# Vocal Repertoire of *Cebus capucinus*: Acoustic Structure, Context, and Usage

**Julie J. Gros-Louis · Susan E. Perry ·
Claudia Fichtel · Eva Wikberg ·
Hannah Gilkenson · Susan Wofsy · Alex Fuentes**

**Abstract** Researchers studying nonhuman primate vocal repertoires suggest that convergent environmental, social, and motivational factors account for intra- and interspecific vocal variation. We provide a detailed overview of the vocal repertoire of white-faced capuchins, including acoustic analyses and contextual information of vocal production and vocal usage by different age-sex classes in social interactions. The repertoire is a mixture of graded and discrete vocalizations. In addition, there is general support for structural variation in vocalizations with changes in arousal level. We also identified several combined vocalizations, which might represent variable underlying motivations. Lastly, by including data on the social contexts and production of vocalizations by different age-sex classes, we provide preliminary information about the function of vocalizations in social interactions for individuals of different rank, age, and sex. Future studies are necessary to explore the function of combined vocalizations and how the social function of vocalizations relate to their

J. J. Gros-Louis (✉)
Department of Psychological and Brain Sciences, Indiana University, Bloomington, IN 47405, USA
e-mail: jgroslou@indiana.edu

S. E. Perry · H. Gilkenson · A. Fuentes
Proyecto de Monos, Apdo 5, Bagaces, Guanacaste 50401, Costa Rica

S. E. Perry
Department of Anthropology, Behavior, Evolution and Culture Program,
University of California–Los Angeles, Los Angeles, CA 90095, USA

C. Fichtel
Department of Behavioral Ecology and Sociobiology, German Primate Center,
37077 Göttingen, Germany

E. Wikberg
Department of Anthropology, University of Calgary, Calgary, AL T2N 1N4, Canada

S. Wofsy
School of International and Public Affairs, Columbia University, New York, NY 10027, USA

acoustic structure, because social use of vocalizations may play an important role in shaping vocal evolution.

**Keywords** capuchin · *Cebus capucinus* · communication · social behavior · vocal repertoire

# Introduction

An investigation of repertoires across primate species indicates that one can group vocalizations into ≥3 broad behavioral contexts: social contact, agonistic inter-actions, and alert or alarm calls (Zimmerman 1985), with many monkey and ape species also having distinct calls for contact/spacing (proximity), affiliative interactions (social), feeding behavior, sexual behavior, and intergroup encounters (Bermejo and Omedes 1999; Cleveland and Snowdon 1982; Hammerschmidt and Fischer 1998; Palombit 1992; Range and Fischer 2004). Researchers studying nonhuman primate communication often focus on particular calls within a single context to examine stimuli that elicit calling and behavioral contexts that influence calling, e.g., alarm calls (Fichtel and Kappeler 2002; Fischer and Hammerschmidt 2001; Macedonia 1990; Seyfarth *et al.* 1980; Zuberbühler 2000), food-associated calls (Di Bitetti 2003; Dittus 1984; Evans and Evans 1999; Gros-Louis 2004a), and intergroup encounters (Mitani 1985; Robinson 1979). In addition, some researchers have focused on the mediating effects of vocalizations in social interactions (Cheney *et al.* 1995; Gros-Louis 2002; Harcourt *et al.* 1993; Palombit *et al.* 1999; Rendall *et al.* 1999).

The aforementioned studies have provided detailed information about the proximate factors that influence signaling and how signals influence the behavior of call recipients, thus indicating the presumed function of the signals. However, to understand fully the relationship between vocal and social behavior, it is important to investigate not only the calls in a particular context, but also the relationship among call types within the vocal repertoire of a species. Information about the acoustic structure, context of call production, and call usage for different age-sex classes, when considered across the vocal repertoire, informs the relationship between signal structure and function. In addition, cross-specific comparisons of vocal repertoires enable assessment of hypotheses related to the evolution of particular call structures under different socioecological conditions (Marler 1976, 1977; Morton 1977; Owings and Morton 1998; Owren and Rendall 2001). Lastly, with vocal repertoires available, one can compare studies that assess the context and function of calls across species. We aimed to provide a comprehensive overview of the structure, function, and usage of vocalizations in white-faced capuchins (*Cebus capucinus*) to guide future studies on their vocal communication in that of other species.

Like studies in other species, prior studies in white-faced capuchins examined individual call types from diverse categories of the repertoire, including spacing, food-associated, and alert calls (trills: Boinski 1993; Boinski and Campbell 1995; Gros-Louis 2002; food-associated calls: Boinski and Campbell 1996; Gros-Louis 2004a, b; alarm calls: Digweed *et al.* 2005; Fichtel *et al.* 2005; lost calls: Digweed *et al.* 2007). Though the studies provide a detailed examination of the function of

particular calls in exemplar categories of vocal communication (contact, spacing, alert), there has been no attempt to examine the entire vocal repertoire, aside from 2 very early nonquantitative descriptive studies (Freese and Oppenheimer 1981; Oppenheimer 1973). We add to the early descriptions by providing acoustic analyses and more detailed information on the social and ecological covariates of vocal production to contribute to a better understanding of the vocal repertoire variation across primate species.

## Methods

### Study Site and Subjects

We recorded and observed 3 social groups of white-faced capuchins —Abby's, Rambo's, and Fonz's groups— with the exception of recordings of human alarm calls from 2 unhabituated groups. The 3 groups range in Lomas Barbudal Biological Reserve, a 2279-ha reserve in Guanacaste Province, Costa Rica, adjacent private ranches, a community reserve, and government-managed IDA property (Instituto para Desarollo Agricultura). The habitats are composed of riparian and tropical dry deciduous forest (Frankie *et al.* 1988).

### Vocal Usage Data

Perry and Perry's field assistants collected the data on vocal usage from 1991 to 2003 as part of long-term studies on development, social behavior, and vocal communication. The total database consisted of >13,000 h of data, though we used different subsets for different analyses. Due to call rarity, the size of subsets varied across call types and across analyses, as follows: 1) age at first call, 64–800 focal h; 2) call rate, 70–920 focal h; and 3) social context, 198–1822 focal h. Perry analyzed the vocal usage data, with coding assistance from Wofsky and Wikberg. For common calls for which more data were available, we provide more detailed usage analyses.

### Call Sample

We based the analysis of acoustic structure of calls primarily on 46 h of recordings Perry made in 1999. We supplemented the database with 94 h of recordings Perry and field assistants made from 2001 to 2003, and 7 h of recordings Gros-Louis made in 2000. We used a Sony Professional Walkman and a Sennheiser ME66 directional microphone, with high bias IEC type II ($CrO_2$) audio tapes. We made recordings opportunistically, at any hour of day when it was not raining or windy, and when the monkeys were not near noisy water sources.

### Acoustic Analyses

Fichtel, Gilkenson, Wikberg, and Fuentes acquired calls, based on recording quality, via Cool Edit (Syntrillium, Phoenix, AZ) and AVISOFT-SASLab Pro 4.12 (R. Sprecht,

Berlin, Germany). We used different sampling frequencies to digitize calls depending on their frequency ranges (22.05 kHz, 32 kHz, 44.1 kHz).

We performed fast Fourier transforms on digitized calls via AVISOFT-SASLab Pro 4.2 (R. Specht, Berlin, Germany). We used a 1024-point fast-Fourier transform, Hanning window function. We analyzed resulting frequency-time spectra via LMA (version 9.2), a custom acoustic analysis program for extracting and deriving variables from acoustic signals (Hammerschmidt and Todt 1995). Researchers have employed LMA in numerous studies of animal vocal communication (Fichtel *et al.* 2005; Fischer and Hammerschmidt 2002; Gros-Louis 2006; Manser 2001). The algorithms used to calculate acoustic parameters and to derive acoustic measurements are per Schrader and Hammerschmidt (1997).

We calculated 14 acoustic parameters via LMA related to time, frequency, and amplitude characteristics for the majority of calls except the ones consisting of pulsed elements (trills and staccato screams). First, we calculated several characteristics of the first 2 dominant frequency bands (DFB). Dominant frequency bands are characterized by amplitudes that exceed a given threshold in a consecutive number of frequency bins (Schrader and Hammerschmidt 1997). We calculated the duration, start, end, and mean frequency for the first and second dominant frequency bands. In addition, we derived the mean frequency range of each call by averaging the difference between the highest and lowest frequencies across all time segments.

In addition to measurements on frequency characteristics of each call, we performed measurements on the statistical distribution of spectral energy in the call. First, we determined the overall amplitude for each time segment and derived the frequency at which the amplitude reached the first and second quartile of the total amplitude distribution (Schrader and Hammerschmidt 1997). Then, we averaged the frequencies of the first quartile for each time segment to derive the mean frequency of amplitude distribution for the first quartile, and likewise for the second quartile of amplitude distribution. From the measurement, we determined the start and end frequency of the mean frequency for the first and second quartiles of the amplitude distribution. We derived the mean value of the frequencies with the highest amplitude across the call by averaging across all time segments (mean peak frequency). Lastly, we included a measure of the relative position in the call of the frequency with the highest amplitude [1/call duration (ms) × location of peak frequency (ms)].

For pulsatile calls (trills and staccato screams), we determined the mean peak frequency and the location of the peak frequency as with the other call types. In addition, we determined the location at which the amplitude was at a minimum in the call. To capture the contoured shape of the calls and their pulsatile nature, we also included the following measurements: 1) We derived the frequency range encompassing the spectral energy in the call from the frequencies at which the minimum and maximum amplitude were reached. 2) We calculated the average number of gaps in the call (spaces between elements). 3) We derived the mean gap length by averaging the gap lengths across the call.

Statistical Analyses

Different numbers of individuals and calls contributed to analyses for different call types (range: 2–17 individuals contributing 1–22 calls each). When calculating mean

values of call parameters, we first calculated means for each individual and then averaged across individuals so as to control for any bias by 1 individual contributing more vocalizations to the sample.

To examine differences between acoustically similar call types, we used discriminant function analyses. To cross-validate the discriminant function that was generated, we used the leave-one-out classification procedure, whereby each call is classified by the functions derived from all calls other than that one. For each analysis, we randomly selected an equal number of calls from individuals because the discriminant function analysis is sensitive to unbalanced data sets.

Before performing the discriminant function analyses, we first conducted principal components analyses (PCA) to reduce the 14 original variables to a smaller set of uncorrelated variables (Dunteman 1989). For the subsequent discriminant function analyses, we used a stepwise procedure, employing the *F*-to-enter criterion for entering variables (Klecka 1980). We included all variables whose associated *F* statistics had a *p*-value of <0.05. To determine the factors that differed between call types, we performed univariate analyses of variance using the factor scores from the PCA (Gros-Louis 2006).

We conducted analyses via SPSS version 12.0.1. All statistical tests are 2-tailed.

## Results

We summarized vocalizations into 5 functional categories based on extensive observations of context of emission: affiliative and appeasement, agonistic, cohesion and group movement, sociosexual, and alarm calls. We based individual call terminology on call labels that we and other researchers had published. Table 1 contains an overview of the vocalizations in the repertoire including the age-sex classes that produce each vocalization, the age that particular vocalizations appear in the repertoire, the rate of occurrence of different vocalizations, and the general context in which subjects produce each vocalization. Acoustic measurements of calls are in Tables 2 and 3.

