

Acoustics and behavioral contexts of “gecker” vocalizations in young rhesus macaques (*Macaca mulatta*)

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Loud, pulsed “gecker” vocalizations are commonly produced by young rhesus macaques in distressful circumstances. The acoustics, usage, and responses associated with these calls were examined using audio recordings and observational data from captive, socially living rhesus up to 24 months old. One-hundred-eleven gecker bouts were recorded from ten individuals (six males, four females), with most geckers produced during the first 6 months of age. A gecker call consisted of a bout of up to 28 pulses of spectrally structured noise with a single prominent frequency peak. Nine contexts of calling were identified, but little evidence of context-specific acoustic variation was found. While geckering often triggered responses by the vocalizer’s mother, the most common outcome was the absence of any reaction. Females geckered longer and at higher rates than did males, while also showing acoustic evidence of greater vocal effort. Mothers nonetheless responded more often and more positively to males. Overall, results show that gecker acoustics vary somewhat with vocalizer sex, age, and likely arousal level, but do not reflect detailed aspects of behavioral context. Circumstances of production suggest that geckers function primarily to draw the attention of mothers, who in turn are selective in responding. © 2007 Acoustical Society of America.

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I. INTRODUCTION

Young nonhuman primates produce a variety of vocalizations when in distress, which in rhesus macaques (*Macaca mulatta*) include “coos,” “squeaks,” “screams,” “pant threats,” “girneys,” and “geckers” (Maestripieri and Call, 1996; Maestripieri *et al.*, 2000; Tomaszycki *et al.*, 2001). Geckers in particular have been described as a distress-related vocalization in rhesus monkeys, occurring in large numbers when infants are ignored, rejected, or otherwise separated from their mothers. Often accompanied by dramatic, convulsive bodily jerking, these loud, explosive, and distinctive-sounding vocalizations have received some attention and mention from a variety of researchers, but predominantly through qualitative rather than quantitative description. Thus, while geckers have also been documented in a number of other macaque species, details of their form and function remain unclear (Newman, 1995; Green, 1981).

Altmann (1962) first named geckers onomatopoeically as “ik, ik, ik.” He noted that the call is accompanied by spasmodic jerking and occurs during weaning and other circumstances of evident infant distress. The sounds were subsequently referred to as “geckers” and “geckering screeches” by Rowell (1962; Rowell and Hinde, 1962), who described them as a series of 0.1 s squeaks separated by 0.5–1.0 s intervals (illustrated in Fig. 1). Several subsequent studies have shown geckers to be among the most common vocalizations produced by young rhesus. For example, Owren

et al. (1993) reported that geckers comprised approximately 38% of the total number of vocalizations produced by rhesus monkeys during the first year of life, and 12% in the second year. Figures from Maestripieri *et al.* (2000) were comparable, with geckers making up 43.3% of all vocalizations in the first three months of life. Tomaszycki *et al.* (2001) similarly noted that geckers were the most common vocalization over the first 8 months, accounting for 34% of vocal output.

In spite of the prevalence of these sounds, little quantitative information is available concerning their acoustics or function. On the one hand, Newman (1995) notes that geckers can routinely occur without apparent cause, and suggests that they “may largely be a reflection of the immature state of the central nervous systems underlying vocal expression” (p. 79). On the other hand, many researchers are likely to agree with Maestripieri and Call’s (1996) characterization that geckers, like most primate infant distress calls, occur “when the infant is not in contact with its mother” and “signal the infant’s need for nursing, transport, or protection” (Maestripieri and Call, 1996, p. 620). Critical issues thus include whether rhesus geckers are in fact occurring primarily or exclusively in instances of distress, whether geckers have specific, context-dependent signaling value, and how other animals respond to these sounds.

Relatively few studies of primate infant vocalization have examined the co-occurrence of call acoustics and context (e.g., Kalin *et al.*, 1992; Jovanovic and Gouzoules, 2001), or found evidence of context-specific vocal subtypes (e.g., Bayart *et al.*, 1990). Although also limited, some information is available concerning responses to geckers and other distress-related calls. Across primate species, for instance, it has generally been found that mothers are most responsive to young infants that vocalize at relatively low

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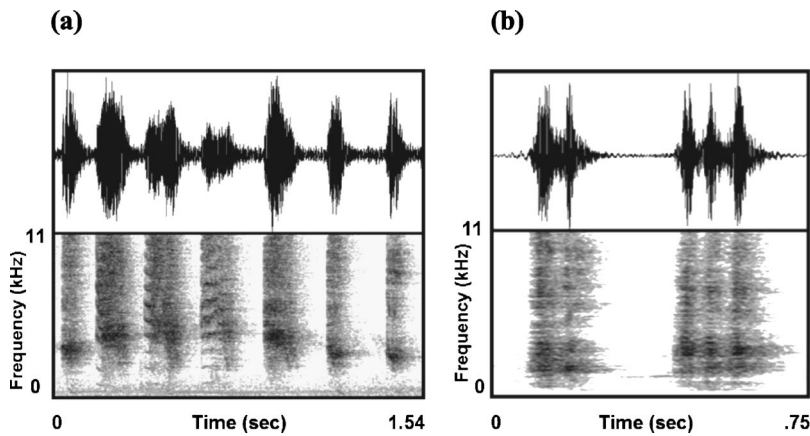


FIG. 1. (a) A representative gecker bout consisting of seven pulses, shown as (top) a wave form and (bottom) a narrowband FFT spectrogram (20 ms Hanning analysis window, 22.05 kHz sampling rate). The third and fourth pulse shown produced higher HNR values than elsewhere, but are nonetheless still likely to reflect deterministic chaos in underlying vocal-fold vibration. (b) A gecker bout illustrating pulse reduplication in the wave form and a narrowband FFT spectrogram. Pulses are first doubled and then tripled.

rates (Maestriperi, 1995; Hauser, 1993). Furthermore, females in several species have been reported to produce distress-related calls comprised of more call types, emitted at higher rates, and for longer durations than males (Locke and Hauser, 1999; Wallen, 2005; Green, 1981). Overall, rhesus females do show greater volubility than males, not only in infancy (Newman *et al.*, 1990; Tomaszycycki *et al.*, 2001), but also in adolescence and adulthood (Erwin, 1975). Thus, while sex differences in maternal treatment of primate infants tends to be rare (Wallen, 2005), Tomaszycycki *et al.* (2001) have nonetheless reported that rhesus mothers are more likely to respond to vocalizations by male than by female infants. Despite this evidence, rather little is as yet known about the ontogeny or extent of sex differences in vocal behavior (Gautier and Gautier 1977; Green, 1981). Furthermore, the few studies that are available have typically examined time periods of less than a year (Hammerschmidt *et al.*, 2000; Hammerschmidt *et al.*, 2002; Seyfarth and Cheney, 1986; Newman, 1995; Snowdon *et al.*, 1997; Owren *et al.*, 1993).

The current study sought to extend previous work on rhesus geckers by examining the acoustics and contexts of these vocalizations as systematically as possible in animals up to 24 months of age. The work began with a detailed characterization of gecker acoustics and the contexts in which infants produce these calls. The data were then used to test for possible specificity in acoustics and contexts, age and sex-related differences, and factors that might affect the likelihood of responding by mothers or other animals. These questions were examined using a large database of calls recorded during a long-term study of two groups of socially housed rhesus monkeys living in outdoor cages at a national primate center.

