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# Versatility in a loud call: Dual affiliative and agonistic functions in the blue monkey *boom*

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**Abstract**

To investigate the selective agents that shape signals, we examined function (adaptive benefit to signaler) in the *boom* loud call by male blue monkeys. Using natural observation and playbacks in a wild population in Kenya, we characterized *boom* function from conspecifics' behavioral responses and also variation in call usage relating to context and reproductive season. *Booms* occurred in several contexts and after varied stimuli, including falling branches, yet were strongly associated with intragroup activity and, in particular, affiliative interactions between callers and females. Males produced more *booms* during the mating season and, congruently, when more females in their groups were sexually active. After hearing *booms*, compared to no call, females spent more time near groupmates and the caller and were more likely to approach and have mating interactions with him. Males tended to move away after hearing a *boom*. In the aggregate, results indicate that *booms* achieve multiple functions relating to facilitating group cohesion, affiliative interactions, and mating opportunities, while also repelling rival males. An observed association with falling branches is puzzlingly distinct from these social functions. We explore the hypothesis that *booms* enable affiliative encounters by acting as signals of benign intent, and discuss the functional versatility of signals perceived by multiple receivers that vary in age, sex, and relationship to signalers.

**KEYWORDS**
*Cercopithecus*, communication, primates, signal evolution, vocal signals

## 1 | INTRODUCTION

Animal social interactions rely on consistent use of and response to signals. Among acoustic signals, the so-called "loud calls"—high amplitude, species-stereotyped vocalizations—have received particular research attention across insects, amphibians, birds, and mammals (Searcy & Nowicki, 2005). Relative to other call types in a species' repertoire, loud calls are more detectable over longer distances (Mitani & Stuht, 1998), and callers incur greater costs in terms of energy investment and exposure to predators and competitors (Vehrencamp, 2000; Woods, Hendrickson, Mason, & Lewis, 2007). For species to maintain such conspicuous and costly traits, the calls should provide compensatory adaptive benefit, making loud calls particularly useful for investigating the evolution of animal communication and sociality.

To understand a call's function (used here to mean its adaptive benefits to signalers), researchers examine receiver responses as well as variation in the contexts and stimuli associated with the call's production. Across taxa, functional explanations for loud calls typically fall into only a few categories relating to predator avoidance, social cohesion, mate attraction, or mate defense (Gautier & Gautier, 1977; Gustison & Townsend, 2015; Ryan, 1985; Snowdon, 2004). Importantly, loud calls are perceived simultaneously by multiple receivers who, depending on variation in characteristics such

as age, sex, or social status, might respond differently: In some frog and deer species, for example, one call type attracts females and simultaneously repels rival males (Bernal, Akre, Baugh, Rand, & Ryan, 2009; Charlton, Reby, & McComb, 2007). Therefore, and at odds with the appealing convenience of single-function labels (e.g., "eagle call"), one signal may thus achieve multiple functions by simultaneously evoking multiple responses (Fuller & Cords, 2017).

In this study, we explored the selective agents that shape signals by investigating signal function in a primate loud call. In at least nine Old World monkey species in the genus *Cercopithecus*, adult males produce low frequency, tonal loud calls referred to as *booms* (*C. campbelli*, *C. hamlyni*, *C. lomamiensis*, *C. mitis*, *C. mona*, *C. neglectus*, *C. nictitans*, *C. lhoesti*, *C. pogonias*; Gautier, 1988; Hewitt, MacLarnon, & Jones, 2002; Hart et al., 2012). The calls' distinctive sound (Audio S1; Figure S1) and their production only by adult males reflects *booms*' dependence on a supralaryngeal air sac that is much larger in males (Hewitt et al., 2002). Gautier's (1971) experimental work with *C. neglectus* confirmed the *boom's* reliance on inflating this air sac, evidenced also by callers' distinctive postural behavior: To produce *booms*, males sit upright, swell at the thorax, and *boom* with the mouth completely or nearly closed (Figure S2). Exactly how the inflated air sacs modify vocalizations remains uncertain, but they likely act as resonance chambers that amplify vocal fold vibrations (de Boer, 2009).

The *boom's* loudness and the sexually dimorphic, specialized anatomy underlying its production suggest the call is an adaptive trait, yet the *boom's* usage and function(s) remain poorly understood. The most frequently referenced studies focused on male Campbell's monkeys (*C. campbelli*) who typically *boom* just before producing another call type: Researchers found that receivers' response to the second call differed if preceded by *booms* and suggested *booms* act as syntactic modifiers (Ouattara, Lemasson, & Zuberbuhler, 2009; Zuberbühler, 2002). Other species, however, such as blue monkeys (*C. mitis*), typically produce the *boom* by itself (>97% of observations; Fuller, 2014), suggesting a function other than "semantic" modification.

We investigated the *boom* of blue monkeys, an arboreal monkey that inhabits forests across east and central Africa and maintains unimale–multifemale social groups (Lawes, Cords, & Lehn, 2013). The adult male vocal repertoire—entirely distinct from that of adult females or juveniles of either sex—comprises six acoustically distinct call types: *ant*, *boom*, *ka*, *katrain*, *nasal scream*, and *pyow* (Fuller, 2014). Adult males in groups produce *booms* regularly (typically ca. three a day; Fuller, 2014) and the audible distance for conspecifics may be >1,000 m (Brown, 1989), which exceeds typical home range size; the *boom's* low pitch (center frequency is typically near 122 Hz; Fuller, 2014), however, makes it difficult for humans to hear from far away.

We examined four distinct yet not mutually exclusive hypotheses for *boom* function (Table 1), using evidence from receivers' responses to *booms*, close proximity interactions between males and females, and variation in *boom* production in relation to context, season, and number of sexually active females. If *booms* function in **predator avoidance**, they should occur in predator contexts and elicit protective responses (run, hide) by members of the caller's group. If *booms* facilitate **within-group cohesion**, we predicted that females would spend more time near groupmates after *booms* by their group's male. To investigate whether *booms* increase males' **mating opportunities**, we examined whether females increased their likelihood of moving closer to, spending more time near, or mating with a male who *boomed*; additionally, we predicted that males would *boom* more during the mating season or when there were more sexually active females and that male–female close proximity interactions would be more "successful" (last longer, with more affiliative and less aggressive behavior) if a male *boomed* than if he did not. Lastly, if *booms* function in **mate defense**, rival males should move away from a caller after he *booms*, and *booms* should occur with agonistic encounters between males and be more frequent during the mating season or when more females are sexually active.

## 2 | METHODS

This study adhered to the Association for the Study of Animal Behaviour's principles for the ethical treatment of animals. Fieldwork protocols were approved by the Columbia University Institutional Animal Care and Use Committee and by the Kenya Wildlife Service and National Commission on Science, Technology and Innovation.

### 2.1 | Study site, species, and subjects

Fieldwork took place in the Kakamega Forest, Kenya (0°15′N, 34°52′E; elevation 1,580 m; Cords, 2012), a rain forest that supports a relatively dense blue monkey population (ca. 192 per km$^2$; Fashing et al., 2012). Predators here include crowned eagles (*Stephanoaetus coronatus*), Gaboon vipers (*Bitis gabonica*), and sometimes humans hunting with dogs (Cords, 2012). The main data collection period occurred from September 2010 through September 2011 (hereafter: data Period 1). We collected additional records for male–female interactions from April to December 2017 (data Period 2).

