Original Article

Differences in combinatorial calls among the 3 elephant species cannot be explained by phylogeny

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Understanding why related species combine calls in different ways could provide insight into the selection pressures on the evolution of combinatorial communication. African savannah elephants (*Loxodonta africana*), African forest elephants (*Loxodonta cyclotis*), and Asian elephants (*Elephas maximus*) all combine broadband calls (roars, barks, and cries) and low-frequency calls (rumbles) into single utterances known as "combination calls." We investigated whether the structure of such calls differs among species and whether any differences are better explained by phylogenetic relationships or by socioecological factors. Here, we demonstrate for the first time that the species differ significantly in the frequency with which they produce different call combinations using data from multiple study sites. *Elephas maximus* and *L. africana* mostly produced roar–rumble combinations, whereas *L. cyclotis* produced a more even distribution of roar–rumble, rumble–roar, and rumble–roar–rumble combinations. There were also significant differences in favored structure among populations of the same species. Moreover, certain call orders were disproportionately likely to be given in particular behavioral contexts. In *L. africana*, rumble–roar–rumble combinations were significantly more likely than expected by chance to be produced by individuals separated from the group. In *E. maximus*, there was a nonsignificant trend for rumble–roar–rumbles to be given more often in response to a disturbance. Site-specific socioecological conditions appear more influential for call combination structure than phylogenetic history.

Key words: **combinatorial communication, comparative, elephant, syntax, vocal communication.**

INTRODUCTION

The potential parallels between human language and the ways in which nonhuman animals combine different calls together have led to much interest in the structure and function of such call combinations (Arnold and Zuberbühler 2006; Suzuki 2014; Hedwig et al. 2015; Engesser et al. 2016). Although some species combine vocal elements in multiple orders with different functions (Arnold et al. 2008; Engesser et al. 2015), others always combine the units in only one or a few of the possible orders (Hailman and Ficken 1986; Suzuki et al. 2016). Still other species produce many different permutations of the same components, but without any change in function (Kroodsma and Momose 1991). The reasons behind this variation in the degree to which species exploit call combinations remain poorly understood.

As with any behavior, similarities among the communication systems of different species can either result from common ancestry (homologs) or from convergence due to similar selection pressures (analogs) (Collier et al. 2014). Social selection pressures

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and nonsocial ecological pressures are themselves alternative axes of variation to consider in comparative studies of communication (Manser et al. 2014). Substantial evidence supports a link between social structure and vocal repertoire (Freeberg et al. 2012). For instance, in primates, vocal repertoire size is positively associated with both social group size and time spent grooming, and is a key predictor of evolutionary changes in time spent grooming (McComb and Semple 2005). Similarly, experimentally increasing or decreasing group size in Carolina chickadees (*Poecile carolinensis*) led, respectively, to an increase or decrease in the maximum potential information encoded in their combinatorial chick-a-dee calls (Freeberg 2006). Habitat can also have a profound effect on the evolution of vocal signals, by influencing the transmission properties of different sounds. For example, absorption and reflection of sound is greater in forests than in open environments, and thus species in forested habitat may be selected to produce lower frequency, longer duration vocalizations with less rapid modulation to enhance propagation (Ey and Fischer 2009). Comparing related species that differ in socioecological attributes is one means of understanding the evolution of communication systems (Collier et al. 2014). However, such an approach has not yet been used to study the evolution of call combinations.

The extant Proboscidea consist of 3 widely distributed and highly vocal species: the Asian elephant (*Elephas maximus*), African savannah elephant (*Loxodonta africana*), and African forest elephant (*Loxodonta cyclotis*) (Table 1). *Elephas maximus* occurs in multiple geographically isolated populations across south and southeast Asia (Leimgruber et al. 2003). *Loxodonta africana* is found in Eastern, Central, and Southern Africa with a small population in Mali (West Africa), whereas *L. cyclotis* primarily inhabits the rainforests of Central Africa with some small remnant populations in West Africa (Roca et al. 2001). *Loxodonta* and *Elephas* diverged an estimated 5–6 Ma (Thomas et al. 2000), whereas *L. africana* and *L. cyclotis* diverged at most 2.63 ± 0.94 Ma (Roca et al. 2001). Comparing combinatorial vocalizations in these species, which occupy different habitat types and exhibit different social organization, could help to identify the selection pressures on combinatorial communication.

Loxodonta africana is most commonly associated with grassy savannah habitat, but is also found in forest, scrub, and desert (Viljoen 1989; Galanti et al. 2006). By contrast, *L. cyclotis* is found almost exclusively in forests, although it also occurs at the transition zone between forest and savannah (Tchamba and Seme 1993; Roca et al. 2001; Maisels et al. 2013). *Elephas maximus* occurs in a variety of habitats, from rainforest (primarily in the south-eastern part of its range) to drier deciduous scrub jungle and grassland (primarily in India and Sri Lanka) (Leimgruber et al. 2003). For this study, data were collected from *L. cyclotis* populations in forest ecosystems, *L. africana* populations in savannah ecosystems, and an *E. maximus*

population occupying dry-deciduous scrubland (further described in Methods).

All elephants live in sexually segregated societies, where females and calves for the most part range separately from postadolescent males. Females exhibit differences in social structure across species and locations. *Loxodonta africana* in savannah environments exhibits multitiered societies with strong associations between members of the same core group and a high degree of connectedness within a population (Moss and Poole 1983; Wittemyer et al. 2005; de Silva and Wittemyer 2012). Core group members are usually close relatives, and closely affiliated core groups typically consist of related matrilines (Archie et al. 2011). *Elephas maximus* in southern Sri Lanka exhibits multiple levels of association as well with the closest social affiliates typically being matrilineal kin (Fernando and Lande 2000), but without the clear, hierarchical tiers of *L. africana* society. *Elephas maximus* also has smaller groups, weaker associations between social affiliates, and fewer social ties per individual than *L. africana* (de Silva et al. 2011; de Silva and Wittemyer 2012). Although less is known about the social structure of *L. cyclotis*, it appears to be the least visibly gregarious of the 3 species, with smaller group sizes and more fluid social ties within a wider network of associating individuals that are likely to be related (Fishlock and Lee 2013; Turkalo et al. 2013; Schuttler et al. 2014).

All 3 species produce a wide range of vocalizations, many of which appear to be identical or at least homologous between the 3 species (Stoeger and de Silva 2014). Moreover, both *L. africana* and *E. maximus* in captivity have demonstrated the capacity to imitate sounds outside their normal vocal repertoire (Poole et al. 2005; Stoeger et al. 2012). In addition to "trumpets," all elephants produce low-frequency tonal vocalizations, termed "rumbles" or "growls," and higher-frequency noisy broadband vocalizations called "cries," "husky cries," "barks," "roars," or "long-roars" (Nair et al. 2009; de Silva 2010; Poole 2011; Stoeger and de Silva 2014). *Elephas maximus* additionally produces a unique class of high-frequency vocalizations known collectively as "chirps" or as "squeaks" and "squeals" (Nair et al. 2009; de Silva 2010). In all elephant species, rumbles and noisy broadband calls can be given as stand-alone calls or as "combination calls," in which at least one rumble and one broadband call are produced together with no intervening silence (Stoeger-Horwath et al. 2007; de Silva 2010; Poole 2011). The lack of intervening silence distinguishes combination calls from mere repetition. The number and order of components in these combination calls is variable (Figure 1).

