elements than males from Gombe. While genetic factors, anatomical differences, variations in the use of calls at the two sites, and changes in calling over time may account for the variability between populations, we suggest the additional possibility that differences in pant hooting may be due to learning. © 1992 Wiley-Liss, Inc.

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INTRODUCTION

Recent studies of primate vocal behavior have shown that learning plays an important role in determining how individuals use and respond to calls [review in Snowdon and Elowson, in press]. In contrast, a growing body of evidence suggests that the acoustic morphology of calls is not learned and undergoes little developmental modification in the absence of anatomical changes during maturation. For example, animals raised in acoustic or social isolation during youth give many of their species-typical vocalizations [Winter et al., 1973; Gautier, 1974], and hybrid individuals emit calls that do not resemble those of either of their parents [Brockelman & Schilling, 1984; Geismann, 1984]. In addition, infant monkeys raised with heterospecific foster mothers produce their species-typical calls upon maturation [Owren et al., in press], and while attempts to train monkeys to call selectively in certain situations have been successful, call morphology remains largely unchanged [Sutton et al., 1973; Pierce, 1985].

Primates learn many critical aspects of behavior during long periods of infant dependency and are well known for their learning abilities shown both in the

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laboratory and in the field [Rumbaugh & McCormack, 1967; Nishida, 1987]. Viewed within this context, the conclusion that learning does not play a role in the development of the acoustic structure of nonhuman primate calls is paradoxical and deserves closer scrutiny. Since one correlate of the vocal learning process is the formation of dialects, an examination of variation between the calls of conspecific individuals living in different populations provides a means to investigate the issue of learning in the wild. In this paper we explore the possibility of vocal learning in our closest living relative, the chimpanzee, by examining geographic variation in the calls of individuals from two neighboring populations, the Mahale Mountains and Gombe Stream National Parks in Western Tanzania. Our results reveal subtle differences in the manner in which chimpanzees from the two populations emit their species-typical long distance calls, and provide the first suggestion of vocal learning in these animals.

MATERIALS AND METHODS

Study Site and Subjects

Tape recordings of chimpanzee pant hoots were made at the Gombe Stream and Mahale Mountains National Parks, Tanzania. Both areas have been the sites of long-term field investigations of chimpanzee behavior [Goodall, 1986; Nishida, 1990]. The Mahale study site lies at 6°07'S, 29°44'E along the eastern shore of Lake Tanganyika. The Gombe study population is approximately 150 km north of the Mahale Park. The two populations are found on the eastern-most edge of the geographic range of chimpanzees and belong to the same subspecies, the eastern or long-haired race *Pan troglodytes schweinfurthii*. Pant hoots were tape recorded from members of one unit-group or community from each population, the M-group at Mahale and the Kasakela community at Gombe [Goodall, 1986; Nishida, 1990]. While it is likely that gene flow was possible between the two populations in the past, recent deforestation and increasing human habitation along the coast of Lake Tanganyika have resulted in the effective isolation of the two populations within historical time.

The Calls

Chimpanzees utter a distinctive loud call known as the pant hoot [Goodall, 1968; Marler & Hobbett, 1975]. Animals pant hoot in several contexts, including in response to other pant hooting individuals, after rejoining other community members, in response to strange conspecifics, upon arriving at a particularly rich food source, during agonistic displays, and upon capture of animal prey items [Goodall, 1986]. Calls are individually distinctive [Marler & Hobbett, 1975], and announce the presence of animals within and between groups.

Pant hoots vary from 2 to 23 sec and can include four distinct phases [Marler & Hobbett, 1975] (Fig. 1). Calls may begin with a brief "introduction" consisting of a series of unmodulated tonal elements. A progressively louder "build-up" follows containing elements that are typically shorter than those in the introduction and produced both on inhalation and exhalation. The third phase, the "climax," is characterized by one or a series of long, frequency-modulated elements resembling a scream in its acoustic properties. Male chimpanzees frequently utter a climax section during pant hooting, but females typically do not. Pant hoots conclude with a "let-down" portion, which includes elements similar in acoustic morphology to the build-up section.