Blue monkey social groups comprise multiple adult females, their offspring, and typically one adult "resident" male. Groups are thus characterized as unimale, though sometimes (ca. 25% of group-years in Kakamega) multiple "influx" males temporarily join a group, usually in the mating season (Cords, 2000, 2002a). Females are territorial and philopatric, whereas males disperse at ca. 7 years old (Cords, 2002a; Ekernas & Cords, 2007) and live alone or loosely associated with other "non-resident" males unless and until they become a resident by taking over a group. Resident males are typically aggressive toward other adult males—unsurprising given that extragroup males sire ~40% of a group's offspring (Roberts, Nikitopoulos, & Cords, 2014) and can forcefully depose a resident or move in after his departure; furthermore, infanticide by incoming males accounts for ≥17% of infant mortality (Cords & Fuller, 2010). The population in Kakamega exhibits reproductive seasonality, with a peak in conceptions from June to October (Cords & Chowdhury, 2010).

**TABLE 1** Hypotheses for *boom* function (benefit to signalers) and their predictions examined in this study

| Hypothesis | Predictions | | | |
|---|---|---|---|---|
| | Variation in *boom* usage | Male receiver response | Female receiver response | Male–female proximity events |
| Predator avoidance: *Booms* decrease likelihood caller or his kin/mates are killed by predators | *Boom* production is associated with the presence of predators | No predictions | Responses are consistent with predator avoidance:<br>• Flee (run, dive, hide)<br>• increase visual monitoring[†]<br>• spend more time near more group members[†] | No predictions tested |
| Within-group Cohesion: *Booms* increase/maintain time caller's group members spend in proximity | No predictions tested | No predictions | After *booms*, ♀ receivers:<br>• spend more time near more group members[†] | If male *booms* during MFP, then MFP:<br>• duration is longer[†]<br>• more likely to include affiliative behavior[†]<br>• less likely to include aggression[†] |
| Mate Attraction: *Booms* increase caller's likelihood of mating | *Boom* production rate:<br>• is higher in mating season than other seasons[†]<br>• correlates with number of sexually active females in callers' groups[†] | No predictions | After *booms*, ♀ receivers:<br>• look toward call origin<br>• move toward caller<br>• spend more time near caller<br>• increase proceptive behavior toward caller | If male *booms* during MFP, then MFP:<br>• duration is longer[†]<br>• more likely to include affiliative behavior[†]<br>• less likely to include aggression[†]<br>• more likely to include<br>• mating behavior |
| Mate Defense: *Booms* reduce likelihood that other males mate with females in caller's group | *Boom* production:<br>• is associated with male-male agonism<br>• rate is higher in mating season than other seasons[†]<br>• correlates with number of sexually active females in callers' groups[†] | After *booms*, ♂ receivers:<br>• look toward call origin<br>• increase visual monitoring<br>• move away from call origin | No predictions tested | No predictions tested |

*Note:* Hypotheses are not mutually exclusive (i.e., *boom* could achieve multiple functions), and some predictions (marked†) support more than one hypothesis

[†]Prediction supports more than one hypothesis.

In Period 1, subjects were 32 adult males and 61 adult females that were each identifiable and habituated from long-term research (Cords, 2012). Females came from five groups that varied in size (range: 16–50 group members). Male subjects included residents ($N$ = 17, in 12 groups), influx males ($N$ = 9, in two groups), and non-residents ($N$ = 16); nine males held multiple statuses during the study period (Table S1). In Period 2, data for male–female interactions came from 33 males and 84 females in seven groups (size range: 8–65).

## 2.2 | Data collection

Period 1 data were collected by JF and eight observers who each received ≥1 month training on data protocols and identifying behavior (including all call types) and socioecological variables such as inter-group encounters and presence of predators. JF "shadowed" each observer at least 1 day each month and compared observers' records to ensure reliability and ≥95% agreement. Daily monitoring of study

groups (by a separate team as part of MC's long-term study) provided records of all monkeys present (including extragroup males), births, and all observed sexual activity. On each field day (≥22 per month), eight observers monitored three groups and one to two non-resident males from ~0720 to 1,730 hr (with a 90-min break at 1,300 hr, a time when the monkeys usually rested). In each group, one observer followed the resident male continuously (unless lost), while another monitored different adult females for 20- to 30-min focal follows. We adjusted observation schedules regularly to ensure females' behavioral samples (below) were distributed similarly across individuals, months, and morning, midday, and afternoon hours. Males were sampled unequally, with most data coming from the residents of the five main study groups (Table S1).

During Period 2, observers, monitoring groups for a separate, long-term study, documented close-proximity interactions between adult males and females. Data were collected when interactions occurred during or between systematic focal animal follows of adult females.

## 2.3 | Male vocal behavior

We describe male vocal behavior in nested categories, with *Call* being a single, discrete utterance (1 *boom*) and *Episode* any vocal occurrence, including all his calls spaced <1 min apart. We documented vocal behavior on an all occurrence basis (Altmann, 1974): Whenever any male vocalized, observers noted the time, caller's location and identity, and the sequence of calls (most episodes included one call type only, though ~6% were combinations—e.g., *boom* then *pyows*; Fuller, 2014).

### 2.3.1 | Call context

Observers documented vocal episodes using a checklist of social and ecological states relating to the presence of other conspecific groups or males, predators, or other heterospecifics within 100 m, and also narratively described the activity of the caller and associated conspecifics (feeding, resting, moving, agonistic/affiliative interactions) before and after calls. Observers were typically with groups throughout the 2-km$^2$ study area, and we therefore examined records from multiple observers to assess each episode.

Extensive field observations and post hoc examination of nearly 4,000 records for which data were sufficient to assess context identified 14 contexts in which males vocalized (Table 2). Calls were associated with (occurred within 2 min of) several ecological disturbances, including predators, non-predator heterospecifics, and falling trees. Though infrequent, loud trucks or airplanes typically evoked predator-consistent behavior, so we grouped such episodes with terrestrial or aerial threats. Males also called in association with social disturbances, including agonism between the caller and conspecifics or between groups. We labeled some episodes "unknown disturbance" if the caller and nearby monkeys exhibited conspicuous high-arousal behavior (scanning, intense

staring, rapid moving), but observers could not identify a particular stimulus.

Males called in non-disturbance contexts also, characterized by an absence of the above variables and with the caller and group members resting, feeding, grooming, and sometimes mating. We labeled some well-observed episodes "spontaneous," but did so conservatively only when it was very clear no observable stimulus or interaction occurred and the caller and nearby monkeys exhibited no increased arousal. Lastly, males called in association with approaching or being approached by females (without aggression) or when rejoining groups (after being away ≥20 min), each of which occurred in disturbance and non-disturbance contexts.