II. METHODS

A. Study site and subjects

Data were collected during the course of a long-term project on vocal development (Owren *et al.* 1992a, 1992b; Owren *et al.*, 1993). The subset analyzed here drew on audio recordings and behavioral data collected between 1986 and 1989 from ten rhesus macaques (six males and four females) ranging in age from newborn to 24 months of age (see Table I). The overall project involved cross fostering a small num-

ber of neonatal infants between different-species foster mothers (Owren and Dieter, 1989), but no such offspring are represented in the data analyzed here. The ten subjects included here represented all the rhesus offspring born into the study groups during the course of the project and from whom there were any usable gecker recordings. The subjects were offspring of a total of seven different mothers, all of whom were multiparous. Five mothers were represented by a single study subject, one by two study subjects, and one by three study subjects. All animals were located at the California National Primate Research Center (CNPRC; University of California, Davis), as part of two socially living groups. Group composition varied somewhat over time, with each of the two cages including 1–2 adult males, one or no unrelated juvenile males, 4–6 adult females, and 6–8 offspring of those females.

Each group was housed outdoors in a separate cage constructed from two modified commercial corn cribs connected by a rectangular inter-cage unit (Hoffman and Stowell, 1973). The cages were approximately $13.6 \times 4.3 \times 3.0$ m (with additional space created by conical roofs), and contained capture chutes, perches, and pea gravel used as replaceable ground cover. During the winter months, screens were installed as wind shields and infrared lamps provided heat. The monkeys had continuous access to fresh water and received Purina monkey chow twice daily in quantities that ensured a plentiful supply for all. Detailed physical examinations of the animals were conducted three times per year by the CNPRC veterinary staff and general health was checked daily.

TABLE I. Subject demographics and representation in the gecker sample.

Subject	Sex	Age (mo)	No. of Bouts	No. of Pulses
JN	M	1–5	3	9
JS	M	2–5	16	76
LN	F	4–14	27	281
ML	F	2–4	7	47
MS	M	1–16	28	98
MY	F	3–17	6	55
NK	M	4–7	9	33
RK	M	3–17	4	15
SM	M	5–14	8	18
SV	F	5	3	19

TABLE II. The 24 variables used in acoustic analysis.

Acoustic measure	Definition
Bout-Dur	Duration of a gecker bout (s)
Pulse-Dur	Duration of a single gecker pulse within a bout (s)
Pulses-Bout	Number of gecker pulses within a bout
Pulse-Redup	Number of re-duplicated pulses within a bout
SNR (signal-to-noise ratio)	Difference between rms amplitude of a pulse and adjacent background noise (dB)
Peak1	Frequency of the first LPC peak (Hz)
Spectral-Tilt	Overall slope of the LPC function
LPC1 to LPC12	Values of the 12 coefficients of the LPC function
Spectral-Mean	Mean of the normalized frequency spectrum (Hz)
Spectral-StDev	Standard deviation of the normalized spectrum
Spectral-Skew	Relative symmetry of the normalized spectrum
Spectral-Kurtosis	Relative peakedness of the normalized spectrum
HNR (harmonic-to-noise ratio)	Ratio of wave form periodicity to noisiness (dB)

B. Apparatus and procedure

1. Observation and recording

Behavioral observations were conducted in 10 min continuous focal sessions (Altmann, 1974) occurring in the morning (7:30 AM to noon) in the spring, summer, and fall, and in the afternoon (noon to 5 PM) in winter, up to six days per week. The daily sampling order was determined quasi-randomly. During sampling, behaviors exhibited by the focal animal and others it interacted with were entered as codes on a handheld computer, with each entry noting animal identities, any one or more of 63 concomitant behaviors, as well as the onset time of occurrence. This approach allowed documentation of all vocalizations produced by a focal animal during the session, as well as the behavior associated with these calls.

Audio recording was conducted with a four-channel Tascam 234 cassette deck (Teac Corporation, Tokyo), and two Sennheiser ME88 microphones (Sennheiser Electronic, Old Lyme, CT) placed on stands in fixed positions outside the cage. Calls from all animals were routinely recorded, including ad libitum samples that were described through supplementary commentary using a lapel microphone connected to a separate channel of the cassette deck. Vocalizations were later transferred to $\frac{1}{4}$ in. audio tape using either a Uher 4200 Report Monitor (Uher Werke Munchen, Munich) or a Fostex A-2 reel-to-reel deck (Fostex America, Norwalk, CA). Calls were separated, numbered, and annotated during this process using the coded behaviors and any additional, audio-recorded comments.

2. Call selection and analysis

The vocalization sample was identified by examining the entire database of more than 10,000 separately cataloged calling episodes available from the project. Gecker vocalizations were identified based on previous annotations in the database (Owren *et al.*, 1992a), by matching acoustic features to published descriptions of gecker calls (e.g., Rowell and Hinde 1962; Jovanovic and Gouzoules 2001), and by ear. A total of 111 analyzable gecker bouts comprising 651 individual gecker pulses from the ten vocalizers were iden-

tified in this manner (see Table I). A bout was defined as an uninterrupted emission of pulsed vocalization by a single animal with less than a 5 s pause between pulses.

Vocalizations were digitized and archived using a sampling rate of 44.1 kHz with 16 bit accuracy. Calls were subsequently downsampled to 22.05 kHz for analysis, which was conducted using the ESPS/waves+ 5.3 “xwaves” package (Entropic Research, Washington, DC), running on an SGI O2 workstation (Silicon Graphics Incorporated, Mountain View, CA). The Praat speech analysis package was also used in some analyses (Boersma, 2001; available at www.praat.org). Statistical analyses were conducted using NCSS 2004 (Jerry Hintze, Kaysville, UT) and SPSS 13.0 (SPSS Inc., Chicago, IL).

3. Acoustic variables

Twenty-four acoustic measures were extracted (definitions are provided in Table II), spanning temporal, amplitude, and frequency-spectrum aspects of the calls. Temporal measures of geckering at bout and pulse levels included absolute durations (Bout-Dur, Pulse-Dur), and number of pulses per bout (Pulses-Bout). As illustrated in Fig. 1(b), gecker pulses sometimes occur in doubled, tripled, quadrupled, and even quintupled form without intervening silent intervals. This phenomenon was referred to as “twinning” by Maestriperi *et al.* (2000), and here is considered as a single phenomenon labeled “reduplication” (Pulse-Redup). Call amplitude was characterized based on calculating a signal-to-noise ratio (SNR) for individual bouts, defined as the root-mean-square (rms) amplitude of the pulse minus the rms amplitude of a representative, adjacent segment of background noise. No attempt was made to measure the absolute amplitude of calls. This indirect approach was used as an attempt to obtain relative amplitude information for comparisons such as possible age-, sex-, and context-related differences. It was arguably justified by the fact that microphones were placed in the same locations outside the cages for every session, and based on the assumption that general background noise levels remained roughly constant over time. Sources of error for SNR

TABLE III. Codes used to characterize behavior occurring before/during and after a geckering event.

Code	Type	Definition
Affil	Before/during	Infant engages in “friendly” prosocial behavior with mother or others, such as touching, grooming, and play.
Aggr	Before/during	Infant engages in or receives aggressive behavior with mother or others, such as threatening, pushing, hitting, biting, and nipple rejections.
Inf-Follow	Before/during	Infant follows its locomoting mother.
Mth-Leave	Before/during	Mother moves out of proximity to her infant.
Inf-Leave	Before/during	Infant moves out of proximity to her mother.
Spon	Before/during	Absence of any evident antecedent or co-occurrence.
Pos-Outcome	After	Infant experiences Affil and/or attention from mother or others.
Neg-Outcome	After	Infant experiences Aggr from its mother or others.
No-Outcome	After	Infant experiences neither Aggr nor Affil from mother or others.
Rsp	Response	Any immediate discernible maternal action occurring in response to her infant’s gecker (includes looking, touching, shifting position, threatening, pushing, hitting, or biting an infant that is in contact, and vocalizing, looking, approaching, reaching, touching, threatening, pushing, hitting, biting, as well as Affil or Aggr toward an infant that is not in contact).
No-Rsp	Response	Absence of discernible maternal behavior in response to her infant’s gecker.

measurements would then be any moment-to-moment variation in background noise, and the vocalizer’s distance from and relative orientation to the microphone.