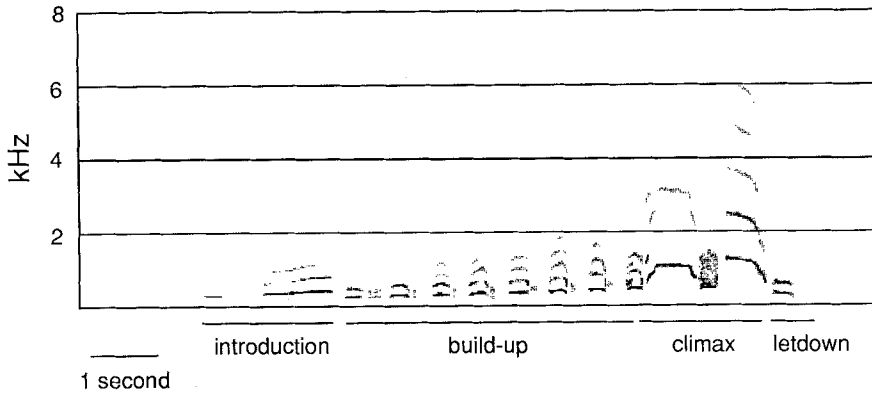


Fig. 1. Audiospectrogram of a representative pant hoot illustrating its four stages. The spectrogram was produced on a Macintosh IIfx computer using MacRecorder sound analysis software. Analysis range = 11 kHz. Frequency resolution = 22 Hz.

Field Methods

Recordings from Gombe were made by Peter Marler, who from June through August 1967 conducted a systematic study of chimpanzee vocal behavior around the banana provisioning station [Marler, 1969, 1976; Marler & Hobbett, 1975; Marler & Tenaza, 1977]. Tape recordings from Mahale were made from August through November 1984 by Richard Byrne ($n = 9$ calls), August through November 1988 by Toshikazu Hasegawa ($n = 31$), and December 1989 through June 1990 by John Mitani ($n = 126$). All recordings from Mahale were made while following chimpanzees in their natural habitat. Individuals recorded during Byrne's study were fed small amounts of banana and sugar cane; provisioning at Mahale ceased after 1987. Tapes from Gombe were recorded with a Nagra III recorder and Sennheiser MKH 804 directional microphone, while those from Mahale were made with Sony TCD-D10, TC-D5M, and WM-D6C recorders and Sennheiser ME80, ME88, and MKH 816 microphones.

Acoustic Analyses

Audiospectrograms of pant hoots were first produced on a Kay 5500 DSP sonagraph to examine the gross acoustic morphology of pant hoots. Visual inspection of spectrograms coupled with aural monitoring proved useful in identifying acoustic features that could potentially serve to differentiate populations. Subsequent acoustic measurements of these features were made digitally using a Dolch 486/25 computer and signal processing program designed especially for the analysis of animal vocalizations [Engineering Design, 1990]. Pant hoots were sampled at 20,000 points/second yielding an effective analysis bandwidth of 8 kHz. Temporal and spectral characteristics of waveforms were examined after performing 512 point Fourier transforms (time resolution = 26 msec).

Since the acoustic structure of pant hoots varies as a function of the age-sex class of individuals [Marler & Hobbett, 1975], only calls from adult males were used in the following analyses. Male chimpanzees reach adulthood at 15 years [Goodall, 1986], and animals whose known or estimated age exceeded this figure were included in the sample. The number of pant hoots analyzed from each individual ranged from 2 to 31. Sample sizes and the animals included in the following

analyses vary because masking noise due to environmental sources or other animals precluded measuring all features in every call.

Three acoustic features of build-up elements were examined: their rate of delivery, duration, and fundamental frequency. We extracted the last five build-up elements prior to the climax and multiplied the reciprocal of the length of this section by five to calculate a rate of delivery. Measurements of duration were made on the last exhaled build-up element prior to the climax. The last element was also used in computations of fundamental frequency. Fundamental frequency was measured by performing a 1024 point Fourier transform beginning at the midpoint of each element. These transforms included 51 msec, yielding a frequency resolution of 20 Hz. We also measured the duration and two spectral features of climax elements: the average frequency of the fundamental and the frequency range it spanned. The climax element whose fundamental reached the highest frequency in the call was selected for analysis. Since the fundamental frequency of climax elements varies over time, a cepstral algorithm was employed to compute an average frequency for each element. One hundred calculations based on 128 points (= 6 msec) were performed over each element. The first measurement was made at the start of the signal, with successive measurements performed at intervals equal to 1/100 of the duration of the element. A few sections of climax elements were aperiodic, and in these cases the cepstral algorithm was unable to extract a fundamental frequency value. These missed values were rare (<10% of the total sample), and they were excluded in the computations of average frequencies.

