

Peer Review Information

Journal: Nature Ecology & Evolution

Manuscript Title: African elephants address one another with individually specific name-like calls

Corresponding author name(s): Michael A. Pardo

Editorial Notes:

Reviewer Comments & Decisions:

Decision Letter, initial version:

6th December 2023

*Please ensure you delete the link to your author homepage in this e-mail if you wish to forward it to your co-authors.

Dear Dr Pardo,

Your manuscript entitled "African elephants address one another with individually specific name-like calls" has now been seen by three reviewers, whose comments are attached. The reviewers have raised a number of concerns which will need to be addressed before we can offer publication in Nature Ecology & Evolution. We will therefore need to see your responses to the criticisms raised and to some editorial concerns, along with a revised manuscript, before we can reach a final decision regarding publication.

We therefore invite you to revise your manuscript taking into account all reviewer and editor comments. Please highlight all changes in the manuscript text file [OPTIONAL: in Microsoft Word format].

We are committed to providing a fair and constructive peer-review process. Do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

When revising your manuscript:

* Include a "Response to reviewers" document detailing, point-by-point, how you addressed each reviewer comment. If no action was taken to address a point, you must provide a compelling argument. This response will be sent back to the reviewers along with the revised manuscript.

* If you have not done so already please begin to revise your manuscript so that it conforms to our Article format instructions at <http://www.nature.com/natecolevol/info/final-submission>. Refer also to any guidelines provided in this letter.

* Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

Please use the link below to submit your revised manuscript and related files:

2



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

[REDACTED]

Note: This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

We hope to receive your revised manuscript within four to eight weeks. If you cannot send it within this time, please let us know. We will be happy to consider your revision so long as nothing similar has been accepted for publication at Nature Ecology & Evolution or published elsewhere.

Nature Ecology & Evolution is committed to improving transparency in authorship. As part of our efforts in this direction, we are now requesting that all authors identified as 'corresponding author' on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with their account on the Manuscript Tracking System (MTS), prior to acceptance. ORCID helps the scientific community achieve unambiguous attribution of all scholarly contributions. You can create and link your ORCID from the home page of the MTS by clicking on 'Modify my Springer Nature account'. For more information please visit www.springernature.com/orcid.

Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

[REDACTED]

Reviewer expertise:

Reviewer #1: mechanisms of vocal learning, primates

Reviewer #2: random forest models, animal communication research

Reviewer #3: elephant communication

Reviewers' comments:

Reviewer #1 (Remarks to the Author):

The authors tested the hypothesis that elephants use name-like calls to interact with each other. Using observation data in the field, they found evidence that the elephants use calls specific to each receiver. The authors also used a playback experiment to show that the name-like calls elicited more

2



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

robust behavioral responses when related to the receiver. The authors executed a beautiful work. The manuscript is well-written and a joy to read. The authors describe the analyses in detail and implement the most relevant controls. I found the playback experiment the most impressive. Overall, the evidence is strong to support the authors' conclusion. I have only a few minor comments.

Major points

1) Although the authors provide important information about the data structure, I would like to understand better which animals interacted with which animals in the call data. Please provide a table showing how many calls the caller produced to which receiver. I understand the table is large, so I suggest putting it in an Excel sheet.

2) It would be interesting to know if the name-like calls differed from other contact calls that did not elicit responses to conspecifics.

3) The mixed result for "different callers addressing same receiver" is slightly puzzling. Could a better classifier show a better classification result (mainly because the prediction accuracy is relatively low)? It is worth trying another classifier only for this case. One state-of-the-art classifier is the tweety net by Cohen et al. (2022, eLife).

4) In the discussion, I think it is reasonable that authors suggest that there is production learning. Still, it might be safer to acknowledge that the name-like calls could result from auditory learning (maybe the elephants learn to associate the calls and identity), especially given that the "different callers addressing the same receiver" result was less conclusive.

