

Individuality in a Contact Call of the Ringtailed Lemur (*Lemur catta*)

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A vocalization of the ringtailed lemur (*Lemur catta*) was examined for individual differences according to several temporal- and frequency-dependent variables. Vocalizations were tape recorded at the Duke University Primate Center (Durham, NC) and spectrographically analyzed. Significant differences were found in pair-wise comparisons of call structure among the study subjects, thus providing the physical basis for individual discrimination. A separate analysis comparing degree of kinship and vocal similarity revealed a positive but nonsignificant correlation between these two variables. This study represents an initial examination of vocal individuality in prosimian primates.

Key words: vocal individuality, primate communication, spectrographic analysis

INTRODUCTION

In order for animals to identify one another by sound, consistent differences in signal structure must exist among individuals. Spectrographic analyses of individual differences in the vocalizations of conspecifics have been carried out on numerous taxa, including amphibians, birds, and mammals. Anthropoid primates represent one such group whose vocalizations have been examined for individual differences, or "vocal signatures" [eg, marmosets: Snowden & Cleveland, 1980; tamarins: Snowden et al, 1983; Snowden & Hodun, 1985; squirrel monkeys: Symmes et al, 1979; Lieblisch et al, 1980; Smith et al, 1982; Symmes & Biben, 1985; Masataka & Symmes, 1986; spider monkeys: Masataka, 1986; mangabeys: Waser, 1977; macaques: Lillehei & Snowden, 1978; vervets: Cheney & Seyfarth, 1980; gibbons: Tenaza, 1976; Haimoff & Gittins, 1985; Haimoff & Tilson, 1985; and chimpanzees: Marler & Hobbett, 1975]. No studies of vocal individuality have yet been published for prosimian primates. However, several vocalizations of the ringtailed lemur (*Lemur catta*) consist primarily of distinct, narrow-frequency bands, making their quantitative analysis precise and reliable.

One such vocalization is the "cohesion call" ("cohesion miaouw" of Petter & Charles-Dominique [1979]). This call is given by all individuals except infants. It appears to serve an intragroup contact function by providing an auditory cue for the location of group members who are dispersed during routine daily activities [Jolly,

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1966; Petter & Charles-Dominique, 1979; personal observation]. This is particularly evident when the call is emitted just prior to troop movement or after a disturbance which has caused troop dissociation.

Snowdon et al [1983] have suggested that the ability to distinguish one's own group members from other conspecifics is a requisite of a call system used in intragroup cohesion. Thus, in addition to its discrete structural qualities, the cohesion call of the ringtailed lemur appears to represent a socially functional model for examining vocal individuality in a prosimian primate.

Although experience may play some role in shaping the vocalizations of nonhuman primates [eg, Larson et al, 1973; Sutton et al, 1973; Newman & Symmes, 1974; Green, 1975; Hodun et al, 1981], it is generally accepted that genetic mechanisms are primarily responsible for determining primate vocalizations [eg, Winter et al, 1973; Gautier, 1974; Eisenberg, 1976; Liebllich et al, 1980; Newman & Symmes, 1982]. The inheritance of vocal characteristics in primates has been further clarified in studies of interspecific hybrid individuals [eg, Gautier & Gautier, 1977; Marler & Tenaza, 1977; Geissmann, 1984; Tenaza, 1985]. However, only one study of primate vocalizations [Liebllich et al, 1980] has examined the relationship of vocal traits among nonhybrid kin.

Documentation of the presence of kin-group traits might not only represent empirical evidence for testing theoretical selection models (see "Discussion") but also may provide phenotypic markers for determining genetic relatedness of animals in the field.

In this study, the cohesion call of the ringtailed lemur is examined spectrographically for acoustic features that may facilitate individual recognition. Additionally, a preliminary investigation of kin-group traits in this vocalization is made.

METHODS

Study Site and Subjects

Tape recordings of cohesion calls were obtained from the study group between May and August, 1985, at the Duke University Primate Center (DUPC, Durham, NC). The study group consisted of 20 semi-free-ranging ringtailed lemurs (*Lemur catta*) inhabiting a 3.5-ha natural habitat enclosure at the DUPC. An additional pair of *L. catta* included in the study (Attis and Hypocrates) were housed apart from this group in a smaller outdoor wire enclosure (2.0 × 1.4 × 2.6 m). Only eight of these individuals were included in the analyses owing to the difficulty of obtaining a reasonably sized sample of calls under nonmanipulative conditions. The degree of relatedness among the eight ringtailed lemurs was determined from the DUPC animal records.

Recordings and Measurements

Vocalizations were recorded with a Sony TC-D5M cassette tape recorder onto TDK-SA High Bias recording tape, using a Sennheiser ME-88 microphone. This equipment provides accurate frequency response from 50 to 15,000 Hz. Cohesion calls were recorded by standing within 2–3 m of one or several individuals, who were somewhat isolated from other troop members, and waiting for a periodic round of these vocal exchanges to occur. Samples were obtained throughout the diurnal activity cycle, but success was greatest during the morning and late afternoon hours when the lemurs were most active. Only calls of good recording quality were used in the analyses. A sample of sonograms (approx 4–6 calls per individual) was produced initially on a Kay 6061-B Sonograph to discover the salient physical features of the cohesion call. All individual calls were then measured using a Niscan II digital real-time audio spectrum analyzer (frequency resolution: ± 16 Hz;

time resolution: $\pm .006$ sec at the 0–2-kHz setting). Although five to six energy bands were usually discernible in each call, only the first three bands were considered consistent enough in quality to be measured precisely. Measurements were taken from the monitor of the Uniscan II using calibrated frequency and time cursors supplied via the system's keyboard interface. Dot-matrix printouts of the calls were made on an Epson MX100III printer as direct output from the Uniscan II. A representative cohesion call from each study animal is displayed in Figure 1.