Statistical Methods

Pant hoots are known to differ between individuals [Marler & Hobbett, 1975]. We planned to control for this variation by performing nested analyses of variance on each measured variable in the sample. Acoustic measurements did not conform to the assumptions of ANOVA, however; the data set remained non-normal and heteroscedastic after performing a variety of arithmetic transformations. To evaluate population differences, we compared the mean values of each measured variable between individuals from Mahale and Gombe using nonparametric procedures [Sokal & Rohlf, 1981]. Nonparametric one-way analysis of variance was also employed to examine variability between individuals within populations. Statistical tests were two-tailed with the criterion of significance set at $P < .05$.

RESULTS

Aural monitoring and visual inspection of spectrograms suggested that pant hoots from the Mahale and Gombe populations differ in their build-up and climax phases (Fig. 2). Acoustic measurements of pant hoots were made to examine these qualitative impressions in greater detail.

Male chimpanzees at Mahale delivered significantly shorter build-up elements at faster rates than did males from Gombe (Mann-Whitney U -tests, $P < .03$, $N_1 = 10$, $N_2 = 6$ for both comparisons; Fig. 3a,b). These differences give the Mahale pant hoots a rushed quality that is clearly audible to a human listener. Population differences appeared to exist despite variability between individuals within populations. Build-up rates showed significant heterogeneity among the males from Gombe (Kruskal-Wallis test, $P < .03$, $N = 6$), but the mean values of all individuals from this population were less than those of every male from Mahale (Fig. 3b). Similarly, although the durations of build-up elements varied among the males from Mahale (Kruskal-Wallis tests, $P < .01$, $N = 10$), the majority of measurements from this population were less than those from Gombe (Fig. 3a). In one additional

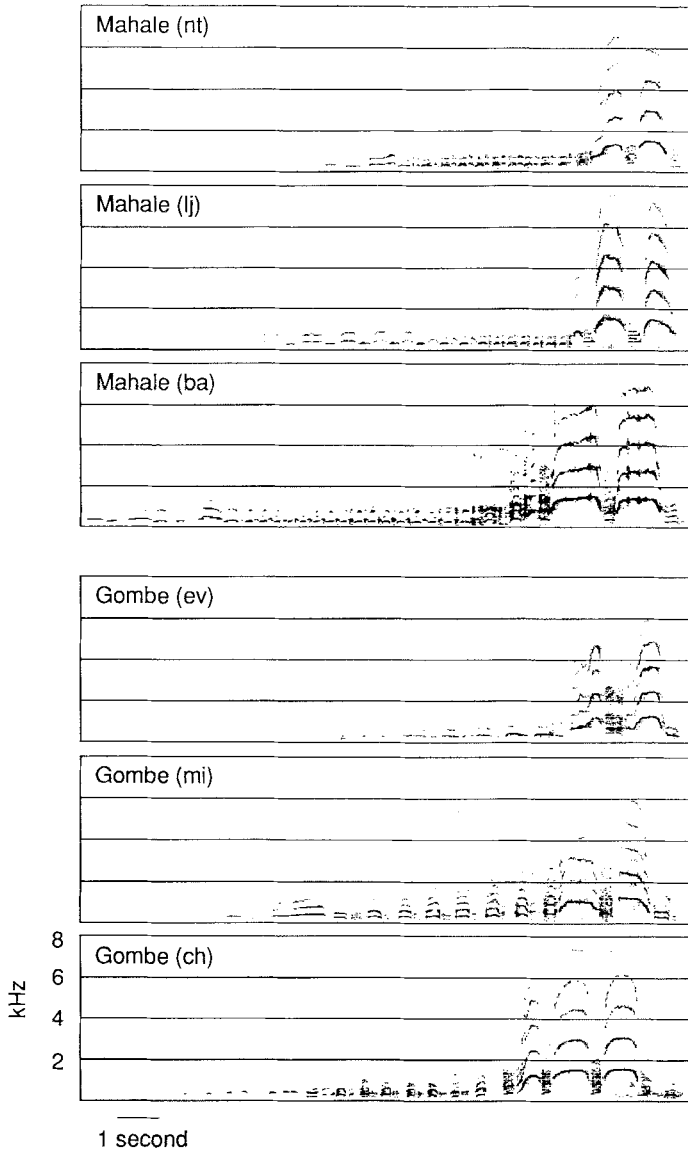


Fig. 2. Audiospectrograms of representative pant hoots from Mahale and Gombe. Spectrograms were produced as in Figure 1. Letters within parentheses stand for individual animals.

comparison, the fundamental frequencies of elements did not differ between the two populations (Mann-Whitney U -test, $P > .05$, $N_1 = 10$, $N_2 = 6$; Fig. 3c).

