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RESEARCH ARTICLE

The Vocal Repertoire of Adult Male Blue Monkeys (*Cercopithecus mitis stulmanni*): A Quantitative Analysis of Acoustic Structure

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Vocal signals are key elements in understanding species' behavior, sociality, and evolution. Quantified repertoires serve as foundations for investigating usage and function of particular signals, and also provide a basis for comparative analyses among individuals, populations, and taxa to explore how entire signal systems evolve. This study presents a descriptive catalogue of all vocal signals used by adult male blue monkeys (*Cercopithecus mitis stuhlmanni*). During 12 months in the Kakamega Forest, Kenya, I observed and digitally recorded vocal behavior of 32 adult males across a variety of socioecological contexts. From recordings, I measured 18 temporal-frequency parameters. Undirected ordination and hierarchical cluster analysis identified six distinct call types regularly used by males: *ant*, *boom*, *ka*, *katrain*, *nasal scream*, and *pyow*. Cross-validated discriminant function analysis supported the classifications. The repertoire is best described as discrete, though some gradation occurs between *pyows* and *ants*. Summary of acoustic structure and exemplar spectrograms are provided for each call type, along with preliminary examination of socioecological contexts in which they were produced. Discussion addresses repertoire structure, similarity to other taxa, and potential for functional inferences. Am. J. Primatol. 9999:1–14, 2013.

Key words: blue monkeys; *Cercopithecus mitis*; communication; repertoire; vocal behavior

INTRODUCTION

It has been asserted that systematic ethography should serve as both "foundation and starting point of behavioral research" [de Waal, 1988]. In communication studies, signal repertoires are such a starting point, and serve as critical foundations for investigating proximate and ultimate explanations for individual signals, as well as exploring how entire signal systems evolve. Quantified signal catalogues provide the basis for comparative analyses among individuals, populations, and taxa, as well as data for examining specific selection factors [Maynard Smith & Harper, 2003], phylogenetic hypotheses [e.g. Gautier, 1988], and the evolution of signal systems [e.g. Gustison et al., 2012; McComb & Semple, 2005]. Repertoires also establish common referents and terminology for researchers, helping to standardize observations and avoid confusion among studies.

Cataloguing vocal signals traditionally relied on human observers' aural and visual (via spectrographs) assessment of acoustic differences among vocalizations. As a classification method, however, qualitative assessment risks categories that reflect differences humans perceive and assume biologically meaningful, yet possibly disregard differences salient to the species [Green, 1975]. Though challenges remain, advances in acoustic technology and analytic approaches have greatly increased the precision and objectivity of establishing signal ethograms. Undirected, multivariate ordination (e.g. cluster analyses), for example, allows distinct structures (i.e. call types) to reveal themselves, with post hoc validation (e.g. discriminant function analysis [DFA]) providing objective assessment of the appropriateness of types [e.g. Boisseau, 2005; Melendez et al., 2006; Range & Fischer, 2004].

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Here, I present the first comprehensive vocal repertoire of adult male blue monkeys (*Cercopithecus mitis stuhlmanni*), an arboreal guenon found across central, eastern, and southern Africa. Blue monkey social groups comprise several adult females, their offspring, and typically one adult male (hereafter: resident male). Females are philopatric and territorial [Cords, 2002a, 2007], whereas males leave natal groups at around seven years old [Ekernas & Cords, 2007] and live alone or in loose associations with other "bachelors" (hereafter: non-resident males). Resident males are typically aggressive toward other males, and blue monkey social structure is aptly characterized as unimale; in ~25% of group years, however, multiple males occupy a group for extended periods during the July–September mating season and, during such multimale influxes, females may mate with all present males (hereafter: influx males) [Cords, 2000, 2002b]. Some non-resident and influx males eventually become a group's sole resident male by expelling the prior resident or moving in after his disappearance. After takeovers, new males may kill infants ≤9-month-old, with infanticide accounting for ≥17% of infant mortality [Cords & Fuller, 2010].

Only a handful of researchers have examined blue monkey vocal behavior, most notably Marler [1973], Brown [1989], Brown & Waser [1984], and Butynski et al. [1992]. These studies, along with recent work by Papworth et al. [2008] and Murphy et al. [2013], each contribute to understanding the species' vocal behavior. The absence of a comprehensive, objectively derived repertoire, however, constrains interpretation of different studies' named "call types," and precludes robust comparative studies among populations and taxa.

Some blue monkey vocal signals have been described based on subjective assessment of distinctiveness. Adult females and juveniles of both sexes use signals that include *chirps*, *trills*, and *grunts* [Marler, 1973], as well as *growls*, *screams*, staccato *geckers*, and low tone *long grunts*; infant calls, typically quieter and more variable than most by older individuals, include *trills*, *geckers*, and tonal *girns* [Cords, pers. comm., unpublished data]. Adult males' vocal signals appear to be completely distinct from those of other age–sex classes, being considerably louder, lower frequency, and less common, and emerge quite suddenly at maturity (a pattern observed in other *Cercopithecus* species [Gautier, 1971]). Calls described for adult males include the *boom*, *pyow*, and *ka* or *katrain* [Marler, 1973], with observations of other possible calls including *ants* and *nasal screams* [Cords, pers. comm.].

This paper presents a quantified catalogue of all vocal signals used by adult male blue monkeys in the Kakamega Forest, Kenya. I used recordings and behavioral data from >12 months of continuous fieldwork to establish a detailed repertoire. Emphasis here is on acoustic structure, though I also provide general characterizations of social and ecological contexts in which calls occurred; functional hypotheses are addressed in forthcoming papers.

METHODS

This study adhered to the American Society of Primatologists' principles for the ethical treatment of primates. Fieldwork protocols were approved by the Columbia University Institutional Animal Care and Use Committee and by the Kenyan government's National Council on Science and Technology.

Study Site and Subjects

Fieldwork took place from September 2010 to September 2011 in the Kakamega Forest, a semi-deciduous rain forest in western Kenya (0° 16′ N, 34° 52′ E; elevation 1,580 m; for detailed site description, see Cords [2012]). The area supports a relatively dense population of blue monkeys (*C. m. stuhlmanni*), approximately 192 individuals per km^2 [Fashing et al., 2012], and is home to five other primate species: *Cercopithecus ascanius*, *Cercopithecus neglectus*, *Colobus guereza*, *Papio anubis*, and *Perodicticus potto*. Natural predators of blue monkeys, including crowned hawk eagles (*Stephanoaetus coronatus* [Struhsaker & Leakey, 1990]) and Gaboon vipers (*Bitis gabonica* [Foerster, 2008]) occur in Kakamega, though leopards (*Panthera pardus*) have not been reported in the area in >10 years; humans, often with dogs, also sometimes hunt monkeys here.