Minor point

5) The labels in Fig 3-Right seem wrong. I think it should be "Different caller, same receiver" and "Different caller, different receiver"

Reviewer #2 (Remarks to the Author):

Review for Nature Ecology and Evolution

African elephants address one another with individually specific name-like calls

Introduction: This article examines whether elephants possess a trait previously only detected in human communication: referential, arbitrary labels of individuals, or names. The authors test several clearly articulated hypotheses and associated predictions and make an excellent effort to test alternative hypotheses. This is important with an exciting result. I have a few concerns and a handful of minor comments. If these can be addressed, I recommend this manuscript for publication.

Detailed comments:

Methods and Results

3



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

The methods are mostly sound and sufficiently described for reader understanding and future replication. I am somewhat concerned about the small sample size and the uncertainty in the callers and receivers. I'd especially like to see more calls per caller and more calls per receiver. Have you attempted to do some of your analyses after eliminating call sets with 3 or less calls per individual or receiver? I think it's essential for readers to know what proportion of calls were certain vs. uncertain. Were any analyses conducted with only certain calls? I'd especially like to see Extended Figure 3 with only certain calls (or coded as uncertain with a dashed pin line perhaps)

I'm also curious how you accounted for pseudoreplication in the ANOVAs where call pairs were compared. Did each call only occur in a pair once for each analysis?

Discussion and conclusions

I would like to see more discussion about the mixed evidence regarding convergence among callers when addressing the same receiver. For these calls to be "names" in the human sense, wouldn't all the callers need to use similar labels? These mixed results suggest to me there is something else going on. Perhaps this is just an artifact of the small sample size and the uncertainty in the callers and receivers. Do you think this result would have been different with a larger sample size where all calls were from positively identified dyads?

I'd also like to see some discussion of further differences between names and these individually specific calls. While names in humans can also clearly encode information such as context and signaler state, the majority of the variation encodes the identity of the named person. Further, names can be used to discuss the named individuals as a third party. Does your data account for this possibility and could it be affecting your analyses in one way or another?

Are there some calls, especially those from bouts of rumbles that were never (or rarely) classified to correct "receiver" or some that were always (or nearly) correctly classified? This would suggest to me that there are calls in the bout that encode the receiver while others do not and instead encode other information. Perhaps those in a bout that are very commonly classified correctly are a better comparison to human names?

What is the likelihood that some of the calls in the dataset are "addressed to" multiple individuals?

Are there some calls, especially those from bouts of rumbles that were never (or rarely) classified to correct "receiver" or some that were always (or nearly) correctly classified? This would suggest to me that there are calls in the bout that encode the receiver while others do not and instead encode other information. Perhaps those in a bout that are very commonly classified correctly are a better comparison to human names?

Minor comments:

First, I apologize for not having the time to review with a fine-toothed comb, as I prefer when reviewing and receiving reviews. These are the few small mistakes I picked up without that.

Line 692 95% confidence intervals, not internals.

Line 462 – It's unclear what the "focal call" is here.



Line 521 - How old to be considered "adult" female?

Overall, congratulations on an excellent and well-written manuscript!

Reviewer #3 (Remarks to the Author):

This very interesting and thorough study investigates whether the rumble vocalizations of savanna elephants contain individually specific signatures, similar to the use of names in human language, using an observational and experimental approach.

They authors found that the identity of an intended receiver (an individual either separated or approaching the caller) can be successfully predicted based on the acoustic structure of a call, irrespective of callerID and social relationship between recipient and caller. The result indicates that call structure varies by receiver as expected if elephants use vocal labels for other group members. Albeit a proportion larger than expected by chance, interestingly only 20% of calls were classified correctly. However, this may not be surprising given that names are only used in specific contexts in other species, including humans. The authors also found that these vocal labels do not reflect characteristics of the intended recipient's calls. Combined these results suggest that the vocal labels are not genetically predetermined, nor a result of a particular emotional state (associated with the type of relationship) nor based on imitation but learned arbitrary vocal labels. This is a key similarity to names and the referential nature of human languages, and in contrast to closest analogies to date found in non-human animals, for instance the dolphins and parrots. Yet, the results are ambiguous and the author's refrained from a definitive conclusion on the role of imitation in the investigated system.