Currently, it is unknown how the functions of elephant combination calls relate to the functions of their components. In the wild, *E. maximus* produces bark–rumbles and roar–rumbles most commonly during movement and when searching for group members, which partially, but not completely, overlaps with the contexts in

Table 1

Ecological and social differences between the 3 species of elephant

Species	Geographic range	Habitat	Social behavior	Divergence time
Loxodonta africana	East, Central, Southern, and West Africa	Savannah, scrub, dry woodland, montane forest, desert	Large, tightly affiliated groups, hierarchically organized social tiers	2.63 Ma from *L. cyclotis*; 5–6 Ma from *E. maximus*
Loxodonta cyclotis	Central and West Africa	Rainforest, forest-savannah edge	Small core groups (mother–calf), unknown if hierarchical tiers exist	2.63 Ma from *L. africana*; 5–6 Ma from *E. maximus*
Elephas maximus	South and Southeast Asia	Rainforest, dry woodland, scrub, grassland	Medium sized, loosely affiliated groups, no clear hierarchical tiers	5–6 Ma from *Loxodonta* sp.
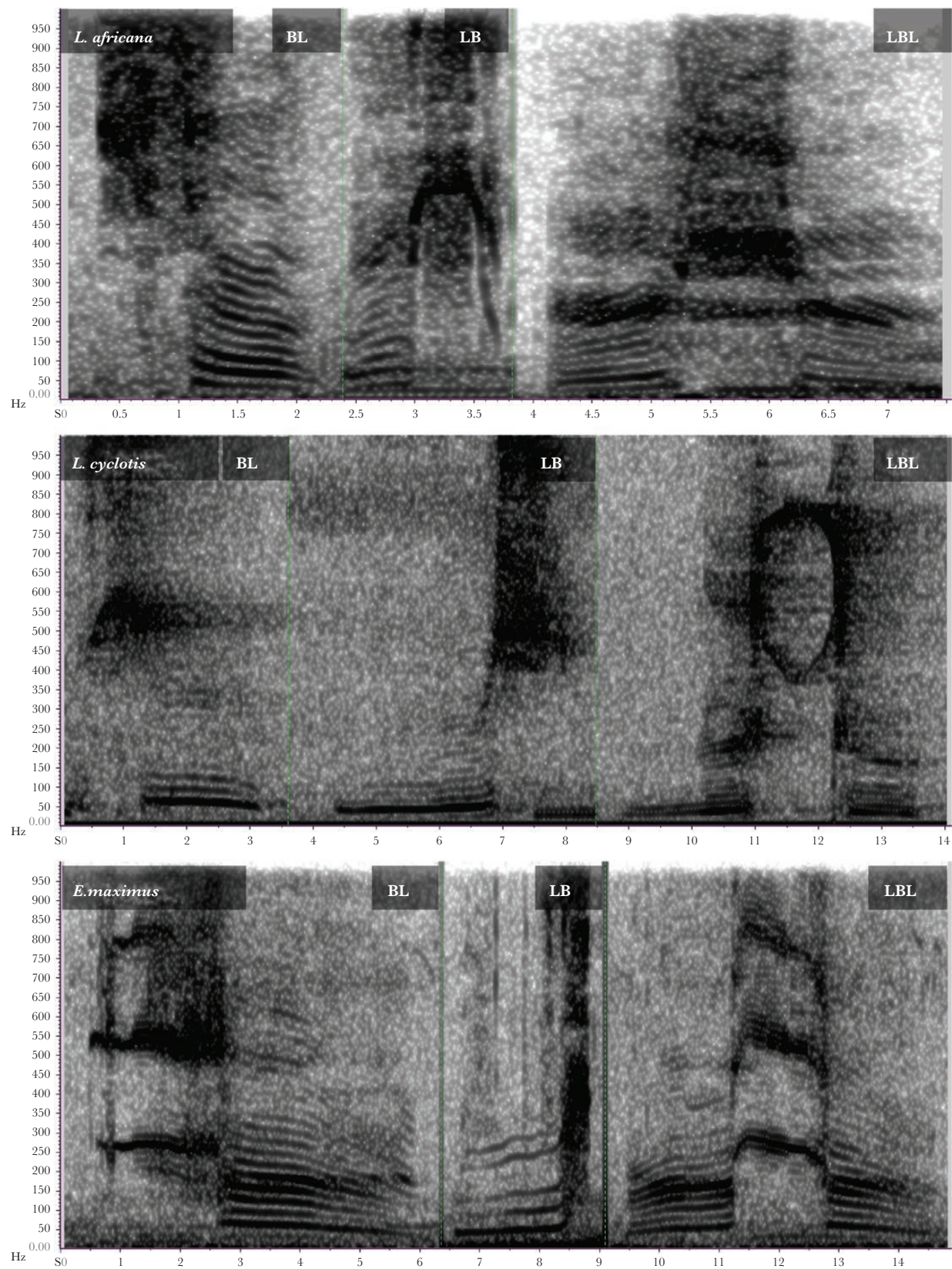
Figure 1

Sample combination calls of the 3 elephant species. All calls were converted to a 2 kHz sampling rate, and spectrograms created in Raven Pro 1.5 (Hann window, window size = 270 samples, overlap = 90%, Discrete Fourier Transform (DFT) = 512 samples). There is considerable variation in all of these call types within each species, not shown here. BL, broadband-low frequency (e.g., roar-rumble); LB, low frequency-broadband (e.g., rumble-roar); LBL, low frequency-broadband-low frequency (e.g., rumble-roar-rumble).

which stand-alone roars, barks, and rumbles are given (de Silva 2010). *Loxodonta africana* often produces rumble–roar–rumbles during intense social excitement, whereas stand-alone roars are more commonly produced during distress, and stand-alone rumbles are produced in almost every behavioral context (Poole 2011). However, it is not known whether combination calls have the same function as one of their components, a sum or average of the each of the constituent components' functions, or an entirely different function than their components. Because roars, long-roars, barks, cries, and husky cries may not contain reliable cues to individual identity while at least some types of rumbles are known to convey identity information (McComb et al. 2000), it has also been hypothesized that the rumble component of combination calls serves to add individual identity information to the broadband component of the call (Stoeger et al. 2011), but this remains untested. Furthermore, it is unknown whether the number or order of elements within a combination call affects its function.