Frequency-spectrum (spectral) measurements were made from all 651 total pulses in the sample, based on a spectral slice located midway through each pulse. This slice was characterized by overlaying a ten-coefficient, autocorrelation-based linear predictive coding (LPC) function (0.023 s Hanning window) on a 512-point fast Fourier transform (FFT) spectrum (Hanning window) of the same segment (further described by Owren and Bernacki, 1998), with frequency and amplitude values recovered from the LPC envelope through cursor-based measurement. Variables used were the first LPC peak (Peak1), the overall slope of the LPC spectrum (Spectral-Tilt), values of each of the 12 coefficients used in the LPC function (LPC1 to LPC12), and the first four spectral moments of the Fourier spectrum (Spectral-Mean, Spectral-StDev, Spectral-Skew, Spectral-Kurtosis). Spectral-moment measures are particularly well suited to characterizing global features of noisy, broadband frequency spectra (Forrest *et al.*, 1988), and are computed by normalizing the Fourier power spectrum and treating it as a statistical distribution. The first four moments of this distribution are its mean, standard deviation, skewness, and kurtosis, in the normal sense of these terms. The last measure was the harmonic-to-noise ratio (HNR) of each pulse, extracted using Praat’s pitch-based algorithm (Boersma, 1993).

4. Behavioral variables

The behavioral contexts of each of the 111 gecker bouts were coded in binary fashion according to whether the offspring’s mother exhibited any discernible response to the vocalizations (Rsp/No-Rsp), as well as being scored as to which of six possible behaviors were occurring just before or during the bout (Before/During) and whether vocalizing was followed by aggression, affiliation, or neither (After). Behav-

ioral codes are defined in Table III. Coding for Before/During and After variables was based on behavioral codes recorded just before, during, and after each gecker bout. Behaviors included as the context of each vocalization event were determined by the observer, who also transcribed the relevant codes for each episode on a daily basis during the course of the project. Contexts were thus not inherently limited in time either before or after the vocalization, but rarely exceeded a few seconds on either side. In four cases, data were insufficient to determine the Before/During context and those gecker bouts were excluded from analyses involving this variable. In 34 cases, mothers were out of view, and Rsp/No-Rsp could not be coded.

III. RESULTS

A. Gecker acoustics

1. General features

Descriptive statistics for the acoustic features of gecker vocalizations are shown in Table IV. On average, geckers were emitted in 1 s bouts of four pulses, though both bout duration (Bout-Dur) and number of pulses per bout (Pulses-Bout) were highly variable. The longest bout observed was nearly 9 s in duration, and as many as 28 pulses were observed in a single bout. Reduplication (Pulse-Redup) occurred in 34% of all bouts, could include as many as five pulses, but usually consisted of just two (72% of total reduplication events). Pearson’s correlation coefficients revealed that Pulse-Redup was strongly correlated with Bout-Dur ($r = 0.83$, $p < 0.001$) and Pulses-Bout ($r = 0.78$, $p < 0.001$).

Although geckers are likely among the loudest vocalizations emitted by young rhesus macaques, mean SNR values were relatively modest (just over 6 dB), while showing high overall variability with the loudest geckers at 19.1 dB. The broadband noisiness of the sounds was reflected in generally low HNR values and spectral slopes that were virtually flat.

TABLE IV. Descriptive features of gecker vocalizations, based on 111 total bouts and 651 total pulses.

Variable	M	SE	Min	Max	Range	COV _{mean}
Age (mo)	5.32	0.41	1	17	16.0	0.80
Bout-Dur (s)	0.98	0.12	0.03	8.96	8.9	1.26
Pulse-Dur (s)	0.18	0.01	0.03	0.71	0.68	0.52
Pulses-Bout	4.29	0.37	1.00	28	27.0	0.92
Pulse-Redup	1.06	0.28	0.00	26	26.0	2.79
SNR (dB)	6.40	0.44	-1.35	19.1	20.5	0.72
Peak 1 (Hz)	2923	74.9	1208	4488	3280	0.27
Spectral-Tilt	-0.01	0.01	-0.22	0.33	0.55	-12.6
Spectral-Mean (Hz)	2087	127.2	114.2	5932	5818	0.64
Spectral-StDev	1480	66.1	136.5	3661	3524	0.47
Spectral-Skew	2.70	0.40	-0.92	22.7	23.6	1.55
Spectral-Kurtosis	41.5	14.5	-1.53	1066	1068	3.67
HNR (dB)	4.13	0.24	-0.67	10.4	11.0	0.60
HNR-SD	3.75	0.11	1.25	7.24	5.99	0.31
LPC1	0.63	0.07	0.03	6.1	6.10	1.18
LPC2	0.66	0.07	0.05	6.1	6.10	1.14
LPC3	0.30	0.03	-0.64	0.92	1.60	1.09
LPC4	-0.35	0.03	-0.84	0.43	1.27	-0.86
LPC5	-0.17	0.03	-0.66	0.54	1.20	-1.69
LPC6	-0.38	0.02	-0.75	0.33	1.08	-0.61
LPC7	-0.10	0.02	-0.57	0.53	1.10	-2.24
LPC8	-0.20	0.02	-0.71	0.31	1.01	-1.02
LPC9	-0.01	0.02	-0.47	0.59	1.06	-15.47
LPC10	-0.09	0.02	-0.60	0.49	1.09	-1.93
LPC11	0.02	0.01	-0.42	0.42	0.84	6.16
LPC12	-0.05	0.01	-0.40	0.27	0.67	-2.57

HNR values did become significantly higher in a few cases (see, for example, the third and fourth pulses shown in Fig. 1(a)), but were never clearly or purely harmonically structured. LPC analysis revealed a one consistent frequency peak just below 3000 Hz (Peak1), with the spectral-moment mean falling just above 2000 Hz. LPC analysis revealed a second peak occurring above 7000 Hz in some cases, but associated frequency values were highly variable. This peak was not discernible in the majority of bouts, and therefore was also not included as a reliable component of gecker acoustic structure. When it did occur, the peak was not harmonically related to Peak1.

2. Age and sex

The effects of age and sex on geckering are shown in Fig. 2, based on 2-mo age blocks during which gecker bouts were available from at least three different individuals (i.e., months 1–2, 3–4, 5–6, 7–8, and 13–14, respectively). Repeated-measures General Linear Model analysis of variance (ANOVAs) were used to test for possible age effects on acoustics, but independent of individual variation. Results revealed that younger infants emitted the fewest pulses per bout, $F(4,96)=6.75$, $p<0.05$, the shortest pulses, $F(4,96)=8.39$, $p<0.05$, and the shortest bouts, $F(4,96)=7.55$, $p<0.01$. Results from associated Tukey-Kramer multiple-comparison posthoc tests are displayed in Fig. 2.

A number of sex differences were also found, even when controlling as well as possible both for body-size differences between males and females, and for differences among individuals. As could be expected, analysis of covariance

(ANCOVA) with vocalizer age entered as a covariate showed males ($M=1.62$ kg) to be significantly heavier than females ($M=1.41$ kg), $F(1,110)=14.2$, $p<0.001$. Infant body weight was therefore entered as a covariate in further repeated-measures ANCOVAs. With vocalizer sex as the independent variable, these tests revealed sex differences in four temporal, amplitude, and frequency-spectrum aspects of the calls (see Table V). The strongest effect sizes were found for Peak1, with frequency peaks in female being almost 700 Hz higher than in male calls, and for Bout-Dur, where female bouts were more than twice as long as male bouts. Other outcomes showed male geckers to be higher in amplitude (SNR), and also less noisy (HNR).

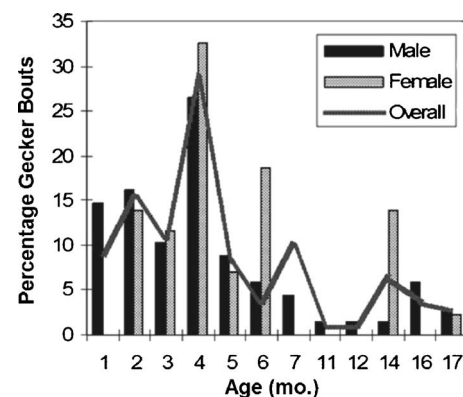


FIG. 2. Mean percentage of gecker bouts occurring by sex and age, based on 2 month age blocks, tallied separately for each individual caller.