Statistical Analyses

A step-wise discriminant analysis program of SPSS [SPSS Inc, 1986] was used to select those variables most useful in discriminating among the cohesion calls of individual ringtailed lemurs. Canonical correlation also was performed in this procedure in order to transform the discriminating variables into classification functions. Smith et al. [1982:271] have pointed out that "this procedure guarantees that the first classification function (most heavily weighted) always contains the best single combination of discriminant variables, whereas the last function (least heavily weighted) contains the poorest combination of discriminators." Step-wise discriminant analysis has also been applied elsewhere to vocal discrimination of individual primates [eg, Snowdon et al, 1983]. The five different methods of step-wise variable selection in SPSS (MAHAL, RAO, WILKS, MAXMINF, and MINRESID) were used to find the best discriminant model. An F-value of 4.0 was required for variables to enter and to remain in the model once entered. An F-value of this magnitude causes a smaller subset of highly discriminating variables to be chosen than that chosen by the program's default F-value of 1.0. Two structural parameters (duration and frequency) were used to define nine measured and three computed variables (Fig. 2). Gender and age class also were added to this set of discriminating variables.

Because the classification functions were derived from the same data set that they were used to classify, a cross-validation of the analysis was performed in a fashion similar to that of Smith et al [1982]. A random sample of 40% of the calls ($n = 74$) was used to derive the classification functions. These functions were then used to classify the remaining 60% of the calls ($n = 111$).

Further statistical examinations included a Pearson correlation of the dependent variables, a one-way analysis of variance (ANOVA), and a series of Duncan multiple range tests, which compared the dependent variables between pairs of individuals. Finally, Spearman rank correlation coefficients were generated in an investigation of the possible relationship between kinship and shared vocal characteristics. This nonparametric test was used in this case because of small sample sizes. The degree of relatedness (r) was computed for all pairs of the eight study animals using matrilineal ties only. While this approach probably reduced the values of actual relatedness between some of the animals, lack of confidence of paternity in a number of cases favored this method for determining genealogical relationships.

RESULTS

Each of the five variable selection methods produced a model containing a set of five discriminating variables. These models differed slightly, however, in the particular variables chosen and in their classification accuracy (Table I). The first two functions in the MAXMINF and MINRESID models accounted for over 90% of the total explained variation (Table II). On the average, nearly three of every four calls was correctly assigned by these models, indicating a high level of discrimination of individuals by their call structures. However, the uniqueness of certain individual's