Affiliative and Appeasement Vocalizations

*Food-associated Call* (Fig. 1a,b)

Synonyms: huh (Boinski 1993; Boinski and Campbell 1996; Oppenheimer 1973).
Vocalizers: Primarily adult females and immatures (>1 yr, when foraging independently). Adult males rarely emit food-associated calls.
Acoustic structure and analysis: Typically tonal vocalizations with clear harmonics, but a more guttural, noisy variant also exists (Fig. 1b). Individuals often emit calls in bouts rather than singly. Food-associated calls are individually distinctive, and differ between the sexes (Gros-Louis 2006).
Usage and context of emission: Food-associated calls are one of the most common vocalizations in the repertoire. Individuals emit them only in food-related contexts, almost exclusively when they are foraging successfully, such as in the crown of a fruit tree (Boinski 1993; Gros-Louis 2006). Individuals emit the guttural

**Table 1** Demographic groups producing calls, age at onset of call production, call rate, and context of call production for the vocalizations in the white-faced capuchin vocal repertoire

| Call type | Functional category | Vocalizers | Age at first call ($n=16$ infants) | Call rate | Most common context |
|---|---|---|---|---|---|
| Alarm calls | Alarm | All age-sex classes, but rare in young infants | 85 | Adult females: 0.31 bouts/h (0.89 calls/h); adult males: 0.20 bouts/h (1.2 calls/h), infants: 0.07 calls/h | While visually focused on a potential predator, extragroup member, or in response to others' alarm calls |
| Bray | Agonistic | Most often by adult males | >2 yr | Adult males: <1 bout/100 h | Typically accompanied by intense vocal threat; often precedes intergroup encounters |
| Burst | Cohesion/group movement | Most often by adults | 85 | Adults: 0.07 bouts/h | When initiating group movement; accompanied by loud trills |
| Coo | Cohesion/group movement | Most common in infants under 2 yr of age; extremely rare in older animals and absent in adult males | 47 | Immatures: during first year of life: 1.03 bouts (6.84 calls/h); during second year of life: 0.22 bouts (0.56 calls/h) | When separated from mother |
| Cough | Agonistic | Most common in adult males; absent in infants and juveniles | >2 yr | Adult males: 1 call/100 h | While piloerected, often shortly before performing an aggressive behavior |
| Food-associated call | Affiliative/ appeasement | All age-sex classes, but rarer in adult males and very young infants | 33 | Adult females: 20.1 calls/h; adult males: 6.1 calls/h; juvenile females: 10.1 calls/h; juvenile males: 7.6 calls/h | While foraging, particularly for fruit |
| Gargle | Affiliative/ appeasement | All age-sex classes but infrequently by adult males | 12 | Adult females: 0.15 (without infant) to 2.0 (with infant); infants: 0.6–13.0 depending on developmental stage (older immatures gargles less often) | While following or touching an adult male (accompanied by ≥1 of the following behaviors: piloerection, penile/clitoral erection, head-shaking, wrinkly face, self-scratching, cowering); often combined with trills |
| Gecker | Affiliative/ appeasement | All age classes except adult males | 56 | | While inspecting or interacting affiliatively with an infant (often accompanied by fear grins); can grade into staccato screams or scream trills |
| Grunt | Sociosexual | All age-sex classes except for young infants | 221 | Adult females: 0.04 bouts/h; adult males: 0.17 bouts/h | During dances (generally accompanied by duck face, pacing, spinning, and often squeaks, wheezes, or intense gargles); often precedes mating; vocal exchanges between partners are typically rhythmic |

| Call | Category | Age-sex classes | Age at first call | Rate | Context |
|---|---|---|---|---|---|
| Intense gargle | Affiliative/appeasement | Most often by adult males | 159 | Adult males: 0.10 bouts/h; adult females: 0.01 bouts/h; infants: 0.003 calls/h | During dances (see entry for grunt) or in appeasement context, e.g., after or during a fight |
| Intense peep | Affiliative/appeasement | All age-sex classes | >1 yr | 1.3 bouts/mo of observation | When foraging on food that is potentially dangerous, e.g., insects that have urticating hairs or stings, or another form of defense or when encountering an atypical object or substance, e.g., mango pit covered in dirt, maimed insects that are moving |
| Intense vocal threat | Agonistic | Primarily adult males and high-ranking adult females | 89 | Adult females: 2 bouts/100 h; adult males: 11 bouts/100 h | Intergroup encounters; occasionally in predator contexts or severe intragroup aggression |
| Lost call | Cohesion/group movement | All age-sex classes | 77 | Adult females: 2.7 bouts/100 h; adult males: 4.1 bouts/100 h; infants: 4.0 bouts/100 h | When out of visual contact of the rest of the group, or when replying to another lost call |
| Mild vocal threat | Agonistic | All age-sex classes, but rare in infants | 92 | Adults: 0.24 bouts/h; infants: 0.03 bouts/h | When exhibiting mild aggression toward an opponent; always accompanied by open-mouth threat, and often by bouncing |
| Peep | Affiliative/appeasement | All age-sex classes, but primarily adult females | 23 | Adult females: 8.06 calls/h; Adult males: 1.85 calls/h; subadult females: 3.26 calls/h; subadult males: 1.17 calls/h; juvenile females: 0.69 calls/h; juvenile males: 0.36 calls/h; infants: 1.85 calls/h | When presenting for grooming, or when lying next to someone |
| Scream | Agonistic | All age-sex classes, but rare in adult males | 1 | Adult females 0.16 bouts/h; adult males 0.03 bouts/h; infants: 0.13 calls/h | In the most extreme agonistic situations involving physical contact, often followed by undulating screams and then pulsating screams |
| Squeak | Sociosexual | Adults and subadults | 127 | Adult females: 0.02 bouts/h; adult males: 0.12 bouts/h | During dances (see entry for grunts), always accompanied by a duck face |
| Staccato vocalization | Affiliative/appeasement | All age-sex classes, but rare in adult males | 13 | Highly variable | When inspecting a young infant |
| Trill | Affiliative/appeasement and contact/group movement (loud trills) | All age-sex classes, but primarily infants; very rare in adult males | 11 | Infants 42.4 calls/h | When approaching another individual before affiliative interaction; can grade into screamy trill during aggressive interactions; loud trills produced when locomoting |
| Wheeze | Sociosexual | Primarily adults, most common in adult males and high-ranking adult females | 91 | Adult females: 1.2 bouts/100 h; adult males: 7.7 bouts/100 h | Often during dances (see entry for grunts); most commonly shown by dominants and during periods of social tension |

Age at first call is reported in days.

**Table 2** Acoustic measurements of call types (mean±SD) obtained using LMA general analysis

| Call type | Duration (ms) | PF mean (Hz) | Range mean (Hz) | Q1 mean (Hz) | Q2 mean (Hz) | Dfb2 mean (Hz) |
|---|---|---|---|---|---|---|
| Peeps | 174.7± 67.7 | 2352± 1274.8 | 4180.1± 2005.3 | 916.3± 64.4 | 2029.7± 218.0 | 3431.9± 1299.0 |
| | — | — | — | — | — | — |
| | 153.1± 56.9 | 1572.6± 615.1 | 3586.5± 1342.6 | 915.0± 30.5 | 1851.6± 236.0 | 2677.0± 379.5 |
| Alarm calls: Bird | — | — | — | — | — | — |
| | 378.4± 3.8 | 1787.1± 98.8 | 1064.7± 23.7 | 1688.8± 72.2 | 2466.7± 318.9 | 1437.9± 8.4 |
| | — | — | — | — | — | — |
| Human | 421.4± 84.0 | 2024.4± 545.8 | 1032.1± 59.5 | 1719.3± 138.6 | 2774.0± 718.0 | 1273.0± 74.8 |
| | — | — | — | — | — | — |
| Other monkey | — | — | — | — | — | — |
| | 425.7± 34.1 | 1889.0± 231.9 | 977.1± 139.8 | 1619.6± 193.4 | 2510.4± 668.0 | 1331.6± 212.8 |
| | — | — | — | — | — | — |
| Snake | 191.6± 8.4 | 3455.0± 669.8 | 1351.1± 266.8 | 2384.6± 428.8 | 4344.5± 819.9 | 2555.1± 742.6 |
| | 164.2± 17.7 | 2754.5± 1650.0 | 1234.2± 216.7 | 2110.9± 350.8 | 3583.7± 2336.7 | 2187.3± 1595.6 |
| | 184.4± 41.0 | 2779.0± 626.8 | 1199.8± 117.0 | 2171.5± 267.6 | 3363.1± 1171.4 | 1916.7± 423.0 |
| Terrestrial Predator | 213.2± 37.3 | 2668.8± 1243.8 | 1257.8± 482.6 | 2171.5± 724.0 | 3152.4± 1214.0 | 2031.2± 1248.1 |
| | 224.4± 56.2 | 2770.8± 1443.9 | 1369.1± 477.0 | 2476.0± 809.0 | 3221.6± 1250.4 | 2021.6± 1323.3 |
| | 299.4± 77.8 | 2362.6± 371.8 | 960.7± 235.1 | 1694.3± 235.1 | 3547.7± 1340.6 | 1516.4± 442.8 |
| Bray | — | — | — | — | — | — |
| | 285.8± 89.3 | 764.9± 129.6 | 1640.5± 353.4 | 661.5± 51.9 | 1391.1± 85.7 | 1046.4± 232.2 |
| | — | — | — | — | — | — |
| Burst | 181.8± 33.4 | 1716.3± 661.5 | 2872.7± 1345.3 | 1284.5± 353.8 | 2628.6± 898.6 | 2859.0± 1171.1 |
| | 137.0± 43.5 | 1114.5± 294.5 | 2119.5± 803.6 | 1056.6± 159.8 | 2323.8± 210.4 | 1592.5± 345.6 |
| | — | — | — | — | — | — |
| Chirp scream | 131.2± 60.0 | 3644.4± 631.5 | 1855.8± 900.6 | 2814.3± 380.6 | 4039.6± 452.9 | 3767.3± 388.0 |
| | — | — | — | — | — | — |
| Coo | — | — | — | — | — | — |
| | — | — | — | — | — | — |
| | 214.4± 109.8 | 1487.2± 434.8 | 2374.6± 1062.7 | 909.5± 174.8 | 1681.1± 214.4 | 1397.3± 379.7 |
| Cough | Sonogram only | | | | | |
| Food-associated call | 243.3± 99.4 | 2057.0± 623.9 | 3684.7± 716.3 | 1089.8± 153.0 | 1807.4± 190.7 | 1809.1± 377.7 |
| | 202.9± 83.8 | 1664.6± 497.8 | 3462.5± 510.3 | 949.2± 211.0 | 1651.7± 211.0 | 1547.9± 315.2 |
| | — | — | — | — | — | — |