TABLE V. Statistically significant ANCOVA tests for sex differences in gecker acoustics with body weight entered as a covariate.

Acoustic measure	Males (M/SE)	Females (M/SE)	Direction of difference	F(1,5)	Effect Size (<i>d</i>)	<i>p</i> value
Bout-Dur (s)	0.57/0.07	1.60/0.25	F>M	19.3	0.86	.007
SNR (dB)	7.53/0.56	4.59/0.63	M>F	8.74	0.67	.032
HNR (dB)	4.58/0.29	3.40/0.38	M>F	8.73	0.48	.032
Peak1 (Hz)	2654/91.3	3349/99.3	F>M	17.7	0.99	.008

B. Gecker usage

1. Age and sex

During the first two years of life, gecker bouts were emitted by infants from 1 to 17 months of age. Over this period, 75.7% of all gecker bouts occurred during the first 6 months of life (see Fig. 3). Gecker usage peaked at 4 months in both males, 26.5% ($X^2_{(6)}=51.7$, $p<0.001$), and females, 32.6% ($X^2_{(6)}=16.7$, $p<0.05$). However, the percentage of gecker bouts used in each month differed between the sexes ($X^2_{(11)}=25.1$, $p<0.01$), with male geckers tending to occur at younger ages. The greatest proportions of male gecker bouts occurred during months four (26.5%), two (16.2%), and one (14.7%), respectively. Females produced the most gecker bouts during months four (32.6%), two (14.0%), and 14 (14.0%), respectively.

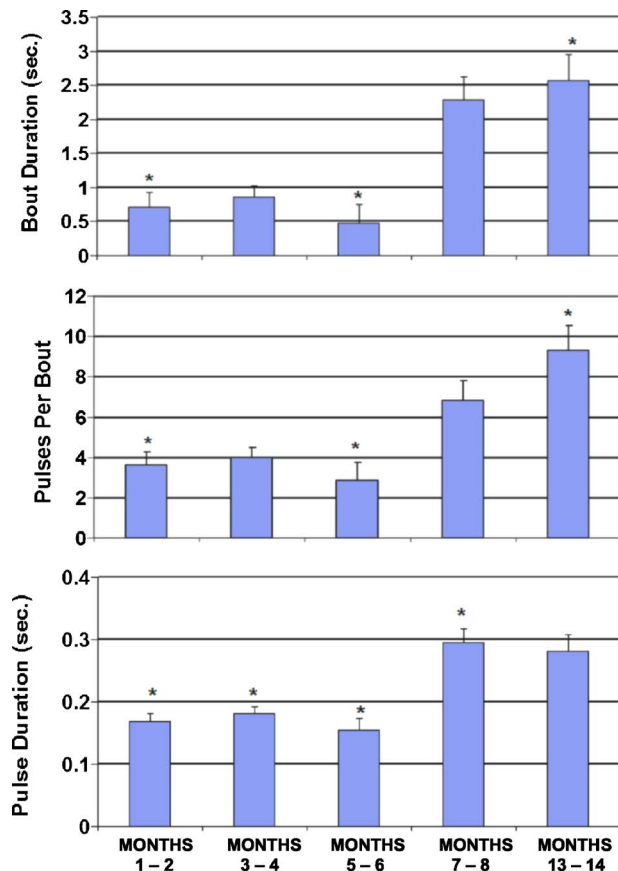


FIG. 3. (Color online) Bout duration (Bout-Dur), the number of pulses per bout (Pulse-Bout), and pulse duration (Pulse-Dur) are shown as a function of offspring age in 2 month blocks. Asterisks signify Tukey-Kramer posthoc tests in which at least one comparison to other outcomes shown in the panel was statistically significant.

2. Contexts

The behavior occurring immediately before or during a gecker bout was clear in all but four of the 111 total cases. Although none of the six categories of Before/During behavior could be considered predominant, relative proportions did show statistically significant heterogeneity ($X^2_{(5)}=26.7$, $p<0.001$). Inf-Follow (25.2%) was the most prevalent, followed by Aggr (22.3%) and Spon (22.3%), Mth-Leave (18.7%), and Affil (9.4%). Inf-Leave (1.9%) could also occur before or during a gecker bout, but was rare. Males and females were found to differ in the proportion of geckers emitted across these categories ($X^2_{(5)}=23.9$, $p<0.001$). Male geckers were most common in Affil (male: 15.4%, female: 0%) and Aggr (male: 27.7%, female: 14.3%) contexts, while female geckers were most common in the Inf-Follow context (male: 10.8%, female: 47.6%). Differences in the Inf-Leave, Mth-Leave, and Spon categories were all less than five percentage points. The influence of infant age on sex differences in Before/During gecker usage was examined in infants up to 6 months old, and results paralleled the overall pattern of sex differences ($X^2_{(5)}=22.0$, $p<0.001$). Males geckered most in the Affil (male: 17.0%, female: 0%) and Aggr (male: 28.3%, female: 14.3%) contexts, while females geckered most in the Inf-Follow (male: 5.44%, female: 10.3%) context. However, the male-female difference in the Inf-Follow context was less pronounced in these younger infants.

C. Acoustics and contexts

A cross-validated, multinomial discriminant-function analysis was conducted with Before/During as an independent variable to determine whether the acoustic measures considered collectively could be used to discriminate among the six contexts associated with geckering. Only 34.8% of the 107 available cases were successfully classified, which was nonetheless statistically significant, $F(52,343)=2.10$, $p<0.001$. Canonical discriminant analysis (Tabachnik and Fidell, 2001) revealed that the first canonical correlation ($r_c=0.59$) was significant, $F(52,343)=2.06$, $p<0.0001$, with Pulse-Redup (1.02), SNR (0.91), and Bout-Dur (-0.67) being the most influential in discriminating among the contexts.

A cross-validated, multinomial discriminant-function analysis was conducted with After as an independent variable to determine whether the acoustic measures considered collectively could be used to discriminate among the three outcome categories associated with geckers. Only 26.6% of the 111 cases were correctly classified, which was not a statistically significant proportion, $F(26,184)=0.94$, $p>0.55$.

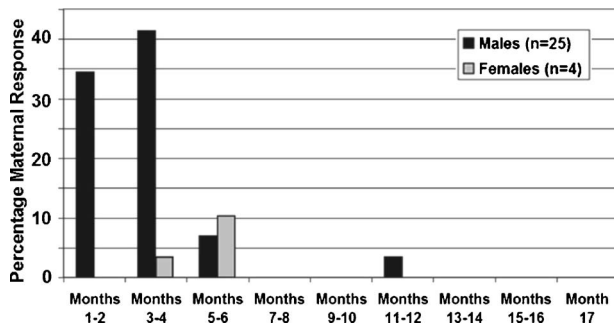


FIG. 4. Percentage occurrence of immediate maternal response by infant age block (mo.) to each gecker bout that received an immediate maternal response. Percentages shown sum to 100%, representing all instances that the mother showed an immediate response to her offspring's geckering (scored as Rsp, as described in TABLE III).

One-way ANOVA did reveal that the means of some acoustic measures differed as a function of the After context, including HNR, $F(2,104)=3.95$, $p<0.05$, Bout-Dur, $F(2,104)=3.91$, $p<0.05$, and Pulse-Dur, $F(2,104)=4.0$, $p<0.05$. Tukey posthoc tests demonstrated that the geckers with the longest Bout-Dur and Pulse-Dur values were associated with negative outcomes significantly more often than either positive outcomes or no outcomes. Geckers with higher HNR values were more often associated with positive outcomes than no outcome.