Furthermore, if the vocal labels in savanna elephant rumbles function similarly to names in human language, different callers are expected to use the same vocal label for the same intended recipient. The findings were also ambiguous. While the authors found that calls from different callers to the same recipient were significantly more similar than calls from different callers to different recipients, they were not able to correctly predict recipient ID based on the call structure of rumbles from different callers.

Lastly, the authors found that recipients reacted more strongly to calls intended for them compared to calls not intended for them, suggesting that elephants recognize the labels and understand that they are being addressed.

The acoustic and statistical approach seems rigorous, and I believe the findings are highly significant and strongly deserve publication. Given the ambiguity of some the results I am concerned that the use of the term "name-like calls" in the title may not be entirely appropriate and overstating the findings.

Much of the ambiguity may be due to uncertainty in the identification of callers and receivers, inconsistent selection of calls and perhaps inappropriate acoustic parameter selection, all adding

5



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

potential “noise” to the dataset. I encourage the authors to find ways to remove some of this “noise” to perhaps substantiate the claim that the vocal labels indeed function as “names” that are used consistently across individuals and are not imitated acoustic signatures of the recipients calls.

Below a few more detailed remarks.

Main Text – The manuscript is generally well written. However, the structure of the manuscript with the method section at the end, combined with the very technical writing style, makes it difficult to understand the results and the reading painful at times. I would suggest moving the “Extended Table 1. Hypotheses and predictions tested in this study” from the supplementary material to the main text and refer to the predictions when talking about the respective statistical test and result.

Data quality - It appears that during data collection callerID, recipientID and behavioral context could not always be discerned with 100% certainty. Ideally, data collection protocols should have provided the opportunity to conduct inter-observer reliability tests, which has not been done or wasn't possible post hoc with the existing datasets. I commend the authors for including the certainty scores as weights into the data analysis. However, to provide some confidence in the data set it would be valuable if the authors could provide some quantification of the scoring certainty (e.g., mean certainty for callerID, proportion of caller identified with 100% certainty etc.). I am wondering why the authors did not include into analysis only data points that were acquired with 100% certainty.

The authors made specific choices regarding the selection of calls to be included in the analysis as well as regarding acoustic parameter extraction. Rumbles are typically produced in sequence or as part of an exchange. A standardization of which call to select for analysis among a sequence of calls, for instance consistently choosing the first call in a sequence, may be preferred. It seems the authors selected calls purely based on recording quality. Why didn't the authors select based on certain assumptions regarding when a vocal label would be most likely?

In addition, the authors state that the measured acoustic features may not be the most appropriate. How could the acoustic feature extraction be improved, and could the analysis be conducted based on more suitable parameters?

II. 60 – 75 The definition of the behavioral contexts of the analysed rumbles could be a bit more concise. If I understood correctly, you looked at rumbles produced by elephants when one adult female affiliate had walked away from the group to at least 50m and rumbles produced by elephants when an adult female affiliate returns to the group after having spent time more than 50m away from the group? The recipient is the adult female separated or reuniting. I suggest revising the text to bring this across more clearly. The current text is a bit convoluted. Please define separation in terms of how long the recipient had been >50m away from the caller, and what counts as an “approach”, particularly in the context of the little greeting.

I. 92 Why did you chose random forest classification? Would it make sense to try additional alternative classification methods to see if classification accuracy can be improved? Would an unsupervised classification (e.g., model based cluster analyses) based solely on the acoustic features be suitable?



II. 106 - 118 "correlation" between caller and recipient ID. I think this would be easier to understand if you could add a sentence explaining what you mean by "correlation" and add a prediction. This is explained more concisely in the methods section and I recommend moving some of the verbiage from the methods to the main text.

II. 119 You really need to include additional verbiage to explain the different tests you performed here. The table with predictions would help.

I. 237 Above you mention acoustic features that predict receiver ID. Aren't those candidate parameters that encode receiver ID?