Data came from >5500 hr of direct observation of 32 adult males, including resident and influx males of 11 groups, and non-residents from the surrounding area. Subjects were individually known and habituated to observers from long-term research in this population [Cords, 2012]. I considered males adults if older than 7 years (mean age of natal group dispersal [Ekernas & Cords, 2007]); when age was unknown, body size, descended testes, and elongated canines differentiated adults and sub-adults.

Recordings and Acoustic Analyses

I recorded vocalizations with a Marantz PMD-660 digital recorder, at a 44.1-kHz (16 bits) sampling rate, using a Sennheiser ME67 directional microphone with windscreen. Recording took place during systematic 3-hr focal samples between 0700–1800 hr, and opportunistically throughout the study. Distance to callers varied from ~3 to 80 m. Prior to analyses, I excluded recordings of poor quality and those from unidentified callers.

I used Raven Pro 1.4 [Cornell Laboratory of Ornithology, Ithaca, NY] to perform discrete Fourier transform (Hann window function, 1,024-pt DFT, 20 ms window size, 46.9 Hz resolution) on recordings. I used the resulting spectrograms, power-time

oscillograms, and power-frequency spectra in a visualizing window of 0.5 sec and frequency range of 0–3,000 Hz to measure samples. Temporal and frequency limits of calls were determined using power-time oscillograms (waveform) and power-frequency spectra to identify energy above ambient noise. To avoid conflating echo with source, I identified ends of calls by the terminus of the fundamental frequency band (F0) in spectrograms and the emergence of a repeating oscillation pattern in waveforms. The first three dominant frequency bands (F0, DF1, and DF2) were identified by consistent energy peaks in consecutive frequency bins.

For each call sample, except those comprising a sequence of linked, rapidly pulsed units (identified as *katrains*, below), I measured 18 acoustic parameters. The first six, addressing frequency/amplitude features of the total call, were the center frequency (Cent_tot; the discrete frequency that divided all energy within the total call into two intervals of equal energy), maximum frequency (Max_tot; the frequency at which maximum power occurred in call), the start, middle, and end frequencies (Start-, Mid-, and End_tot; max frequency during first, middle, and last 25% of call), and the rise time (Rise_tot; interval from call's start to time at which maximum power/amplitude first occurred).

The next nine parameters addressed only the fundamental frequency band (F0), and measured its duration (Dur_F0), lower and upper frequency limits (Hi- and Lo_F0), and the start, middle, and end frequencies (Start-, Mid-, and End_F0). I calculated three slopes (i.e. rate of frequency change), including the F0's total slope (Slope_F0; end frequency minus start frequency divided by duration), and similarly slopes of the first and second halves of the F0 (Slope1_F0; Slope2_F0).

Three parameters calculated formant dispersion (i.e. distance between bands) among the first three dominant frequency bands. I selected 3–7 time points (median: 4) across the call in which F0, DF1, and DF2 could be clearly identified. At each point, I subtracted the maximum frequency of F0 from that of DF1 and subtracted the maximum frequency of DF1 from that of DF2. From these values, I derived mean formant dispersion of DF1-F0, of DF2-DF1, and of the entire call (Frmt_Disp_1, _2, and _$\bar{x}$). Formant parameters were not measured for calls identified as *booms*, which had no bands above the F0.

For *katrains*, the only male vocalization comprising linked units or "syllables" (see Results), I measured the six total call parameters as for other calls. I also counted the number of temporally discrete units and the average inter-unit interval (between start of unit and end of previous unit). As *katrains* contained multiple distinct structures, I chose three units (second, middle, and second to last) from each *katrain* as samples for analyses; for these "*kas*-within-*katrains*," I measured the F0 and formant dispersion as for other calls. The Results provide summary description of the *katrain* units as well as the total call.

Vocal Behavior

Every day of the study, 4–14 trained observers were distributed among different males and social groups. At least 21 days per month, observers followed 3–4 males continuously from about 0730 until 1730 hr, while others followed group females; observations typically suspended for 1 hr around 1300 hr.

Vocal behavior data were recorded on an all occurrence basis [Altmann, 1974]. Whenever any male vocalized, observers recorded his identity, location, and call type(s) used, and also context, including conspicuous social and ecological factors (e.g. other male near, predator) and activity of caller and nearby conspecifics just before and after call. When appropriate, combined data from several observers' provided more complete context assessment.

To characterize vocal behavior, I used the nested categories Call, a single, discrete utterance (e.g. one *pyow*), Bout, a sequence of only one call type with $\leq$1-min between calls (e.g. four *pyows*), and Episode, any vocal occurrence by a male, including all calls by him with $\leq$1-min between calls. Most episodes comprised one call type, given singly or in bouts, but combinations (e.g. a *boom* followed by *pyows*) were not uncommon.

Guided by extensive field observations, I coded episodes to broad social/ecological categories, including agonistic encounters with males, presence of other conspecific group, presence of terrestrial threats (e.g. snakes, dogs) or aerial threats (raptors), affiliative interactions with females (e.g. approach, groom), and falling tree or branch. Another category described undisturbed contexts—episodes in which there was no other male or group observed, no indication of predators, and no clear social or ecological disturbance, and caller and conspecifics were generally resting and feeding before and after episode.

For each call type, I calculated hourly usage rates for each male (number of episodes that included a particular call type divided by his hours observed). Using records for which context was unambiguous, I also calculated the proportion of each call's occurrence in different contexts (e.g. *katrains* associated with aerial threats). As this study's focus is acoustic structure, I characterized usage qualitatively; forthcoming articles assess signal function and content quantitatively.

Statistical Analyses

Prior to statistical analyses, I labeled each recording sample based on aural consistency with

one of six putative call types: *ant*, *boom*, *ka*, *katrain*, *nasal scream*, or *pyow*; samples identified as "other" constituted <0.2% of male vocal behavior during the study and were excluded from analyses, but described in Results. Analyses used R version 2.1 [R Development Core Team, 2008]; tests were 2-tailed using $\alpha = 0.05$ unless otherwise specified.

Principal components, cluster, and discriminant function analyses

I conducted ordination and cluster analysis with all recording samples to examine acoustic similarity among samples, using a priori call categories to guide interpretation of observed patterns. Principal components analysis (PCA) identifies linear combinations of variables (principal components; PCs) that maximally account for the variability in a data set, reducing the total parameters to a subset of uncorrelated combinations [Joliffe, 2002]. Because large value differences among variables can exaggerate variability and compromise the explanatory value of PCA, I used scaled unit variance for parameters.