## 2.4 | Receiver response data

Throughout the study period, we conducted focal animal samples of males and females. To assess how receivers respond to *booms*, we compared activity in samples distinguished as No-Vocalization (hereafter: NVs) and After-Vocalization samples (hereafter: AVs). NVs were those samples conducted when no call by any male had been heard in ≥30 min prior. AVs were samples conducted after hearing a *boom* by any male, but only if no other vocalization by any male had been heard in ≥30 min prior.

Focal observations were 23 min long but divided into "short-term" (first 3 min) and "long-term" (subsequent 20 min) samples. For NVs, observers started after a 10-min count or after playback of a control (bird call; see below). For AVs, if observers had a receiver in clear sight when a *boom* occurred, we started a 3-min AV immediately, and a 20-min AV followed consecutively; if we did not see a receiver at the time of the *boom*, we located a subject and started a 20-min AV 3 min after the *boom*.

Three-minute samples used continuous recording to catalog subjects' activity. In the first minute only, we recorded instances of look (reorient face up, down, or, in AVs only, toward call) and flee (run, dive, or hide). For AVs only, if subject moved >5 m net, we recorded the direction relative to the call origin as away (135–225°), toward (≥315° to ≤45°), or parallel (45–135° or 225–315°). We discarded 3-min samples if the subject went out of sight for >20 s or if we heard any male vocalize.

Twenty-minute samples used instantaneous sampling (1 min intervals, marked by an audio-timer's *beep*) to record subjects' number of neighbors (conspecifics within 10 m) and, for females, if these included their group's resident male. In each interval between *beeps*, we used one-zero sampling to record whether subjects exhibited scanning (rapidly shifting gaze with neck extension), mating behavior (mount or other sexual behavior, such as female present or pucker to male, male anogenital inspection; Pazol, 2003), approach (move directly toward, from ≥5 m to ≤2 m, and remain ≥10 s without aggression; given to or received from adult conspecific that was opposite sex of subject), or flee. If a subject went out of sight, we excluded those *beeps* and intervals from analysis. Samples ended immediately if observers heard any call by any male. We discarded samples that lasted <18 min.

**TABLE 2** Observed contexts in which males vocalized, including number of observed vocal episodes (all call types and, in parentheses, *booms*) that were sufficient to assess context

| Context category Any call (*booms*) | Description |
|---|---|
| Terrestrial threat 366 (41) | Dog[†], snake[†] (known predators) |
| | Baboon, civet, truck, chainsaw (not known predators, but consistently evoked predator-consistent behavior) |
| Aerial threat 321 (7) | Raptor[†] (species not distinguished) |
| | Airplane (evoked predator-consistent behavior) |
| Tree fall 59 (5) | Entire or most of tree falls nearby |
| Branch fall 94 (71) | Branch falls nearby; quieter than tree |
| Male–male agonism 409 (143) | Adult male nearby[†] |
| Intergroup aggression 612 (207) | Group other than caller's nearby. Aggression includes vocalizing, lunge, chase, physical contact |
| Intragroup aggression (not w/caller) 75 (39) | Aggression (lunge, chase, grab, bite) between members of caller's group |
| Intragroup aggression (w/caller) 91 (41) | Aggression between caller and member(s) of his group |
| Unknown disturbance 278 (37) | High arousal in group and caller, consistent with predator or other male presence, but not identified |
| Affiliative (non-mating) 292 (226) | Non-aggressive interaction (e.g., groom, co-feed) between caller and group member(s) |
| Affiliative (mating) 187 (68) | Mating interaction (w/caller): mount, copulation, proceptive behavior (e.g., present, anogenital inspect) |
| Spontaneous 128 (7) | No conspicuous stimulus preceded call. Caller and group rest and feed |
| Rejoins Group 205 (59) | Caller moves to within group after being ≥75 m from group's edge >20 min |
| Approach 391 (354) | Caller approaches or approached by other(s) from ≥5 m to ≤2 m and remain ≥10 s w/no aggression |

*Note:* Some variables (marked†) were replicated in field experiments.
[†]Replicated in field experiments.

At the start and end of all samples, we recorded subjects' location (to nearest 25 m on a gridded map) and, for female subjects, approximate distance to their group's resident male. For females, in both NVs and AVs, we used these data to derive a subject's change in proximity to her resident male (closer, farther, same). For males, in AVs only, we derived a subject's change in distance to the call's origin (closer, farther, same).

In addition to AV samples of male and female receivers, we also conducted focal samples on males after they *boomed* (hereafter: AV-Caller), using the protocols described above. These samples documented interactions between a caller and female receivers (approaches, mating, and time in proximity), and we therefore included them as indirect measures of female receiver response.

## 2.5 | Experimental stimuli

To supplement our examinations of contexts in which males call and also responses by male receivers to *booms* (above), we exposed seven resident and seven non-resident males to simulated "intruder" males or predators. To simulate a male nearby, we broadcast various call types (*boom, katrain, ants* or *pyows*) recorded from five males in the study area. To minimize subjects' likelihood of familiarity with callers, each trial used calls by a male whose home range border was ≥500 m from the subject's. Predator simulations included recordings of crowned eagles (Macaulay Library, Cornell Laboratory of Ornithology) or dogs, or a fiberglass model of a Gaboon viper. As controls, we used recordings of local birds (hornbills, *Bycanistes subcylindricus*; doves, *Streptopelia semitorquata*) or a plastic bag similar in size to the snake model. To avoid pseudoreplication, we used different recordings of a predator or male in each playback trial. We aimed for each subject to receive one trial of each of the seven experimental stimuli and one control, with ≥4 days between trials.

For playbacks we used an iPod Classic (Apple, Inc.) and a GO + PLAY Portable Loudspeaker (Harman Kardon International) at source amplitudes of ~90–105 dB measured from 2 m with an Extech Digital Sound Level Meter (Flir Systems). Trials began when a subject (and group) was resting or feeding, and only after we confirmed that no predator events, severe aggression, or male vocalizations had occurred ≤30 min before a trial. One observer monitored the subject, another checked the area for other groups or males, and one hoisted the speaker (in camouflage fabric) ~5 m up a tree, 30–50 m from (and outside the view of) the subject. We aborted trials if subjects appeared to detect the speaker prior to playback. Snake trials used the same protocol, with the model on the ground in a camouflage bag covered in leaves. When a subject moved to a position with unobstructed view, the experimenter, 25 m away, pulled a translucent line to drag the model slowly along the ground (Figure S3).

During trials, if the subject vocalized in response to the stimulus, we recorded data for call context the same as for naturally occurring calls (above). For trials in which the playback was a *boom* by another male, we conducted 3- and 20-min focal samples as for natural receiver responses (above).

## 2.6 | Male–female proximity data

In Period 2, during daily follows of adult females, we documented male–female proximity events (MFPs)—instances in which a male

and female came within 2 m of each other, initiated by either, and remained ≥3 s. Observers recorded start time (when subjects first came <2 m) and all subsequent affiliative (present for groom, groom, co-sit), mating (present, mount), and aggressive (threat, lunge, hit) behavior, and if the male *boomed* before the end time (when subjects separated to >2 m; Figure S4).

## 2.7 | Data analysis

We describe the analyses grouped by the different hypotheses and evidence examined. Analyses used R version 3.5.1 (R Core Team, 2018). All reported *p*-values were two-tailed, except where noted.