D. Responses to geckers

Immediate maternal response coding (Rsp/No-Rsp) was available for 76 geckering episodes, with mothers found to respond in only 38.2% of these cases, and doing so predominantly when the vocalizers were relatively young ($M=3.52$ mo). Although offspring as old as 17 months were still producing geckers, no responses were noted to individuals older than 12 months (see Fig. 4). A clear sex difference also emerged, with 47.2% of the gecker bouts emitted by males eliciting an immediate maternal response (25/53), compared to only 17.4% from females (4/23), $X^2_{(1)}=6.03$, $p<0.014$. Male geckers were also responded to ($M=3.32$ mo) earlier in life than females ($M=4.75$ mo), Mann-Whitney U , $z=2.44$, $p<0.02$.

Gecker usage did not deviate significantly from expected proportions across the three outcome categories scored for geckers ($X^2_{(2)}=2.65$, $p>0.25$). Furthermore, no sex difference was found in the outcomes experienced when examining offspring across the entire 24 months, $X^2_{(2)}=0.72$, $p>0.68$. However, significant differences were apparent for infants that were 7 months of age or older. Here, 50% of male bouts were ultimately associated with positive outcomes, but only 26.7% of female bouts. Conversely, 66.7% of female bouts but only 8.3% of male bouts ultimately resulted in negative outcomes, $X^2_{(2)}=10.2$, $p<0.01$.

Multivariate logistic regression analysis was used to identify independent acoustic predictors of maternal response as coded through Rsp/No-Rsp. Two subjects, female infant LN and male infant MS, contributed a disproportionately high number of bouts to this sample, 17 and 23 bouts, respectively. Using a random number generator, 15 bouts

from each were selected for analysis, which reduced the sample to 66 bouts from nine individuals (six males, three females), with equivalent numbers of male ($M=7.7$, $SD=6.68$, range 1–15) and female bouts ($M=7.0$, $SD=6.93$, range 3–15). All variables that achieved univariate statistical significance at the 0.2 level were entered into a forward stepwise model selection procedure for the multivariate logistic regression analysis. Two variables, HNR and Peak1, were determined to be statistically significant predictors of maternal response in a multivariate model. Like HNR, Peak1 can be interpreted as a measure of relative noisiness, as this LPC coefficient tends to co-vary with the overall slope of the LPC function. However, the measures were nonetheless largely independent. After adjusting for Peak1, the odds of a maternal response were 1.42 times greater for each unit increase in HNR (95% confidence interval 1.2–2.1). After adjusting for HNR, the odds of a maternal response were 3.3 times greater for each unit increase in Peak1 (95% confidence interval 1.2–9.1). Overall, the likelihood of a maternal response significantly increased for vocalizers with higher HNR and Peak1 values. The multivariate logistic regression model correctly predicted the presence or absence of maternal response in 80.3% of cases, although prediction accuracy was substantially higher for instances of no response (92.9%) compared to when a response did occur (58.3%).

IV. DISCUSSION

Acoustic analyses of rhesus monkey gecker vocalizations during the first 24 months of life revealed age, sex, and maternal response differences across several temporal, spectral, and amplitude measures, but little context-specific acoustic differentiation. Geckers of the youngest infants had the shortest bout durations, pulse durations, and fewest pulses per bout. Female geckers showed higher spectral peaks and bout durations, while male geckers were higher in amplitude and less noisy. Developmentally, gecker usage peaked at four months of age for both sexes, with male geckers nonetheless tending to occur at younger ages than those of females. More than 75% of gecker bouts were produced by infants 6 months of age or less, but offspring as old as 17 months could also gecker. Over 20% of gecker bouts appeared to be spontaneous, while the majority of these calls were emitted when the offspring were following their mothers, receiving aggression from their mothers, or had been left behind. Acoustic measures showed some statistical power in discriminant-function classification of calls according to six different behavioral contexts associated with geckering, but modestly so. The measures discriminating most among these contexts were bout duration, pulse reduplication, and signal-to-noise ratio. Mothers responded most, and most positively to the geckers of young infants, while also clearly favoring males. Maternal response was also more likely when geckers showed a pronounced spectral peak and less noisiness.

A. Acoustics

1. Structure and function

Acoustic analysis confirmed that geckers are composed solely of multiple short pulses. With just one reliable fre-

quency peak (at just below 3000 Hz), geckers can be considered “spectrally structured noise” (Beeman, 1998). The noisiness of gecker pulses was reflected in a virtually flat spectral slope (Spectral-Tilt), low tonality (HNR), and high spectral standard deviation (Spectral-StDev) relative to spectral mean (Spectral-Mean). While the absolute amplitude of geckers was not measured, they are likely among the loudest vocalizations produced by young rhesus. Their noisiness therefore almost certainly reflects chaotic vocal-fold vibration (e.g., Tokuda *et al.*, 2002) rather than simple airflow turbulence. The occasional occurrence of periodic components within this noise-based spectral structure is also consistent with interpreting the sounds as example of deterministic chaos (Wilden *et al.*, 1998). This kind of chaos is often a hallmark of elevated vocal effort, for example, occurring as subglottal air pressures and vocal-fold tensions increase during vocal production (Wilden *et al.*, 1998; Fitch *et al.*, 2002; Brown *et al.*, 2003; Riede *et al.*, 2004). The occurrence of pulse reduplications in 34% of all gecker bouts can thus be taken as an indicator of additional vocal-fold instability due to vocal effort, with these events being particularly prevalent in longer geckers with a large number of pulses.

This acoustic structure suggests that geckers are both salient and localizable to listeners. Several features, including their abrupt, high-amplitude pulses and broadband atonal spectra, likely make geckers particularly difficult to ignore as an auditory event (see Owren and Rendall, 1997, 2001). These same features also suggest that geckers should be easy to localize in both vertical and horizontal dimensions (Brown, 1982; Heffner, 2004; Recanzone and Beckermann, 2004). Moreover, auditory localization is facilitated when sounds are produced in conjunction with salient visual events (e.g., Heffner, 2004), such as the dramatic, spasmodic whole-body jerking that can accompany geckering. Geckers are thus well designed to serve as signals of distress, and communicative significance likely adds additional salience for species-specific listeners. However, these same perceptual features can contribute to these sounds becoming annoying as well, particularly with prolonged use (e.g., Todt, 1988). In humans, for instance, there is ample evidence both that infant distress vocalizations are aversive to caregivers, and that the sounds become significantly more noxious when produced in long bouts (Frodi and Senchak, 1990; Levitzky and Cooper, 2000; Soltis, 2004). Noisy, so-called “dysphonia” is also prominent among the features found to have the greatest negative impact in human infant cries (Wood and Gustafson, 2001; Gustafson and Green, 1989; Dessureau *et al.*, 1998), a phenomenon now shown to be chaotic vocal-fold vibration (Herzel, 1993).

2. Age and sex

Ontogenetic trends mainly involved producing longer pulses, longer bouts, and more pulses per bout. Consistent with previous work on primate vocal production, these changes likely reflect maturational and growth processes rather than vocal learning per se (Hammerschmidt *et al.*, 2000; Hammerschmidt *et al.*, 2002). Sex differences, such as

female gecker bouts lasting more than twice as long as those of males, were similar to outcomes reported for other distress calls in rhesus (Tomaszycki *et al.*, 2001; Erwin, 1975) and Japanese macaques (Green, 1981). The single characteristic spectral peak in geckers was also nearly 700 Hz higher in females than in males. Male geckers were somewhat less noisy (HNR), as well as being substantially higher in amplitude (SNR). These differences were apparent even after statistically controlling for body weight, suggesting that the critical factors may involve neuroanatomy, hormones, or vocal-fold size and shape, rather than body size and associated differences in vocal-tract length (Fitch, 1997).