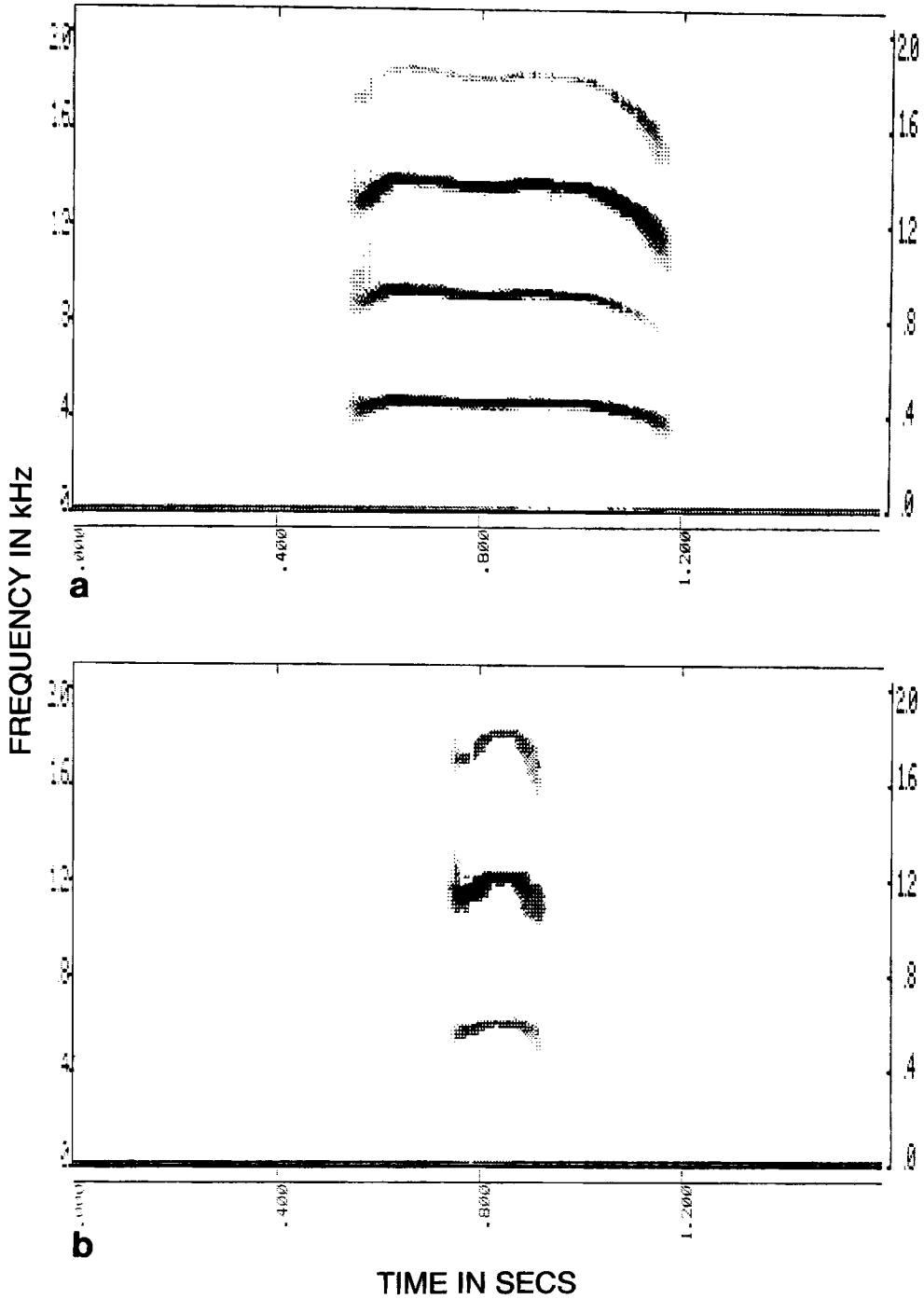
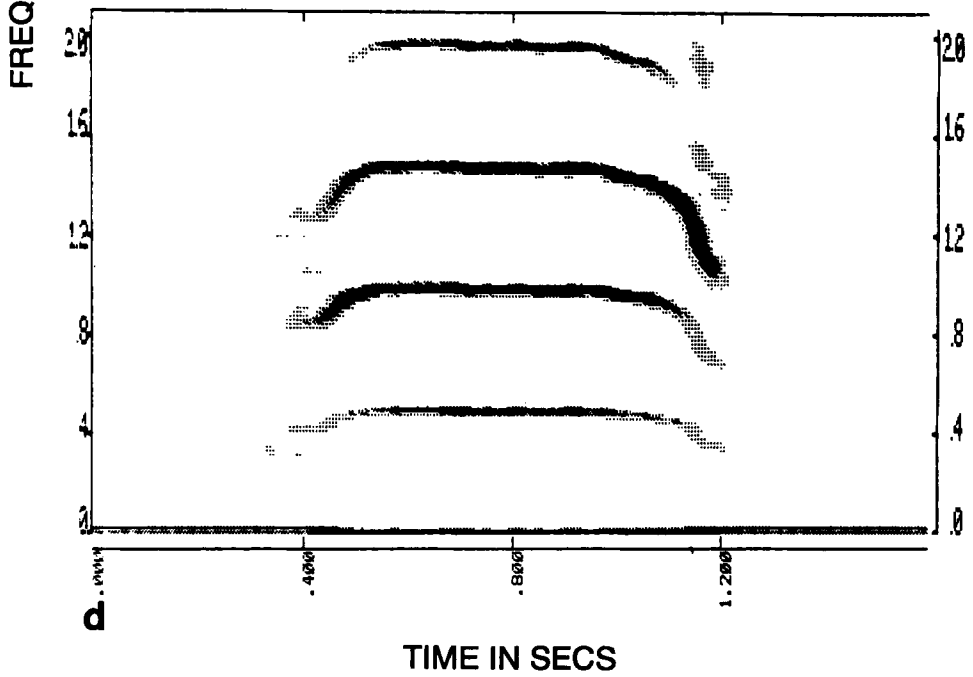
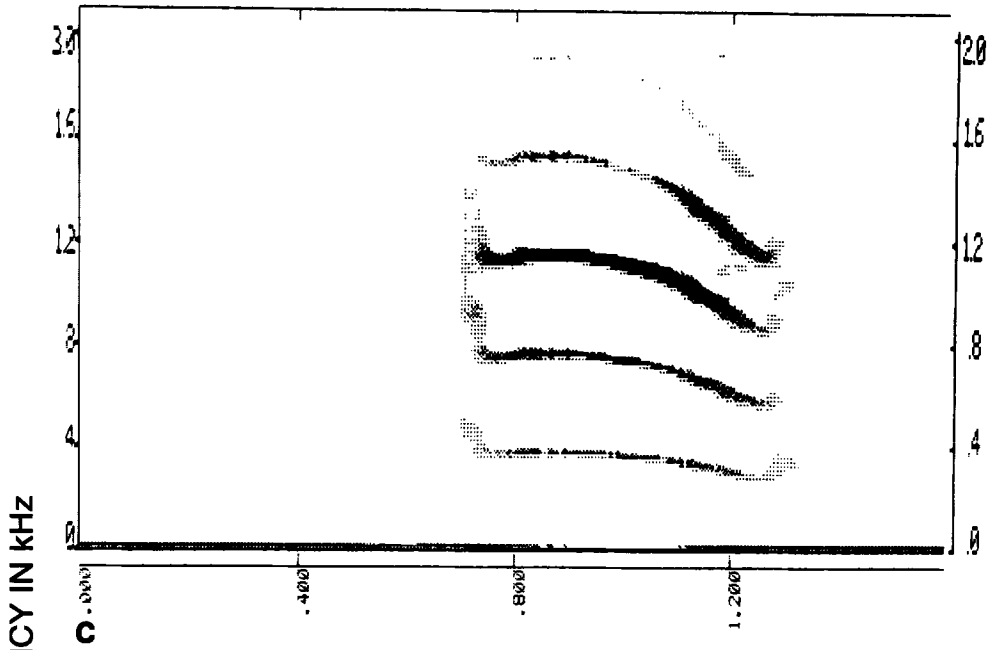