### 2.7.1 | Usage patterns

For each month, we used daily records to calculate each male's hourly *boom* rate and each group's number of sexually active females (we used two measures: average daily number of females observed copulating; month's total observed copulating plus those inferred to have copulated from timing of subsequent birth, assuming a 176 ± 14-day gestation; Pazol, Carlson, & Ziegler, 2002). We used linear mixed models (LMM; R function: lmer; with male identity as random effect because of repeated measures) to test whether males' *boom* rates varied with the number of sexually active females in their group. We used similar LMMs to test whether males' *boom* rates were higher in the June-October mating season than other months.

To characterize association with context, we examined the *boom's* usage relative to that of other call types in across vocal episodes (Table 2). Using only the contexts in which males vocalized (and not total time spent in each context, which we did not record), we tested whether *booms'* occurrence in some contexts was more than that expected if different call types were used randomly. If, in those instances that males did vocalize, different call types were used randomly, the *boom's* occurrence in each context (Table 2) should be predicted by its proportion of all vocal episodes. Thus, the expected occurrence of *booms* in a particular context ($B_C$) would be $B_N \times (V_C/V_N)$, where $B_N$ is the total number of *boom* episodes (in any context), $V_N$ is the total number of vocal episodes (any call type, any context), and $V_C$ is the number of episodes (any call type) in that context.

### 2.7.2 | Male receiver response

To identify differences in males' behavior after hearing a *boom* versus after not hearing any call, we used matched comparisons of AV and NV samples. We examined responses of non-resident and resident males separately and excluded responses by influx males because of low sample size. We matched each male's AV to a corresponding NV (hereafter: mNV): Matched AV-mNV pairs for a subject were conducted within 1–10 days of each other, at the same time of day (±2 hr) and with the subject (if resident male) in the same location relative to his group (In: within an imaginary circle centered on group's center of mass and containing 75% of

members; Out: >50 m beyond a circle encompassing ≥90% of members; or Edge). We examined data from responses to natural vocal episodes and playbacks of *booms* separately but similarly. As the sample size for non-resident males was relatively small, we also present an analysis of combined responses to playback and natural stimuli.

Using only those 3-min AV samples in which subjects moved >5 m, we used a binomial test to see whether male receivers moved away from the caller more than the 25% expected if movement away, toward, and each of two parallels were equally likely. To test whether males increased visual monitoring (scanning) after hearing *booms*, we used 20-min AV-mNV pairs: We modeled the proportion of each sample that included scanning (intervals/20) with a generalized additive mixed model (GAMM; R function: gamlss; with identity as random effect). These models are appropriate for proportional data and easily implement zero-inflated beta distributions. To identify the appropriate error distribution, we used a Cullen and Frey graph (a skewness-kurtosis plot; R function: descdist) and, because data included zeros and ones, modeled the association using the beta inflated distribution (R family: BEINF). For males' 20-min AVs only, we determined whether subjects ended the sample closer, farther, or the same distance relative to the call origin; we then used a binomial test to test whether receivers' likelihood of increasing distance to the call (end farther) was greater than the 33% expected if ending farther, closer, or the same were equally likely.

### 2.7.3 | Female receiver response

As with male receivers (above), we used matched AV-mNV pairs to compare behavior of females after hearing *booms* (by resident males of their own group only) versus no call.

Using only those 3-min AV samples in which subjects moved >5 m, we used a binomial test to see whether female receivers moved toward the caller more than the 25% expected by chance. To test whether females spent more time scanning after *booms* than in mNVs, we used a GAMM with 20-min AV-mNV pairs, as described above for male scanning. We used similar GAMMs to compare females' AVs versus mNVs for proportion of time (instantaneous *beeps*/20) spent with different numbers of neighbors (1–2, 3–4 and >4 neighbors).

Analyses treated some infrequent responses as binary for the entire sample. Specifically, we coded each 3-min sample "Y/N" for whether predator avoidance (flee followed by continued looking at ground or sky) occurred, and each 20-min sample for whether it included any time with the male as a neighbor, approaches, mating behavior, or ended with the female closer to the male. We then used mixed-effects logistic regressions (hereafter: GLMMs; R function: glmer, family: binomial; link: logit; fixed effect: sample type; random effect: identity), to compare females' likelihood in AVs versus mNVs to exhibit predator avoidance behavior and also to increase proximity to (end closer), approach, or have a sexual interaction with resident male.

To further assess female responses to *booms*, we also examined males' matched 20-min mNV and AV-Caller (after *booming*) samples,

using GAMMs to compare males' proportion of time spent with neighbors (1–2, 3–4, and >4). We used mixed-effects logistic regressions (GLMMs; R function: glmer; family: binomial; link: logit; fixed effect: sample type; random effect: identity) to test whether a male was more likely to be approached or have mating interactions with females after *booms* versus mNVs.

## 2.7.4 | Male–female proximity

We separated male–female proximity events into those in which the male *boomed* ($MFP_B$) or did not ($MFP_0$) and compared duration of time in proximity using a linear mixed model (LMM; R function: lmer; random effect: male identity). We treated some behavior as binary, coding the entire MFP "Y/N" for occurrence of affiliative, mating, or aggressive behavior. We tested whether likelihood of including these behaviors differed for $MFP_B$ versus $MFP_0$, using GLMMs as above (R function: glmer; family: binomial; link: logit; fixed effect: MFP type; random effects: male and female identities).

## 3 | RESULTS

Observers logged >12,000 observation hours with subjects over 12.5 months (Table S1). We documented 10,427 male vocal episodes, of which 49% included *booms*. Data were sufficient to assess context for 33% of all vocal episodes, including 25% of all *booms*. In April–December 2017, we observed 1,177 close

proximity interactions between adult males and females (MFPs). Below, we present results grouped by the different types of evidence examined.

## 3.1 | Boom rates and mating patterns

For resident males observed for ≥60 hr per month for 12 months ($n = 5$), the annual mean *boom* rate was 0.40 per hour (range: 0.23–0.57), but rates varied by season. During June–October (mating season), males' *boom* rates were significantly higher than in other months (Figure 1), with each male exceeding his own annual mean by 9% on average (range: −2% to 37%).

Although mating frequency exhibited seasonal variation, mating occurred throughout the year in all study groups. We tested, therefore, also whether resident males' *boom* rates varied with the number of sexually active females in their groups. To standardize comparisons of different males and groups, we centered each month's value for each male/group ($n = 5$) around their annual means (subtracted their mean monthly value). Monthly *boom* rates were positively associated with the total number of sexually active females in the group (Figure 1) and also the daily average number (LMM, $\beta$: 0.40, $t$: 4.69, $p < .001$).