To characterize grouping of and distance between samples, I performed agglomerative hierarchical (i.e. connectivity-based) cluster analysis with the PC scores of all samples. I first calculated dissimilarity between samples using a Euclidean distance matrix, and then used Ward's linkage [Ward, 1963] to group samples according to similarity of PC scores.

To assess the appropriateness of a priori categories and examine differences among types, I used DFA, which identifies linear combinations of predictor variables (linear discriminant functions; LDs) that best distinguish among preset groups [Klecka, 1980]. Because an unbalanced data set can influence DFA adversely, I randomly selected equal numbers of samples of each call type from each male. To control for colinearity among acoustic variables, I used each sample's PC scores in the DFA.

To validate the call type classifications, I used a forward stepwise linear discriminant procedure to construct LDs. To cross-validate resultant LDs (i.e. determine the degree to which samples could be "correctly" assigned), I used the *leave-one-out* classification, using all samples except the one being classified, to assign samples to call types.

RESULTS

Observers logged >5,500 direct observation hours with 32 different males in each social status, with the majority of recordings and observation hours from resident males (Table I). From >450 recording hours, I extracted 1,171 samples of calls by ≥27 males, reduced to 772 calls by 20 males after excluding recordings of low quality or from unidentified callers. The number of recordings of each call type differed and different individuals contributed different numbers of call samples (Table II).

Analysis of recordings ($N = 772$ call samples) and field observations ($N = 6{,}490$ episodes) identified six distinct call types used by adult male blue monkeys: *boom*, *pyow*, *ant*, *ka*, *katrain*, and *nasal scream*. Three other vocalizations collectively constituted <0.2% of observed male vocal behavior: *grunts*, *geckers*, and *eerns*. Males in resident ($N = 17$) or influx ($N = 10$) status regularly produced each of the six primary call types. Males in non-resident status ($N = 16$), including males that had been or later became residents ($N = 3$) or influx males ($N = 9$), were never observed to use any call except the *nasal scream*, even in contexts in which residents typically called (e.g. predator events, presence of other males).

Principal Components Analysis

The first three principal components (PC1-PC3) explained 82% of the sample variance (Table III), with PC4-PC5 capturing another 8%. Factor loadings indicate PC1 was heavily influenced by many variables, but primarily formant dispersion and various frequency peaks. PC2 was driven by variation in calls' rise (i.e. time to peak amplitude) and duration of F0. PC3 was dominated by frequency peaks of the total call as well as slopes of the F0.

Plotting samples in principal component space revealed patterns consistent with a priori call type categories, but that acoustic separation among types is not equal (Fig. 1). PC1 and PC2 easily segregated

TABLE I. Observation Hours and Number of Vocal Episodes Observed and Recorded for Male Subjects ($N = 32$) in Each Social Status

Status	Subjects observed[a]	Hours observed, total (per subject mean) (per subject range)	Vocal episodes observed, total (per subject mean) (per subject range)	Vocal episodes audio recorded, total (per subject mean) (per subject range)
Resident	17	4294.3 (613.5) (20.7–939.6)	5,589 (328.8) (6–1231)	537 (31.6) (0–117)
Influx	10	906.3 (129.5) (23.3–381.9)	901 (90) (3–389)	73 (7.3) (0–21)
Non-resident	16	350.6[b] (21.9) (7.8–48.8)	0	0

[a]Seven males occupied multiple statuses during the study period.
[b]This reported observation time for non-residents is extremely conservative, reflecting only times reported for the last 6 months of the study; non-residents were observed throughout the entire study period, but observation times were not systematically recorded in the first 6 months.

TABLE II. Sample Size of Analyzed Recordings of Calls From Different Males

Call Type	Recording samples	Number of males	Samples per male
Ant	66	9	3–10
Boom	211	16	4–29
Ka	28	7	2–6
Katrain	39	8	2–9
Nasal Scream	11	4	1–5
Pyow	417	19	8–62

three distinct clusters, with *booms* and *nasal screams* each separate from others and *ants*, *pyows*, *kas*, and *katrain* units agglomerated in a wide cloud. Adding PC3 shows that all calls cluster distinctly, though *pyows* and *ants* overlap somewhat; the near total overlap of *kas* and *katrain*-units indicates acoustic affinity close to equivalency (though *katrains* are unmistakably distinguished by their multi-unit structure).

Hierarchical Cluster Analysis

Cluster analysis results (Fig. 2) were consistent with the above patterns. Samples clustered distinctly by putative call type, with *kas* and *ka-train* units clustering together, and some overlap between *ants* and *pyows*. The *booms* cluster was the most segregated, with a linkage distance more than double that of any other nearest join (that of *nasal screams*) and nine times that of the average join distance of samples excluding *booms*. Average branch length within clusters, reflecting acoustic variation within call types, was longest for *nasal screams*—nearly 15 times that of *booms*, which had the shortest.

Discriminant Function Analysis

The discriminant functions classified 85% of call samples ($N = 84$) to their named call type (cross validation = 83.4%), better than the 16.7% expected by random chance (binomial test, $P < 0.001$), indicating that the acoustic variables used are sufficient to differentiate calls and that a priori call types are appropriate. Correct classification was 100% for *booms* and *nasal screams*, 96% for *pyows*, and 88% for *ants*. Correct classification was lower for *katrain*-units (68%) and *kas* (60%), yet all *kas* and *katrain*-units were classified as either *kas* or *katrain*-units, highlighting their acoustic similarity. The first three linear discriminant functions (LD) collectively explained 91% of the variance among call types (LD1: 44%; LD2: 33%; LD3: 14%). LD1 was primarily explained by calls' rise and LD2 correlated most strongly with rise and duration of the F0.

All call types were distinguished in DFA and clustered distinctly in PCA (Fig. 1); *ants* and *kas*, however, appeared the most structurally similar (Fig. 3). To identify acoustic variables that differed between *ants* and *kas*, I compared these two call types on each of the 18 parameters. With the Bonferroni adjustment ($\alpha = 0.0028$), eight acoustic variables differed (Mann–Whitney U-test: $U = 81.5$–909.5, $P < 0.0000$–0.91): Cent_tot, Max_tot, Strt_tot, Mid_tot, Lo_F0, End_F0, Slope_F0, and Slope1_F0.

Call Types

The following provides summary description of each signal in the adult male vocal repertoire. Table IV summarizes call types in terms of the acoustic parameters used in analyses. To avoid unequal sampling giving some males' greater influence on characterization of some call types, I followed Gros-Louis et al. [2008] and derived mean values for variables for each call type for each male and then summarized call types using the pooled sample of males. Exemplar spectrograms are provided in Figures 3 and 4.