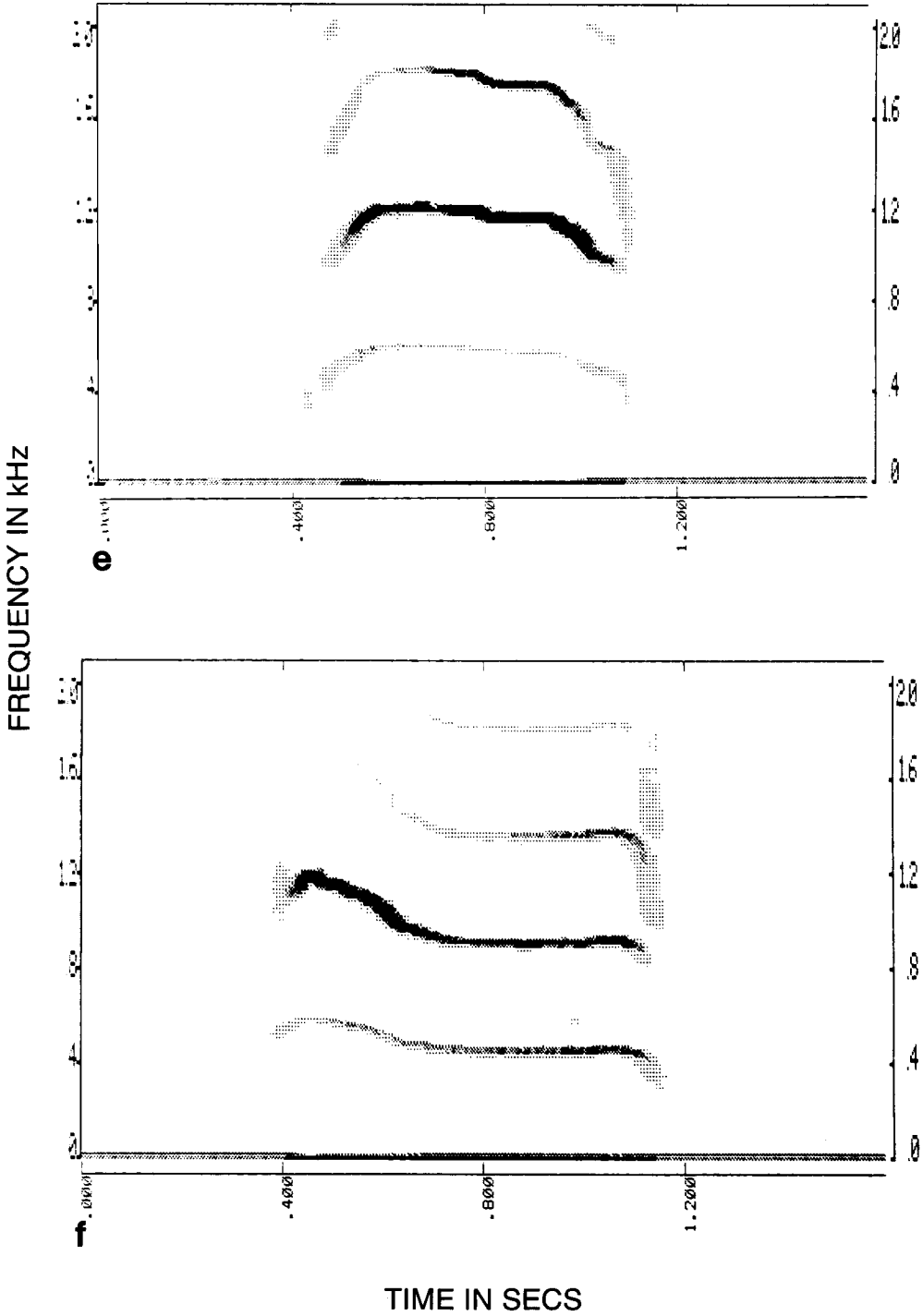
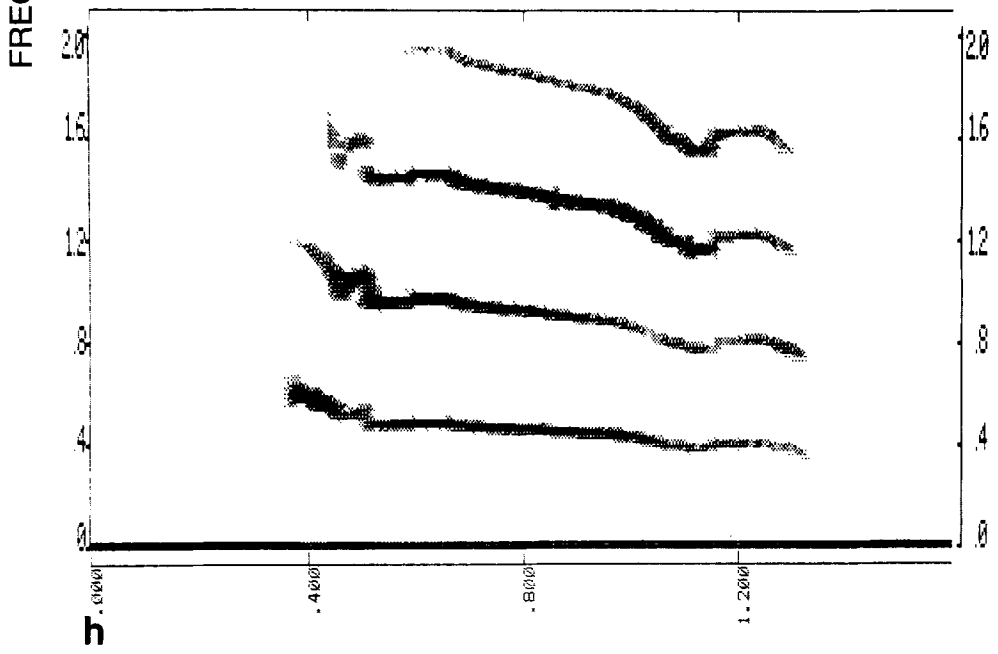
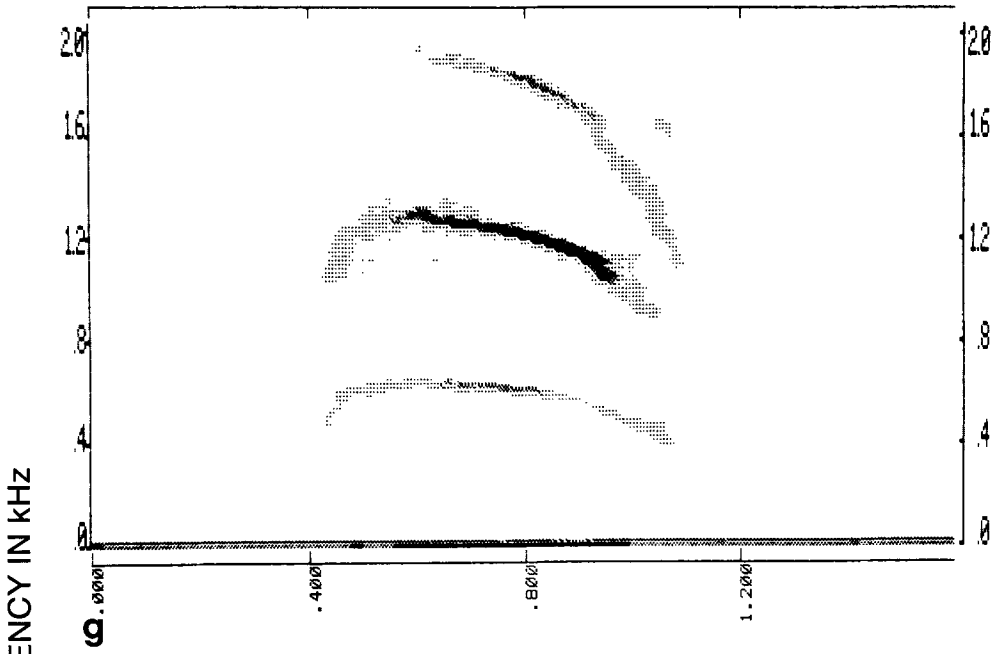