## 3.2 | Call context

Of the male vocal episodes for which data were sufficient to assess context unambiguously ($V_N = 3,415$), 37% included *booms*
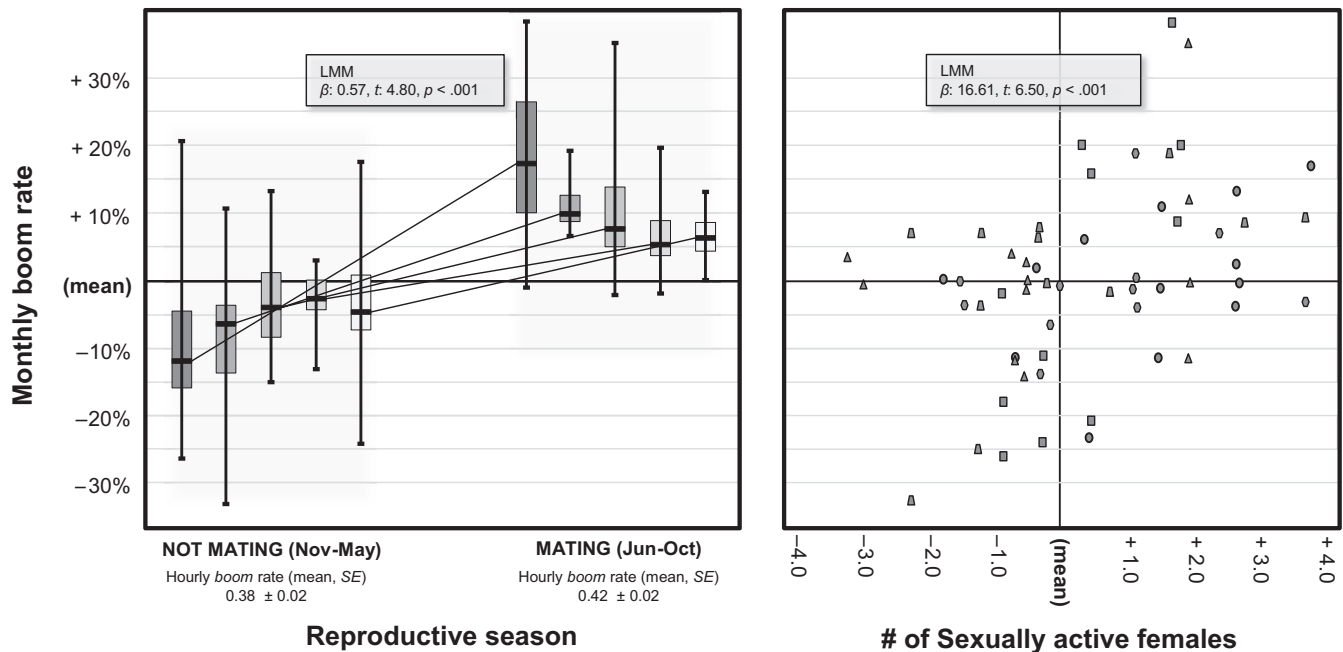


**FIGURE 1** Variation in resident males' ($N = 5$) monthly *boom* rates (per hour) in relation to reproductive season (*left*) and monthly variation in their groups' total number of sexually active females (*right*). Boxes (*left*) are different males' means and IQRs (whiskers show range). Shapes (*right*) are different males and their groups. All the values shown here (both axes) are each male's/group's divergence each month from their own annual mean

($B_N$ = 1,277). *Booms* occurred in all 14 of the contexts in which males vocalized (Table 2), and more than expected if use of different call types were random in four (Figure 2). Nearly 55% of *booms* occurred in non-disturbance contexts, and particularly in association with approaches and affiliative interactions (groom, co-sit) between the caller and groupmates. We also observed that *booms* regularly were preceded by nearby female(s) producing *long grunts*, low-frequency calls used exclusively by adult females when near or interacting with males (Audio S1). This pattern (noted also by Tsingalia & Rowell, 1984) was so consistent that observers often could "predict" *booms* from hearing *long grunts*. When nearing a male, females' behavior typically appeared solicitous—"hesitating" (alternating between advancing and retreating) and producing successively longer and louder *long grunts*—until the male *boomed* (Audio S1). Data from Period 2 showed that *long grunts* preceded 79% (26 of 33) of *booms* during MFPs. *Booms* occurred also in disturbance contexts, though more than expected by chance only during intragroup aggression and after branches falling nearby.

To supplement context data from naturally occurring episodes, we examined data from stimulus experiments similarly, yet separately. Experiments exposed 14 males, separately, to a simulated snake, eagle, dog, and another male nearby (using 1 of 4 call types), and also a control; due to time constraints, seven males each missed one experimental trial and five missed a control trial. Non-residents ($N$ = 7) never called during any of their 48 trials. Residents ($N$ = 7) never called in controls but did in 28 (62%) of the 45 experimental trials (Figure 3). Of the trials in which males produced any call, they *boomed* in 7 (25%), including with snakes and another male calling. *Booms* were <25% of vocal responses to trials with each stimulus except for hearing another male's *boom* (Figure 3), for which they were 100% of the responses ($N$ = 4) and significantly greater than 25% (expected if using *booms*' proportion of calls in experiments) or

37% (if using *booms*' proportion of naturally occurring call contexts; binomial tests, $p$ = .004, 0.02).

## 3.3 | Male receiver response

In 88 natural 3-min AVs, resident males ($N$ = 8) usually (86% of AVs) oriented toward the call in the first min after *booms* (Table 3). Males moved >5 m in 29 AVs and, of these, the direction was away from the call in 12 (41%), which was more than the 25% expected by chance; interestingly, movement toward the call was practically the same (45%; Table 3).

For 20-min samples, there were 150 matched AV-mNV pairs for eight residents. Males scanned more in AVs than in mNVs (Table 3). Residents ended samples farther from the call in 47% of AVs, which was more than the 33% expected if ending farther, closer, or the same were equally likely, and more than double the 18% of AVs in which males ended closer (Table 3). In playbacks of *booms* to residents ($N$ = 7), responses were similar to those for natural observations, but differences were significant for scanning only (Table 3).

Non-resident males' lower observation times (Table S1) and tendency be far away from calling males contributed to a small sample of observations after natural *booms*, reducing analytic power. We report, however, that non-residents, in ten 3-min AVs, oriented toward the call in 100% and, of the six in which they moved >5 m, moved away in 4 (67%), which was more than expected by chance (Table 3).