**Table 2** (continued)

| Call type | Duration (ms) | PF mean (Hz) | Range mean (Hz) | Q1 mean (Hz) | Q2 mean (Hz) | Dfb2 mean (Hz) |
|---|---|---|---|---|---|---|
| Gargle | — | — | — | — | — | — |
| | 224.3±117.8 | 1252.0±0.28 | 2689.8±1068.5 | 1191.0±13.9 | 2289.7±194.7 | 2446.2±194.3 |
| | 228.6±42.7 | 1094.3±368.6 | 3119.6±955.1 | 867.7±114.7 | 2023.8±366.8 | 1927.4±472.6 |
| Gecker | Sonogram only | | | | | |
| Grunts | 195.7±63.6 | 1542.2±409.3 | 2967.1±1167.9 | 1148.6±162.9 | 2068.5±261.4 | 2430.1±188.6 |
| | 306.8±88.1 | 1440.3±320.7 | 3059.6±560.3 | 1190.3±201.6 | 2091.7±282.7 | 2220.1±459.5 |
| | — | — | — | — | — | — |
| Intense gargle | — | — | — | — | — | — |
| | 148.1±60.6 | 1566.9±354.2 | 3394.2±1210.6 | 1137.8±202.7 | 2135.5±437.6 | 2573.2±603.9 |
| | — | — | — | — | — | — |
| Intense vocal threat | 112.6±26.4 | 2330.0±306.6 | 4154.6±739.4 | 1395.2±278.4 | 2304.1±259.2 | 2904.6±148.7 |
| | 95.3±27.3 | 2532.5±1216.0 | 4100.2±943.5 | 1486.8±298.4 | 2422.4±381.8 | 3247.1±1078.12 |
| | — | — | — | — | — | — |
| Lost calls | 197.6±29.3 | 1178.5±58.6 | 1858.1±482.0 | 1105.9±62.8 | 2225.0±259.8 | 1677.9±242.4 |
| | 202.0±42.7 | 1133.2±44.8 | 1236.8±235.1 | 1098±45.7 | 2153.0±109.0 | 1443.5±329.4 |
| | — | — | — | — | — | — |
| Staccato gargle | — | — | — | — | — | — |
| | — | — | — | — | — | — |
| | 291.5±77.4 | 1126.8±418.8 | 2987.0±1428.2 | 913.1±151.5 | 1942.1±399.5 | 2181.2±903.6 |
| Staccato vocalization | Sonogram only | | | | | |
| Mild vocal threat | 101.8±36.4 | 2964.1±1958.7 | 4009.1±1160.1 | 1784.8±726.8 | 3118.3±903.1 | 3604.8±1316.3 |
| | 97.7±34.4 | 2186.8±1041.4 | 2875.3±1191.8 | 1504.7±706.5 | 2905.4±1221.5 | 2745.3±980.1 |
| | — | — | — | — | — | — |
| Roar scream | 945.9±321.0 | 3501.4±794.8 | 1877.1±309.3 | 1653.3±310.7 | 2681.8±372.3 | 1868.7±368.9 |
| | — | — | — | — | — | — |
| | 966.4±326.9 | 4088.7±182.4 | 2023.8±480.7 | 1772.9±352.7 | 2893.6±313.2 | |
| Squeak | Sonogram only | | | | | |
| Twargle | 354.6±108.8 | 3260.5±1770.6 | 4009.1±986.6 | 2021.0±892.9 | 4992.8±1809.2 | 3629.6±1468.6 |
| | — | — | — | — | — | — |
| | 170.4±105.2 | 2662.1±212.0 | 3122.5±785.6 | 2073.1±641.9 | 2823.8±311.4 | 3362.9±273.1 |
| Undulating scream | 649.3±190.1 | 3737.2±1663.0 | 4591.4±1876.6 | 2644.4±1519.4 | 3788.0±1601.6 | 4260.4±1257.4 |
| | — | — | — | — | — | — |
| | 640.7±328.8 | 4790.1±2042.2 | 5360.6±1615.3 | 3064.1±1435.2 | 4422.7±1563.9 | 4181.2±1401.8 |

**Table 2** (continued)

| Call type | Duration (ms) | PF mean (Hz) | Range mean (Hz) | Q1 mean (Hz) | Q2 mean (Hz) | Dfb2 mean (Hz) |
|---|---|---|---|---|---|---|
| Wheeze | 204.5± 39.9 | 4462.5± 1263.6 | 2759.5± 928.8 | 2108.5± 610.7 | 3418.0± 1147.8 | 4530.1± 812.3 |
|  | 701.8± 88.9 | 6320.9± 1556.4 | 5591.4± 927.9 | 2257.6± 1106.3 | 4416.8± 885.0 | 6286.4± 1206.7 |
|  | — | — | — | — | — | — |
| Yelp | — | — | — | — | — | — |
|  | — | — | — | — | — | — |
|  | 136.4± 29.1 | 1950.6± 684.4 | 2468.8± 701.5 | 1373.1± 220.7 | 2254.5± 403.0 | 2408.0± 464.3 |

The first number listed is for adult females. The second number is for adult males. The third number is for juveniles. A — denotes that we obtained no measurement for a given age class.
Duration=time between the start and the end of the call; PF mean=frequency with the highest amplitude, averaged across all time segments; Range mean=average frequency range; Q1 mean=frequency at which the amplitude distribution reaches the first quartile of the total distribution, averaged across all time segments; Q2 mean=frequency at which the amplitude distribution reaches the second quartile of the total distribution, averaged across all time segments; Dfb2 mean=frequency of the second dominant frequency band, averaged across all time segments.

variant of the food-associated call in contexts of highly productive fruit foraging on preferred foods, e.g., mangoes (*Mangifera indica*) and bromeliad fruits (*Bromelia pinguin*); however, individuals sometimes call in anticipation of food, typically as they approach a fruit patch or as they visually search for ripe fruit after arriving at a fruit patch. By contrast, individuals rarely emit food-associated calls when foraging for insects or vertebrates except when eating coati pups (*Nasua narica*; Perry and Gros-Louis, *unpub. data*).

Field experiments indicate that food-associated calls appear to serve the function of announcing food possession, thereby deterring approach and aggression from others (Boinski and Campbell 1996; Gros-Louis 2004a; Robinson 1982).

*Gargle* (Fig. 1c)

Synonyms: guttural chatter (Oppenheimer 1973).

Vocalizers: All age-sex classes, but primarily infants, juveniles, and adult females. One of the first vocalizations that infants produce.

Acoustic structure and analysis: A low-frequency, atonal guttural sound emitted in bouts rather than singly. More staccato-like variants of the gargle infants produce resemble staccato vocalizations, which we label staccato gargles (Fig. 1e).

Usage and context of emission: A caller produces the gargle when following, grooming, or otherwise affiliating with the target of the gargle. Garglers often exhibit signs of emotional arousal, such as penile/clitoral erection, piloerection, head-shaking, scratching, squirming, and grimacing. Recipients of gargles either remain neutral or respond by mildly swatting at the gargler. Quite often, particularly in very young individuals, starting by the end of the first month of life, the gargle is combined with a downward falling trill to produce a hybrid vocalization that we term a twargle (Fig. 1f). A trill accompanied 37% of all gargles that infants produced. Adult females also produce twargles, but much more infrequently than infants do.

**Table 3** Acoustic measurements of call types (mean±SD) obtained using LMA contour analysis

| Call type | Duration (ms) | No. gaps | Gap mean | PF mean (Hz) | Freq range (Hz) | PF max location | PF min location |
|---|---|---|---|---|---|---|---|
| Ascending trill | — | — | — | — | — | — | — |
| | — | — | — | — | — | — | — |
| | 308.7± 65.9 | 4.1± 0.96 | 21.3± 8.2 | 8202.7± 1187.1 | 2138.3± 1087.3 | 0.85± 0.08 | 0.12± 0.10 |
| Descending trill | 249.9± 70.1 | 3.4± 0.87 | 18.5± 6.5 | 6951.2± 1759.3 | 3526.5± 2356.4 | 0.18± 0.20 | 0.95± 0.04 |
| | — | — | — | — | — | — | — |
| | 315.2± 116.2 | 4.0± 2.8 | 20.9± 0.2 | 7483.8± 1172.0 | 2138.5± 1071.3 | 0.08± 0.09 | 0.82± 0.21 |
| Inverted u trill | Sonogram only | | | | | | |
| Staccato scream | 351.5± 55.5 | 4.8± 1.1 | 24.0± 2.2 | 3236.2± 613.1 | 4615.3± 3252.2 | 0.39± 0.06 | 0.46± 0.27 |
| | — | — | — | — | — | — | — |
| | 289.4± 110.5 | 2.3± 1.8 | 11.9± 9.3 | 4556.4± 1861.2 | 4540.5± 2645.1 | 0.43± 0.24 | 0.35± 0.24 |
| Screamy trill | 312.1± 115.8 | 2.1± 1.6 | 10.8± 1.1 | 11019.9± 2676.9 | 6338.3± 1302.9 | 0.21± 0.28 | 0.26± 0.29 |
| | — | — | — | — | — | — | — |
| | 328.3± 152.1 | 3.9± 1.5 | 13.4± 4.8 | 9448.8± 1721.5 | 8805.1± 2794.1 | 0.69± 0.14 | 0.46± 0.17 |

The first number listed is for adult females. The second number is for adult males. The third number is for juveniles. A — denotes that we obtained no measurement for a given age class.
Duration=time between the start and the end of the call; No. gaps=the average number of spaces between elements in the call; Gap mean=duration of the spaces between elements in the call, averaged across time segments; PF mean=frequency with the highest amplitude in the frequency spectrum, averaged across all time segments; Freq range=difference between the maximum and minimum frequencies with the highest amplitude in the call; PF max location=relative position of the maximum peak frequency of a call [1/call duration (ms) × position of maximum frequency with the highest amplitude in the call (ms)]; PF min location=relative position of the minimum peak frequency of a call [1/call duration (ms) × position of minimum frequency with the highest amplitude in the call (ms)].

Adults do not emit gargles to same-sexed adults, and, with extremely rare exceptions, adult males are the only recipients of gargles. In 1991–1993, adult females gargled exclusively to the α-male, and they promptly switched to gargling to the new α-male after a rank reversal (Perry 1998). Immature individuals are less consistent in their gargling patterns: though immatures, too, gargle only to adult males and primarily to the α-male, they direct gargles to non-α-males at a fairly high rate (Perry 1998). Also, peripheral adult females that subsequently left the group in a fission performed anomalous gargles to non-α-males. We replicated the results in subsequent years (1997, 1999) in 2 social groups.

*Intense Gargle* (Fig. 1d)

Synonyms: Not described previously.
    Vocalizers: Primarily adult females and adult males.
    Acoustic structure and analysis: A low-frequency, atonal guttural sound of higher amplitude and more plosive than gargles, emitted more rhythmically in a sequence.

Springer
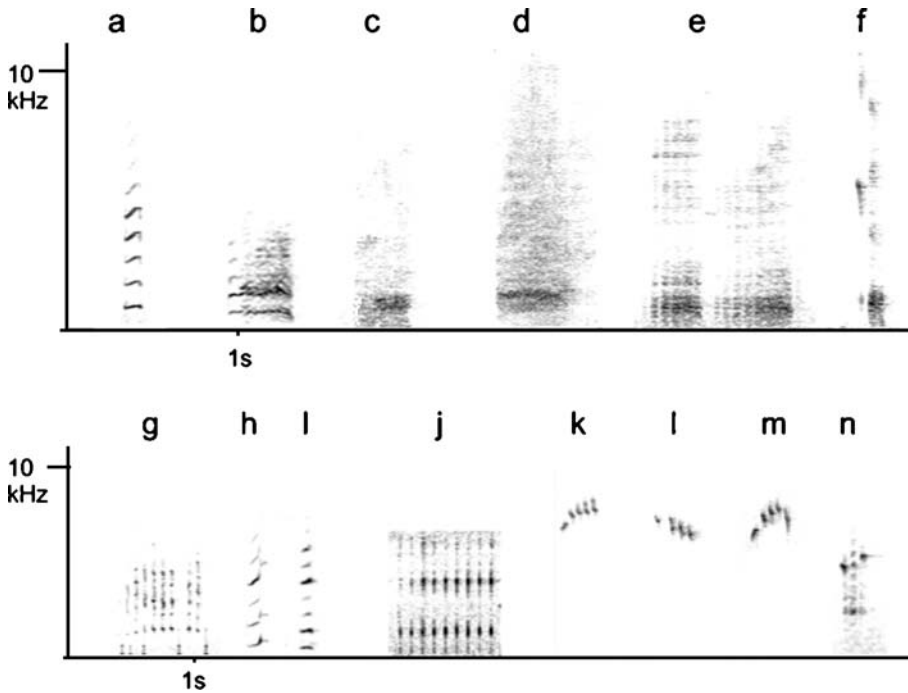
**Fig. 1** Affiliative and appeasement vocalizations. We digitized calls via AVISOFT-SASLab Pro 4.12 at a sample rate of 22 kHz. We generated spectrograms via a 1024-point FFT, 93.75% overlap, resulting in a frequency resolution of 22 Hz and a temporal resolution of 47 ms. *a*) food-associated call; *b*) guttural food-associated call; *c*) gargle; *d*) intense gargle; *e*) staccato gargle; *f*) twargle; *g*) gecker *h*) peep; *i*) intense peep; *j*) staccato vocalizations; *k*) ascending trill; *l*) descending trill; *m*) inverted u trill; *n*) screamy trill.