Fig. 1. a-h. Typical cohesion calls from the eight study animals. a, Arachne; b, Hypocrates; c, Kryos; d, Lysis; e, Megara; f, Sosthenes; g, Attis; h, Corinna.







TIME IN SECS

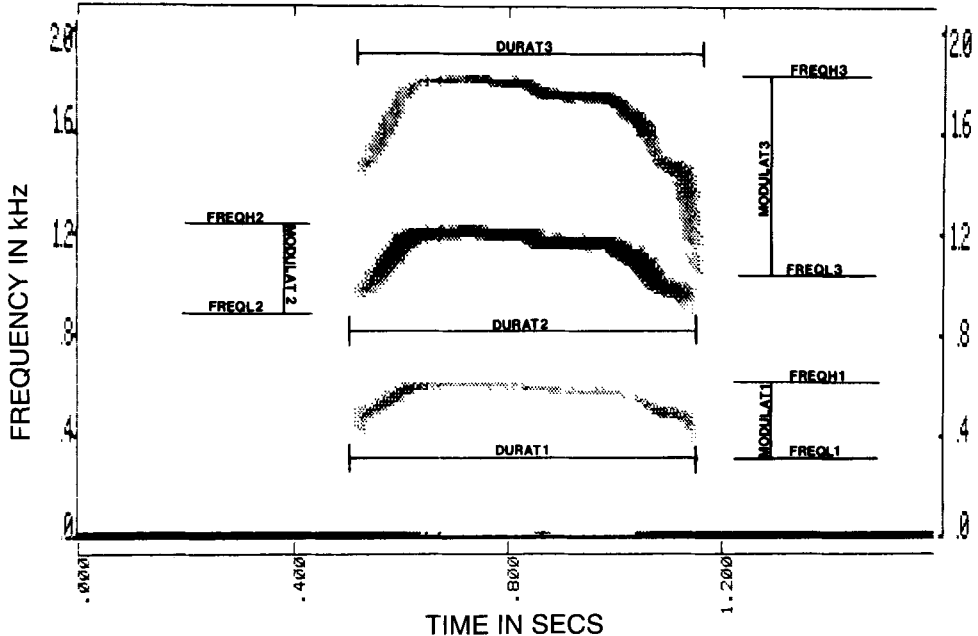


Fig. 2. Illustration of the 12 acoustic variables used in this study. In each energy band (1, 2, and 3) DURAT = duration, FREQ_L = lowest frequency, FREQ_H = highest frequency, and MODULAT = modulation (FREQ_H minus FREQ_L).

calls (eg, Hypocrates) led to differential discrimination among the study animals (Table III). Nevertheless, all individuals were correctly classified by their calls far above the level of random probability (12.5%). Gender and age class were found to be nonsignificant in individual discrimination, and did not pass the initial tolerance test ($F \geq .001$) to enter any of the discriminant models.

The classificatory ability of the cross-validation analysis was found to be slightly less precise than the initial analysis. The predictive accuracy of the five cross-validating models (Table IV) ranged from 51.35 to 63.06%, while the original five models (Table I) ranged from 73.51 to 74.05%. Several factors could have accounted for this decrease in accurate prediction of call ownership when the data set was sampled randomly.

First, unlike the initial analysis in which five variables were included in each model, only four variables for predicting call ownership were used in each cross-validation model. As fewer variables were used, less of the variation was explainable. Second, the greater predictability of the original classification models may have been an intrinsic property of the data set used. That is, the initial classification functions may have partially reflected the particular features of the 185-call data set rather than the general differences between the calls of different individuals. However, as the best cross-validation models (WILKS and MINRESID) correctly predicted only about 11% fewer calls and utilized far fewer calls per individual to derive the classification equations (median = 9 calls; range = 4–18 calls) than the original models (median = 21 calls; range = 14–39 calls), the acoustic variables used in this study still appear to be effective predictors of call ownership. Had the initial sample sizes been larger for some individuals, it seems probable that the discrepancy between the original and cross-validation results would have been diminished.

