

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed
☐	☒ The exact sample size (<i>n</i>) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒ The statistical test(s) used AND whether they are one- or two-sided <i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i>
☐	☒ A description of all covariates tested
☐	☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒ For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i>) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted <i>Give P values as exact values whenever suitable.</i>
☒	☐ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒ Estimates of effect sizes (e.g. Cohen's <i>d</i> , Pearson's <i>r</i>), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection	No software was used to collect data in this study.
Data analysis	Rough segmentation of calls was performed in Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA). All other acoustic and statistical analyses were performed in R version 4.1.3. The following R packages were used: AER: testing overdispersion of Poisson GLM car: type III ANOVA caret: data partitioning for machine learning coxme: mixed-effects Cox regression data.table: data wrangling dplyr: data wrangling emmeans: post-hoc comparisons ggplot2: plotting gridExtra: combining plots lme4: mixed effects models lubridate: handling dates in R moments: skewness and kurtosis multitaper: multi-taper spectral estimation (for deriving some acoustic features) patchwork: combining plots party: conditional inference random forest (for variable importance scores) ranger: fast random forest robustbase: calculating robust skewness

rsvd: robust principal components
 Raven: importing Raven Pro selection tables into R
 rsvd: robust principal components analysis (for derived acoustic features)
 runner: control running operations
 scatterplot3d: 3D plotting
 seewave: acoustic analysis
 soundgen: acoustic analysis
 stringr: string manipulation
 survival: cox regression
 survminer: plotting survival curves
 tuneR: acoustic analysis
 viridis: more color palettes (for spectrogram)

We did not create any new software or R packages for this study. All of our code is available on Zenodo at this link: doi:10.5281/zenodo.10576772

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

Data are available on Dryad at the following link: doi:10.5061/dryad.hmgqnk9nj

Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

Reporting on sex and gender

Use the terms *sex* (biological attribute) and *gender* (shaped by social and cultural circumstances) carefully in order to avoid confusing both terms. Indicate if findings apply to only one sex or gender; describe whether sex and gender were considered in study design; whether sex and/or gender was determined based on self-reporting or assigned and methods used. Provide in the source data disaggregated sex and gender data, where this information has been collected, and if consent has been obtained for sharing of individual-level data; provide overall numbers in this Reporting Summary. Please state if this information has not been collected. Report sex- and gender-based analyses where performed, justify reasons for lack of sex- and gender-based analysis.

Reporting on race, ethnicity, or other socially relevant groupings

Please specify the socially constructed or socially relevant categorization variable(s) used in your manuscript and explain why they were used. Please note that such variables should not be used as proxies for other socially constructed/relevant variables (for example, race or ethnicity should not be used as a proxy for socioeconomic status). Provide clear definitions of the relevant terms used, how they were provided (by the participants/respondents, the researchers, or third parties), and the method(s) used to classify people into the different categories (e.g. self-report, census or administrative data, social media data, etc.) Please provide details about how you controlled for confounding variables in your analyses.

Population characteristics

Describe the covariate-relevant population characteristics of the human research participants (e.g. age, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."

Recruitment

Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.

Ethics oversight

Identify the organization(s) that approved the study protocol.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences
 ☐ Behavioural & social sciences
 ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description

We investigated the hypothesis that elephants address individual members of their family group with name-like calls. We recorded contact and greeting calls from wild African elephants in Samburu & Buffalo Springs National Reserves, northern Kenya and Amboseli National Park, southern Kenya, noting when possible the identity of the caller and the identity of the receiver.

We measured a suite of acoustic features on each call ($n=469$ calls) and used a random forest model to show that calls could be assigned to individual receivers based on acoustic structure with greater than chance accuracy. To determine if elephants rely on imitation of the receiver's calls to address receiver, we examined random forest classification accuracies separately for calls that were more similar to the receiver's calls than typical for that caller (convergent calls, $n=95$) and calls that were less similar to the receiver's calls than typical for that caller (divergent calls, $n=141$). We found that calls could be assigned to receiver ID with greater than chance accuracy regardless of whether they were convergent with or divergent from the receiver's calls. We calculated pairwise proximity scores between each call in the dataset and ran an ANOVA which showed that call pairs with the same caller and same receiver were more similar on average than call pairs with the same caller and different receivers who had the same type of relationship with the caller. We ran a logistic regression to assess the factors influencing the probability that the random forest would correctly predict the receiver for a call. We found that the receiver was more likely to be correctly predicted for contact rumbles and caregiving rumbles than for greeting rumbles and more likely to be correctly predicted for adult callers than for juvenile callers. This suggests that contact and caregiving rumbles may be more likely to contain a vocal label than greeting rumbles and adults may be more likely than juveniles to use vocal labels.