Usage and context of emission: Similar to gargles, individuals producing intense gargles often exhibit signs of emotional arousal, such as penile/clitoral erection, and piloerection. Adult males sometimes produce intense gargles alone or in exchange with adult females when they reunite with the group after intergroup encounters, or after a fight within the group in which they were involved. Also, both adult males and adult females may produce intense gargles during dances. Dances occur during periods of high tension, such as after fights, reunion of males with the group, and during courtship and mating (Perry 1996). Dances are so named because they involve 2 individuals continually approaching and retreating from one another as they perform a series of gestures and postures, including eye contact, piloerection, slow-motion pacing, pirouetting, and duck faces [pursed, closed lips, which Oppenheimer (1973) termed protruded lips].

*Gecker* (Fig. 1g)

Synonyms: Not described previously.
   Vocalizers: Infants, juveniles, and adult females. One of the first vocalizations that infants produce.
   Acoustic structure and analyses: The calls seem to be the infant version of staccato vocalizations, a rapid sequence of soft, low-pitched pulsatile sounds, but they are louder and more tonal.

Usage and context of emission: Individuals most commonly produce the calls to other infants in affiliative interactions, such as when inspecting or embracing an infant. They are often accompanied by a fear grin. Infants also produce geckers that grade into screamy trills (Fig. 1n), during tantrums, such as after failed nursing attempts. In aggressive interactions that escalate, geckers grade into staccato screams (Fig. 2e). Juveniles and adult females occasionally produce geckers when inspecting infants, which may grade into staccato vocalizations.

*Peep* (Fig. 1h)

Synonyms: Not described previously.

Vocalizers: All age-sex classes, but primarily adult females and immatures (>1 yr of age). Adult males rarely emit peeps.

Acoustic structure and analysis: Single-syllable, tonal calls similar to food-associated calls, but of slightly higher frequency. Peeps often end with a frequency upsweep. Also, whereas food-associated calls can vary widely in duration within and across individuals, peeps are always short in duration, and shorter than food-associated calls (Gros-Louis 2006).

Given that peeps and food-associated calls are acoustically similar, we performed a discriminant function analysis using 6 calls each from 8 females to
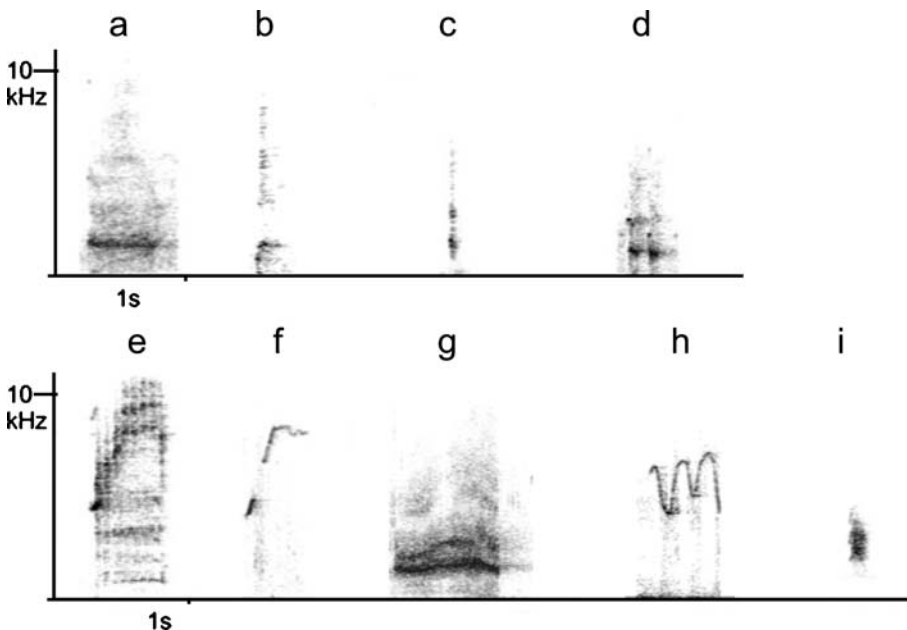


**Fig. 2** Agonistic vocalizations. We digitized calls via AVISOFT-SASLab Pro 4.12 at a sample rate of 22 kHz. We generated spectrograms via a 1024-point FFT, 93.75% overlap, resulting in a frequency resolution of 22 Hz and a temporal resolution of 47 ms. *a*) bray; *b*) cough; *c*) mild vocal threat; *d*) intense vocal threat; *e*) staccato scream. *f*) tonal scream; *g*) roar scream; *h*) undulating scream; *i*) yelp.

determine if there were acoustic differences between peeps (Fig. 1h) and food-associated calls (Fig. 1a). A principal components analysis using the 14 acoustic variables generated 5 independent components. Three of them generated a discriminant function that explained a significant amount of variation between call types (Wilk's $\lambda=0.290$, $\chi^2=55.1$, df=3, $p<0.001$). The discriminant function correctly classified 91.7% of the original calls. The leave-one-out cross validation procedure similarly classified 91.7% of calls correctly. A multivariate analysis of variance (ANOVA) utilizing the factor scores employed in the discriminant function analysis revealed that 1 of the 3 principal components differed between the call types when we controlled for the identity of the caller (component 2: $F=14.960$, $p<0.001$). The mean frequency value of the first dominant frequency band loaded heavily on this component.

Usage and context of emission: Individuals emit peeps in close-range dyadic interactions; thus, they are of very low amplitude. The most common context of emission is when an individual presents for grooming, but individuals sometimes emit peeps when they are resting. Generally the apparent target of the vocalization is within a body length of the peeper, but on rare occasions we have seen subordinate peripheral individuals lie down several meters from the nearest monkey, but in visual contact of the group, and peep while presenting for grooming.

*Intense Peep* (Fig. 1i)

Synonyms: Not described previously.

Vocalizers: All age-sex classes, with the exception of infants <1 yr of age.

Acoustic structure and analysis: Intense peeps are acoustically similar to food-associated calls, but they are of shorter duration and more forcefully emitted, giving an urgent quality.

Usage and context of emission: Individuals emit intense peeps infrequently relative to other vocalizations in the repertoire (30 in 23 mo of observation on 2 groups; because of the small sample size, we could not compare them quantitatively with the other 2 types of peeps). Individuals emit intense peeps to unknown or potentially noxious or dangerous stimuli. The stimuli that have elicited calling include biting/stinging insects, swarming insects, dead animals or insects (often decomposing and swarming with ants or maggots); dirt-covered fruit/fruit pit; monkey feces on the fur of a monkey, often after a monkey puts its hand on it; blood clotting on the fur of a monkey, often as the individual or other individuals groom and inspect it.

In almost all of the contexts of intense peep emission, at least a couple of individuals approach the signaler to inspect the stimulus that is eliciting the calls, suggesting an investigatory function. The caller or other individuals may touch the offensive stimulus. In many cases, individuals also will emit single-syllable threats (Perry 1996), also termed heh (Boinski 1993; Robinson 1982), and in some cases 2 monkeys will do an overlord toward the eliciting stimulus. An overlord is a coalitionary posture in which 2 monkeys are aligned vertically, one on top of the other, threatening a common opponent (Perry 1996), also termed a double threat (Fedigan 1993).

*Staccato Vocalizations* (Fig. 1j)

Synonyms: Not described previously.
   Vocalizers: All age-sex classes, but adult males rarely produce them.
   Acoustic structure and analysis: A rapid sequence of soft, low-pitched pulsatile sounds.
   Usage and context of emission: The vocalization was so rare that in the absence of small infants, observers went for months without hearing it. Independently locomoting infants and young juveniles sometimes perform the vocalization to one another while cuddling, but by far the most common context is by alloparents to very young infants that are typically in the company of their mothers. This was true in all but 2 of the 23 cases we observed in the 1999 data set for Abby's group. The caller always visually inspected the infant, and often physically handled it. Sometimes the caller crouches, bares the teeth in a grimace, looks at the infant upside down, or nuzzles the infant while performing the vocalization. Also, in 18 of the 23 cases, there was affiliative contact between the caller and the mother of the infant being inspected, which took the form of grooming, nonconceptive sex, or affiliative vocalizations such as trills and peeps. In many cases, monkeys alternate between producing staccato vocalizations and geckers when inspecting infants.

*Trill* (Fig. 1k–m)

Synonyms: purr, twitter (Oppenheimer 1973).
   Vocalizers: Primarily infants, but also adult females and juveniles. Adult males rarely produce trills. Trills are one of the first vocalizations that infants produce.
   Acoustic structure and analysis: Trills are series of pulsed, high-frequency elements delivered in rapid succession. Elements within trills ascend in frequency (Fig. 1k), descend in frequency (Fig. 1l), or form an inverted u (Fig. 1m). In addition, some descending trills end in a chirp-like sound (Oppenheimer 1973).
   Usage and context of emission: Individuals use trills most commonly in close-range interactions, such as approaching, huddling with or climbing on another monkey, grooming, nursing, or showing interest in another's food. The social trills account for 90% of infant trills in the 1991–1993 data set (Gros-Louis 2002) and 81% of trills in the 2002 data set. Infants that emitted trills when approaching another individual were significantly more likely to engage in affiliative interactions with the monkey than infants that approached silently were (Gros-Louis 2002). Infants were also significantly less likely to receive aggression from the juveniles and adult males they approached if they trilled when approaching, though trilling did not affect the probability of receiving aggression from adult females (Gros-Louis 2002). Further studies are necessary to determine how trill subtypes differ across social contexts, e.g., *Cebus apella* (Robinson 1984).

*Screamy Trill* (Fig. 1n)

Synonyms: twitter (Oppenheimer 1973).
   Vocalizers: Infants and juveniles.
   Acoustic structure and analysis: Pulsed, high-pitched vocalizations that have an atonal, strained quality versus the tonal quality of a trill.

Usage and context of emission: In rare instances (2.5% of infant trills: Gros-Louis 2002), trills precede or follow aggressive interactions; they grade into screamy trills, and the lips pull back into a grimace while the individual produces the trill. The monkey producing a screamy trill often palpates the nipple of the individual with which it is having the aggressive interaction while trilling. In addition, infants may produce screamy trills when they attempt to nurse and are refused.