I. 246 Are there specific parallels in the social system/cognition between these species which would point towards convergent evolutionary drivers? The manuscript would benefit from a deeper discussion on functions and drivers behind the use of names and/or vocal learning.

*****END*****

Author Rebuttal to Initial comments

We thank the reviewers for their helpful comments. In response to the reviewers' suggestions, we have restricted all analyses to only calls where the identity of the receiver was known for certain. For analyses involving caller ID or behavioral context, we further restricted the dataset to calls where caller ID and behavioral context were known for certain as well. To mitigate the reduction in sample size caused by these restrictions we added calls from one additional behavioral context (caregiving rumbles) to the dataset. Initially, we had not included caregiving rumbles in the analysis because we thought that the vast majority of caregiving rumbles would be produced by the receiver's mother, thus allowing receiver ID to be predicted from caller ID alone. However, on closer examination of our data we realized that many calves in our dataset received caregiving rumbles from multiple different callers, as allomothering is common in elephants. Our responses to each of the reviewers' comments are in bold italics below.

Reviewer #1 (Remarks to the Author):

The authors tested the hypothesis that elephants use name-like calls to interact with each other. Using observation data in the field, they found evidence that the elephants use calls specific to each receiver. The authors also used a playback experiment to show that the name-like calls

7



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

elicited more robust behavioral responses when related to the receiver. The authors executed a beautiful work. The manuscript is well-written and a joy to read. The authors describe the analyses in detail and implement the most relevant controls. I found the playback experiment the most impressive. Overall, the evidence is strong to support the authors' conclusion. I have only a few minor comments.

Major points

1) Although the authors provide important information about the data structure, I would like to understand better which animals interacted with which animals in the call data. Please provide a table showing how many calls the caller produced to which receiver. I understand the table is large, so I suggest putting it in an Excel sheet.

Done. This table is now included in the Supplementary Material as Table S1.

2) It would be interesting to know if the name-like calls differed from other contact calls that did not elicit responses to conspecifics.

We would first like to clarify that a contact call did not have to elicit a detectable response in order for us to identify the receiver and include it in our analysis. In many cases, contact calls were produced by an individual who was together with the majority of the family group while a single other member of the family group was absent (often lagging a few hundred meters behind the group). In these cases, we assumed that the one individual who was separated from the group was the intended receiver of the call, regardless of whether we recorded a response from her or not.

With that said, we have included some additional analyses in the revised manuscript to examine differences between calls that likely contain a vocal label and calls that likely do not. We ran the random forest model 2000 times and for each call we recorded the proportion of model runs in which it was classified correctly. We found that contact rumbles and caregiving rumbles were disproportionately likely to be classified correctly across most runs, while greeting rumbles were disproportionately unlikely to be classified correctly across most runs. This suggests that contact rumbles and caregiving rumbles may be more likely to contain vocal labels than greeting rumbles. We also found that calls made by adult females were more likely to be classified correctly than calls made by juveniles, suggesting that adults may be more likely to use vocal labels (lines 216-226).



3) The mixed result for "different callers addressing same receiver" is slightly puzzling. Could a better classifier show a better classification result (mainly because the prediction accuracy is relatively low)? It is worth trying another classifier only for this case. One state-of-the-art classifier is the tweety net by Cohen et al. (2022, eLife).

We acknowledge the compelling results that have been obtained with Deep Neural Network (DNN) models, but such models require massive training sets. Re-tuning an existing DNN model to provide leverage for a small data set explicitly assumes that the modes of variation in the borrowed training data align with modes of variation in the smaller data set. It is questionable whether models trained on birds and syringeal mechanics would yield informative results for elephant rumbles that lack syllabic structure and involve different vocal production mechanisms.

During our analyses, we explored some alternative classifiers such as gradient boosted machines. We obtained marginal improvements over our published results with some alternatives. However, these marginal improvements did not change our interpretation of the data, and we deemed that any benefit of such improvements was negated by the cost of introducing another complex procedure that did not connect to the call proximity scores we obtained from random forest.