To determine if elephants imitated the calls of the receiver they were addressing, we ran another ANOVA to test if call pairs in which the receiver of one call produced the other call had higher proximity scores than call pairs in which this was not the case. There was no significant difference, indicating no evidence for imitation. To determine if different callers use the same label to address a given receiver (i.e., if calls could be assigned to receiver ID independent of caller ID), we ran a second random forest with the training and test sets partitioned so the model was trained and tested on different callers. This random forest failed to assign calls to receiver ID any better than chance, suggesting that different callers do not use the same label for the same receiver. However, an ANOVA showed that call pairs with different callers and the same receiver were more similar (had higher proximity scores) on average than call pairs with different callers and different receivers, suggesting that different callers do use similar labels for the same receiver.

Finally, we conducted a playback experiment to determine if elephants perceive and respond to putative labels in their calls. We played 17 elephants a recording of a call that was originally addressed to them (test) and a recording of a call from the same caller that was originally addressed to someone else (control). One subject received two different sets of test and control playbacks, one subject received just 1 test playback (no control) and one subject received just one control playback (no test). All other subjects received exactly one test playback and one control playback each. Subjects approached the speaker more quickly, vocalized more quickly, and produced more vocalizations in response to test playbacks than controls, further supporting the hypothesis that calls are specific to individual receivers.

Research sample

Subjects were wild African savannah elephants (*Loxodonta africana*) from two Kenyan populations: Samburu & Buffalo Springs (northern Kenya) and Amboseli (southern Kenya). Acoustic analyses were conducted on 371 rumbles from 52 adult females, 16 juvenile females, 2 females recorded as both juveniles and adults (cutoff for adulthood was 10 years of age), and 14 juvenile males in Samburu, as well as 98 rumbles from 13 adult females, 3 juvenile females, and 1 juvenile male in Amboseli. Playbacks were conducted to 17 individuals in Samburu (15 adult females, 1 adolescent female, and 1 adolescent male).

Sampling strategy

Calls were recorded using all-occurrence sampling. There was no predetermined sample size as we attempted to record as many calls as possible. Subjects for playbacks were chosen based on which individuals we were able to record a test stimulus and control stimulus for. We did not predetermine the sample size for playbacks and instead did as many playbacks as we were able to given what recordings were available.

Data collection

Calls were recorded during daylight hours from a vehicle using a handheld Earthworks microphone. Callers and receivers were identified using behavioral cues, and elephants were identified individually using naturally-occurring marks on the ears and other distinct physical features. Playbacks were conducted from 50 meters away from a loudspeaker placed on the ground or in a Landcruiser with all the doors and windows open. Data in Samburu (recordings and playbacks) were collected by MP and DL. Data in Amboseli (recordings) were collected by JP and PG.

Timing and spatial scale

Calls were recorded in Samburu in Nov 2019-Mar 2020 and Jun 2021-Apr 2022. Calls were recorded in Amboseli in 1986-1990 and 1997-2006. Playbacks were conducted from Oct 2021 to Apr 2022. Playbacks to the same subject were spaced apart by at least 7 days which previous studies on elephants have suggested as a rule of thumb to minimize the risk of habituation. Samburu and Buffalo Springs National Reserves cover an area of about 296 km² and Amboseli covers an area of about 392 km².

Data exclusions

We only analyzed rumbles that were produced in the contexts of contact calling, greeting, and caregiving. We also only included calls with minimal overlapping sounds, a high enough signal-to-noise ratio for the first two formants to be clearly visible in the spectrogram. Finally, we only included calls where the identity of the receiver was known for certain and for which there was only one receiver. For analyses involving caller ID or behavioral context, we also made sure that the identity of the caller/behavioral context was known for certain.