Agonistic Vocalizations

*Bray* (Fig. 2a)

Synonyms: Not described previously.
    Vocalizers: Almost exclusively adult males.
    Acoustic structure and analysis: The bray is a short, plosive vocalization with a sharp onset and descending pitch across the call.
    Usage and context of emission: Individuals bray almost exclusively in the context of intergroup encounters. They rarely bray alone, but instead, brays precede a sequence of intense vocal threats as a lead-in vocalization.

*Cough* (Fig. 2b)

Synonyms: Not described previously.
    Vocalizers: Almost exclusively adult males, primarily the $\alpha$-male.
    Acoustic structure and analysis: The cough is a short, harsh, plosive vocalization of low amplitude.
    Usage and context of emission: The cough is one of the rarer vocal types, along with staccato vocalizations and intense peeps. Individuals performed it *ca.* once per 100 h of focal male data in the 1997 data set. We have heard females cough only once or twice in 15 yr of observation. $\alpha$-Males cough *ca.* 3 times as often as other males do. During production of a cough, the male is generally vigilant on the ground, with his hair erect. After the cough, he typically stiff-walks or gallops toward the periphery of the group, and then often threatens another individual.

*Mild vocal threat* (Fig. 2c)

Synonyms: heh: *Cebus apella* (Robinson 1982).
    Vocalizers: All age-sex classes, although infants rarely produce the threat.
    Acoustic structure and analysis: A mild-vocal threat is a low-frequency slightly atonal squeak that is typically produced as single syllables and interspersed with silent open-mouth threats.
    Usage and context of emission: Individuals emit mild vocal threats most commonly to other monkeys during low-level aggression with no physical contact. However, individuals also produce mild vocal threats to other, nonthreatening mammals, e.g., cows, and nonthreatening stimuli, e.g., a smashed, writhing insect. During mild vocal threats, the mouth is open and teeth are bared, and sometimes the tongue wags up and down as the individual emits the squeaky threat. Often monkeys

producing mild threats are in the overlord position, and they frequently bounce while threatening.

*Intense Vocal Threat* (Fig. 2d)

Synonyms: chortle (Oppenheimer 1973).

Vocalizers: Primarily adult males and high-ranking adult females, and occasionally immatures.

Acoustic structure and analysis: An intense vocal threat is a sequence of high-amplitude, atonal plosive sounds typically emitted in bouts of multiple calls (typically 3–5). Intense vocal threats differ acoustically from the mild vocal threats not only in that they are delivered in longer bouts of more closely spaced elements but also in their frequency structure.

We randomly selected 6 calls each from 6 individuals for each call type for the discriminant function analysis to explore acoustic differences between mild and intense vocal threats. Four of the original 14 acoustic variables met the preselected criterion of the *F*-to-enter stepwise procedure. The components generated a discriminant function that explained a significant amount of variation between call types (Wilk's $\lambda=0.822$, $\chi^2=13.3$, df=4, $p<0.02$). The discriminant function correctly classified 70.8% of the original calls and 62.5% of the calls in the leave-one-out cross-validation analysis. A multivariate ANOVA utilizing the factor scores employed in the discriminant function analysis revealed that 2 of the 4 principal components differed between the call types when we controlled for the sex and the identity of the caller (component 2: $F=10.16$, $p<0.002$; component 3: $F=10.86$, $p<0.002$). Component 2 represents the amplitude and frequency characteristics at the end of the call. The frequency of the first dominant frequency band and the frequency at the end of the call where the amplitude reaches 25% of the total energy in the call, i.e., first quartile of amplitude distribution, both loaded heavily on component 2. Component 3 represents the location of the highest amplitude of the call. Reviewing call measurements reveals that the frequency and amplitude concentration at the end of intense vocal threats are higher than the ones of mild vocal threats are. Also, the location of the peak frequency is later in the call for intense vocal threats than for mild vocal threats.

Usage and context of emission: Intense vocal threats are fairly rare, and produced primarily in response to other groups (Perry 1996). Males face the direction of the other group, breaking branches, bouncing, and emitting intense vocal threats as the intergroup interaction ensues. In some cases, the males of one group will chase males of another group while emitting intense vocal threats. Other less common contexts of intense vocal threats are intragroup contexts during periods of social instability, such as rank reversals (Perry 1998) and in response to predators. The hair is usually erect during the production of intense vocal threats.

*Screams* (Fig. 2e–i)

Synonyms: chatter-scream, scream, whistle (Freese and Oppenheimer 1981; Oppenheimer 1973).

Vocalizers: All age-sex classes, though adult males rarely produce screams.

Acoustic structure and analysis

Staccato scream (chatter-scream: Oppenheimer 1973; Fig. 2e): A staccato scream is a rapid sequence of pulsed loud, high-frequency atonal sounds. Though sharing the same pulsatile quality with staccato vocalizations, the screams are much louder and sound forceful and strained.
Tonal scream (whistle: Oppenheimer 1973; Fig. 2f): A tonal scream is a loud, high- frequency tonal call of fairly long duration.
Roar scream (scream: Oppenheimer 1973; Fig. 2g): A roar scream is a loud, high- frequency atonal call of fairly long duration.
Undulating scream (Fig. 2h): An undulating scream is a loud, high-frequency, frequency-modulated call.
Yelp (Fig. 2i): A yelp is a loud, atonal plosive sound with abrupt onset and of short duration. In some cases, a yelp or a series of yelps is followed by a roar scream if aggression continues and escalates.

Usage and context of emission: Individuals emit screams either in response to an aggressive gesture from another monkey, or sometimes to initiate an aggressive interaction. Individuals emit the staccato scream and tonal scream in the context of fairly mild aggression, whereas an individual emits the undulating scream and the roar scream when under greater stress, either because the type of aggression received is more severe, or because the opponents are more formidable, e.g., they are very high-ranking, or they are individuals that normally side with the screamer but have unexpectedly sided against the screamer (Perry, *pers. obs.*). Undulating screams can grade into roar screams, which individuals often produce when physical contact occurs, such as biting. Lastly, an individual emits a yelp when it is the victim of an aggressive act that is typically mild and extremely short in duration, e.g., a dominant stealing food, pushing to supplant, or hitting. Yelps also appear to occur in response to swiftly delivered, unexpected aggression not preceded by threats or other behaviors that typically lead to an aggressive encounter.
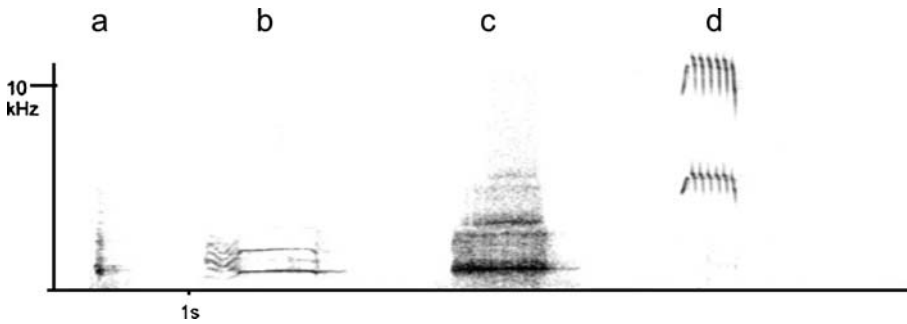
Cohesion and group movement vocalizations

*Bursts* (Fig. 3a)

Synonyms: Not described previously.
Vocalizers: Almost exclusively adults, primarily the α-male and female emit bursts.
Acoustic structure and analysis: Bursts are slightly atonal, bell-like bursts of sound.
Usage and context of emission: Individuals emit bursts most typically while locomoting. Extremely loud trills accompanied 62% of bursts in the 1999 data set. The vocalization appears to function to initiate and to coordinate group movement similar to loud trills (Boinski 1993; Boinski and Campbell 1995). In Abby's group, the α-male was by far the most frequent producer of bursts, calling at a rate of 78 times/100 h, but adults of all ranks produced them at lower rates. In Rambo's group, which has an unusually low-key α-male (Perry, *pers. obs.*), there was no particular tendency for the α-male or female to produce bursts more often than other group members did, and individuals produced bursts on average *ca.* 3.5 times/100 h.

**Fig. 3** Contact and group movement vocalizations. We digitized calls via AVISOFT-SASLab Pro 4.12 at a sample rate of 22 kHz. We generated spectrograms via a 1024-point FFT, 93.75% overlap, resulting in a frequency resolution of 22 Hz and a temporal resolution of 47 ms. *a*) burst; *b*) coo; *c*) lost call; *d*) loud trill.

Peripheral individuals and central dominant ones were prone to produce bursts in Rambo's group. Individuals produced 60% of all bursts when no capuchin was in close proximity, i.e., ≤5 body lengths.

*Coos* (Fig. 3b)

Synonyms: Not described previously.

Vocalizers: Primarily infants emit coos. Individuals >1 yr of age very rarely emit coos except, on very rare occasion, by mothers separated from their infants. Adult males never coo.

Acoustic structure and analysis: Coos are low-frequency tonal calls typically emitted as single syllables of long duration, sometimes grading into lost calls.

Usage and context of emission: Coos are commonly produced by infants that are separated from their mothers. In 83% of coo bouts ($n=203$), the caller also produced trills. Typically, infants coo until they are reunited with the mother. Mothers returned to their infants right away in 30 of the 203 coo bouts. In 93% of cases in which mothers returned during a coo bout, the infant immediately stopped cooing. By contrast, infants continue to coo when non-mothers give them rides or otherwise affiliate with them. Thus, coos seem to be produced specifically by infants in the absence of their mothers. On very rare occasions, mothers have cooed when separated from their infants, but more often they will respond to coos by approaching the infant silently or perhaps trilling, and then crouching to invite the infant to ride. Adults very rarely coo, and when they do, it is most often when they are the victims of coalitionary aggression and appear extremely stressed, e.g., they are kneading or chewing their own tails.

*Lost calls* (Fig. 3c)

Synonyms: arrawh (Oppenheimer 1973).

Vocalizers: All age-sex classes produce lost calls.

Acoustic structure and analysis: Lost calls are low-frequency, atonal calls typically uttered in bouts of 1–3 elements. The call is one of the loudest in the repertoire, carrying ≤0.5 km through wooded terrain.

Usage and context of emission: Typically, a caller that was separated from the group emitted loud contact calls (58% of lost calling bouts, *n*=33), but individuals also emitted them in response to another's lost call (36% of bouts; see alo Digweed *et al.* 2007) or apparently searching for a missing individual that had not yet called (6% of bouts). Adults within hearing range of the lost monkey respond in one of the following ways: 1) by producing a lost call (6%), 2) by producing an intense vocal threat or other vocal response, such as an alarm call, intense gargle, trill or burst (10%), 3) by looking or moving toward the caller (7%), or 4) by ignoring the lost caller (77%). Sometimes monkeys produce lost calls when individuals are separated from the group when they themselves are in the center of the group, even when the missing individual is known by observers to be far out of hearing range and not producing lost calls (Perry 1998). Females receive responses to their lost calls more often than males do (65% response rate for female callers, versus 14% for male callers).