Boom

An extremely low frequency, tonal call, sounding somewhat dampened to human ears. Though *booms*

TABLE III. Proportion of Variance Contained in First Four Principal Components, With Acoustic Variables Ranked by Factor Loadings

	PC1		PC2		PC3		PC4	
Proportion of variance explained	0.466		0.232		0.119		0.046	
(cumulative)	(0.466)		(0.698)		(0.817)		(0.863)	
Loading variables	Frmt_Disp_$\bar{x}$	9%	Rise_tot	19%	Max_tot	15%	Range_F0	42%
	Frmt_Disp_2	9%	Dur_F0	19%	Cent_tot	14%	Hi_F0	16%
	Hi_F0	9%	End_F0	13%	Mid_tot	14%	Lo_F0	12%
	Start_F0	9%	Mid_F0	10%	Start_tot	12%		
	Cent_tot	8%	Slope_F0	10%	Slope1_F0	11%		
	Max_tot	7%	Lo__F0	9%	Slope_F0	8%		
	Range_F0	7%	Slope1_F0	8%	Start_F0	7%		
	Mid_tot	7%	Slope2_F0	8%				
	Start_tot	7%						

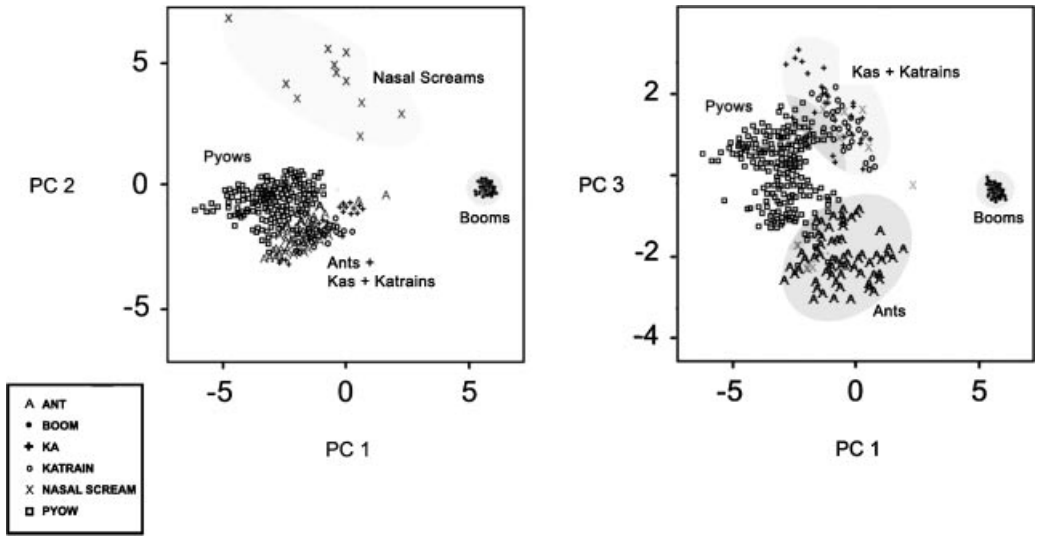

Fig. 1. Recording samples ($N = 772$) plotted in principal component space. Symbols and cluster labels refer to putative call types assigned a priori to samples. PC1 and PC2 (left) account for 70% of variance and easily segregate *booms* and *nasal screams* from a cluster containing the other call types. Plotting on PC1 and PC3 (right) (59% of variance) shows the distinctiveness of *pyows*, *ants*, and the combined cluster of *kas* and *katrain* units.

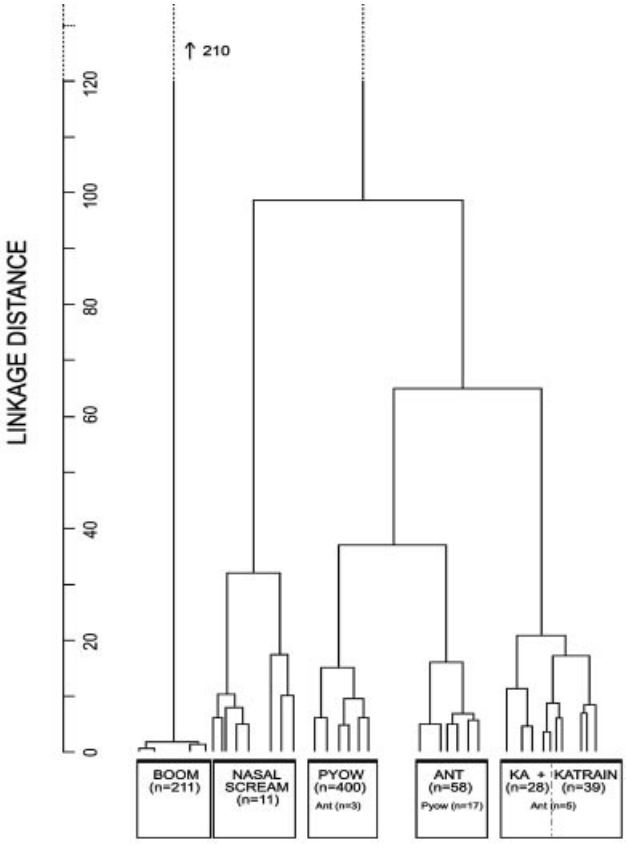

Fig. 2. Dendrogram from hierarchical cluster analysis using samples' ($N = 772$) PC scores. Between-cluster distance (vertical lines) for *booms* was twice other distances, so its linkage is not shown. Nodes below 5.0 (except *booms*) are contracted into a single node. Clusters are labeled by a priori call types ($n =$ number of samples contained below the join).

may be audible to other blue monkeys up to 1,000 m [Brown, 1989], human observers have difficulty hearing them sometimes even as close as 40 m. *Booms* undoubtedly depend on the supralaryngeal air sac, as in other *Cercopithecus* species (e.g. *C. neglectus* [Gautier, 1971]). *Booms* were typically given alone, though episodes in which a *boom* was followed by *pyows* were frequent enough to suggest a possible pattern. Males nearly always produced a single *boom* in an episode, though one subject often "double *boomed*," giving a second ~15 sec after a first.

Booms were the most common call, with most resident males typically producing about three *booms* per all day observation (~8 hr). Observations indicate *booms* relate to interactions between callers and nearby females, though the long audible distance suggests possible extra-group functions as well. In *boom* observations in which context was clearly known ($N = 1{,}255$), 52% were cases in which, with no aggression, a male approached or was approached by group females, then *boomed*, and then was groomed or co-fed; nearly half of these occurred in non-disturbance contexts, with others during encounters with other groups or after predator events. In approach contexts, adult females typically produced *long grunts* (low frequency calls used only around adult males; syn: *croak* [Tsingalia & Rowell, 1984]) prior to the male's *boom*. The next most common context (9%), notably different from the previous, was branches falling nearby; though deemed disturbance, these cases did not relate to any substantive threat to callers or group members. Other contexts included snakes, inter-group aggression, and unknown contexts that included intense arousal behavior by members of callers' groups.