Gonadal sex steroids are particularly likely to play a critical role, with Tomaszycki *et al.* (2001) finding that female rhesus up to 8 months emitted longer call bouts and used a greater variety of call types than did males of comparable age. However, when female fetuses were treated with androgen during the second trimester of gestation, the sex difference in later calling behavior was eliminated. The hormone treatment was likely to be operating via effects both on inferior temporal cortex (Newman and Bachevalier, 1997; Newman *et al.*, 1990) and on the vocal folds themselves (Aufdemorte *et al.*, 1983; Saez and Martin, 1976; Hollien *et al.*, 1994). Vocal-fold dimensions are largely unrelated to overall body size (Fitch, 1997; Rendall *et al.*, 2005), consistent with the current finding that sex differences in gecker acoustics persisted after statistically controlling for body size.

B. Usage

1. Age and sex

Although rhesus from 1 to 17 months of age emitted geckers, 75.7% of these calls occurred during the first 6 months of life. Geckering peaked at 4 months of age in both males and females, similar to results from Berman *et al.*'s (1994) more general study of rhesus distress calling. Ontogenetic peaks have also been found in other primate infant distress calls: stump-tail macaque “trilled whistles” at 8 weeks (Maestriperi *et al.*, 1995), vervet monkey “care-elicitation” calls at 8–10 weeks (Hauser, 1993), chimpanzee “crying” at 6–8 weeks (Bard, 2000), and human infant crying at 6 weeks (Barr, 1990).

The time course involved may reflect the changing quality of the mother-infant relationship, with both free-ranging and captive rhesus infants beginning to spend time away from their mothers at about 4 months of age (Berman, 1980). A mother's first postpartum estrus also occurs around the same point, potentially causing significant increases in separation, distress calling and infant tantrums (Berman *et al.*, 1994). Males both began and stopped geckering earlier than females (also see Green, 1981), consistent with Newman *et al.*'s (1990) finding that female rhesus vocalize more than males during social separation in the second half of their first year. Erwin (1975) has argued that this sex difference in rhesus vocalization rates is very general, extending to “every age other than the period when the females have reached puberty and the males have not” (p. 376).

2. Accompanying context

Gecker production was not associated with any single behavioral context, with most geckers occurring when an offspring received maternal aggression (22%), when there was a proximity change such as mother moving away (19%), or when the vocalizer was following its mother (25%). Spontaneous geckers (22%) were also common. This finding is compatible with Newman's (1995) argument that at least some geckers are artifacts of basic nervous-system development rather than having signaling function per se. In a similar vein, Blass (1994) argues that human infant crying may function to maintain ideal levels of brain activation during early development. Nonetheless, spontaneous geckers may also reflect distress with purely internal causes, or could be related to external circumstances that the observer cannot readily see. At present, this issue must be considered unresolved.

Male geckering was found to be significantly more likely in the context of experiencing either aggression or affiliative behavior than was female geckering. However, the most striking sex difference appeared for offspring following their mothers, a context that accounted for almost half of all gecker bouts in females, but only 11% in males. One interpretation of this discrepancy is that females are less independent of their mothers than are males, particularly in early infancy (Lindell *et al.*, 2003; Simpson *et al.*, 1986; although see Brown and Dixon, 2000). If so, females might also become more distressed and vocal when following an inattentive mother (Lovejoy and Wallen, 1988).

C. Acoustics and context

The contexts found to be associated with geckering are consistent with interpreting these sounds as "separation-rejection" vocalizations, but the lack of context-specificity suggests they are not differentiated signals of specific need. While gecker acoustics supported statistically significant discriminant-function classification according to preceding or co-occurring context, categorization success was only 35% correct overall. The upshot is that the degree of acoustic differentiation is unlikely to attain the "just noticeable difference" (*sensu* Nelson and Marler, 1990) necessary for conspecifics to reliably infer the context of calling from acoustics alone. Gecker variation appears more likely to reflect differences in vocalizer arousal, particularly as pulse reduplication, signal-to-noise ratio, and bout duration were the primary variables contributing to successful statistical classification. Each of these measures probably reflects overall vocal effort, with increasing arousal plausibly associated with higher subglottal air pressures, greater vocal-fold tension, and more prolonged calling. This interpretation is consistent with Bayart *et al.*'s (1990) compelling results with coo calls produced by rhesus infants being separated from their mothers. Both infant behavior and associated coo acoustics were differentially affected by the degree of isolation, with concomitant effects found on hormone levels, monoamine neurotransmitter measures, and behavioral arousal. Total isolation produced increases in each of these domains, and triggered coos that were longer, harmonically

richer, and more frequency modulated than those produced when mothers were visible to the infants in an adjacent cage.

D. Maternal response

Mothers showed an immediate response to only 38% of gecker bouts, and these reactions depended on a combination of gecker acoustics, offspring age, and whether the vocalizers were male or female. Mothers were most responsive to infants aged 4 months or less, and mothers were never observed to react to offspring older than 12 months. Maestripieri (1995) and Hauser (1993) have reported similar outcomes for stump-tailed macaques (*Macaca arctoides*) and vervet monkeys (*Cercopithecus aethiops*), respectively. Overall maternal responsiveness here was lower than in those studies, but probably because the current subjects were observed over a wider age range. Mothers were also more likely to react to male than to female geckers, and began to show responses earlier in the infant males' lives. Tomaszycski *et al.* (2001) similarly found that rhesus mothers responded more to males than to females across a variety of distress vocalizations, consistent with a general pattern of rhesus females showing somewhat greater parental investment toward sons than daughters (Bercovitch *et al.*, 2000).

Overall, the outcomes experienced by geckering infants were about equally likely to be positive or negative, and based again on discriminant-function analysis, gecker acoustics could not be used to predict the nature of the outcome, or whether there would be any discernible outcome. However, univariate analyses did show that geckers with longer bout and pulse durations tended to be associated with more negative outcomes such as aggression, while less noisy geckers were associated with more positive outcomes. An additional, striking difference was that for offspring 7 months or older, geckering was followed by aggression from mothers or other group members more than 50% of the time for females, but less than 10% of the time for males. Similarly, about half the gecker bouts from older male infants were associated with positive outcomes such as affiliation and attention, while the comparable figure for females was only about one-quarter.

These differences probably reflect a combination of factors, including the vocalizer's age and sex, as well as the potential aversiveness of geckers as auditory events. On the one hand, rhesus mothers could be less responsive to, but more negative toward females due to their higher calling rates, noisier geckers, and older ages when calling. Reinforcement learning has often been proposed as the mechanism by which rat pups (D'amato *et al.*, 2005), bird nestlings (Lotem, 1998; Stamps *et al.*, 1989), or rhesus monkey infants (Berman *et al.*, 1994) adjust their vocalizing towards optimal rates of effectiveness. Female rhesus infants may vocalize more often and intensively than males because mothers are rarely responding. Mothers may respond less to females because females are geckering excessively beyond the ages at which maternal response to geckers is crucial to offspring well being.

On the other hand, females may be more likely to exhibit these calling characteristics precisely because their mothers are less responsive and behave less positively to-

ward them. If the latter, mothers are behaving differently toward males and females for other reasons, and can in fact likely distinguish their respective geckers due to differences such as spectral peak frequencies. In addition, mothers were simply less likely to respond to calls from older individuals, which in most instances of which were females. Overall, then, while sex differences in both geckering and maternal responsiveness are apparent in these animals, the direction of causality involved between remains unclear.

V. CONCLUSIONS

Taken together, gecker vocalizations are likely to be highly salient and localizable to receivers. Gecker acoustics appear to be well designed to draw the attention of mothers and other listeners, while also potentially becoming aversive. These sounds become even more salient by virtue of regularly being accompanied by spasmodic jerking, occurring in lengthy bouts, and being associated with situations of evident vocalizer distress. While thus potentially being an effective distress cue, geckers are not highly specific to particular circumstances, and only infrequently elicit maternal response. The likelihood of maternal response was greatest when geckers exhibited pronounced spectral peaks and less noisiness (HNR).