For 20-min samples, non-residents ($N$ = 9) had 30 AV-mNV pairs. Males scanned more in AVs than in mNVs (Table 3). Non-residents ended samples farther from the call in 8 (53%) AVs, which was quadruple the 13% in which they ended closer but not significantly more than the 33% expected by chance (Table 3). In playbacks of *booms*, non-residents' ($N$ = 6) responses were similar to those for natural observations, though differences were

**FIGURE 2** Naturally occurring *boom* episodes ($B_N$ = 1,277) observed in different contexts compared to the expected if association with context were random. Values are the proportion of all naturally occurring vocal episodes for each context category. Light shading shows episodes of any call type ($V_C$), with dark shading showing those with *booms* ($B_C$). Inset dotted lines indicate the expected proportion of *booms*, and stars indicate where *booms* occurred more than expected (Binomial tests). Vertical line separates contexts relating primarily to extragroup (*left*) versus within-group (*right*) events
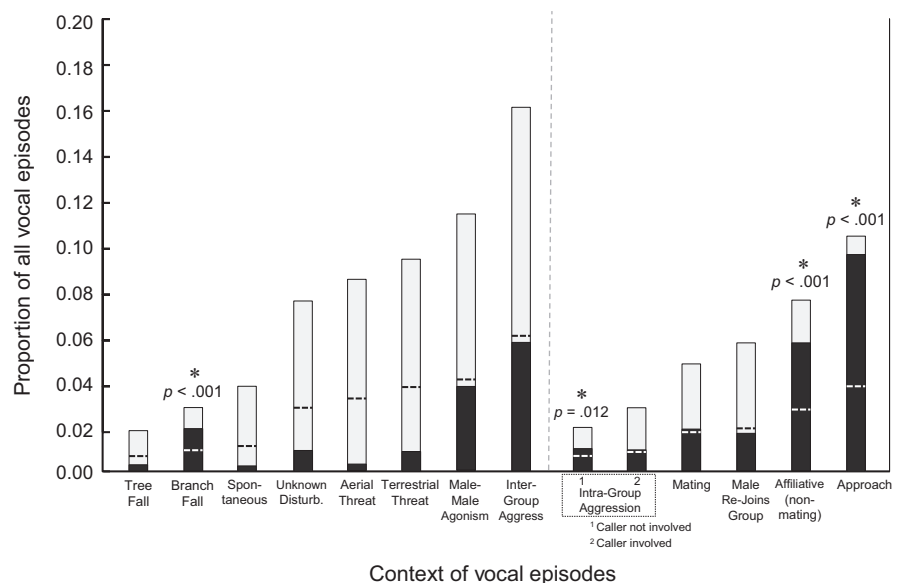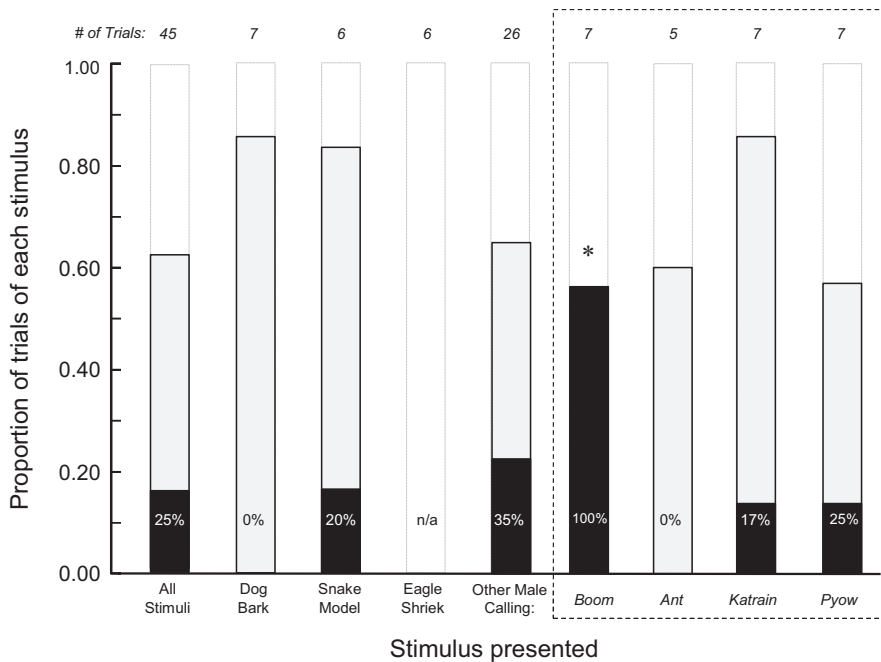
**FIGURE 3** Experimental stimulus trials (N = 45) for resident males (N = 7). Separate trials simulated another male nearby using recordings of different call types (in box). Columns show proportions of trials of each stimulus type in which subjects produced any call type (light shading) and *booms* (dark shading). Inset percentages indicate proportion of all vocal responses to each stimulus type that were *booms*

significant for scanning only (Table 3). Pooling data for non-residents' responses to playbacks and natural *booms* provided similar, but uniformly significant, results: In 3-min AVs (n = 16), males moved away in 7 of the 12 (58%) in which they moved >5 m, which was more than expected (binomial test, p = .01). In 20-min AV-mNV pairs (n = 21), non-residents scanned more in AVs (median, range: 60% of *beeps*, 45%–80%) than in mNVs (median, range: 45%, 20%–80%; GAMM, $\beta$: 1.3769, t: 3.152, p = .004), and ended AV samples farther from the call in 12 (57%), which was more than expected (binomial test, p = .02).

## 3.4 | Female receiver response

We examined responses of females to naturally occurring *booms* by resident males of their own group. In matched 3-min AV-mNV samples (Table 4), females' likelihood of predator avoidance behavior was the same after *booms* and after no calls. Females oriented to the call in the first min after *booms* in most (74%) AV samples. In the 71 AVs in which they moved >5 m, females moved toward the caller in 39 (55%), which was more than the 25% expected if direction were random (Table 4), and also more than away (20%) or parallel (25%).

In matched pairs of 20-min AV-mNV samples, females scanned the same amount after *booms* as in mNVs (Table 4). Females increased proximity (ended closer) to their resident male in 24% of AVs, which was more than the 9% in mNVs (Table 4). Females were more likely to have the male as a neighbor after he *boomed* (42% of AVs) than in mNVs (28%), and similarly were more likely to approach him after he *boomed* (7% of AVs) than in mNVs (4%), and to have mating interactions after *booms* (4% of AVs vs. 1% of mNVs; Table 4). Females spent roughly the same amount of time with 1–2 and 3–4 neighbors after *booms* and in mNVs. Time with >4 neighbors, however, was greater after *booms* than in mNVs (Table 4).

To further test whether females' interactions with a male differed after he *boomed*, we compared matched pairs of natural 20-min AV-Caller–mNVs of six resident males (Table 4). After *booming*, males had ≥1 female within 10 m longer than after no call. In particular, time with 3–4 and >4 females was much greater after *booming* than in mNVs, though the difference was significant for time with 3–4 neighbors only (Table 4). Males were more likely to be approached after *booming* than after no call, and also to have sexual interactions (Table 4).

We acknowledge that, as subjects' behavioral samples were used in multiple analyses, some of the above constitute repeated measures. Applying the Benjamini and Hochberg (1995) procedure with false discovery rates >0.056 did not change whether any results were significant.

## 3.5 | Male–female proximity

Of the 1,177 male–female proximity events, 3% included *booms*. Although the median duration of interactions with *booms* (113 s, range: 8–1361) was greater than those without *booms* (86 s, range: 3–2401), the difference was not significant overall (LMM, $\beta$: −3.68, t: −0.09, p = .93). MFPs that included *booms* (MFP$_B$) were more likely to include affiliative behavior than those without *booms* (70% of MFP$_B$ vs. 46% of MFP$_0$; GLMM, OR: 2.99, $\beta$: 1.10, z: 2.77, p = .01), yet the difference in likelihood of including mating behavior (12% of MFP$_B$; 11% of MFP$_0$) or aggression (0% of MFP$_B$; 2% of MFP$_0$) was not significant.