*Loud trill* (Fig. 3d)

Synonyms: trill or twitter (Freese and Oppenheimer 1981).
    Vocalizers: Adult females, adult males, and sometimes immatures (>1 yr of age) emit loud trills. Acoustic structure and analysis: A loud trill is a series of pulsed, high-frequency elements of high amplitude delivered in rapid succession.
    Usage and context of emission: At Lomas Barbudal, as in Santa Rosa (Boinski 1993; Boinski and Campbell 1995), individuals sometimes use loud trills in the context of coordinating group movement, wherein the trills are of louder amplitude than in social contexts (*cf.* Trills), and they are often accompanied by burst vocalizations (Fig. 3a). In the 2002 data set for infants, individuals emitted 12% of trills in a nonsocial context that may have served to maintain contact during group movement. In the 1999 data set, individuals emitted 25% of adult female trills and 26% of adult male trills in a nonsocial context, potentially qualifying as group movement signals. Further analyses are needed to determine if there are acoustic differences between trills and loud trills.
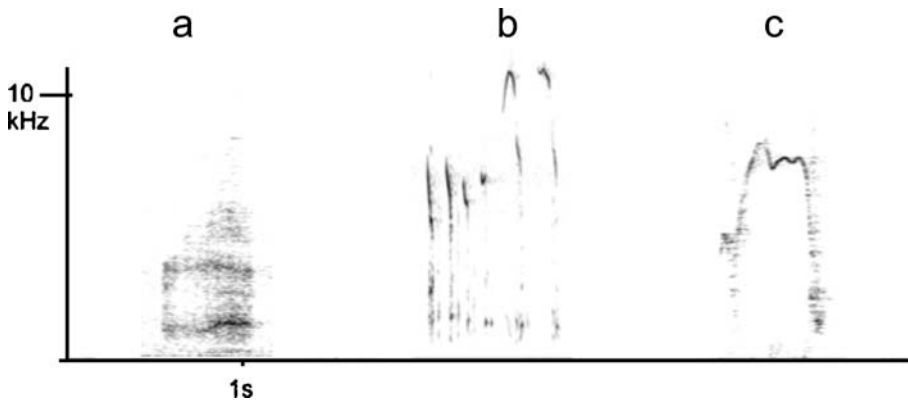
Sociosexual Vocalizations

Sociosexual vocalizations occur most commonly in the context of dances. Dances occur, as described under the entry for intense gargles, occur during periods of high tension, e.g., after fights, reunion of males with the group, and during courtship and mating. In dances, 2 individuals approach and retreat from one another, while often piloerected and maintaining eye contact, and performing any combination of the following behaviors: pacing in slow motion, pirouetting, and duck faces (pursed, closed lips).

*Grunts* (Fig. 4a.)

Synonyms: Not described previously.
    Vocalizers: All age-sex classes, with the exception of young infants (<6 mo), emit grunts.

**Fig. 4** Sociosexual vocalizations. We digitized calls via AVISOFT-SASLab Pro 4.12 at a sample rate of 22 kHz. We generated spectrograms via a 1024-point FFT, 93.75% overlap, resulting in a frequency resolution of 22 Hz and a temporal resolution of 47 ms. *a*) grunt; *b*) squeak; *c*) wheeze.

Acoustic structure and analysis: A grunt is an atonal, plosive sound that in some cases seems muffled because the vocalizer has pursed lips.

Usage and context of emission: The hair of the grunter is usually erect, and the monkey may assume a crouching posture if it is not already pacing or mounting the target. Two individuals often emit grunts as part of a rhythmic exchange between them, one or both of which are dancing (Manson *et al.* 1997). Grunts may continue throughout copulation. Sometimes one monkey will produce grunts while the other produces wheezes (24% of grunting bouts) or squeaks (38% of grunting bouts). Fourteen percent of dances in which at least one partner grunted resulted in copulation ($n=28$); however, the presence or absence of grunting did not have a statistically significant effect on the probability of a dance ending in copulation (grunt: 19% vs. no grunt: 14%; Fisher exact, $n=84$, $p=0.7$).

*Squeaks* (Fig. 4b)

Synonyms: warble (Freese and Oppenheimer 1981).

Vocalizers: All age-sex classes, though infants rarely produce squeaks.

Acoustic structure and analysis: Squeaks are highly frequency-modulated, tonal vocalization with pulsatile elements.

Usage and context of emission: Individuals emit squeaks while lips are pursed in a duck face and while one monkey is stalking another before initiation of a dance, during courtship dances, and during copulation. Of 58 occurrences of squeaks, 17 involved mutual squeaking with the dance partner. Squeaks were accompanied by grunts by one or both partners in 25% of cases. Copulation followed squeaking in 28% of cases. Only 2% of squeaks were accompanied by wheezes or intense gargles. Males and females are equally likely to squeak in a male-female courtship dance.

Because we found that nonconceptive sex is common in same-sex dyads and may serve to reduce tension (Manson *et al.* 1997), we were interested in the function of squeaks in same-sex dyads. In adult male-male dyads, squeaking decreases the probability of mounting and thrusting (Fisher exact, $n=36$, $p<0.005$), whereas in

adult male-female dyads, squeaking seems to increase the probability of copulation (Fisher exact, $n=84$, $p<0.005$). For male-male dyads, the proportion of dances resulting in copulation was 55% if neither squeaked, 8% if one partner squeaked, and 0 if both partners squeaked. For male-female dyads, the proportion of dances ending in copulation was 7% if neither squeaked, 25% if one partner squeaked, and 54.5% if both partners squeaked.

*Wheezes* (Fig. 4c)

Synonyms: warble (Freese and Oppenheimer 1981).
   Vocalizers: Primarily adult males and high-ranking adult females and extremely rarely immatures emitted wheezes.
   Acoustic structure and analysis: A wheeze is a high-frequency, long tonal whistle, often starting with a sharp upsweep and ending with a sharp downsweep in frequency.
   Usage and context of emission: Wheezes are one of the loudest vocalizations in the vocal repertoire, and also one of the rarest. Wheezes are often accompanied by pacing, eye contact, piloerection, pirouetting (28% of 28 observations), and sometimes mounting and thrusting (14%). Occasionally the wheezing monkey will rear back on its hind legs, arching the back and flailing the arms, while wheezing. Loud grunts (28%), intense gargles (14%), or squeaks (7%) are sometimes interspersed with wheezes during wheeze dances. In 21% of cases, both partners in the interaction wheezed.
   Wheeze rates vary wildly across groups and time periods and can be essentially absent from the repertoire for months if there is complete social stability (Perry 1995). Individuals emit wheezes more frequently in times of social tension, such as rank reversals, male-male competition for access to estrous females, reunions of missing individuals within the group (particularly if a major fight was the reason for the individual's absence), and immigrations (Perry 1995). Dominant monkeys tend to wheeze more often than low-ranking ones do (Perry 1995). $\alpha$-Males most commonly interrupt wheeze dancers, emitting vocal threats and charging toward the dancers (pairs of subordinate males), but high-ranking females and subordinate males sometimes respond similarly to wheeze dances (Perry 1995).
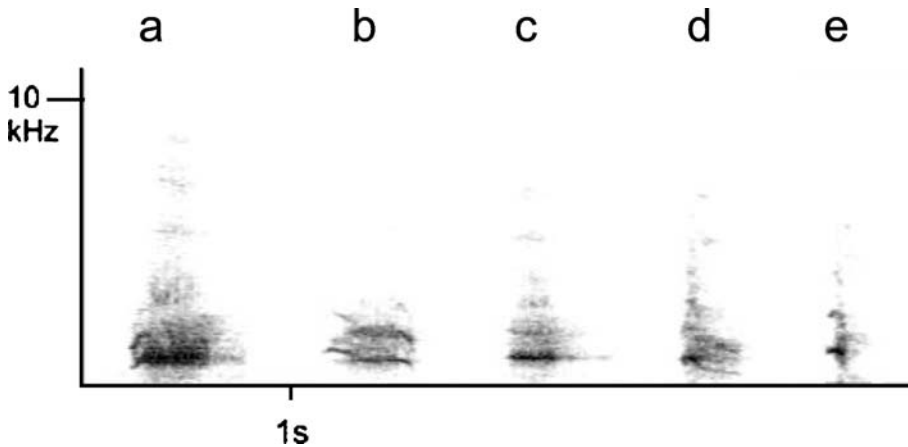
Alarm Vocalizations

*Alarm calls* (Fig. 5a–e)

   Synonyms: gyrrah (Oppenheimer 1973).
   Vocalizers: All age-sex classes emit alarm calls.
   Acoustic structure and analysis: Alarm calls comprise 2 broad acoustic categories that differ in structure (Digweed *et al.* 2005; Fichtel *et al.* 2005). Alarm calls emitted in response to aerial predators, unfamiliar humans, and unfamiliar monkeys comprise the first category (Fig. 5a–c). The alarm calls vary across several acoustic dimensions and are associated with predator-specific escape responses and thus may contain context-specific information. Alarm calls of the second acoustic category, composed of alarms given in response to terrestrial predators and snakes, also differ in several acoustic variables and are associated with specific responses (Fig. 5d,e); however, because

**Fig. 5** Alarm vocalizations. We digitized calls via AVISOFT-SASLab Pro 4.12 at a sample rate of 22 kHz. We generated spectrograms via a 1024-point FFT, 93.75% overlap, resulting in a frequency resolution of 22 Hz and a temporal resolution of 47 ms. *a*) aerial predator; *b*) unfamiliar human; *c*) unfamiliar monkey; *d*) terrestrial predator; *e*) snake.

individuals also emit similar calls in highly aggressive situations and in response to caiman, one can consider the calls general alert calls (Digweed *et al.* 2005).

Usage and context of emission: Capuchins produce alarm calls in response to many types of animals: rattlesnakes, boas, caiman, guapote, large raptors, canids, felids, unfamiliar monkeys, and unfamiliar humans.

The behavior of individuals varies depending on what type of alarm call they are producing. In general, monkeys emit all alarm calls while looking toward the location of the predator or disturbance. In the case of alarms to aerial predators, a single individual emits an alarm call while cowering down and, in some cases, descending from its location in a tree as it looks skyward. When monkeys encounter unfamiliar humans, typically a few of them emit alarm calls intermittently while remaining hidden in the trees, occasionally branch-shaking. When an individual detects an unfamiliar monkey or other group, it looks in their direction and produces alarm calls, which may be followed by intense vocal threats when intergroup interactions ensue. In the case of alarms to snakes and terrestrial predators, the caller looks toward them and in some cases may mob the predator with other group members that are often attracted by the alarms of the initial caller. Lastly, when an individual sees a caiman, it looks into the river and emits a series of intense, rapidly delivered calls that immediately attracts virtually every group member, all of which scan the river. We report the behavior of callers and call recipients in detail elsewhere (Fichtel *et al.* 2005).

## Discussion

An examination of *ca.* 27 different calls in the repertoire shows that while some calls show distinct differences in acoustic structure, e.g., vocal threats versus trills, others

grade into one another: staccato vocalization and screamy trill. Therefore, the vocal repertoire is a mixed repertoire, consisting of both discrete and graded call types, much like several other New World species, e.g., *Cebus apella* (Di Bitetti 2001), *Saguinus oedipus* (Cleveland and Snowdon 1982), *Saimiri sciureus* (Schott 1975). Researchers have proposed several factors to account for acoustic variation in the repertoire of a species, including internal, motivational factors, habitat, and social complexity (Marler 1965, 1976; Morton 1977; Wiley and Richards 1978).