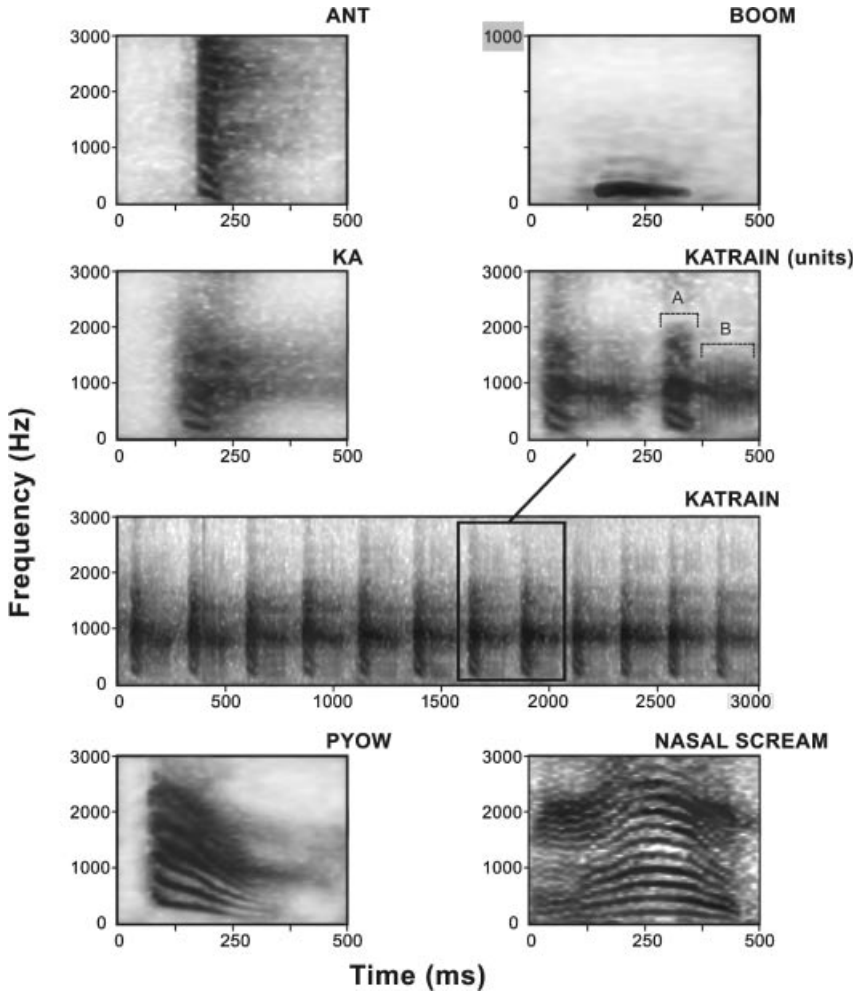

Fig. 3. Exemplar spectrograms of the six call types of adult male blue monkeys at Kakamega. For the mult-unit *katrain*, spectrograms depict an entire call and also two units within the call, with marks indicating one unit (A) and the inter-unit *urr* syllable (B).

Pyow

A loud, tonal call with a relatively slower onset than other types and a characteristic "descending" sound resulting from its long duration and negative slope. Brown [1989] calculated *pyows* are likely audible to other blue monkeys >1,000 m away; human observers can typically perceive *pyows* and reliably approximate caller location from up to 400 m. *Pyows* vary significantly among individuals [Butynski et al., 1992], with experienced observers able to distinguish some males by the sound of *pyows*. Bouts of 3–4 were typical (range: 1–16), with *pyows* separated by ~10–15 sec; the intercall interval of the last *pyow* in a bout was typically longer than preceding ones. *Pyows* were most often given alone, but *pyows* in combination with *ants*, *booms*, or *katrains* were not uncommon.

Pyows were the second most common call, with residents typically producing 2–3 *pyow* bouts per all day (~8 hr) observation. Observations in which context was clear ($N = 1{,}174$) included a variety of disturbances and non-disturbances, and often group movement. Male–male agonism was associated with >30% of episodes (after chasing a male, 12%; with another male nearby and caller continuously oriented to him, 19%); males also frequently *pyowed* after other males called. Terrestrial predators (e.g. dogs) were associated with another 19% of episodes, and raptors with 7%. Nearly 12% of *pyow* episodes occurred in undisturbed contexts, consistent with what some refer to as "spontaneous" calls; importantly, many similarly undisturbed contexts were conservatively labeled "unknown," suggesting the proportion of "spontaneous" *pyows* might actually be higher.

Ant

A short, harsh call with an abrupt clipped sound. *Ants* are easily distinguished from other calls, though "*ant*-like" *pyows* are common in episodes in which *pyow* bouts transition to *ant* bouts, suggesting

TABLE IV. Summary Measurements (mean ± SE) of the Acoustic Structure of Call Types (N = Number of Males that Contributed Recordings to Analyses)

Call type	Cent_tot (Hz)	Max_tot (Hz)	Start_tot (Hz)	Mid_tot (Hz)	End_tot (Hz)	Rise_tot (sec)	Dur_F0 (sec)	Lo_F0 (Hz)	Hi_F0 (Hz)
Ant ($N=9$)	1,765 ± 54	1,832 ± 85	1,946 ± 98	1,566 ± 91	1,247 ± 97	0.028 ± 0.001	0.058 ± 0.002	124 ± 4	461 ± 19
Boom ($N=16$)	122 ± 2	131 ± 1	131 ± 2	127 ± 2	115 ± 2	0.054 ± 0.002	0.147 ± 0.003	64 ± 2	191 ± 2
Ka ($N=7$)	903 ± 29	912 ± 36	864 ± 44	888 ± 44	925 ± 35	0.029 ± 0.002	0.049 ± 0.002	166 ± 5	475 ± 16
Katrain (units) ($N=8$)	857 ± 10	868 ± 13	847 ± 15	881 ± 13	850 ± 10	0.029 ± 0.001	0.051 ± 0.001	155 ± 3	419 ± 5
Nasal Scream ($N=4$)	1086 ± 136	994 ± 172	1099 ±174	927 ± 157	820 ± 165	0.300 ± 0.021	0.536 ± 0.043	241 ± 13	478 ± 25
Pyow ($N=19$)	1533 ± 35	1668 ± 49	1653 ± 89	1561 ± 45	1249 ± 27	0.068 ± 0.002	0.139 ± 0.003	152 ± 4	635 ± 14
Katrain (call) ($N=8$)	833 ± 11	853 ± 21	872 ± 16	862 ± 19	858 ± 28	1.91 ± 0.2	n/a	n/a	n/a