## 4 | DISCUSSION

Blue monkey resident males *boom* regularly and in a variety of situations, but most *booms* (>60%) relate to intragroup interactions

**TABLE 3** Results of analyses of male receivers' responses to hearing a *boom* by another male

| Resident male (N = 8) natural observation | 3-min AV (N = 88) | 20-min NV (N = 150) | 20-min AV (N = 150) | Test | p |
|---|---|---|---|---|---|
| Move away from call origin | 12 (41% of samples w/ movement) | n/a | n/a | Binomial test 1-tailed[†] | .039 |
| Visual monitoring (scanning) | n/a | Median: 37% of *beeps* Range: 30%–80% | median: 49% of *beeps* range: 25%–71% | GAMM $\beta$: 0.25, t: 2.41 | .017 |
| End farther from call origin | n/a | n/a | 71 (47%) | Binomial test 1-tailed[†] | <.001 |
| **Resident male (N = 7) Playbacks** | **3-min AV (N = 7)** | **20-min NV (N = 7)** | **20-min AV (N = 7)** | **Test** | **p** |
| Move away from call origin | 2 (50% of samples w/ movement) | n/a | n/a | Binomial test 1-tailed[†] | .26 |
| Visual monitoring (scanning) | n/a | Median: 39% of *beeps* Range: 10%–55% | median: 61% of *beeps* range: 35%–80% | GAMM $\beta$: 0.89, t: 2.50 | .034 |
| End farther from call origin | n/a | n/a | 4 (57%) | Binomial test 1-tailed[†] | .168 |
| **Non-Res male (N = 9) natural observation** | **3-min AV (N = 10)** | **20-min NV (N = 15)** | **20-min AV (N = 15)** | **Test** | **p** |
| Move away from call origin | 4 (67% of samples w/ movement) | n/a | n/a | Binomial test 1-tailed[†] | .038 |
| Visual monitoring (scanning) | n/a | Median: 45% of *beeps* Range: 25%–80% | Median: 60% of *beeps* Range: 45%–80% | GAMM $\beta$: 0.79, t: 5.72 | <.001 |
| End farther from call origin | n/a | n/a | 8 (53%) | Binomial test 1-tailed[†] | .084 |
| **Non-Res male (N = 6) playbacks** | **3-min AV (N = 6)** | **20-min NV (N = 6)** | **20-min AV (N = 6)** | **Test** | **p** |
| Move away from call origin | 3 (50% of samples w/ movement) | n/a | n/a | Binomial test 1-tailed[†] | .169 |
| Visual monitoring (scanning) | n/a | Median: 45% of *beeps* Range: 20%–50% | Median: 65% of *beeps* Range: 55%–80% | GAMM $\beta$: 1.09, t: 9.18 | .007 |
| End farther from call origin | n/a | n/a | 4 (67%) | Binomial test 1-tailed[†] | .097 |

[†]Test was 1-tailed because the prediction was specifically that males move away *more* than expected.

and the association with approaches between the caller and females is strong (Figure 2). Our study found no evidence that *booms* have an "alarm" function: Less than 4% of *boom* episodes were associated with predators (compared to 80% of *katrains*, 72% of *ants*; Fuller, 2014), and typical receiver responses were to feed or rest calmly. Instead, the results suggest the call's adaptive functions relate primarily to facilitating interactions between adult males and group members. Some characteristics of the *boom*, however, such as its long audible distance and the way it predictably follows *booms* by other males and also falling branches, suggest a more complex communicative role.

### 4.1 | Within-group cohesion

Group living, common in primates, provides benefits such as improved predator avoidance, resource acquisition, and mating opportunities (Rubenstein, 1978). Selection, however, does not directly favor "group living" (an emergent property of many individuals) but rather favors mechanisms that maintain mutual proximity and group

cohesion. Our results indicate that the *boom* is one such mechanism. After *booms* by their group's male, females tended to move toward him (observed also in *C. campbelli*; Ouattara et al., 2009) and subsequently spent more time in proximity to more neighbors (including the caller).

### 4.2 | Mate attraction

Results supported nearly every prediction for a mate attraction function (Table 1). Males *boomed* more during the mating season and when there were more sexually active females, and females were more likely to approach, spend time near, and—crucial to inferring sexual selection (Snowdon, 2004)—have mating interactions with a male after he *boomed*. Unlike signals that warrant a "courtship display" label (e.g., Túngara frog *whine*; Ryan, 1985), however, *booms* occurred regularly in many contexts and, though interactions typically followed, only a small portion (5%) included mating behavior. In group-living animals, male–female proximity can relate to non-reproductive functions such as foraging

**TABLE 4** Results of analyses of female receivers' responses to *booms* by their group's resident male

| Female receivers (N = 61) | 3-min NV (N = 226) | 3-min AV (N = 226) | 20-min NV (N = 597) | 20-min AV (N = 597) | Test | p |
|---|---|---|---|---|---|---|
| Predator avoidance | 19 (8%) | 23 (10%) | n/a | n/a | GLMM, OR: 1.23, z: 0.65 | .518 |
| Move toward caller | n/a | 39 (55% of samples w/movement) | n/a | n/a | Binomial test | <.001 |
| Visual monitoring (scanning) | n/a | n/a | Median: 25% of *beeps*, range: 7%–49% | Median: 25% of *beeps*, range: 11%–42% | GAMM, β: 0.03, t: 0.58 | .56 |
| End sample closer to resident male | n/a | n/a | 53 (9%) | 144 (24%) | GLMM, OR: 4.83, z: 7.83 | <.001 |
| Have male as neighbor | n/a | n/a | 167 (28%) | 253 (42%) | GLMM, OR: 1.94, z: 5.30 | <.001 |
| Approach male | n/a | n/a | 23 (4%) | 40 (7%) | GLMM, OR: 1.74, z: 2.07 | .039 |
| Have mating interaction with male | n/a | n/a | 6 (1%) | 24 (4%) | GLMM, OR: 4.42, z: 2.95 | .003 |
| Proportion of sample with 1–2 neighbors | n/a | n/a | Median: 36% of *beeps* | Median: 32% of *beeps* | n/a | n/a |
| Proportion of sample with 3–4 neighbors | n/a | n/a | Median: 28% of *beeps* | Median: 27% of *beeps* | n/a | n/a |
| Proportion of sample with >4 neighbors | n/a | n/a | Median: 19% of *beeps*, range: 0%–43% | Median: 24% of *beeps*, range: 6%–59%; | GAMM, β: 0.18, t: 1.97 | .048 |
| **Resident males (N = 6)** | | | **20-min NV (N = 522)** | **20-min AV-Caller (N = 522)** | **Test** | **p** |
| Approached by female | | | Median: 28% of samples, range: 11%–46% | Median: 39% of samples, range: 29%–62%; | GLMM OR: 1.89, z: 4.73 | <.001 |
| Have mating interaction | | | Median: 14% of samples, range: 4%–44% | Median: 22% of samples, range: 9%–46% | GLMM OR: 1.64, z: 3.21 | .001 |
| Time with any neighbors | | | Median: 61% of *beeps*, range: 21%–68% | Median: 79% of *beeps*, range: 62%–90% | n/a | n/a |
| Proportion of sample with 3–4 neighbors | | | Median: 16% of *beeps*, range: 7%–18% | Median: 26% of *beeps*, range: 21%–33% | GAMM β: 0.19, t: 2.41 | .016 |
| Proportion of sample with >4 neighbors | | | Median: 7% of *beeps*, range: 3%–23% | Median: 19% of *beeps*, range: 5%–37% | GAMM, β: 0.10, t: 0.86 | .393 |

*Note:* Lower table shows female responses recorded in samples of males after they *boomed*.

efficiency and predator avoidance, and any trait that enables or prolongs affiliative interactions likely achieves multiple benefits. Nonetheless, *booms* clearly increase the likelihood and duration of interactions with females, and thereby increase callers' opportunities to mate.