We compared the order of combination calls in all 3 elephant species and investigated the relationship between call order and behavioral context for *L. africana* and *E. maximus*, the 2 species for which we had behavioral context data. We predicted that if call orders are phylogenetically conserved, *L. africana* and *L. cyclotis* should be more similar to one another than to *E. maximus*. We predicted that if combinatorial structures are shaped by social communication needs, then *L. cyclotis* and *E. maximus* should be more similar to one another than to *L. africana*, and if driven by habitat type, then the species should be distinct, but *L. africana* and the population of *E. maximus* in our study might be more similar to one another. We expected that if call order has functional relevance, there would be a relationship between call order and behavioral context.

METHODS
Recording methods and locations

Loxodonta africana
We recorded *L. africana* calls between 1984 and 1990 and between 1998 and 2006 in Amboseli, Kenya (Poole 2011). During 1998, we also recorded from elephants in Loisaba, Kenya and Maasai Mara, Kenya. The habitat at all 3 sites is open savannah grassland, with annual rainfall varying from 350 mm in Amboseli to 1400 mm in Maasai Mara. Recording took place only during daylight hours. Until 1990, we recorded on a Nagra IVSJ (Poole 1999); between 1998 and 2003, we used an HHB PDR 1000 DAT recorder at 44.1 kHz (frequency response: 8 Hz: −0.43 dB; 12 Hz: −0.26 dB; 15 Hz: −0.22 dB; 20 Hz: −0.15 dB; 60–1000 Hz no roll off); and after 2003, we recorded on a modified Nagra Ares BB (frequency response: 10 Hz: −1 dB; 20 Hz: −0.4 dB, 50 Hz: −0.2 dB, 100 Hz: −0.1 dB; 200–20 000 Hz no roll off). The majority of recordings were made with an Earthworks QTC1 omnidirectional microphone (frequency response: 4 Hz–40 kHz ± 1 dB). Using the sound analysis program SIGNAL RTSD (Engineering Design, Berkeley, CA), we acquired calls through a low-pass anti-alias filter and saved them to disk as .wav files for analysis.

We recorded elephants from a vehicle, recording continuously and using all-occurrence sampling for calls (Altmann 1974). Whenever a call was heard, we noted the elapsed time in the recording, the behavioral context, and when possible, the sex and age of the caller. In Amboseli, where the elephants are under long-term

study and are individually identified, we also noted the identity of the caller when possible. We categorized elephant age class as calf (0–4.9 years), juvenile (5–9.9 years), and adult (>10 years). We were able to identify the age class of the caller for 85.2% of the combination calls, the sex of the caller for 65.9% of the combination calls, and the individual identify of the caller for 39.8% of the combination calls. We identified at least 17 unique callers in Amboseli.

We also recorded *L. africana* calls from the Mushara waterhole in Etosha National Park, Namibia, in 2014 and 2015. The Mushara waterhole is located within sandveld habitat on the edge of a scrub desert, with a mean annual rainfall of about 460 mm. This waterhole is located 10 km away from the nearest other water source, so the site is a focal point for social interaction among elephant family groups and for conflict over access to the resource. We recorded at night from approximately 1700 to 0200 h, whenever family groups were present at the waterhole. Recordings were made using all-occurrence sampling (Altmann 1974) and were captured at distances of approximately 5–300 m. We placed a Neumann KM131 omnidirectional condenser microphone (frequency response: 20 Hz–20 kHz) 20 m from the waterhole and connected it via a shielded sound cable to a Tascam DA-P1 DAT recorder (sampling rate 48 kHz, 16 bits of amplitude resolution, frequency response: 4 Hz to 20 kHz ± 0.5 dB). An observer operated the recorder from a 7-m observation tower 80 m away from the waterhole. We collected a total of 35 h of recordings in 2014, and a total of 101 h of recordings in 2015. However, 79.4% of the combination calls were recorded in 2014. Age, sex, and behavioral context information were unavailable for these recordings.

Loxodonta cyclotis
We recorded *L. cyclotis* calls at a forest clearing within the forestry concession of the Compagnie Equatorial des Bois, Gabon (CEB1), on 41 different days between 14 April and 15 November 2009 (1–8 days/month). CEB1 is located in continuous low altitude mixed-species semievergreen rainforest with 2 wet seasons and 2 dry seasons per year and a mean annual rainfall of about 1431 mm. We also recorded at Bai Jobo, a forest clearing within Plateaux Batéké National Park, Gabon (Jobo), from 16 May to 15 June 2009 and from 6 June to 29 June 2010. Jobo is located in mixed-species semievergreen gallery forest adjacent to open savannah-scrub habitat with one long wet season and one dry season per year and a mean annual rainfall of about 1770 mm. CEB1 and Jobo are over 240 km apart and separated by the Ogooué River, so the elephants that visit these 2 locations are most likely from separate populations. Recordings were made with a custom-built autonomous recording unit (sampling rate 2 kHz, 12 bits of amplitude resolution), placed near the edge of the clearing and operating 24 h/day, except on 16 May 2009 and 6 June 2010 at Jobo, when the recorder was started at 1300 h, and on 29 June 2010 at Jobo, when the recording was stopped at 1159 h. Although we could not identify individual callers, individuals visit such clearings only a few times each year, for only a few days on each visit (Turkalo et al. 2013). Therefore, the sample probably includes many different individuals. Age and sex of callers were unknown. At CEB1, we collected a total of 984 h of recordings, and at Jobo, we collected a total of 755 h. Although the recorders ran 24 h/day (except on 16 May 2009, 6 June 2010, and 29 June 2010 at Jobo), at CEB1, 93.9% of combination calls were recorded at night (1800–0600 h), and at Jobo, 97.4% of combination calls were recorded at night.

Elephas maximus

We recorded *E. maximus* calls from January 2007 to December 2010, September to December 2011, January to August 2012, and February to June 2014 in Udawalawe National Park, Sri Lanka. Udawalawe contains a mix of grassland, dense scrub, and dry forest habitat with 2 wet seasons and 2 dry seasons per year and a mean annual rainfall of about 1500 mm. Recordings were made between 0600 and 1845 h from an open jeep using all-occurrence sampling (Altmann 1974), with a handheld Earthworks QTC50 microphone (frequency response: 3 Hz–50 kHz ±1.5 dB) and a Fostex FR-2 field recorder (sampling rate 22.5 or 48 kHz, 16 bits of amplitude resolution, frequency response: 20 Hz–20 kHz ±1 dB). Whenever possible, we recorded the individual identity, sex, and age of the caller. We recorded the behavioral context of calls using a mix of focal sampling (Altmann 1974) and ad libitum field notes. We categorized elephant age class as infant (0–2 years), juvenile (3–7 years), subadult (8–12 years and nulliparous for females), and adult (>10 years and parturient for females) based on either known age or height relative to that of an adult female (de Silva 2010). We were only able to individually identify the caller for 68 of 1034 combination calls (6.6%) and identified at least 37 unique callers. We were able to identify the age class of the callers for 35.1% of the calls (363/1034) and the sex of the callers for 13.3% of the calls (138/1034). One hundred and thirty of 138 combination calls from known-sex callers were produced by females, probably due at least in part to the greater sampling effort we devoted to female groups.