Reproducibility

Due to the logistical constraints of conducting this type of experiment in the field and the time constraints of available funding, we did not attempt to replicate the experiment.

Randomization

For the playback experiment, we attempted to conduct both a test playback and control playback to each individual (within-subjects design), only failing to do so for 2/17 subjects. The order of presentation of test and control playbacks was balanced across subjects.

Subjects were randomly assigned to receive the test or control playback first, with the constraint that 50% of subjects should receive the test first and 50% should receive the control first.

Blinding

The experimenters were blind to the condition of each playback trial until after all playback trials had been conducted and all videos of those trials were scored. The same observer (MP) conducted the playback trials and scored the videos.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions

The habitat of both field sites is a mixture of open grassland, bushy shrubs, and patches of woodland and permanent swamp. Both sites are semi-arid, receiving an average of about 350 mm of rain per year with peaks in November and April. Fieldwork was conducted in both wet and dry seasons. Average annual temperature is about 21.6 degrees Celsius in Amboseli and 24.5 degrees Celsius in Samburu.

Location

Samburu & Buffalo Springs: (0.61 N, 37.5 E), 800-1230 m above sea level
Amboseli National Park: (2.7 S, 37.3 E), 1100-1200 m above sea level.

Access & import/export

Permits were obtained from the Wildlife Research & Training Institute (WRTI) of Kenya and the National Commission for Science, Technology, and Innovation (NACOSTI) of Kenya, in consultation with local county governments (Samburu, Isiolo, and Kajiado counties). Permit numbers: NACOSTI/P/19/2735, WRTI-0061-06-21, NACOSTI/P/21/14091.

Disturbance

Elephants were not physically handled as part of this study. They may have been temporarily and slightly disturbed by playback stimuli. To minimize potential disturbance, we only played back a single call in any given trial and waited a minimum of 7 days between playbacks to the same subjects. Subjects did not always exhibit any response to playbacks, and when they did, they returned to baseline behavior in <10 min. The elephants in Samburu and Amboseli are habituated to research vehicles so it is unlikely that they were disturbed in any substantial way by our presence. To avoid damage to vegetation, we only drove off road when absolutely necessary to access the elephants and returned to an existing road as soon as possible.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

Methods

- | | |
|-------------------------------------|---|
| n/a | Involved in the study |
| ☒ | ☐ Antibodies |
| ☒ | ☐ Eukaryotic cell lines |
| ☒ | ☐ Palaeontology and archaeology |
| ☐ | ☒ Animals and other organisms |
| ☒ | ☐ Clinical data |
| ☒ | ☐ Dual use research of concern |
| ☒ | ☐ Plants |

- | | |
|-------------------------------------|---|
| n/a | Involved in the study |
| ☒ | ☐ ChIP-seq |
| ☒ | ☐ Flow cytometry |
| ☒ | ☐ MRI-based neuroimaging |

Animals and other research organisms

Policy information about [studies involving animals](#); [ARRIVE guidelines](#) recommended for reporting animal research, and [Sex and Gender in Research](#)

Laboratory animals

This study did not involve laboratory animals.

Wild animals

This study involved wild African savannah elephants (*Loxodonta africana*). No elephants were captured or handled as part of this study. We used audio recordings from 65 adult females, 19 juvenile females, and 15 juvenile males, as well as 2 females who were considered juveniles (<10 yo) in earlier recordings and adults (>10 yo) in later recordings. Playbacks were conducted to 17 individuals in Samburu (15 adult females, 1 adolescent female, and 1 adolescent male).

Reporting on sex

We focused on female-calf groups for this study because females and calves are much more vocal than adult males in elephants. As most of the elephants (and all the adults) in our study were female, these results may only be applicable to females. We did not conduct a sex-based analysis because we did not have sufficient data from males to consider them separately from females.

Field-collected samples

This study did not involve samples collected from the field (only audio and video recordings)

Ethics oversight

This study was approved by the Institutional Animal Care and Use Committee of Colorado State University (protocol #19-9229A)

Note that full information on the approval of the study protocol must also be provided in the manuscript.