TABLE I. The Five Discriminant Models Examined*

Model	Variables	Calls correct	Percent correct
MAHAL	DURAT1, FREQL2, FREQL3, MODULAT2, MODULAT3	136	73.51
RAO	DURAT1, FREQL2, FREQL3, MODULAT2, MODULAT3	136	73.51
WILKS	DURAT1, FREQL2, FREQL3, FREQH2, FREQH3	136	73.51
MAXMINF	DURAT2, FREQL2, FREQL3, MODULAT2, MODULAT3	137	74.05
MINRESID	DURAT2, FREQL2, FREQL3, FREQH2, FREQH3	137	74.05

*n = 185 calls for all models.

TABLE II. Canonical Discriminant Functions (MAXMINF/MINRESID Models)

Function	Percent of variance	Cumulative percentage	Canonical correlation
1	80.95	80.95	0.94
2	10.76	91.71	0.72
3	5.21	96.92	0.59
4	2.72	99.63	0.46
5	0.37	100.00	0.19

TABLE III. Classification Results*

Actual group	No. of cases	Predicted group membership (%)							
		1	2	3	4	5	6	7	8
Group 1 Arachne	21	11 (52.4)	0 (0.0)	1 (4.8)	3 (14.3)	1 (4.8)	3 (14.3)	0 (0.0)	2 (9.5)
Group 2 Hypocrates	39	0 (0.0)	39 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Group 3 Kyros	20	0 (0.0)	0 (0.0)	15 (75.0)	3 (15.0)	0 (0.0)	1 (5.0)	1 (5.0)	0 (0.0)
Group 4 Lysis	32	4 (12.5)	0 (0.0)	2 (6.3)	23 (71.9)	1 (3.1)	1 (3.1)	0 (0.0)	1 (3.1)
Group 5 Megara	16	4 (25.0)	0 (0.0)	0 (0.0)	0 (0.0)	8 (50.0)	1 (6.3)	3 (18.8)	0 (0.0)
Group 6 Sosthenes	22	2 (9.1)	0 (0.0)	0 (0.0)	0 (0.0)	1 (4.5)	18 (81.8)	1 (4.5)	0 (0.0)
Group 7 Attis	21	0 (0.0)	0 (0.0)	0 (0.0)	1 (4.8)	2 (9.5)	1 (4.8)	15 (71.4)	2 (9.5)
Group 8 Corinna	14	2 (14.3)	0 (0.0)	0 (0.0)	2 (14.3)	0 (0.0)	1 (7.1)	1 (7.1)	8 (57.1)

*Percent of "grouped" cases correctly classified: 74.05%.

TABLE IV. The Five Discriminant Models Examined in the Cross-Validation Analysis*

Model	Variables	Calls correct	Percent correct
Mahal	FREQL2, FREQH2, FREQH3, MODULAT3	57	51.35
Rao	FREQL1, FREQL2, FREQH2, MODULAT3	62	55.86
Wilks	DURAT1, FREQL2, FREQL3, FREQH2	70	63.06
Maxminf	FREQL1, FREQL2, MODULAT2, MODULAT3	62	55.86
Minresid	DURAT1, FREQL2, FREQL3, FREQH3	70	63.06

*n = 111 calls for all models.

A one-way ANOVA showed that variation in call structure was significantly greater between than within individuals ($P \leq .001$) for all 12 structural variables. Individual means for these variables are presented in Table V. Pair-wise comparisons of all individuals for each variable were then performed with the Duncan multiple range test. This test showed that usually more than one variable differed significantly between all pairs of individuals (Table VI). The striking number of significant differences between individuals may be misleading, however, as most of the structural variables were found to be highly correlated among themselves (Table VII).

The correlation between degree of relatedness (Table VIII) and the number of calls misclassified with other individuals was found to be nonsignificant ($r_s = -.0012$; $P = .497$; $n = 56$). A strong positive but nonsignificant correlation was found between degree of kinship and the number of variables differing significantly between pairs of individuals ($r_s = .2564$; $P = .094$; $n = 28$). Thus, the data in this study do not unequivocally support the presence or absence of kin-group traits in the cohesion call of the ringtailed lemur but do indicate a need for further investigation.

DISCUSSION

Results of the discriminant analysis show that individual ringtailed lemurs can be distinguished on the sole basis of acoustic differences present in their cohesion calls. The percent of correct classifications in this analysis of a prosimian vocalization (74.05%) lies intermediate to similar analyses of anthropoids by Smith et al [1982] for squirrel monkeys (95.16%) and Snowdon et al [1983] for tamarins (62.35%—mean between two analyses). Numerous factors may be involved in these different levels of accuracy (eg, stereotypy of the particular call analyzed, inclusion or exclusion of individuals in the sample with particularly unusual vocal characteristics, or resolution and accuracy of measurements).

Furthermore, it is conceivable that varying classification accuracy of individuals by their vocalizations may reflect a differential in some inherent "need" across primate taxa to possess vocal traits that would permit individual discrimination. If so, such a variable might perhaps be a function of taxon-specific social and/or ecological factors, such as group size and dispersion patterns or degree of visibility in a given habitat. Whatever the selective forces involved, some species, such as squirrel monkeys, appear to strongly and consistently exhibit the acoustic products of selection for vocal individuality.