Call classification

We converted all recordings to a 2 kHz sampling rate and 16 bits of amplitude resolution using SoX 14.4-2.2 (sourceforge.net), the last date accessed is Feb. 6, 2019. We then created spectrograms of all the recordings (Hann window, window size = 438 samples, overlap = 90%, Discrete Fourier Transform (DFT) = 512 samples) using Raven Pro 1.5 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY). We defined a combination call as any combination of at least one rumble-like component and at least one bark, cry, or roar-like component in which the components are immediately adjacent to one another with no temporal overlap and no intervening silence. To facilitate unambiguous scoring of combination calls, we lumped all the rumble-like components of combination calls together as "L"s (low-frequency call elements) and all the bark, cry, and roar-like components together as "B"s (broadband call elements). The first author identified all combinations of Ls and Bs by eye and scored them according to their order. Any call combinations that could not be reliably scored (primarily due to extensive overlap with other calls) were not included in analysis. To cross-validate call classifications, we randomly selected 10% of the calls from each species and 4 other authors each scored one quarter of this subsample, while blind to the first author's classifications. The percent agreements between the first author and the other authors were 85.9%, 89.1%, 89.1%, and 95.3% (mean: 89.9%).

Behavioral context

We aggregated the behavioral contexts for *E. maximus* and the Kenyan populations of *L. africana* into the following 11 discrete categories: suckling, agonistic interaction, affiliative social interaction, disturbance, separation, calf requiring help, sexual behavior, playing, eating, moving, and resting (Table 2). Ten of these 11 contexts were observed in *E. maximus* (all except calf requiring help), and 7 of the 11 contexts were observed in *L. africana* (all except playing, eating, moving, and resting).

Table 2

Observed behavioral contexts of combination calls in Asian elephants and African savannah elephants

Behavioral context	Definition
Agonistic	Receiving or performing aggressive behavior
Disturbance	External disturbance: humans, lions, canids, etc.
Eating	Grazing or browsing
Moving	Any movement that does not fit into another category
Playing	Calves mounting, chasing each other or running around with no apparent purpose
Requiring help	Calf in distress (e.g., stuck in ditch)
Resting	Standing still with no other obvious behaviors
Separation	Separated from group and attempting to rejoin
Sexual behavior	Copulation, sexual behavior chase, females reacting to another female copulating (mating pandemonium), or females reacting to musth bull
Social affiliation	Touching one another nonaggressively, greeting one another
Suckling	Calf attempting to suckle

We excluded from analysis all contexts observed less than 5 times. Thus, "eating," "playing," and "calf requiring help" were excluded from analysis altogether, and "disturbance" was excluded from analysis for *L. africana* because it was only observed 3 times in this species. No behavioral context information was available for *L. cyclotis* on a per-call basis, but most of the contexts observed for *L. africana* are typically observed in forest clearings.

Noncombination calls

To compare the rate of occurrence of combination calls (of any order) to the rate of occurrence of their stand-alone components, we also assessed the number of stand-alone rumbles, stand-alone roars, and stand-alone barks/cries in Amboseli, Etosha, CEB1, Jobo, and Udawalawe, the 5 populations for which we had a substantial amount of data. To assess the rate of occurrence of combination calls relative to other call types in Amboseli (*L. africana*), we used the ElephantVoices database (Poole 2011), which contains most of the calls recorded over the course of a long-term study at Amboseli classified by general call type. The ElephantVoices database overlaps substantially with the set of Amboseli recordings used in our analyses of combination call order; however, some of the combination calls from Amboseli that we included in our analyses of call order had not yet been entered into the ElephantVoices database at the time of writing. To assess the rate of occurrence of combination calls relative to other call types in Udawalawe (*E. maximus*), we used the numbers reported in de Silva (2010), which also partially overlaps with the recordings used in our analyses of combination call order. For Etosha (*L. africana*), CEB1 (*L. cyclotis*), and Jobo (*L. cyclotis*), the first author manually identified and classified non-combination calls from a subset of our data, according to descriptions in the literature (Poole 2011). All of the Mushara recordings from 2014 (24.9% of the Mushara recording time) were manually searched for non-combination calls. In CEB1, all recordings from 14 April 2009 (2.4% of the CEB1 recording time) were searched for non-combination calls, and in Jobo, all recordings from 9 June 2010 at 1300 h through 23 June 2010 at 0445 h (45% of the Jobo recording time) were searched for non-combination calls. We searched a much higher percentage of the Jobo recordings because vocalizations occurred less frequently at Jobo than at

CEB1 during our sampling periods. To compare rates of occurrence of combination calls and other call types, we also counted the number of combination calls (of any order) within the data subsets that we searched for non-combination calls.

In the Udawalawe data, we combined calls originally scored as "growls" and "rumbles" into a single "rumble" category, so that they would be more directly comparable with the data from other populations, where no distinction was made between growls and rumbles. Similarly, we combined the "roars" and "long-roars" in the Udawalawe data set into a single "roar" category. We also combined barks and cries into a single category due to uncertainty about the difference between these call types.

Statistical analysis

All statistical tests were conducted in R 3.4.3 (R Core Team 2018). For all chi-square tests, we calculated a permutation-based (simulated) *P* value with 2000 replications. We used this approach because it is nonparametric and makes no assumptions about the underlying distribution of the data. Significance level was chosen to be 0.05 for all tests.

Caller age and sex

Using the existing data on caller age in the ElephantVoices database (Amboseli) and in de Silva (2010) (Udawalawe), we conducted permutation-based chi-square tests to determine whether age classes differed in their propensity to produce combination calls compared with other call types. We tested these 2 populations separately because the age classification systems for *L. africana* and *E. maximus* were not directly comparable. We did not have age information for Etosha, CEB1, or Jobo. We also used permutation-based chi-square tests to investigate whether age class or sex was related to call combination order in *E. maximus* and *L. africana*, considering each species separately.

Comparing call order across species and populations

We used permutation-based chi-square tests to determine whether the relative proportions of each combination call order differed between species and populations. We first compared the proportions of each combination call order in the 3 species, with all populations of a single species combined together. We then conducted all 3 possible pairwise comparisons of species, again with all populations of the same species pooled. Finally, we compared the 2 *L. cyclotis* populations (CEB1 and Jobo) to each other and also compared the Amboseli and Etosha populations of *L. africana*. As we only recorded a total of 11 combination calls from Loisaba and Maasai Mara combined, these populations could not be compared. Combination calls other than "BL" (broadband–low frequency), "LB" (low frequency–broadband), and "LBL" (low frequency–broadband–low frequency) were very rare, so we aggregated all other orders into a single category called "other."