Internal Influences on Call Variation

Morton (1977, 1982) proposed predictable changes in the vocalizations of birds and mammals relative to levels of arousal (motivational-structural or MS rules), suggesting that animals produce low-frequency atonal vocalizations in aggressive situations and high-frequency tonal vocalizations in nonaggressive or fearful situations. Overviews of primate repertoires broadly support expected differences across contexts that putatively correspond to different levels of motivation, but there are exceptions that indicate additional influences of external referents and social contexts on call structure (Fischer *et al.* 1995; Gouzoules and Gouzoules 2000; Hauser 1993; Schrader and Todt 1993). More convincing support comes from empirical observations of changes in call structure in a variety of species in which researchers experimentally manipulated affective states (Fichtel *et al.* 2001; Watts *et al.* 1999; Weary *et al.* 1998). Results reveal a more complex relationship than simply changes in absolute frequency and tonality. The studies have shown that during more aversive situations, calls exhibit more nonharmonic energy, increased duration, increased frequency range, and higher frequencies at which the maximum amplitude was reached in the power spectrum (peak frequency; Fichtel and Hammerschmidt 2002, 2003).

Call variation in the repertoire of white-faced capuchins is generally consistent with the empirical observations. Whereas affiliative vocalizations and the ones produced in nonaggressive situations are generally tonal —peeps, food-associated calls and trills— calls produced in more aversive situations, such as encounters with predators and aggressive situations are more harsh, atonal, and broadband: screams, threats, alarm calls. In addition, within the category of agonistic calls, victims of aggression emitted high-frequency, frequency-modulated calls (screams) in submissive, potentially fearful situations, whereas aggressors emitted low-frequency, atonal calls (threats), which generally is consistent with calls across primate taxa (Hauser 1993).

It may be more instructive to consider Morton's original hypothesized structural changes with arousal level within call type rather than across call types, because structural changes can reflect an increase in the intensity of arousal (Fichtel *et al.* 2001). For example, though we have no independent evidence on underlying motivation, the contexts of production of intense and mild vocal threats differ relative to the elevation of aggression, which presumably relates to elevation of arousal. Analyses reveal that intense vocal threats are differentiated from mild vocal threats based on their higher overall frequencies and higher peak frequencies. Individuals also typically repeat intense vocal threats in sequences, which also can indicate heightened arousal (Manser 2001). In addition, individuals emit roar screams during the most severe aggressive encounters that, accordingly, are of longer duration and exhibit more atonality than other types of screams do.

Using predictions about structural changes related to presumed motivational levels, when combined with information on social relationships, also can provide potential information about call function. For example, Morton predicted that calls whose frequencies fall and rise with equal frequency reflect a conflict of motivation to approach or withdraw from a stimulus. Sociosexual vocalizations emitted during dances seem to fit the description, in that harsh, low-frequency grunts are combined with frequency-modulated squeaks and high-frequency wheezes with sharp upsweeps and downsweeps. Further, 2 individuals exchange the calls as they approach and retreat from one another continually over a period of several minutes in situations of high tension in which aggression can erupt (Perry, *pers. obs.*).

There are also transitional calls with mixed acoustic structure (harmonic/noisy) in the repertoire of white-faced capuchins, including twargles (trill-gargle), geckers (harsh trill grading into a screamy trill), staccato gargles (staccato vocalizations-gargle), and screamy trills. Researchers have suggested that transitional calls serve an affiliative function while also exhibiting qualities of submissive vocalizations (Robbins and McCreery 2003). Given that typically only infants emit most of the calls, it is unclear whether the calls are simply representative of intermediate stages of social and vocal development or they independently represent particular call types, or are a result of intermediate motivational states (*cf.* Cleveland and Snowdon 1982; Robinson 1984).

External Influences on Call Variation

Marler (1965, 1976) first suggested that species that live in relatively open habitats and that interact at close range, or those that use vocalizations relatively more in intragroup interactions, should evolve graded vocal repertoires because visual and contextual cues accompany auditory signals. By contrast, discrete vocal repertoires should evolve in species that live in habitats with low visibility, such as forest-dwelling species, or in species that rely heavily on long-distance intra- or intergroup communication. However, a revised view of Marler's hypothesis is that a combination of habitat characteristics, group spread, and social complexity will play a role in influencing call structure (Fichtel and Kappeler 2002; Fischer and Hammerschmidt 2002; Fischer *et al.* 2002; Schott 1975; Schrader and Todt 1993).

There are a few studies that support the hypothesis that vocal structure and diversity of calls in a repertoire is associated with variation in social parameters. For example, in a phylogenetic analysis of vocal repertoire size across primate species, McComb and Semple (2005) revealed an association with increased repertoire size, social group size, and time spent grooming. Similarly, a relationship exists between measures of social complexity and alarm call repertoire size in some, but not all, sciurid species (Blumstein and Armitage 1997). Most relevant to the current study, Cleveland and Snowdon (1982), Fischer and Hammerschmidt (2002), Macedonia (1993), McShane *et al.* (1995), and Range and Fischer (2004) related variation of calls in a repertoire to the quality and type of interactions within groups.

*Cebus capucinus* exhibit complex social interactions and social relationships that involve social negotiation behaviors, alloparenting, coalitions in which they show triadic awareness, and cultural traditions (Perry *et al.* 2003, 2004). Individuals often emit vocalizations in dyadic interactions, some of which influence the behavior of

call recipients, e.g., trills and food-associated calls (Gros-Louis, 2002, 2004a). We propose that the extent to which individuals use vocalizations differentially in social interactions may influence call diversity as well. Thus, a fruitful line of research would be to compare vocal usage in social interactions among species and corresponding call complexity. Similarly, calls that individuals emit in succession and combine syntactically (*cf.* Marler 1977; Robinson 1984), such as bray/intense vocal threat during intergroup interactions, burst/loud trill during group movement or to initiate group movement, and coo/lost call by infants separated from their mothers, may provide information different from calls produced individually (Arnold and Zuberbühler 2006; Crockford and Boesch 2005; Zuberbühler 2002), thereby increasing call diversity.

By documenting not only how vocalizations vary within and across call types but also how call structure changes within individuals as their social rank changes over time, researchers can gain better insight into call function than by documenting the contexts in which they occur. For example, Fischer *et al.* (2004) demonstrated that fundamental frequency characteristics of baboon loud calls change with age and changing dominance status. In addition to examining changes in the acoustic structure of calls, changes in call usage can be illuminating. In white-faced capuchins, infants show a steady decline in their gargle and coo production over the first 2 yr of life (Perry, *unpub. data*). Similarly, young males and females emit food-associated calls at similar rates, but as males mature, they decrease their production of food-associated calls. Given that food-associated calls appear to serve an appeasement function (Gros-Louis 2004a), the distribution of calls across age-sex classes elucidates the role of the vocalizations in social interactions. Similarly, the observation that adult females shift their gargles to a new $\alpha$-male sheds light on the possible appeasement or bond-testing function of this call (*cf.* Perry *et al.* 2003).

The evolutionary origin of the link between structure and function has attracted new interest in recent years. Though changes in call structure may be related to changes in callers' internal states, they may also have been selected to influence call recipients' behavior via physiological mechanisms (Owren and Rendall 2001; Todt *et al.* 1995). Though it is clear that many primate calls influence the behavior of call recipients, e.g. affiliative calls (Bauers 1993; Bauers and deWaal 1991; Blount 1985; Cheney and Seyfarth 1997; Palombit *et al.* 1999), alarm calls (Fichtel and Hammerschmidt 2002; Fichtel and Kappeler 2002; Fischer 1998; Fischer *et al.* 2001; Macedonia 1990; Manser 2001; Seyfarth *et al.* 1980; Zuberbühler *et al.* 1999), and food-associated calls (Di Bitetti 2003; Evans and Evans 1999; Gros-Louis 2004b; Hauser 1998), researchers debate the mechanism underlying the phenomenon. Though many calls in the vocal repertoire of white-faced capuchins fit the predictions of calls that should increase attention and arousal in listeners, it is likely that calls influence the behavior of others via both physiological mechanisms elicited by physical characteristics of the calls and through learned associations (Fichtel and Kappeler 2002; Owren and Rendall 2001).

Our results suggest the need to consider how social behavior and vocal communication are related. By exploring in depth how calls function in social interactions and how calls vary across broadly defined similar social interactions (Cleveland and Snowdon 1982), or how they change as social interactions change across a continuum (affiliative-aggressive: Robinson 1984), it is possible to identify

more distinct vocal types and the meaning of combined vocal types. Such examination of call structure and complexity can uncover the relative influence that social structure and interactions can have on the evolution of vocal repertoires (Macedonia 1993; Robinson 1984). Researchers can understand better the multivariate nature of diversity in vocal communication by considering all of the factors in studies of vocal repertoires across species.

# References

Arnold, K., & Zuberbühler, K. (2006). The alarm calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. *Animal Behavior*, *72*, 643–653.

Bauers, K. A. (1993). A functional analysis of staccato grunt vocalizations in the stumptailed macaque (*Macaca arctoides*). *Ethology*, *94*, 147–161.

Bauers, K. A., & de Waal, F. B. M. (1991). "Coo" vocalizations in stump-tailed macaques: a controlled functional analysis. *Behaviour*, *119*, 143–160.

Bermejo, M., & Omedes, A. (1999). Preliminary vocal repertoire and vocal communication of wild bonobs (*Pan paniscus*) at Lilungu (Democratic Republic of Congo). *Folia Primatologica*, *70*, 328–357.

Blount, B. (1985). "Girney" vocalizations among Japanese macaque females: Context and function. *Primates*, *26*, 424–435.

Blumstein, D., & Armitage, K. B. (1997). Does social complexity drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *American Naturalist*, *150*, 179–200.

Boinski, S. (1993). Vocal coordination of troop movement among white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, *30*, 85–100.

Boinksi, S., & Campbell, A. F. (1995). Use of trill vocalizations to coordinate troop movement among white-faced capuchins: A second field test. *Behaviour*, *132*, 875–901.

Boinski, S., & Campbell, A. F. (1996). The "huh" vocalization of white-faced capuchins: A spacing call disguised as a food call? *Ethology*, *102*, 826–840.

Cheney, D. L., & Seyfarth, R. M. (1997). Reconciliatory grunts by dominant females influence victims' behaviour. *Animal Behavior*, *54*, 409–418.

Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The role of grunts in reconciling opponents and facilitating social interactions among female baboons. *Animal Behavior*, *50*, 249–257.

Cleveland, J., & Snowdon, C. T. (1982). The complex vocal repertoire of the adult cotton-top tamarin (*Saguinus oedipus oedipus*). *Zeitschrift für Tierpsychologie*, *58*, 231–270.

Crockford, C., & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour*, *142*, 397–421.

Di Bitetti, M. S. (2001). Food-associated calls in the tufted capuchin monkey (Cebus apella): Unravelling the mysteries of an apparently altruistic behavior in an apparently selfish animal. Ph.D. dissertation, State University of New York, Stony Brook, NY.

Di Bitetti, M. S. (2003). Food-associated calls of tufted capuchin monkey (*Cebus apella nigritus*) are functionally referential signals. *Behaviour*, 140, 565–592.

Digweed, S. M., Fedigan, L. M., & Rendall, D. (2005). Variable specificity in the anti-predator vocalizations and behaviour of the white-faced capuchin, *Cebus capucinus*. *Behaviour*, 142, 997–1021.

Digweed, S. M., Fedigan, L. M., & Rendall, D. (2007). Who cares who calls? Selective responses to the lost calls of socially dominant group members in the white-faced capuchin (*Cebus capucinus*). *American Journal of Primatology*, 69, 1–7.

Dittus, W. P. J. (1984). Toque macaque food calls: Semantic communication concerning food distribution in the environment. *Animal Behavior*, 32, 470–477.