Most gecker bouts were emitted within the first 6 months of life, with peak occurrence when infants were 4 months of age and mothers were experiencing their first postpartum estrus. After this age, maternal responsiveness diminished markedly. Male infants both began and stopped geckering earlier in life than females, and mothers responded more to their calls. Sex differences were also found in gecker acoustics, albeit based on an imperfectly balanced sample. Female vocalizations were characterized by longer durations and higher-frequency spectral peaks, while male geckers were generally less noisy (HNR) and higher in amplitude. Differences in neuroanatomy, hormones, and vocal-fold size and shape are all likely to contribute to these acoustic differences. Sex-biased maternal responsiveness is likely attributable to sex differences in gecker acoustics as well as the fact that females are emitting geckers at older ages than males.

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- Altmann, J. (1974). "Observational study of behavior: Sampling methods," *Behaviour* **49**, 227–265.
- Altmann, S. (1962). "A field study of the sociobiology of rhesus monkeys (*Macaca mulatta*)," *Ann. N.Y. Acad. Sci.* **102**, 338–435.
- Aufdemorte, T. B., Sheridan, P. J., and Holt, G. R. (1983). "Autoradiographic evidence of sex steroid receptors in laryngeal tissues of the baboon," *Laryngoscope* **93**, 1607–1611.
- Bard, K. A. (2000). "Crying in infant primates: Insights into the development of crying in chimpanzees," *In Crying As a Sign, a Symptom, & a Signal: Clinical Emotional and Developmental Aspects of Infant and Toddler Crying*, edited by R. G. Barr, B. Hopkins, and J. A. Green (Cambridge University Press, New York), pp. 157–175.
- Barr, R. G. (1990). "The normal crying curve: What do we really know?," *Dev. Med. Child Neurol.* **32**, 356–362.
- Bayart, F., Hayashi, K. T., Faull, K. F., Barchas, J. D., and Levine, S. (1990). "Influence of maternal proximity on behavioral and physiological responses to separation in infant rhesus monkeys (*Macaca mulatta*)," *Behav. Neurosci.* **104**, 98–107.
- Beeman, K. (1998). "Digital signal analysis, editing and synthesis," *In Animal Acoustic Communication: Sound Analysis and Research*, edited by S. L. Hopp, M. J. Owren, and C. S. Evans (Springer-Verlag, Berlin), pp. 59–104.
- Bercovitch, F. B., Widdig, A., and Nuernberg, P. (2000). "Maternal investment in rhesus macaques (*Macaca mullata*): Reproductive costs and consequences of raising sons," *Behav. Ecol. Sociobiol.* **48**, 1–11.
- Berman, C. M. (1980). "Mother infant interaction among free ranging rhesus monkeys: A comparison with captive pairs," *Anim. Behav.* **28**, 860–873.
- Berman, C. M., Rasmussen, K. R., and Suomi, S. J. (1994). "Responses of free ranging rhesus monkey infants to a natural form of social separation: Parallels with mother infant separation in captivity," *Child Dev.* **65**, 1028–1041.
- Blass, E. M. (2004). "Changing brain activation needs determine early crying: A hypothesis," *Behav. Brain Sci.* **27**, 460–461.
- Boersma, P. (1993). "Accurate short-term analysis of the fundamental frequency and the harmonics-to-noise ratio of a sampled sound," *Proc. Institut. Phonet. Sci. Amsterdam* **17**, 97–110.
- Boersma, P. (2001). "PRAAT, a system for doing phonetics by computer," *Glott Internat.* **5**, 341–345.
- Brown, C. H. (1982). "Auditory localization and primate vocal behavior," *In Primate Communication*, edited by C. T. Snowdon, C. H. Brown, and M. R. Peterson (Cambridge University Press, New York), pp. 144–164.
- Brown, C. H., Alipour, F., Berry, D. A., and Montequin, D. (2003). "Laryngeal biomechanics and vocal communication in the squirrel monkey (*Saimiri boliviensis*)," *J. Acoust. Soc. Am.* **113**, 2114–2126.
- Brown, G. R., and Dixon, A. F. (2000). "The development of behavioural sex differences in infant rhesus macaques (*Macaca mullata*)," *Primates* **41**, 63–77.
- D'amato, F. R., Scalera, E., Sarli, C., and Moles, A. (2005). "Pups call, mothers rush: Does maternal responsiveness affect the amount of ultrasonic vocalizations in mouse pups?," *Adv. Food Res.* **35**, 103–112.
- Dessureau, B. K., Kurowski, C. O., and Thompson, N. S. (1998). "A reassessment of the role of pitch and duration in adults' responses to infant crying," *Infant Behav. Dev.* **21**, 367–371.
- Erwin, J. (1975). "Rhesus monkey vocal sounds," *In The Rhesus Monkey, Vol. 1: Anatomy and Physiology*, edited by G. H. Bourne (Academic, New York), pp. 365–380.
- Fitch, W. T. (1997). "Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques," *J. Acoust. Soc. Am.* **102**, 1213–1222.
- Fitch, W. T., Neubauer, J., and Herzog, H. (2002). "Calls out of the chaos: The adaptive significance of nonlinear phenomena in mammalian vocal production," *Anim. Behav.* **63**, 407–418.
- Forrest, K., Weismer, G., Milenkovic, P., and Dougall, R. N. (1988). "Statistical analysis of word-initial obstruents: Preliminary data," *J. Acoust. Soc. Am.* **84**, 115–123.
- Frodi, A., and Senchak, M. (1990). "Verbal and behavioral responsiveness to the cries of atypical infants," *Child Dev.* **61**, 76–84.
- Gautier, J. P., and Gautier, A. (1977). "Communications in old world monkeys," *In How Animals Communicate*, edited by T. A. Sebeok (Indiana University Press, Bloomington), pp. 890–964.