Call order and behavioral context

We used permutation-based chi-square tests to examine the relationship between call order and behavioral context in *L. africana* and *E. maximus* separately. We then conducted a series of post hoc Fisher's Exact tests to examine the relationships between specific call orders and each behavioral context within each species. For each of the 5 behavioral contexts with at least 5 observations in *L. africana*, we constructed a 2 × 2 contingency table with call order scored as either "BL" or "other" and behavioral context scored as either the context of interest or "other." We did the same for the

call order "LBL," for a total of 10 contingency tables for *L. africana*. We constructed sixteen 2 × 2 contingency tables for *E. maximus*, 8 for BL by each of the 8 behavioral contexts that had at least 5 observations, and another 8 for LBL. We did not conduct post hoc tests for the call order LB because there were too few LBs with a known behavioral context (5 in *L. africana* and 2 in *E. maximus*).

To determine whether *L. africana* and *E. maximus* differed in terms of which call orders were associated with which contexts, we conducted a Cochran–Mantel–Haenszel test on call order by behavioral context with species as the stratifying variable. We then conducted post hoc Fisher's Exact tests to examine how *L. africana* and *E. maximus* differed with respect to the prevalence of a specific call order within a given behavioral context. Each 2 × 2 contingency table was constructed using the observations from only a single behavioral context, with the rows "call order of interest" and "all other call orders" and the columns "*L. africana*" and "*E. maximus*." We constructed such contingency tables for both BL and LBL and for each of the behavioral contexts with at least 5 observations in both *L. africana* and *E. maximus* (agonistic, separation from group, sexual behavior, affiliative social interaction, and suckling).

For the chi-square and Cochran–Mantel–Haenszel tests examining the relationship between call order and behavioral context, we excluded combination calls with any order other than BL, LB, or LBL, as there were very few such calls with a known context. However, for the post hoc 2 × 2 Fisher's Exact tests, call order was condensed into a binary variable (call order of interest vs. all other orders), so we did include rare combination orders, lumping them in with the "all orders besides the order of interest" category. Because we conducted a total of 51 statistical tests, we adjusted the *P* values for all tests using the false discovery rate (FDR) method to control for multiple comparisons.

RESULTS

Observed call combinations

We recorded a total of 156 combination calls from *L. africana* (77 from Amboseli, 1 from Loisaba, 10 from Maasai Mara, 68 from Etosha). We recorded a total of 1177 combination calls from *L. cyclotis*, with 564 recorded at CEB1 and 613 recorded at Jobo. We recorded a total of 1034 combination calls from *E. maximus*. We observed 8 different call combinations across the 3 species: "BL," "LB," "LBL," "BLB," "BLBL," "BLBLB," "LBLB," and "LBLBL," although BL, LB, and LBL accounted for 98.5% of all observed combination calls.

Combination calls versus other call types

The proportion of combination calls relative to their stand-alone components varied across populations, with combination calls occurring most frequently in Udawalawe (*E. maximus*) and least frequently in Amboseli (*L. africana*). In all populations, stand-alone rumbles were far more common than combination calls, ranging from 6.4 times more common in Udawalawe to 75.9 times more common in Amboseli. However, stand-alone roars, barks, and cries collectively occurred at a more comparable rate to combination calls (Table 3).

Caller age and sex

Young individuals were disproportionately likely to produce combination calls. According to the ElephantVoices database, in the Amboseli population of *L. africana* combination calls comprised

2.4% of vocalizations produced by calves (<5 years) and 2.8% of vocalizations produced by juveniles (5–9.9 years), but only 0.4% of the vocalizations produced by adults (>10 years) (chi-square test, $\chi^2 = 193.0$, $N = 3526$ calls, FDR-adjusted simulated $P = 0.004$). Similarly, according to de Silva (2010), in the Udawalawe population of *E. maximus* combination calls comprised 14.3% of vocalizations produced by infants (0–2 years), 28.2% of vocalizations produced by juveniles (3–7 years), 8.5% of vocalizations produced by subadults (8–12 years and nulliparous for females), and 7.9% of vocalizations produced by adults (>10 years, and parturient for females) (chi-square test, $\chi^2 = 30.5$, $N = 3921$ calls, FDR-adjusted simulated $P = 0.004$). However, age was not significantly associated with the order of combination calls in either species (*L. africana*: chi-square test, $\chi^2 = 1.6$, $n = 75$ calls, FDR-adjusted simulated $P = 1.00$;

E. maximus: chi-square test, $\chi^2 = 7.7$, $n = 363$ calls, FDR-adjusted simulated $P = 0.93$). Sex was also not significantly associated with call order in either *L. africana* (chi-square test, $\chi^2 = 1.9$, $n = 58$ calls, FDR-adjusted simulated $P = 0.83$) or *E. maximus* (chi-square test, $\chi^2 = 7.7$, $n = 138$ calls, FDR-adjusted simulated $P = 0.45$).

Species and population differences in combination call order

The 3 species of elephants differed significantly in the relative proportions of each combination call when different populations of the same species were pooled together (chi-square test, $\chi^2 = 772.1$, $N = 2367$ calls, FDR-adjusted simulated $P = 0.004$) (Figure 2). Although *L. africana* and *E. maximus* both heavily favored BL calls and produced more LBL calls than LBs, these 2 species differed significantly from one another, with BLs forming an even higher proportion of combination calls in *E. maximus* than in *L. africana* (chi-square test, $\chi^2 = 43.1$, $n = 1190$ calls, FDR-adjusted simulated $P = 0.004$). *Loxodonta cyclotis* differed much more markedly from the other 2 species, with a far lower proportion of BLs (*L. cylotis–L. africana*: $\chi^2 = 99.5$, $n = 1333$ calls, FDR-adjusted simulated $P = 0.004$; *L. cyclotis–E. maximus*: $\chi^2 = 746.9$, $n = 2211$ calls, FDR-adjusted simulated $P = 0.004$).