Two features of climax elements differed between the populations. First, the average fundamental frequencies of climax elements from Mahale were significantly greater than those from Gombe (Mann-Whitney U -test, $P < .01$, $N_1 = 10$, $N_2 = 7$; Fig. 4a). Second, the climax elements of males from Mahale spanned a greater frequency range than the elements from males at Gombe (Mann-Whitney U -test, $P < .01$, $N_1 = 10$, $N_2 = 7$; Fig. 4b). These two features are evident to the

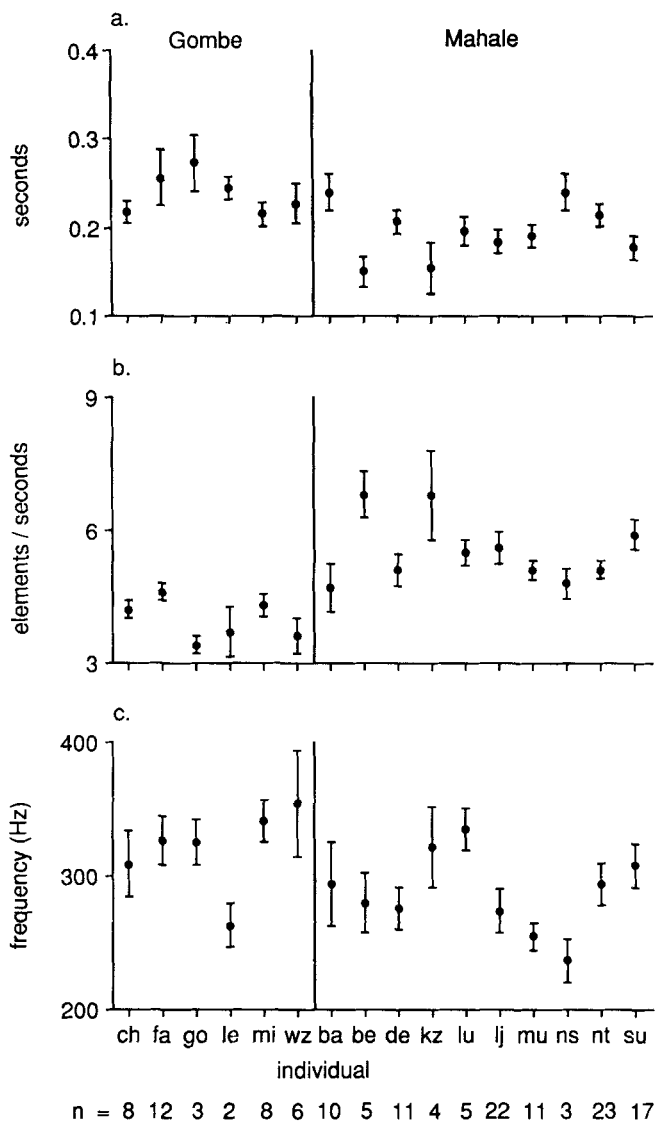


Fig. 3. Comparison of temporal and spectral features of build-up elements from individuals at Gombe and Mahale. a: Element duration. b: Rate of delivery. c: Fundamental frequency of element. Means ± 1 SE are shown for each individual.

human listener, giving the impression that the voices of the Mahale chimps are higher pitched than those from Gombe. An examination of variation between individuals within populations showed that significant heterogeneity existed among values of both variables in each population (Kruskal-Wallis tests, $P < .05$, for all four comparisons). Nevertheless, with the exception of measurements from one male (MU), frequency values from Mahale consistently exceeded those from Gombe (Fig. 4a,b). The durations of climax elements did not differ between the two populations (Mann-Whitney U -test, $P > .30$, $N_1 = 10$, $N_2 = 7$; Fig. 4c).