- Green, S. M. (1981). "Sex differences and age gradations in vocalizations of Japanese and lion-tailed monkeys (*Macaca fuscata* and *Macaca silenus*)," *Am. Zool.* **21**, 165–183.
- Gustafson, G. E., and Green, J. A. (1989). "On the importance of fundamental-frequency and other acoustic features in cry perception and infant development," *Child Dev.* **60**, 772–780.
- Hammerschmidt, K., Newman, J. D., Champoux, M., and Suomi, S. J. (2000). "Changes in rhesus macaque 'coo' vocalizations during early development," *Ethology* **106**, 873–886.
- Hammerschmidt, K., Freudenstein, T., and Juergens, U. (2002). "Vocal development in squirrel monkeys," *Behaviour* **138**, 1179–1204.
- Hauser, M. D. (1993). "Do vervet monkey infants cry wolf?," *Anim. Behav.* **45**, 1242–1244.
- Heffner, R. S. (2004). "Primate hearing from a mammalian perspective," *Anat. Rec.* **218A**, 1111–1122.
- Herzel, H. (1993). "Bifurcation and chaos in voice signals," *Appl. Mech. Rev.* **46**, 399–413.
- Hoffman, R. A., and Stowell, R. E. (1973). "Outdoor housing of nonhuman primates," *Lab. Anim. Sci.* **23**, 74–83.
- Hollien, H., Green, R., and Massey, K. (1994). "Longitudinal research on adolescent voice change in males," *J. Acoust. Soc. Am.* **96**, 2646–2654.
- Jovanovic, T., and Gouzoules, H. (2001). "Effects of maternal restraint on the vocalizations of infant rhesus monkeys (*Macaca mulatta*)," *Am. J. Primatol.* **53**, 33–45.
- Kalin, N. H., Shelton, S. E., and Snowdon, C. T. (1992). "Affiliative vocalizations in infant rhesus macaques (*Macaca mulatta*)," *J. Comp. Psychol.* **106**, 254–261.
- Levitzy, S., and Cooper, R. (2000). "Infant colic syndrome—maternal fantasies of aggression and infanticide," *Clin. Pediatr. (Phila)* **39**, 395–400.
- Lindell, S. G., Shannon, C., Suomi, S. J., and Higley, J. D. (2003). "Sex differences in rhesus macaque mother-infant behavior," *Am. J. Primatol.* **60**, 130–131.
- Locke, J. L., and Hauser, M. D. (1999). "Sex and status effects on primate volubility: Clues to the origin of vocal languages?," *Evol. Hum. Behav.* **20**, 151–158.
- Lotem, A. (1998). "Differences in begging behaviour between barn swallow, *Hirundo rustica*, nestlings," *Anim. Behav.* **55**, 809–818.
- Lovejoy, J., and Wallen, K. (1988). "Sexually dimorphic behavior in group-housed rhesus monkeys (*Macaca mulatta*) at 1 year of age," *Psychobiol.* **16**(4), 348–356.
- Maestriperi, D. (1995). "Maternal responsiveness to infant distress calls in the stump-tail macaque," *Folia Primatol.* **64**, 201–206.
- Maestriperi, D., and Call, J. (1996). "Mother-infant communication in primates," *Adv. Stud. Behav.* **25**, 613–642.
- Maestriperi, D., Jovanovic, T., and Gouzoules, H. (2000). "Crying and infant abuse in rhesus monkeys," *Child Dev.* **71**, 301–309.
- Nelson, D. A., and Marler, P. (1990). "The perception of birdsong and an ecological concept of signal space," in *Comparative Perception, Vol. 2, Complex Signals*, edited by W. D. Stebbins and M. A. Berkley (Wiley, New York), pp. 443–478.
- Newman, J. D. (1995). "Vocal ontogeny in macaques and marmosets: Convergent and divergent lines of development," in *Current Topics in Primate Vocal Communication*, edited by E. Zimmermann, U. Juergens, and D. Symmes (Plenum, New York), pp. 73–97.
- Newman, J. D., and Bachevalier, J. (1997). "Neonatal ablations of the amygdala and inferior temporal cortex alter the vocal response to social separation in rhesus macaques," *Brain Res.* **758**, 180–186.
- Newman, J. D., Bachevalier, J., Michjeda, M., and Suomi, S. J. (1990). "A possible neural substrate for gender differences in vocal behavior by rhesus macaque infants during brief periods of social separation," *Soc. Neuro. Abstr.* **16**, 599.
- Owren, M. J., and Bernacki, R. H. (1998). "Applying linear predictive coding (LPC) to frequency-spectrum analysis of animal acoustic signals," in *Animal Acoustic Communication: Sound Analysis and Research*, edited by S. L. Hopp, M. J. Owren, and C. S. Evans (Springer-Verlag, Berlin), pp. 129–161.
- Owren, M. J., and Dieter, J. A. (1989). "Infant cross-fostering between Japanese (*Macaca fuscata*) and rhesus macaques (*M. mulatta*)," *Am. J. Primatol.* **18**, 245–250.
- Owren, M. J., Dieter, J. A., Seyfarth, R. M., and Cheney, D. L. (1992a). "Food' calls produced by adult female rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques, their normally-raised offspring, and offspring cross-fostered between species," *Behaviour* **120**, 218–231.
- Owren, M. J., Dieter, J. A., Seyfarth, R. M., and Cheney, D. L. (1992b). "Evidence of limited modification in the vocalizations of cross-fostered rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques," in *Topics in Primatology, Vol. 1: Human Origins*, edited by T. Nishida, W. C. McGrew, P. Marler, M. Pickford, and F. de Waal (University of Tokyo Press, Tokyo), pp. 257–270.
- Owren, M. J., Dieter, J. A., Seyfarth, R. M., and Cheney, D. L. (1993). "Vocalizations of rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques cross-fostered between species show evidence of only limited modification," *Dev. Psychobiol.* **26**, 389–406.
- Owren, M. J., and Rendall, D. (1997). "An affect-conditioning model of nonhuman primate vocal signaling," in *Perspectives in Ethology: Vol. 12. Communication*, edited by D. H. Owings, M. D. Beecher, and N. S. Thompson (Plenum, New York), pp. 299–346.
- Owren, M. J., and Rendall, D. (2001). "Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling," *Evol. Anthro.* **10**, 58–71.
- Recanzone, G. H., and Beckermann, N. S. (2004). "Effects of intensity and location on sound location discrimination in macaque monkeys," *Hear. Res.* **198**, 116–124.
- Rendall, D., Kollias, S., Ney, C., and Lloyd, P. (2005). "Pitch (F₀) and formant profiles of human vowels and vowel-like baboon grunts: The role of vocalizer body size and voice-acoustic allometry," *J. Acoust. Soc. Am.* **117**, 944–955.
- Riede, T. R., Owren, M. J., and Clark Arcadi, A. (2004). "Nonlinear acoustics in the pant-hoot vocalizations of common chimpanzees (*Pan troglodytes*): Frequency jumps, subharmonics, biphonation, and deterministic chaos," *Am. J. Primatol.* **64**, 277–291.
- Rowell, T. E. (1962). "Agonistic noises of the rhesus monkey (*Macaca mulatta*)," *Sym. Zool. Soc. London* **8**, 91–96.
- Rowell, T. E., and Hinde, R. A. (1962). "Vocal communication by the rhesus monkey (*Macaca mulatta*)," *Proc. R. Soc. London* **138**, 279–294.
- Saez, S. J., and Martin, P. M. (1976). "Androgen receptors in human pharyngo-laryngeal mucosa and pharyngo-laryngeal epithelium," *J. Steroid Biochem.* **7**, 919–921.
- Seyfarth, R. M., and Cheney, D. L. (1986). "Vocal development in vervet monkeys," *Anim. Behav.* **34**, 1640–1658.
- Simpson, M. J. A., Simpson, A. E., and Howe, S. (1986). "Changes in the rhesus mother-infant relationship through the first four months of life," *Anim. Behav.* **34**, 1528–1539.
- Snowdon, C. T., Elowson, A. M., and Roush, R. S. (1997). "Social influences on vocal development in New World primates," in *Social Influences on Vocal Development*, edited by C. T. Snowdon and M. Hausberger (Cambridge University Press, New York), pp. 234–248.
- Soltis, J. (2004). "The signal functions of early infant crying," *Behav. Brain Sci.* **27**, 443–490.
- Stamps, J., Clark, A., Arrowood, P., and Kus, B. (1989). "Begging behavior in budgerigars," *Ethology* **81**, 177–192.
- Tabachnik, B. G., and Fidell, L. S. (2001). *Using Multivariate Statistics*, 4th ed. (Allyn and Bacon, New York).
- Todt, D. (1988). "Serial calling as a mediator of interaction processes: Crying in primates," in *Primate Vocal Communication*, edited by D. Todt, P. Goedeking, and D. Symmes (Springer-Verlag, Berlin), pp. 88–107.
- Tokuda, I., Riede, T., Neubauer, J., Owren, M. J., and Herzel, H. (2002). "Nonlinear prediction of irregular animal vocalizations," *J. Acoust. Soc. Am.* **111**, 2908–2919.
- Tomaszycycki, M. L., Davis, J. E., Gouzoules, H., and Wallen, K. (2001). "Sex differences in infant rhesus macaque separation-rejection vocalizations and effects of prenatal androgens," *Horm. Behav.* **39**, 267–276.
- Wallen, K. (2005). "Hormonal influences on sexually differentiated behavior in nonhuman primates," *Front Neuroendocrinol.* **26**, 7–26.
- Wilden, I., Herzel, H., Peters, G., and Tembrock, G. (1998). "Subharmonics, biphonation, and deterministic chaos in mammal vocalization," *Bioacoustics* **9**, 171–196.
- Wood, R. M., and Gustafson, G. E. (2001). "Infant crying and adults' anticipated caregiving responses: Acoustic and contextual influences," *Child Dev.* **72**, 1287–1300.