The *L. africana* populations from Amboseli and Etosha also differed significantly from one another (chi-square test, $\chi^2 = 9.0$, $n = 145$ calls, FDR-adjusted simulated $P = 0.04$), with Amboseli exhibiting a lower proportion of BLs (Amboseli: 0.65, Etosha: 0.82) and a higher proportion of LBLs (Amboseli: 0.29, Etosha: 0.09)

Table 3

Number of combination calls and stand-alone rumbles, roars, barks, and cries in a sample of recordings from each of 5 elephant populations
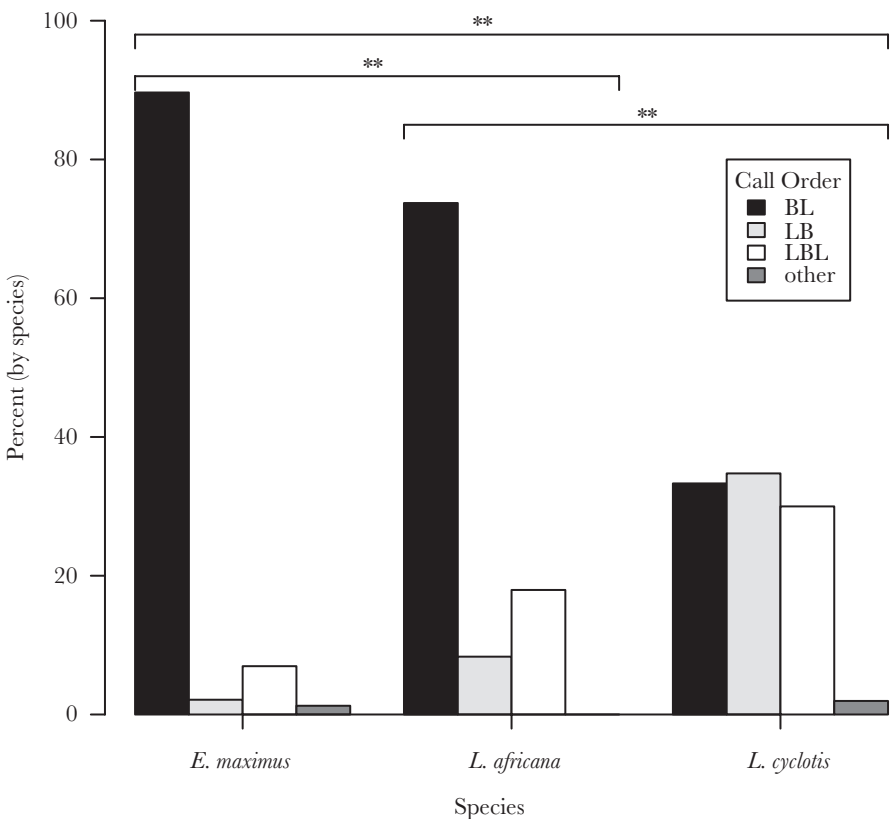
Population	Rumbles	Roars	Barks/cries	Combination calls
Amboseli	3186	85	23	42
Etosha	1223	20	12	56
CEB1	998	54	17	91
Jobo	1801	126	4	71
Udawalawe	2731	203	39	426

Figure 2

Relative percentages of each observed combination call in the 3 elephant species. BL, broadband–low frequency (e.g., roar–rumble); LB, low frequency–broadband (e.g., rumble–roar); LBL, low frequency–broadband–low frequency (e.g., roar–rumble–roar). The percentages add up to 100% within each species. **$P < 0.005$.

(Figure 3a). The 2 *L. cyclotis* populations were also significantly different (chi-square test, $\chi^2 = 50.3$, $n = 1177$ calls, FDR-adjusted simulated $P = 0.004$). BL was the least common of the 3 major combination calls in CEB1, and the most common combination in Jobo, although not nearly to the degree seen in *L. africana* and *E. maximus* (Figure 3b).

Behavioral context

The overall relationship between combination call order and behavioral context in *L. africana* was nonsignificant after correcting for multiple comparisons (chi-square test, $\chi^2 = 20.3$, $n = 74$ calls, FDR-adjusted simulated $P = 0.097$). However, in the specific context of separation from the group in *L. africana*, LBLs were significantly more frequent than expected by chance (Fisher's Exact test, odds ratio = 0.19, $n = 74$ calls, FDR-adjusted $P = 0.04$) and BLs showed a marginally nonsignificant trend toward being less frequent than expected by chance (Fisher's Exact test, odds ratio = 4.8, $n = 74$ calls, FDR-adjusted $P = 0.055$) (Figure 4).

Similarly, the overall relationship between call order and context in *E. maximus* was not significant after correcting for multiple comparisons (chi-square test, $\chi^2 = 22.3$, $n = 125$ calls, FDR-adjusted simulated $P = 0.19$). However, despite being the most common combination call in every behavioral context in *E. maximus*, BLs showed a marginally nonsignificant trend toward being less frequent than expected by chance in the specific context of external disturbance (usually a noisy vehicle, a jackal [*Canis aureus*], or a stray dog [*Canis lupus familiaris*]) (Fisher's Exact test, odds ratio = 0.30, $n = 132$ calls, FDR-adjusted $P = 0.055$).

Conversely, LBLs showed a nonsignificant trend toward being more frequent than expected by chance in this context (Fisher's Exact test, odds ratio = 3.1, $n = 132$ calls, FDR-adjusted $P = 0.097$) (Figure 4).

There was no overall difference between *L. africana* and *E. maximus* in the distribution of call orders across behavioral contexts after correcting for multiple comparisons (Cochran–Mantel–Haenszel test, $M^2 = 14.2$, df = 8, $n = 131$ calls, FDR-adjusted $P = 0.19$). However, in the specific context of separation from the group, *L. africana* was significantly more likely than *E. maximus* to produce LBLs (Fisher's Exact test, odds ratio = 11.6, $n = 34$ calls, FDR-adjusted $P = 0.02$), and *E. maximus* was significantly more likely than *L. africana* to produce BLs (Fisher's Exact test, odds ratio = 0.07, $n = 34$ calls, FDR-adjusted $P = 0.007$). Similarly, in the context of affiliative social interaction, there was a marginally nonsignificant trend for *L. africana* to produce a higher proportion of LBLs than *E. maximus* (Fisher's Exact test, odds ratio = ∞, $n = 30$ calls, FDR-adjusted $P = 0.06$) and for *E. maximus* to produce a higher proportion of BLs than *L. africana* (Fisher's Exact test, odds ratio = 0, $n = 30$ calls, FDR-adjusted $P = 0.06$).