To illustrate, in addition to the work of Smith [1982], three separate studies have employed discriminant analysis as a technique for examining the presence of vocal signatures in squirrel monkeys. Using the nonparametric "nearest neighbor" method, Symmes [1979], Liebllich et al [1980], and Symmes and Biben [1985] have all shown a high degree of vocal individuality among the "isolation peeps" (IP's) of

TABLE V. Individual Means and Standard Deviation by Variable

Variable	ARACHNE (adult, ^a female n = 21)	HYPO- CRATES (adult, male n = 39)	KYROS (subadult, ^a male n = 20)	LYSIS (adult, female n = 32)	MEGARA (subadult, female n = 16)	SOSTHENES (subadult, male n = 22)	ATTIS (subadult, female n = 21)	CORINNA (juvenile, ^a female n = 14)
DURAT1 (sec)	.679 ± .141	.253 ± .073	.746 ± .252	.856 ± .164	.871 ± .352	.641 ± .123	.707 ± .089	.660 ± .182
DURAT2 (sec)	.612 ± .142	.258 ± .072	.705 ± .245	.792 ± .163	.838 ± .332	.620 ± .127	.674 ± .095	.618 ± .201
DURAT3 (sec)	.665 ± .146	.236 ± .073	.686 ± .244	.822 ± .160	.822 ± .340	.606 ± .119	.579 ± .119	.604 ± .166
FREQJ1 (Hz)	345 ± 27	526 ± 41	307 ± 59	328 ± 27	353 ± 20	337 ± 28	371 ± 46	381 ± 48
FREQJ2 (Hz)	752 ± 32	1,081 ± 68	616 ± 103	683 ± 38	841 ± 137	788 ± 55	882 ± 67	823 ± 92
FREQJ3 (Hz)	1,032 ± 65	1,670 ± 83	921 ± 77	983 ± 73	1,073 ± 61	975 ± 39	1,176 ± 73	1,170 ± 81
FREQH1 (Hz)	488 ± 78	716 ± 119	561 ± 173	502 ± 72	613 ± 254	545 ± 145	701 ± 122	575 ± 138
FREQH2 (Hz)	968 ± 57	1,425 ± 177	1,164 ± 79	988 ± 72	1,216 ± 63	1,118 ± 60	1,397 ± 151	1,120 ± 109
FREQH3 (Hz)	1,437 ± 106	2,073 ± 191	1,487 ± 194	1,445 ± 84	1,728 ± 200	1,559 ± 131	1,968 ± 200	1,597 ± 140
MODULAT1 (Hz)	143 ± 41	190 ± 65	254 ± 98	174 ± 53	260 ± 136	207 ± 57	330 ± 97	194 ± 98
MODULAT2 (Hz)	215 ± 98	344 ± 113	549 ± 186	305 ± 110	376 ± 244	330 ± 143	515 ± 131	297 ± 157
MODULAT3 (Hz)	405 ± 94	403 ± 203	566 ± 190	463 ± 120	655 ± 191	583 ± 110	792 ± 277	427 ± 173

^aAdults are animals born prior to 1983. Subadults were born in 1983, and the juvenile was born in 1984.

TABLE VI. Pair-wise Comparison of Study Animals by Variable*

	ARACHNE	HYPO-CRATES	KYROS	LYSIS	MEGARA	SOSTHENES	ATTIS
Hypocrates	1-11						
Kyros	4-8,10-11	1-12					
Lysis	1-3,5,11	1-9	1,3,5,7-8, 10-12				
Megara	1-3,5,7-12	1-10,12	1-6,9,11	5-10,12			
Sosthenes	7-12	1-9,12	4-5,11	1-3,5,7- 9,12	1-3,5-9		
Attis	4-12	1-6,9-12	4-10,12	1-12	1-3,6-11	5-12	
Corinna	4-9	1-9	4-6,10-12	1-9	1-3,6,9- 10,12	4,6,12	5,7-12

*Numbers in columns represent variables (below) that differed significantly between individuals in the Duncan Multiple Range Test ($P \leq .05$). 1 = DURAT1; 2 = DURAT2; 3 = DURAT3; 4 = FREQ1; 5 = FREQ2; 6 = FREQ3; 7 = FREQH1; 8 = FREQH2; 9 = FREQH3; 10 = MODULAT1; 11 = MODULAT2; 12 = MODULAT3.

TABLE VII. Correlation of Acoustic Variables*

	DURAT1	DURAT2	DURAT3	FREQ1	FREQ2	FREQ3	FREQH1	FREQH2	FREQH3	MODU-LAT1	MODU-LAT2
DURAT2	+										
DURAT3	+	+									
FREQ1	-	-	-								
FREQ2	-	-	-	+							
FREQ3	-	-	-	+	+						
FREQH1	-	-	-	+	+	+					
FREQH2	-	-	-	+	+	+	+				
FREQH3	-	-	-	+	+	+	+	+			
MODU-LAT1	+	+	NS	NS	NS	NS	+	+	+		
MODU-LAT2	(+)	+	NS	(-)	(+)	NS	+	+	+	+	
MODU-LAT3	+	+	+	-	(+)	(-)	+	+	+	+	+

*Pluses represent positive correlations; minuses represent negative correlations. Symbols in parens, $P \leq .05$; all other symbols, $P \leq .01$; NS, not significant.