## 4.3 | Mate defense

Evidence that *booms* achieve a mate defense function was equivocal. Males *boomed* more in the mating season and when there were more sexually active females in their group, and thus when their reproductive success was most vulnerable to intrusions by extragroup males (Cords, 2002b; Roberts et al., 2014). When males vocalized in association with male–male agonism (12% of all vocal episodes), however, they typically produced *pyows* (>60%), *ants*, or *nasal screams* (Fuller & Cords, 2017); *booms* constituted <35% of the calls during encounters with other males (Figure 2) and then often appeared related to movement or calls by nearby females. Additionally, more than 54% of *boom* episodes occurred in affiliative or otherwise peaceful contexts and, in even more (>60%), the evoking stimulus or object of attention was a female near the caller, indicating that rival males are not, at a proximate level, a typical stimulus for *booms*.

*Booms*, however, are audible to conspecifics nearly a kilometer away (Brown, 1989), an acoustic property that relies on the air sacs that are much larger (and presumably costlier) in males than in females (Gautier, 1971; Figure S2). This sexual dimorphism suggests sexual selection (Andersson, 1994), though does not shed light on its source. Female mate choice might relate to some male attribute, such as energetic condition, that a quieter, less physically demanding signal could not reliably indicate. Because female blue monkeys are very familiar with their group's male and often near him when he *booms*, however, most of his attributes could be advertised without needing to be perceptible so far beyond his home range.

The *boom's* frequent usage and long audible distance, together with evidence that male receivers increased scanning and typically moved away after *booms*, are consistent with its functioning as an advertisement of occupancy, similar to calls in other taxa used to defend breeding territories (de Kort, Eldermire, Cramer, & Vehrencamp, 2008). Though nearby females might be the typical evoking stimulus, *booms* are simultaneously heard by more distant, rival males. By indicating a resident male's presence (and presumably attributes relevant to his fighting ability such as size or condition; Wyman, Mooring, Mccowan, Penedo, & Hart, 2008) near his group's females, *booms* might deter other males in the area, thereby reducing the threat of group takeover, infanticide, or "sneak" copulations (Cords, 2000; Cords & Fuller, 2010; Roberts et al., 2014). The observation that males often *boomed* in response to hearing another male's *boom* (Figure 3) is also consistent with "counter-calling," commonly considered a mechanism for territorial maintenance (Bradbury & Vehrencamp, 2011).

A noteworthy yet perplexing finding of our study is the consistent relationship between *booms* and falling branches. Branch falls were the context for less than 3% of all male vocal episodes, yet *booms* occurred in 76% of these (Figure 2). Unlike a whole tree falling (which, like predators, typically evoked *pyows* or *katrains*; Fuller, 2014), branches seem to pose little risk to the safety or cohesion of group members. Why falling branches, hardly "alarm-worthy" and so distinct from the social interactions associated with most *booms*, predictably evoke this call remains a puzzle. Any increase in call production might enhance its function as an advertisement of occupancy, yet the *boom's* association with branch falls is perhaps, at a proximate level, simply an evolutionary vestige—a holdover from a time the call had more or different functions—that selection has yet to extinguish.

The adaptive functions described above help explain why selection might favor callers' producing *booms*. Receivers' responses, however, must benefit receivers as well. For selection to favor consistent responses, a signal should exhibit concordance (sensu Fuller & Cords, 2017; association between signal features and attributes of signalers, including their perception of the surrounding environment) that is relevant to receivers' fitness. In future studies, we will examine concordance between *booms* and signaler attributes, but some are already self-evident.

The *boom's* concordance with social status—males in resident status (*n* = 17) *boomed* regularly, whereas non-residents (*n* = 16) never did—is consistent with previous findings that, for blue monkey males, producing any loud call is conditional on being established in a group (Fuller & Cords, 2017). In blue monkeys, like other *Cercopithecus* species that *boom*, it is only adult males that produce *booms* (Gautier, 1988; Lawes et al., 2013), making the call a reliable indicator of age-sex class. Additionally, and of particular relevance to its role in affiliative interactions, the *boom* might exhibit concordance with callers' behavior after calling (discussed below).

## 4.4 | Signal of benign intent?

In many species, some signals reliably indicate a caller's subsequent behavior (e.g., travel, Boinski & Garber, 2000; aggression, Searcy &

Beecher, 2009). Our observations suggest *booms* exhibit concordance with callers' likelihood of affiliative (or unlikelihood of aggressive) behavior, consistent with being a signal of benign intent. As Silk (2002) summarized, "unprovoked" within-group aggression (by males in particular) is common in primates, making "friendly" associations among groupmates difficult to maintain. Evolved signals that facilitate amicable interactions by reliably predicting non-aggression provide some solutions. In chacma baboons, for example, male–female interactions are more likely to be affiliative if males *grunt* as they approach females (Palombit, Cheney, & Seyfarth, 1999). Similarly, in chimpanzees, grooming interactions initiated by "lip-smacking" were longer and more reciprocal than those that were not (Fedurek, Slocombe, Hartel, & Zuberbühler, 2015).

In our study, more than 30% of observed *booms* were preceded immediately by a caller approaching or being approached by females. When nearing a male, females typically appeared solicitous yet hesitant and continued producing *long grunts* until the male *boomed* (Audio S1). Additionally, after *booming*, males spent more time near females and interactions were more likely to include affiliative behavior such as grooming. Though data on males' aggression rates would provide a more robust test, these patterns are consistent with *booms* exhibiting concordance with callers' likelihood of aggression.

In the aggregate, our results indicate *booms* achieve dual functions relating to within-group cohesion and male–male agonism. The concurrence of such disparate functions might appear unusual, especially for a signal evoked most often by within-group stimuli, but the efficiency of males' using one signal to address these distinct yet intertwined fitness concerns perhaps should be expected. It is, indeed, unlikely that any signal – especially a conspicuous one (such as a loud call)—will evolve with a singular function only. Loud calls, by definition, are perceived simultaneously by multiple receivers that vary in age, sex, and social relationship to the caller (Sih, Hanser, & McHugh, 2009). One signal, therefore, may achieve multiple functions by simultaneously evoking very different responses from multiple receivers (Berglund, Bisazza, & Pilastro, 1996; Charlton et al., 2007; Fuller & Cords, 2017) for whom the signal has different relevance to their fitness.

## CONFLICT OF INTEREST

None.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.