Call type	Start_F0 (Hz)	Mid_F0 (Hz)	End_F0 (Hz)	Slope_F0 (Hz/sec)	Slope1_F0 (Hz/sec)	Slope2_F0 (Hz/sec)	Frmt_Disp1 (Hz)	Frmt_Disp2 (Hz)	Frmt_Disp$\bar{x}$ (Hz)
Ant ($N=9$)	357 ± 13	255 ± 6	183 ± 4	−2946 ± 148	−3458 ± 261	−2434 ± 125	249 ± 6	262 ± 7	256 ± 6
Boom ($N=16$)	131 ± 2	127 ± 1	115 ± 2	−107 ± 11	−45 ± 25	−169 ± 24	n/a	n/a	n/a
Ka ($N=7$)	405 ± 15	273 ± 8	225 ± 7	−3685 ± 267	−5419 ± 481	−1952 ± 226	264 ± 9	281 ± 9	273 ± 8
Katrain (units) ($N=8$)	367 ± 8	250 ± 4	199 ± 4	−3435 ± 129	−4822 ± 255	−2047 ± 127	236 ± 5	239 ± 4	237 ± 4
Nasal scream ($N=4$)	405 ± 22	445 ± 23	356 ± 18	−67 ± 40	221 ± 47	−355 ± 78	206 ± 8	219 ± 7	212 ± 7
Pyow ($N=19$)	459 ± 14	328 ± 5	218 ± 12	−1,794 ± 113	−1,992 ± 201	−1,595 ± 58	321 ± 6	325 ± 5	323 ± 6
Katrain (call) ($N=8$)	F0 measures not applicable to whole *katrains*					Number of units: 15.94 ± 1.02 units			
	Parameters describing total call include					Call duration: 4.23 ± 0.29 sec Inter-unit interval: 0.20 ± 0.03 sec			

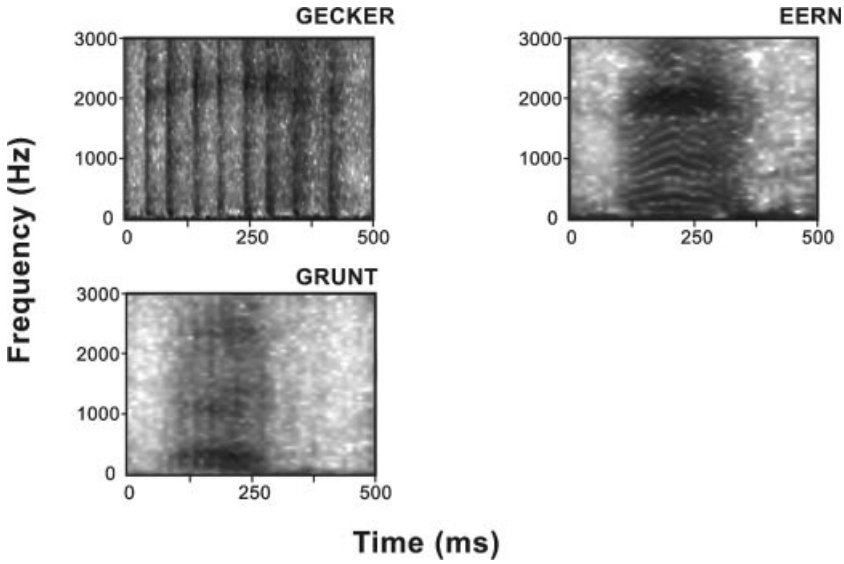

Fig. 4. Exemplar spectrograms of three other vocalizations by males observed during the study. Each was so rare that inclusion in the male repertoire is not warranted.

grading or possibly a transitional form between *pyow* and *ant*. Length of *ant* bouts ranged widely (range: 1–300; median: 21), with calls separated by ~10 sec. Sometimes given alone, *ants* frequently occurred with *pyows*, and then typically at the end of longer bouts of *pyows*.

Usage was low, occurring in only 2% of observed episodes, but a relationship between *ants* and terrestrial predators was clear. In *ant* observations in which context was clearly known ($N = 67$), dogs or snakes were present in 53%, and caller appeared agitated while oriented toward an unseen terrestrial object in another 16%. Other known contexts include male–male aggressive encounters (19%) and the presence of motorcycles, palm civets (*Nandinia binotata*), or baboons (*P. anubis*).

Ka

A loud, short, abruptly clipped call, *kas* sound similar to *ants*, but are distinguished by ear as louder, lower frequency, and more tonal, with a somewhat "hollow" character. Acoustically, *kas* are virtually identical to individual units of *katrains* (below). *Kas* were rarely given alone, with >85% occurring in episodes with *katrains*—typically with one or two *kas* preceding *katrains* by 5–10 sec. When a caller gave multiple *katrains* in an episode, he typically produced *kas* in the 15–20 sec separating them.

Usage was low, occurring in only 3% of observed episodes. Context of *kas* was identical to that of *katrains* (below), and indicates a relationship with aerial predators. In the relatively few cases in which *kas* were not followed by *katrains* or other calls, contexts included tree falls and similar disturbances.

Katrain

A loud string of pulsed units, repeating steadily with a consistent amplitude and tone throughout. The *katrain*, the only male signal with a multi-unit structure, sounds like (and structurally is) a rapid sequence of *kas*, with each separated by a short, guttural "*urrr*" sound. *Katrains* were given alone but most commonly accompanied by *kas*, and sometimes *pyows*. Number of *katrains* per episode varied, but was typically one to three.

Strong relatedness between the *ka* and *katrain* is clear from affinity in both acoustic structure and usage, yet these constitute distinct call types rather than variants of a single, graded type. Graded (sensu Marler [1975]) signals lack distinct boundaries, displaying more or less continuous variation between classes. Field observations, however, included only *kas* produced singly and *katrains* of ≥7 combined units (mean: 15), rather than increasing numbers of sequentially combined *kas*. Furthermore, the *urrr* sound linking units in *katrains* was never observed in recordings of *kas* given singly.

Usage was low, accounting for only 4% of observed calls, but a relationship between *katrains* and aerial predators is unambiguous. Of observations in which context was clear ($N = 157$), raptors were seen in 59%, and in another 22% group members' behavior was consistent with aerial predator avoidance (i.e. diving down, hiding). Consistent with both contagion and the flight patterns of raptors, *katrains* by different males frequently appeared to "spread" across the forest. Other known contexts include trees falling very near caller (8%) and dogs very near (3%).