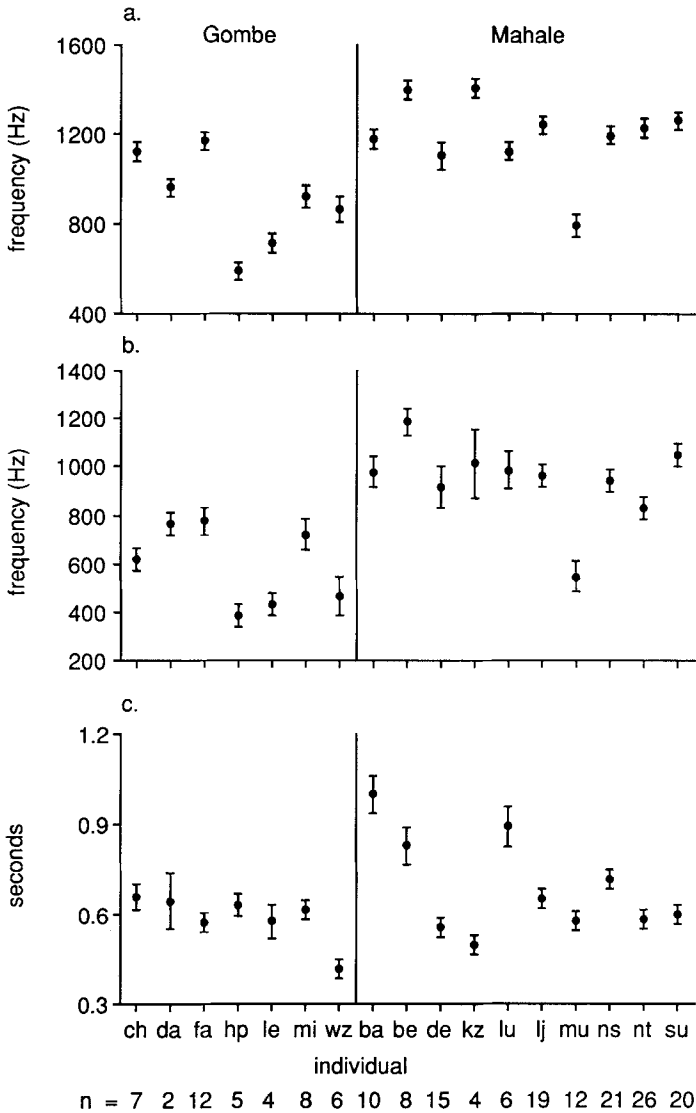


Fig. 4. Comparison of temporal and spectral features of climax elements from individuals at Gombe and Mahale. a: Average frequency of the fundamental. b: Frequency range spanned by the fundamental. c: Element duration. Means ± 1 SE are shown for each individual.

DISCUSSION

Results of the preceding analyses indicate subtle differences in the manner in which chimpanzees from two populations utter their species-typical long distance call. Chimpanzees at the Mahale Mountains emit the build-up portions of their pant hoots at a faster rate with shorter elements than individuals from Gombe Stream. In addition, individuals at Mahale deliver broader-band, higher pitched climax elements than males from Gombe. We propose five factors that may account for these differences. First, the observed variations in pant hoots may reflect ge-

netic differences between the two populations. Vocal differences between genetically isolated populations have been reported in several primate species [Struh-saker, 1970; Hodun et al., 1981; Waser, 1982; Oates & Trocco, 1983; Mitani, 1987]. The Mahale and Gombe chimpanzees belong to the same subspecies, however, and these populations have been effectively isolated only for a few generations. As a result, the degree of genetic differentiation between the two populations is unclear. Recently developed DNA amplification techniques promise to resolve this question [Takasaki & Takenaka, in press]. The existence of a significant amount of genetic variability between the Mahale and Gombe chimpanzees would support the hypothesis that the observed vocal differences are inherited.

Second, genetically or environmentally based anatomical differences might account for vocal variability between the two populations. Chimpanzees at Mahale are significantly larger than those at Gombe [Uehara & Nishida, 1987], and this variation in body size would lead one to predict that the larger Mahale chimps would have deeper voices than the smaller Gombe animals [cf. Davies & Halliday, 1978]. An examination of the climax portion of pant hoots revealed the opposite relationship, however.

Goodall [1986] has suggested that pant hoots delivered in different behavioral contexts vary acoustically. Our sample of calls from Gombe was recorded primarily around the provisioning station, while the majority of pant hoots from Mahale were taped in the chimpanzee's natural habitat. Thus, it is possible that the observed vocal differences may be due to variations in call usage by animals at the two sites. A preliminary analysis of intraindividual variation in the pant hoots of the Mahale chimpanzees does not support this interpretation; consistent acoustic differences between calls used in different situations are not apparent (Mitani, unpublished data). The small number of calls from each individual in our sample, however, precludes a strong test, and more recordings will be needed to evaluate whether variations in call use contributed to vocal differences between the two populations.