DISCUSSION

All 3 species of elephants primarily produced the same 3 call combinations (BL, LB, and LBL), despite the fact that other combinations are clearly possible. However, species and populations differed significantly in the relative proportions of these combinations. Although *L. cyclotis* produced a comparatively uniform distribution
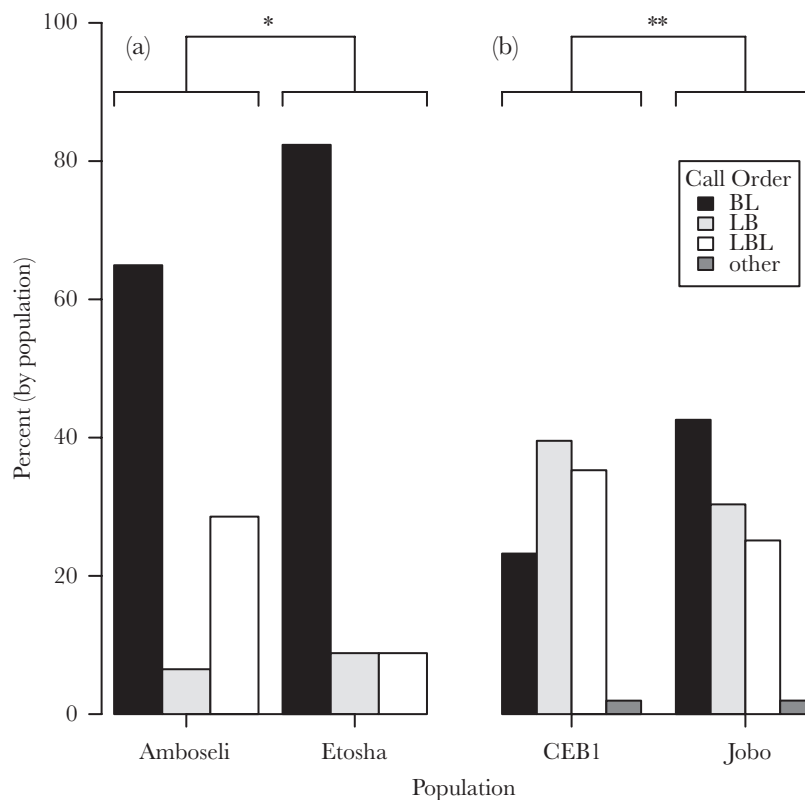
Figure 3

Relative percentages of each observed combination call in each population of *Loxodonta africana* (a) and *Loxodonta cyclotis* (b). BL, broadband–low frequency (e.g., roar–rumble); LB, low frequency–broadband (e.g., rumble–roar); LBL, low frequency–broadband–low frequency (e.g., roar–rumble–roar). The percentages add up to 100% within each population. *$P < 0.05$, **$P < 0.005$.
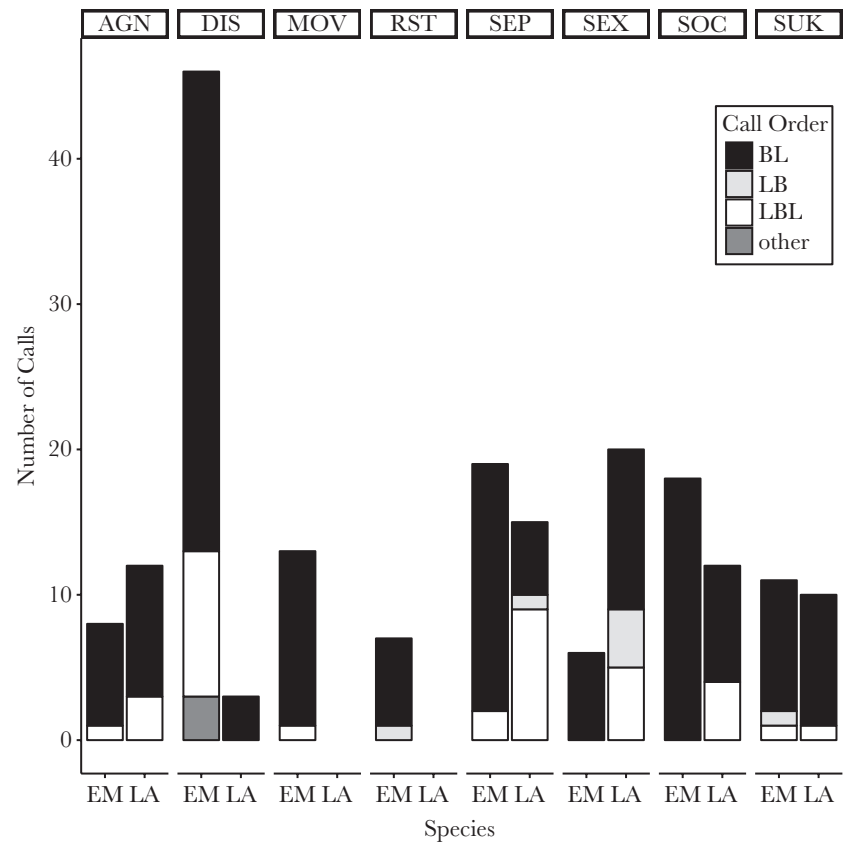
Figure 4

Number of combination calls of each order observed in each behavioral context within *Elephas maximus* (EM) and *Loxodonta africana* (LA). AGN, agonistic; DIS, disturbance; MOV, moving; RST, resting; SEP, separation; SEX, sexual behavior; SOC, social affiliation; SUK, suckling. EAT (eating), PLY (playing), and RHL (requiring help) had fewer than 5 observations each, so they are not included in the graph.

of BLs, LBs, and LBLs, the other 2 species produced mostly BLs (see also Herler and Stoeger 2012). *Loxodonta africana* in Amboseli produced 29% LBLs, which is comparable to *L. cyclotis*, but unlike *L. cyclotis*, produced very few LBs. *Elephas maximus* and the Etosha population of *L. africana* produced very few combinations of any order other than BL. The fact that *L. cyclotis* was the outlier among the 3 species indicates that site-specific factors probably exert a greater influence on combination call structure than phylogenetic relationships.

Because our *L. cyclotis* recordings were recorded primarily at night in forest clearings (*bais*) where elephants gather to access mineral licks and socialize (Turkalo and Fay 1995; Klaus et al. 1998; Fishlock and Lee 2013), it is possible that certain behavioral contexts, and therefore certain combinatorial sequences, were over- or underrepresented in our sample compared to sites with more spatially diffuse resources where we recorded during the day. However, our *L. africana* recordings from the Mushara waterhole in Etosha were also made at night at a spatially concentrated resource. On this basis, we might expect *L. cyclotis* to be more similar to Etosha than to Amboseli, but in fact, the opposite was observed. Similarly, although the recording protocol for Udawalawe was most similar to Amboseli (daytime recording, spatially diffuse resources, mobile observers), the relative proportions of combination call orders in Udawalawe more closely resembled those of Etosha. Thus, sampling protocols alone are unlikely to explain the observed differences among species and populations.

Habitat could potentially explain why the forest-dwelling *L. cyclotis* differed so markedly from the other 2 elephant species, which in this study were both recorded at sites with relatively open habitat. Open environments are windier than forest, and wind disproportionally masks low frequencies (Garstang 2004), so perhaps elephants in more open environments are selected to produce broadband components first to help draw attention to the subsequent low-frequency rumble (Richards 1981). However, it is also possible that the unique distribution of call orders observed in *L. cyclotis* corresponds to social interactions that are poorly understood in this cryptic species.