Nasal Scream

Exceptionally variable, rasping vocalizations, *nasal screams* are quieter and comprise higher frequencies than other adult male calls. Very short (~0.1 sec) *nasal screams* were observed, but calls were typically longer (~0.5 sec), rising in frequency and amplitude in the middle. *Nasal scream* is the only call type observed in non-resident males. *Nasal screams* were rare, observed only 18 times during this study, and unambiguously associated with intense aggression between males. Though residents often threaten and chase "intruder" males, *nasal screams* were observed only during the rare cases of intense physical contact or, with males facing off, when contact appeared imminent. Typically only one combatant *screamed*, usually the recipient of aggression or putative "loser;" in the past, a few observations have included a male screaming while chasing [Cords, pers. comm.]. In some particularly intense fights, males mixed *nasal screams* with other, mostly unclassifiable utterances. Two were somewhat distinguishable, *eerns* and *geckers* (described as "other," below).

Other: Gecker, Eern, and Grunt

Three very quiet vocalizations were also observed, but so rarely that inclusion in the male repertoire is not warranted; they are described here based on four available recordings. *Geckers* and *eerns* were observed only with *nasal screams*. The *gecker* is a rapid sequence of repeated, nearly identical units that are extremely short, raspy, and quiet, with no detectable sound between units. *Eerns* are quiet, nasal, and slightly tonal, with an extremely variable duration, and may be shortened forms of *nasal screams* produced with a partially or fully closed mouth.

Only one adult male produced *grunts*, and only six times in 12 months of continuous observation. *Grunts* were short, quiet, pulsatile, atonal vocalizations, and appear structurally consistent with *grunts* regularly given by adult females and juveniles of both sexes. In all *grunt* observations, the caller appeared calm and group members nearby were feeding; on three occasions, he *grunted* before *booming* several seconds later.

DISCUSSION

The vocal repertoire of adult male blue monkeys comprises six acoustically distinct call types: *ant*, *boom*, *ka*, *katrain*, *nasal scream*, and *pyow*. Three other vocalizations were observed but extremely rarely; *geckers*, *grunts*, and *eerns* likely constitute anomalous rather than stable elements in the repertoire. Each call type is distinguishable by ear, visual inspection of spectrograms, and quantitative analyses of acoustic structure. The results reflect the most extensive study to date of this species' vocal behavior, with data collected during >5500 hr of direct observation and in an immense variety of social and ecological contexts. It thus seems unlikely that any other male calls are typical of this population. Similar studies elsewhere should confirm whether the described repertoire is species-typical, and identify variation relating to population or subspecies differences.

The pattern of separation among samples, revealed by cluster and discriminant function analyses, indicates three primary acoustic structures of the male repertoire, with the multi-unit structure of *katrains* a fourth (Fig. 3). *Ants*, *pyows*, *kas*, and individual *katrain* units share a basic structure of 3–4 distinct, downward sloping energy bands, with the F0 peaking around 300–350 Hz and increasing turbulence (noise) in higher frequencies. *Pyow* duration is typically more than twice that of other calls, permitting its longer rise time and more gradual slope. *Ants*, *kas*, and *katrain* units have very similar duration and F0 measures, yet are distinguished by how energy concentrates at higher frequencies; *ants* have energy distributed evenly through 3,000 Hz, with an average center frequency of 1,765 Hz, whereas *kas* and *katrain* units have relatively little energy above 1,800 Hz and center frequencies closer to 900 Hz (Fig. 3; Table IV). *Nasal screams* differ considerably from other calls, exhibiting more harmonic evenness and energy in higher frequencies, and extreme variability of duration and center frequency.

The *boom's* extreme acoustic dissimilarity to other call types is consistent with a fundamentally distinct production mechanism. The *boom's* center frequency, nearly ten times lower than that of other calls, and conspicuous absence of harmonics (Fig. 3) reflect reliance on an inflated laryngeal air sac [Fitch & Hauser, 1995; Gautier, 1971], with the latter suggesting *booms* may not resonate through the vocal tract. Inflating air sacs likely supplements males' other calls in terms of amplification and lowering the F0 [Fitch & Hauser, 1995; Hewitt et al., 2002], but *boom*s fundamentally depend on it [Gautier, 1971].

The repertoire described here supports other reports of male *C. mitis* vocal behavior, and provides some additions and clarifications. The descriptions of *booms* and *pyows* are consistent with observations in other populations [e.g. Butynski et al., 1992; Marler, 1973]. Marler [1973] and others have also described *kas* (called "*hacks*" by Murphy et al. [2013]), yet considered *kas* given singly and in a series (i.e. *katrains*) variants of one call type; though *kas* and *katrain* units clearly share acoustic features, complete absence of grading between the *ka's* single unit and *katrains'* consistent ≥7-units unquestionably distinguishes the calls. *Ants* have not been described previously for blue monkeys, though some researchers may have observed *ants* and considered them a

short variant of *pyows* [Papworth, pers. comm.]. This is the first study to quantify acoustic features of the *nasal scream*.

Functional Inferences

Signals' acoustic structure and the socio-ecological contexts in which they occur can provide insight into function, and this study's results can thus serve to generate inferences and hypotheses for male calls. Function (i.e. adaptive benefit to signalers [Tinbergen, 1963]), however, should never be assumed based solely on context or structure; functional hypotheses, evaluated based on call usage and receiver response and using data from natural observations and playback experiments, are addressed in forthcoming articles.

Acoustic features

A signal's active space (i.e. distance at which conspecifics can hear it) dictates the number and age–sex classes of potential receivers and thus potential functions. "Except for *ants* and *nasal screams*, male blue monkey calls" are high amplitude, stereotyped, and relatively low pitch, conforming to Gautier and Gautier's [1977] "loud call" description and making them more resistant to attenuation and thus capable of greater audible distances [Wiley & Richards, 1978]. Field observations in Kakamega are consistent with predictions by Brown and colleagues (who used experimentally derived auditory sensitivities of blue monkeys to calculate some calls' audible distances [Brown & Waser, 1984; Brown, 1989; Brown et al., 1995]), and indicate *pyows*, *booms*, *kas*, and *katrains* typically can be heard by a caller's entire group as well as members of adjoining groups and non-resident males hundreds of meters away. Having receivers in such a variety of age–sex classes, social statuses, and reproductive states thus allows calls to potentially achieve multiple within- and between-group functions (e.g. mate defense, spacing, mate attraction [reviewed in Wich & Nunn, 2002]). *Ants* and *nasal screams*, being somewhat quieter and relatively higher frequency, have shorter audible distances, likely limiting function to interactions with nearby animals.