TABLE VIII. Genealogical Relationships of the Study Animals*

	ARACHNE	ATTIS	CORINNA	HYPOCRATES	KYROS	LYSIS	MEGARA
Attis	r = .250						
Corinna	r = .063	r = .063					
Hypocrates	r = .125	r = .125	r = .125				
Kyros	r = .063	r = .063	r = .250	r = .125			
Lysis	r = .125	r = .125	r = .500	r = .250	r = .500		
Megara	r = .250	r = .250	r = .063	r = .125	r = .063	r = .125	
Sosthenes	r = .031	r = .031	r = .125	r = .063	r = .125	r = .250	r = .031

*Genealogies based solely on matrilineal kinship.

infant squirrel monkeys. Classification accuracy of individuals by their IP's ranged from 71% to 99% across the three studies, with a mean of 87% accurate call prediction. That such vocal differences are due to chance seems highly unlikely. Moreover, these vocal signatures do indeed appear to be used by conspecifics in recognition of individuals. This recognition has been inferred from evidence obtained experimentally with squirrel monkeys [eg, Kaplan et al, 1978; Symmes & Biben, 1985] as well as with other primates [Cheney & Seyfarth, 1980; Snowdon & Cleveland, 1980; Snowdon et al, 1983; Masataka, 1986; Pereira, 1986].

Experimental evidence of individual recognition in primates has largely centered around the ability of mothers to recognize the calls of their offspring [cf, Snowdon & Cleveland, 1980; Snowdon et al, 1983; Masataka, 1986], primarily through the use of prerecorded playbacks [cf, Kaplan et al, 1978]. The general level of success found in this body of work seems to suggest that kinship may be one important factor involved in individual recognition in primates. To date, the only study that has attempted to link vocal characteristics and (nonhybrid) kinship is that of Lieblisch et al [1980]. However, although the genealogies of the infant squirrel monkeys used in this study were certain, results were inconclusive because some infants exhibited vocal traits similar to those of their mothers, while other infants' vocalizations either did not resemble those of their mothers or resembled those of some unrelated individual. Lieblisch et al [1980] also noted the seemingly peculiar fact that none of the infants in this study vocally resembled their fathers.

While not the primary focus of the study reported here, a possible correlation between vocal similarity and kinship in the ringtailed lemur's cohesion call was suggested. The adaptive significance of kin recognition through "signature-matching" has been discussed by Beecher [1982], who presented a model for recognizable acoustic (and other) traits in terms of Hamilton's [1964] kin selection hypothesis. Essentially, "the individual might compare its own signature to that of [an] unknown individual, inferring kinship if their signatures are sufficiently similar" [Beecher, 1982:477]. If the cohesion call functions to maintain contact among dispersed group members (of which at least some are close kin), then this vocalization might be expected to harbor acoustic traits that allow relatives to detect each other's locations.

There are a number of structural properties of the cohesion call of *L. catta* that would optimize its ability to encode information regarding the sender's direction and distance from a receiver in addition to individual identity. First, while gradients and fluctuations in temperature, wind, background noise, and broadcast height, in conjunction with more temporally stable factors, such as sound beam absorption, deflection, reverberation, and scattering, will ultimately determine the efficiency of vocal transmissions, calls containing narrow frequency bands (pure-toned, or "clear calls") are inherently better for distance propagation than wide-band calls regardless of amplitude [see Wiley & Richards, 1978; Brown, 1982]. Second, narrow-band calls permit information to be transmitted via both frequency and amplitude modulation, whereas wide-band calls are limited to amplitude changes to convey messages [Wiley & Richards, 1978]. Third, although wide-band calls are more localizable than narrow-band calls, employment of frequency modulation in clear calls provides an optional route toward sound locatability [Waser, 1977; Brown et al, 1978a,b, 1979, 1980]. Fourth, frequency ranges of attenuation minima, or "sound windows," have been found to exist from about 200 Hz to 2 or 3 kHz, depending upon the particular study [eg, Morton, 1975; Marten & Marler, 1977; Marten et al, 1977; Waser & Waser, 1977; Wiley & Richards, 1978; Waser & Wiley, 1979; Richards & Wiley, 1980; Waser & Brown, 1984, 1986], and calls exploiting this region will travel further in the same habitat than calls outside of this range. Fifth, while harmonics above the fundamental (first) frequency band do not provide much information about the direction of a

sound source [Brown et al, 1979], they do appear to degrade in a systematic fashion over transmission distance [Wiley & Richards, 1978] and thus give the receiver of the signal an idea of how close or far the sender may be.

The cohesion call of the ringtailed lemur utilizes all of the above features in that it contains low to intermediate, narrow, modulated frequency bands, and harmonic frequencies that degrade with distance from the broadest source. Thus, this relatively low amplitude vocalization represents a well propagating, high-information-content and localizable auditory signal, and is, therefore, a reasonable suspect for the application of Beecher's [1982] signature-matching model. The results of the present study are, unfortunately, somewhat ambiguous regarding the presence of kin-group traits in the cohesion call. Nevertheless, a strong positive correlation between the number of significant differences in acoustic variables and the degree of genetic relatedness between individuals argues against dismissing the possible presence of these traits.

While statistical analysis has often been shown to be an important tool for investigating the physical basis of vocal discrimination in animals, Snowdon and Cleveland [1980] have pointed out that evidence of structural variation in conspecific vocalizations is not a demonstration that this information is used or even perceived by the animals in question. Complimentary evidence of discrimination by the animals themselves (eg, via playback experiments) is needed before conclusions about communication mechanisms can be drawn.

The study reported here has shown that the physical parameters necessary for individual discrimination by vocalization exist in the structure of the ringtailed lemur's cohesion call. It now remains for research to determine whether or not these primates can identify one another on the basis of these vocal cues.

CONCLUSIONS

1. Significant differences in acoustical structure were found among the cohesion calls of individual ringtailed lemurs (*Lemur catta*).
2. Pair-wise comparisons of the study animals by call variable suggest that each individual exhibits a unique vocal profile with respect to this call.
3. Correlation analyses between genetic relatedness and shared vocal characteristics did not indicate a clear relationship between these two variables. Further investigation is needed to resolve this issue.

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