The fact that certain call orders were more likely to occur in particular behavioral contexts suggests that different call orders may have different functions, at least in *L. africana* and *E. maximus*. Motivation-structure rules predict that broadband vocalizations with nonlinear phenomena, such as elephant roars and combination calls, will be used to signal emotional arousal (Morton 1977), and stand-alone roars have previously been found to signal arousal in infant *L. africana* (Stoeger et al. 2011). A distinct possibility is that in both *L. africana* and *E. maximus*, combination calls signal emotional arousal, with LBLs signaling a higher level of arousal than BLs. The fact that *L. africana* was most likely to produce LBLs in the context of separation from the group, whereas *E. maximus* was most likely to produce LBLs in the context of disturbance by a vehicle, jackal, or dog can be explained if separation from the group is more distressing on average for *L. africana* than for the *E. maximus* population in our study. This is very plausible, given that *L. africana*

groups are more cohesive than *E. maximus* groups (de Silva and Wittemyer 2012), and isolated *L. africana* are susceptible to large predators such as lions that do not exist in Sri Lanka (Joubert 2006). In *L. africana*, LBLs have previously been reported to be associated with intense social excitement such as "greeting ceremonies" and "mating pandemonium" (Poole 2011), which is also consistent with the hypothesis that LBLs signal intense emotional arousal. It is also worth noting that *E. maximus* produces a class of calls (squeaks and squeals) that are unique to this species, and are most often given in high-arousal contexts, including disturbance (de Silva 2010). The low incidence of LBLs in *E. maximus* relative to the other species could potentially be due to functional redundancy with squeaks and squeals.

Age class was not significantly related to the order of combination calls, at least in *L. africana* and *E. maximus*, so population age structure is unlikely to explain the observed population differences in call order. However, the fact that calves were more likely than adults to produce combination calls of any order is noteworthy in its own right. It has been hypothesized that because adult Asian elephants often ignore calf vocalizations, calves may be selected to produce roars or combination calls in situations where adults would use rumbles, as the former have more nonlinear phenomena, which makes them more difficult to habituate to (Fitch et al. 2002; Poole 2011; Stoeger et al. 2011; Herler and Stoeger 2012). Alternatively, combination calls produced by calves could be a form of "babbling" as they learn adult vocalizations, similar to human infants and young songbirds (Brainard and Doupe 2002). Elephants are known to have the capacity for vocal production learning, although it is unknown how or if this ability manifests outside captivity (Poole et al. 2005; Stoeger et al. 2012).

Understanding the function of elephant combination calls could help determine how they relate to the evolution of language. Combinatorial signals can be broadly classified into phonological combinations, idioms, compositional (a.k.a. lexical) expressions, and signals with affixes (Collier et al. 2014; Griesser et al. 2018). Phonological combinations are composed of elements with no inherent meaning on their own, recombined to form multiple signals with different meanings. Idioms, sometimes considered a subcategory of phonological combinations (Collier et al. 2014), are composed of elements that have meaning in isolation but fail to retain their original meanings when combined. In compositional expressions, the individual elements have stand-alone meaning, and the meaning of the combined signal is derived from the meanings of its components. Affixes are vocal elements that do not occur in isolation, but can be added to stand-alone signals to modify their meanings in a consistent way. This is sometimes considered a type of compositional expression (Collier et al. 2014).

Elephant combination calls may be idioms or compositional expressions, as the L and B elements appear very similar to meaningful stand-alone calls (rumbles and roars/barks/cries, respectively). However, when concatenated with a B element, the edge of an L element often sweeps up in frequency to grade into the B, such that the frequency contours of most L elements differ from that of a typical stand-alone rumble. Thus, it is unclear whether the components of combination calls are functionally equivalent to their stand-alone counterparts. Alternatively, the rumble-like (L) components of combination calls could be affixes modifying a roar, bark, or cry, similar to the way in which Campbell's monkeys (*Cercopithecus campbelli*) add "-oo" suffixes to alarm calls to alter their meaning (Ouattara et al. 2009). For example, if combination calls and roars both signal emotional arousal (Stoeger et al. 2011), the number and/or position of the L elements in a combination call might modify the signal's intensity.

Combinatorial signals can further be classified according to whether the order of the elements affects the signal's meaning (syntax) or not (syntax free) (Griesser et al. 2018). Given the associations between call order and behavioral context in both *L. africana* and *E. maximus*, combination calls in these 2 species (especially *L. africana*) are probably not syntax free, although playback experiments are necessary to conclusively determine whether order is functionally significant. A number of other species produce vocal combinations in which the order of the components is critical to the meaning of the signal. For example, Japanese tits (*Parus minor*) produce a call combination of an ABC call followed by a D call, which causes receivers to simultaneously scan their surroundings and approach the caller. If the tits are presented with an artificial sequence in reverse order, they do not respond appropriately, indicating that order is integral to meaning (Suzuki et al. 2016). However, Japanese tits naturally produce ABC-D combinations in only one order. Fewer species are known to produce multiple orderings of the same components with distinct meanings. One such example is chestnut-crowned babblers (*Pomatostomus ruficeps*), which produce 2 different functionally distinct orderings of the same meaningless vocal elements (phonological syntax) (Engesser et al. 2015). If elephant combination calls with different orders have distinct functions, and the calls are found to be compositional, this could be one of the few examples of compositional syntax where multiple functionally distinct call orders occur in nature.

The fact that multiple call orders occurred at least occasionally in most behavioral contexts suggests that the relationship between call order and call function in elephant combination calls is probabilistic rather than absolute. This is similar to a number of other species. For example, black-fronted titi monkeys (*Callicebus nigrifrons*) produce alarm call sequences whose composition is significantly, but not perfectly, associated with the type and location of the predator (Cäsar et al. 2013). Similarly, bonobos (*Pan paniscus*) produce sequences of food calls in which sequence composition is probabilistically associated with food quality (Clay and Zuberbühler 2011). Although much of the work on comparative language evolution has focused on call combinations with highly consistent associations between call order and context (Engesser et al. 2015; Suzuki et al. 2016), human language itself rarely has a clear mapping between syntax, meaning, and context. In fact, although word order is critical to meaning in some human languages, in others, the components of a sentence can be arranged in almost any order without changing the sentence's meaning (Hale 1983; Christianson and Ferreira 2005). Furthermore, the number of utterances that can occur in a given context in human speech is virtually unbounded (Hauser et al. 2002). Thus, it may be worth giving more attention to animal call combinations with weak associations between call order and context.

In conclusion, we found that *E. maximus* in Sri Lanka, *L. africana* in Kenya and Namibia, and *L. cyclotis* at bais in Gabon differ significantly in the frequency with which they produce particular combinations of calls. The difference between species cannot be explained solely by phylogeny, and thus, there is likely a functional reason for the difference, perhaps related to species differences in habitat or social behavior. Certain call orders were significantly more likely to occur in particular behavioral contexts in *L. africana*, and there was a near-significant association between certain call orders and contexts in *E. maximus*, suggesting that combination calls with different orders of call elements may have different functions.

Moreover, some of the associations between call order and context differed significantly across species. Further behavioral studies across species and populations are needed to tease apart the specific social, ecological, and evolutionary factors that shape combinatorial sequences.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Pardo et al. (2019).

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