Signal usage

Four call types—*ant*, *ka*, *katrain*, and *nasal scream*—exhibited high context specificity. All *nasal screams* occurred during intense male–male aggression, indicating a function in agonism and, as losers appear the more likely to *scream*, potentially as a submissive signal. *Kas* and *katrains* were unambiguously associated with aerial threats (consistent with Papworth et al. [2008]), with raptors observed or strongly indicated in nearly 80% of episodes; trees falling nearby also regularly evoked both calls, suggesting high arousal may be a proximate factor in their production. *Ants* occurred reliably with terrestrial disturbances, primarily dogs and snakes, and sometimes vehicles, civets, or baboons, suggesting a terrestrial predator avoidance function.

Repertoires with different calls for terrestrial and aerial threats are common across taxa [Townsend & Manser, 2013]. Data for blue monkey *ants*, *kas*, and *katrains* are consistent with the hypothesis that acoustically distinct, context-specific signals evolve when species face multiple predators whose different hunting styles favor distinct avoidance responses [Marler, 1977; Macedonia & Evans, 1993]. Unlike some primates with distinct snake and leopard calls (e.g. vervet monkeys [Seyfarth et al., 1980]), blue monkeys use *ants* with both snakes and dogs; it may simply be that, for arboreal monkeys, an effective avoidance strategy is the same for both predators (e.g. climb up, keep predator in view).

Unlike other call types, *booms* and *pyows* were not context specific, occurring regularly across various contexts and with apparent stimuli including predators, other males, within-group aggression, and approaches, and often with no apparent antecedent ("spontaneous"). Though such wide usage gives the impression of "generalist" signals, evidence suggests distinct, if potentially overlapping functions. *Booms* appear associated with non-aggressive interactions between resident males and group members, with >50% of *booms* immediately preceded by a caller's approaching or being approached by females. An association with approaches could explain *booms'* occurring across such a wide variety of contexts (i.e. non-aggressive interaction might be equally beneficial in undisturbed contexts and threat events), and suggests a role in facilitating affiliative interactions, possibly as a signal of benign intent (sensu Silk [2002]). The *boom's* long audible distance ($\geq$900 m [Brown, 1989]) seems incongruent with a putative evoking stimulus being females only a few meters away, yet is consistent with mate defense [Wich & Nunn, 2002], suggesting possible multiple functions. The apparent predictability with which a falling tree branch evoked *booms*, even when males were alone, however, remains perplexing.

Pyows similarly occurred in a wide variety of contexts, yet were not associated with affiliative interactions and appeared more often evoked by disturbances. Notably, *pyows* were commonly associated with other males' presence, suggesting a role in agonism and most likely mate defense. That *pyows* were also frequently given "in response" to hearing other males is also consistent with this hypothesis, as it could provide opportunity for rivals to regulate spacing and assess "quality" [Butynski, 1982]. Neighboring males are significant threats to residents' reproductive success—directly ousting them or stealing paternity through "sneak" copulations [Cords,

2000; Tsingalia & Rowell, 1984]—and repelling rivals is thus undeniably important. *Pyows'* having an audible distance beyond callers' home range size [Brown, 1989], coupled with its frequent use, also supports (albeit indirectly) a mate defense function, and is consistent with being an advertisement of occupancy. Some researchers have described the blue monkey *pyow* as an intragroup rallying call [Tsingalia & Rowell, 1984; de Jong & Butynski, 2010; Lawes et al., 2013], a characterization consistent with my observations that group members often moved toward callers after *pyows*. Though likely accurate, this single-function label appears insufficient, with evidence suggesting *pyows* achieve multiple functions (e. g. mate defense).

In recent studies, Papworth et al. [2008] and Murphy et al. [2013] labeled the blue monkey *pyow* an "alarm call," based on use in predator contexts and in response to leopards in particular. My observation that males often *pyowed* in response to seeing or hearing dogs appears consistent with this characterization, yet results indicate (as these authors also noted) that males *pyow* in many other contexts; the label "alarm call" thus seems inappropriate (i.e. that a signal is used in predator contexts is necessary but not sufficient to infer an alarm function). The *pyow's* contextual diversity (e.g. agonism, group travel, and "spontaneous") suggests a functional versatility that might be achieved "simply" by drawing attention to callers, thus potentially serving to facilitate group cohesion, mate attraction, mate defense, and predator avoidance; similar observations and inferences are made for the *pyow* of the closely related *C. nictitans* [Arnold & Zuberbuhler, 2013].

Male blue monkeys' small repertoire and low call rate relative to females [unpublished data] likely reflects males' limited social interactions and may constitute functional constraints on vocal signaling. Acoustic variation within call type, however, may expand the functional capacity of the repertoire, as might combining call types in sequences. The observed use of *booms* followed by *pyows*, for example, may be similar to a pattern observed in Campbell's monkeys (*C. campbelli*) in which *booms* given before another call type evoked different receiver responses than either call on its own [Zuberbuhler, 2002].

Similarities to Congeners

Acoustically, some male blue monkey calls are similar to signals described in other *Cercopithecus* species. The association between phylogenetic relatedness and sharing of call types, however, is not consistent—some calls appear more or less conserved among clades, and others species specific. For example, in putty-nosed monkeys (*C. nictitans*), blue monkeys' nearest congener [Disotell & Raaum, 2002], males use homonymous and acoustically similar *booms* and *pyows*, and *hacks*, similar to *kas*, that are occasionally strung together in multi-unit calls similar to *katrains* [Arnold, pers. comm.; see Arnold & Zuberbuhler, 2006; Gautier, 1988; Price et al., 2008; Struhsaker, 1970]). Interestingly, in the more distantly related redtail monkeys (*C. ascanius*), males use calls extremely similar to *katrains* and *ants*, yet do not *pyow* or *boom* [Marler, 1973; unpublished data]. DeBrazzas monkeys (*C. neglectus*), which are of similar genetic distance from blue monkeys as redtails, use *booms* but apparently not other *C. mitis*-like calls [Bouchet et al., 2012]. Indeed, the *boom* appears to be blue monkeys' most "shared" call type, with similar signals described for several other guenons, including *C. nictitans*, *C. campbelli, C. neglectus*, *C. mona*, and *C. pogonias* [Gautier, 1988].

Given that primate vocal signals appear largely genetically determined [Newman & Symes, 1982], it is not surprising that closely related species should have similar repertoires. The various ecological, social, and phylogenetic factors that explain differences among taxa, however, are difficult to pinpoint. A growing number of studies of vocal behavior across taxa provides opportunities for comparative analyses that might identify particular selection factors and improve understanding of how communication systems evolve. Such research should strive for repertoires derived from extensive, comprehensive observations and objective, quantitative classification methods, and should seek ways to address signals as units within an integrated suite of related behavioral elements.

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