Recordings from the two sites were made at different times, and temporal variation represents a fourth potential cause of the vocal differences that we have uncovered. Pant hoots from Gombe were recorded 23 years ago while most calls from Mahale were recorded recently. The calls of four males from Mahale used in this analysis were collected over a span of 6 years, and the pant hoots of these individuals do not reveal any obvious short-term changes in acoustic morphology. Nevertheless, it is possible that over the intervening 20-year period the calls of the Gombe males have converged with those of present day Mahale chimpanzees. An analysis of recent recordings from the Gombe population will be required to investigate this proposal.

If anatomical, contextual, and short-term temporal factors do not account for the observed population differences in pant hoots, then we may entertain a final possibility that the variation in pant hoots between Mahale and Gombe individuals is dialectal. Dialectal differences are of special interest since they bear on the issue of vocal learning. Learning combined with limited dispersal after vocal acquisition has taken place commonly leads to dialects, and vocal learning in animals is frequently inferred from the existence of dialects [Kroodsmas, 1982]. Intraspecific population vocal differences have been shown only rarely among primates [Green, 1975; Maeda & Masataka, 1987], however, and the absence of dialects is consistent with the paucity of evidence for vocal learning in these animals (see "Introduction"). Studies of young chimpanzees raised in isolation during the first 2 years of life accord with the conclusion that calls are inherited;

social isolates reared in the laboratory were able to emit several species-typical calls characteristically given by adults [Menzel, 1964].

The preceding data regarding call production by social isolates are not consistent with the suggestion of dialectal variation in the pant hoots of chimpanzees. We note, however, the unique nature of the acoustic differences between the Mahale and Gombe populations. The vocal differences between the two populations that we propose as dialectal are subtle and different from those generally described in nonhuman animals. Discrete and easily discernable acoustic differences contribute to the identification of dialects in oscine birds [e.g., Marler & Tamura, 1964]. By analogy, we liken these categorical differences in bird song to variations in vocabulary that contribute to the formation of human dialects. In contrast, the differences described here between two chimpanzee populations, although consistent, are apparent only on close inspection (Fig. 2). The articulatory movements that are involved may be similar to differences in pronunciation which constitute an additional component of dialectal variation among humans.

The acoustic nature of birdsong dialects and variations in pant hoots suggest that different learning processes may be involved in their acquisition. Many oscine birds memorize song patterns during a sensitive period early in life, and in these animals song emerges gradually through vocal practice during a subsequent motor phase [Marler, 1990]. We suggest that such memory-based vocal learning may not occur in chimpanzees and other primates. Instead we hypothesize that if the vocal differences between chimpanzee populations result from learning, they may reflect a process of selective reinforcement over time. Individuals may produce a range of vocal variants and then discard some to match a population-specific standard given repeated exposure to the calls of others with whom they live [cf. Nowicki, 1989]. Alternatively, provisioning at both sites may have led to the reinforcement of different call parameters in the two populations [cf. Green, 1975]. In either case, this process, analogous to what has been described as "action-based" learning in birds [Marler, 1990], would account for the statistical nature of the acoustic differences between the Gombe and Mahale populations since all individuals would not be expected to converge in subtle features of pronunciation. The cases of acoustic modification of nonhuman primate vocalizations [review in Pierce, 1985] are more readily interpretable within the framework provided by reinforcement theory than by memory-based learning, which is typical of oscine birds. Further research will be necessary to clarify whether this form of learning is a characteristic feature of nonhuman primate vocal communication.

We conclude by pointing out that the social system of chimpanzees may have created an appropriate selective milieu favoring the evolution of vocal learning. Male chimpanzees of neighboring communities are typically hostile toward one another; intercommunity interactions may lead to violent conflict during which animals are severely injured or killed [Goodall et al., 1979; Nishida et al., 1985]. Given these circumstances, it would be advantageous for chimpanzees to possess the ability to discriminate the long-distance calls of their fellow community members from those of others. Acoustic similarities between the calls of males from the same community may provide a means for discrimination, with vocal learning the mechanism by which these similarities arise.

CONCLUSIONS

1. Acoustic analyses revealed that the pant hoots of adult male chimpanzees from the Mahale Mountains and Gombe Stream National Parks differ in spectral and temporal features.

2. Males from the Mahale study site delivered the build-up portions of their pant hoots at a faster rate and with shorter elements than individuals from Gombe Stream. Animals at Mahale also delivered broader-band, higher pitched "climax" elements than males from Gombe.

3. Genetic factors, anatomical differences, variations in the use of calls at the two sites, and changes in calling over time may account for the differences in pant hooting between the Mahale and Gombe populations, but an additional possibility is that this variability arises through learning.

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