Dunteman, G. H. (1989). *Principal components analysis*. Beverly Hills, CA: Sage.

Evans, C. S., & Evans, L. (1999). Chicken food calls are functionally referential. *Animal Behavior*, 58, 307–319.

Fedigan, L. M. (1993). Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology*, 14, 853–877.

Fichtel, C., & Hammerschmidt, K. (2002). Responses of redfronted lemurs (*Eulemur fulvus rufus*) to experimentally modified alarm calls: Evidence for urgency-based changes in call structure. *Ethology*, 108, 763–777.

Fichtel, C., & Hammerschmidt, K. (2003). Responses of squirrel monkeys to experimentally modified mobbing calls. *Journal of the Acoustic Society of America*, 113, 2927–2932.

Fichtel, C., Hammerschmidt, K., & Jürgens, U. (2001). On the vocal expression of emotion. A multiparametric analysis of different states of aversion in the squirrel monkey. *Behaviour*, 138, 97–116.

Fichtel, C., & Kappeler, P. M. (2002). Anti-predator behaviour of group-living Malagasy primates: Mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology*, 51, 262–275.

Fichtel, C., Perry, S., & Gros-Louis, J. (2005). Alarm calls of white-faced capuchin monkeys: An acoustic analysis. *Animal Behavior*, 170, 165–176.

Fischer, J. (1998). Barbary macaques categorize shrill barks into two call types. *Animal Behavior*, 55, 799–807.

Fischer, J., & Hammerschmidt, K. (2001). Functional referents and acoustic similarity revisited: The case of Barbary macaque alarm calls. *Animal Cognition*, 4, 29–35.

Fischer, J., & Hammerschmidt, K. (2002). An overview of the Barbary macaque, *Macaca sylvanus*, vocal repertoire. *Folia Primatologica*, 73, 32–45.

Fischer, J., Hammerschmidt, K., Cheney, D. L., & Seyfarth, R. M. (2002). Acoustic features of male baboon loud calls: Influences of context, age, and individuality. *Journal of the Acoustic Society of America*, 111, 1465–1474.

Fischer, J., Hammerschmidt, K., & Todt, D. (1995). Factors affecting acoustic variation in Barbary macaque (*Macaca sylvanus*) disturbance calls. *Ethology*, 101, 51–66.

Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: Acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, 56, 140–148.

Fischer, J., Metz, M., Cheney, D. L., & Seyfarth, R. M. (2001). Categorical responses of Chacma baboons to graded bark variants? *Animal Behavior*, 61, 925–931.

Frankie, G. W., Vinston, S. B., Newstrom, L. E., & Barthell, J. F. (1988). Nest and and habitat preferences of *Centris* bees in the Costa Rican dry forest. *Biotropica*, 20, 301–310.

Freese, C., & Oppenheimer, J. (1981). The capuchin monkeys, genus *Cebus*. In A. Coimbra-Filho, & R. Mittermeier (Eds.), *Ecology and behavior of neotropical primates* (vol. 1). Rio de Janeiro: Academia Brasileira de Ciencias.

Gouzoules, S., & Gouzoules, H. (2000). Agonistic screams differ among four species of macaques: The significance of motivational-structural rules. *Animal Behavior*, 59, 501–512.

Gros-Louis, J. (2002). Contexts and behavioral correlates of trill vocalizations in wild white-faced capuchin monkeys (*Cebus capucinus*). *American Journal of Primatology*, 57, 189–202.

Gros-Louis, J. (2004a). The function of food-associated calls from the perspective of the signaller. *Animal Behavior*, 67, 431–440.

Gros-Louis, J. (2004b). White-faced capuchins' responses to naturalistic and experimentally presented food-associated calls. *Journal of Comparative Psychology*, 118, 396–402.

Gros-Louis, J. (2006). Acoustic description and contextual analysis of food-associated calls in *Cebus capucinus*. *International Journal of Primatology, 27*, 273–294.

Hammerschmidt, K., & Fischer, J. (1998). The vocal repertoire of Barbary macaques: A quantitative analysis of a graded signal system. *Ethology, 104*, 203–216.

Hammerschmidt, K., & Todt, D. (1995). Individual differences in vocalizations of young barbary macaques (*Macaca sylvanus*): A multi-parametric analysis to identify critical cues in acoustic signaling. *Behaviour, 132*, 381–399.

Harcourt, A. H., Stewart, K. J., & Hauser, M. (1993). Functions of wild gorilla close calls. I. Repertoire, context and interspecific comparison. *Behaviour, 124*, 89–122.

Hauser, M. D. (1993). The evolution of nonhuman primate vocalizations: Effects of phylogeny, body size, and social context. *American Naturalist, 142*, 528–542.

Hauser, M. D. (1998). Functional referents and acoustic similarity: Field playback experiments with rhesus monkeys. *Animal Behavior, 55*, 1647–1658.

Klecka, W. (1980). *Discriminant analysis*. Beverly Hills, CA: Sage.

Macedonia, J. M. (1990). What is communicated in the antipredator calls of lemursh: Evidence from playback experiments with ringtailed and ruffed lemurs. *Ethology, 86*, 177–190.

Macedonia, J. M. (1993). The vocal repertoire of the ring-tailed lemur (*Lemur catta*). *Folia Primatologica, 61*, 186–217.

Manser, M. B. (2001). The acoustic structure of suricate's alarm calls vary with predator class and response urgency. *Proceedings of the Royal Society of London Series B, 268*, 2485–2491.

Manson, J. H., Perry, S., & Parish, A. R. (1997). Nonconceptive sexual behavior in bonobos and capuchins. *International Journal of Primatology, 18*, 767–786.

Marler, P. (1965). Communication in monkeys and apes. In I. DeVore (Ed.), *Primate behavior: Field studies in monkeys and apes* (pp. 544–584). New York: Holt, Rinehart and Winston.

Marler, P. (1976). Social organization, communication and graded signals: the chimpanzee and the gorilla. In P. Bateson, & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 239–280). Cambridge, U.K.: Cambridge University Press.

Marler, P. (1977). The structure of animal communication sounds. In T. H. Bullock (Ed.), *Recognition of complex acoustic signals* (pp. 17–35). Berlin: Springer.

McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters, 1*, 381–385.

McShane, L. J., Estes, J. A., Riedman, M. L., & Staedler, M. M. (1995). Repertoire, structure and individual variation of vocalizations in the sea otter. *Journal of Mammology, 76*, 414–427.

Mitani, J. (1985). Sexual selection and adult male orangutan long calls. *Animal Behavior, 33*, 272–283.

Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist, 111*, 855–869.

Morton, E. S. (1982). Grading, discreteness, redundancy, and motivational-structural rules. In D. Kroodsma, & E. H. Miller (Eds.), *Acoustic communication in birds* (pp. 183–212). New York: Academic Press.

Oppenheimer, J. R. (1973). Social and communicatory behavior in the *Cebus* monkey. In C. R. Carpenter (Ed.), *Behavioral regulators of behavior in primates* (pp. 251–271). Cranbury, N J: Associated University Presses.

Owings, D. H., & Morton, E. S. (1998). *Animal Vocal Communication: A new approach*. Cambridge, U. K: Cambridge University Press.

Owren, M. J., & Rendall, D. (2001). Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology, 10*, 58–71.

Palombit, R. A. (1992). A preliminary study of the vocal communication in wild long-tailed macaques (*Macaca fascicularis*), I. Vocal repertoire and call emission. *International Journal of Primatology, 13*, 143–182.

Palombit, R. A., Cheney, D. L., & Seyfarth, R. M. (1999). Male grunts as mediators of social interaction with females in wild chacma baboons (*Papio cynocephalus ursinus*). *Behaviour, 136*, 221–242.

Perry, S. (1995). *Social relationships in wild white-faced capuchin monkeys, Cebus capucinus*. Ph.D. thesis, University of Michigan, Ann Arbor.

Perry, S. (1996). Intergroup encounters in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology, 40*, 167–182.

Perry, S. (1998). Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour, 135*, 139–172.

Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K., et al. (2003). Social conventions in wild white-faced capuchin monkeys: Evidence for traditions in a neotropical primate. *Current Anthropology, 44*, 241–268.

Perry, S., Barrett, H. C., & Manson, J. H. (2004). White-faced capuchins show triadic awareness in their choice of allies. *Animal Behavior, 67*, 165–170.

Range, F., & Fischer, J. (2004). Vocal repertoire of sooty magabeys (*Cercocebus torquatus atys*) in the Taï National Park. *Ethology, 110*, 301–321.

Rendall, D., Seyfarth, R. M., Cheney, D. L., & Owren, M. J. (1999). The meaning and function of grunt variants in baboons. *Animal Behavior, 57*, 583–592.

Robbins, R. L., & McCreery, E. K. (2003). African wild dog pup vocalizations with special reference to Morton's model. *Behaviour, 140*, 333–351.

Robinson, J. G. (1979). Vocal regulation of use of space by groups of titi monkeys *Callicebus moloch. Behavioral Ecology and Sociobiology, 5*, 1–15.

Robinson, J. G. (1982). Vocal systems regulating within-group spacing. In C. T. Snowdon, C. H. Brown, & M. R. Petersen (Eds.), *Primate communication* (pp. 94–116). Cambridge, U.K.: Cambridge University Press.

Robinson, J. G. (1984). Syntactic structures in the vocalizations of wedge-capped capuchin monkeys, *Cebus olivaceus. Behaviour, 90*, 46–79.

Schott, D. (1975). Quantitative analysis of the vocal repertoire of squirrel monkeys (*Saimiri scieureus*). *Zeitshrift für Tierpsychologie, 38*, 225–250.

Schrader, L., & Hammerschmidt, K. (1997). Computer-aided analysis of acoustic parameters in animal vocalizations: A multi-parametric approach. *Bioacoustics, 7*, 247–265.

Schrader, L., & Todt, D. (1993). Contact call parameters covary with social context in common marmosets, *Callithrix j. jacchus. Animal Behavior, 46*, 1026–1028.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to 3 different alarm calls: Evidence for predator classification and semantic communication. *Science, 210*, 801–803.

Todt, D., Hammerschmidt, K., Ansorge, V., & Fischer, J. (1995). The vocal behavior of Barbary macaques (*Macaca sylvanus*): Call features and their performance in infants and adults. In E. Zimmerman, J. D. Newman, & U. Jurgens (Eds.), *Current topics in primate vocal communication* (pp. 141–160). New York: Plenum Press.

Watts, J. M., & Stookey, J. M. (1999). Effects of restraint and branding on rates and acoustic parameters of vocalization in beef cattle. *Applied Animal Behavior Science, 62*, 125–135.

Weary, D. M., Braithwaite, L. A., & Fraser, D. (1998). Vocal response to pain in piglets. *Applied Animal Behavior Science, 56*, 161–172.

Wiley, R. H., & Richards, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalization. *Behavioral Ecology and Sociobiology, 3*, 69–94.

Zimmerman, E. (1985). The vocal repertoire of the adult Senegal bushbaby (*Galago senegalensis senegalensis*). *Behaviour, 94*, 212–233.

Zuberbühler, K. (2000). Referential labelling in Diana monkeys. *Animal Behavior, 59*, 917–927.

Zuberbühler, K. (2002). A syntactic rule in forest monkey communication. *Animal Behavior, 63*, 293–299.

Zuberbühler, K., Cheney, D. L., & Seyfarth, R. M. (1999). Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology, 113*, 33–42.