Any analysis of these data will be limited by the small and unbalanced number of calls per receiver.

4) In the discussion, I think it is reasonable that authors suggest that there is production learning. Still, it might be safer to acknowledge that the name-like calls could result from auditory learning (maybe the elephants learn to associate the calls and identity), especially given that the "different callers addressing the same receiver" result was less conclusive.

We have added an acknowledgement of this possibility to the Discussion (lines 271-273).

Minor point

5) The labels in Fig 3-Right seem wrong. I think it should be "Different caller, same receiver" and "Different caller, different receiver"

Thank you for pointing this out. We have fixed the labels.



Reviewer #2 (Remarks to the Author):

Review for Nature Ecology and Evolution

African elephants address one another with individually specific name-like calls

Introduction: This article examines whether elephants possess a trait previously only detected in human communication: referential, arbitrary labels of individuals, or names. The authors test several clearly articulated hypotheses and associated predictions and make an excellent effort to test alternative hypotheses. This is important with an exciting result. I have a few concerns and a handful of minor comments. If these can be addressed, I recommend this manuscript for publication.

Detailed comments:

Methods and Results

The methods are mostly sound and sufficiently described for reader understanding and future replication. I am somewhat concerned about the small sample size and the uncertainty in the callers and receivers. I'd especially like to see more calls per caller and more calls per receiver. Have you attempted to do some of your analyses after eliminating call sets with 3 or less calls per individual or receiver? I think it's essential for readers to know what proportion of calls were certain vs. uncertain. Were any analyses conducted with only certain calls? I'd especially like to see Extended Figure 3 with only certain calls (or coded as uncertain with a dashed pin line perhaps)

We have redone all the analyses in the paper using only the calls for which the identity of the receiver and caller were known for certain, and the overall conclusions have not changed. We acknowledge that the imbalanced dataset and small average number of calls per receiver and per caller are a limitation of our study. Per your suggestion, we also ran the random forest models using only receivers that received >3 calls (n=302 calls). However, the results did not differ qualitatively from the original models so we have not included them in the manuscript so as not to add unnecessary complexity. When restricting the analysis to receivers with >3 calls, the random forest predicting receiver ID non-independently of caller ID correctly predicted the receiver for 38.5% of calls (randomly permuted models: 12.1±0.73% correct, $P<0.0001$). The random forest predicting receiver ID independently of caller ID correctly

10



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

predicted the receiver for 1.6% of calls (randomly permuted models: $2.0 \pm 0.49\%$ correct, $P=0.870$). We suspect that the reason why we were unable to predict receiver ID independently of caller ID even when restricting the analysis to receivers with >3 calls is because even after this restriction, most of the receivers still received the majority of their calls from a single caller. However, as we have noted in the Discussion, we cannot rule out the possibility that callers or subsets of callers have different labels for the same receiver, something akin to “nicknames” rather than “names” (lines 246-269).

I’m also curious how you accounted for pseudoreplication in the ANOVAs where call pairs were compared. Did each call only occur in a pair once for each analysis?

Thank you for pointing out this issue. We initially failed to account for pseudoreplication in the ANOVAs, which was an oversight. We have now added a random effect to all the models to account for pseudoreplication. This random effect is “pair ID”, which is an identifier of each unique combination of “caller A + receiver A + caller B + receiver B” (the unit of replication for all of our models dealing with pairwise proximity scores).

Discussion and conclusions

I would like to see more discussion about the mixed evidence regarding convergence among callers when addressing the same receiver. For these calls to be “names” in the human sense, wouldn’t all the callers need to use similar labels? These mixed results suggest to me there is something else going on. Perhaps this is just an artifact of the small sample size and the uncertainty in the callers and receivers. Do you think this result would have been different with a larger sample size where all calls were from positively identified dyads?

We have added more discussion of this result to the paper (lines 246-269). We do not claim that elephant vocal labels work in exactly the same way as human names, but rather that elephants address one another with individually specific calls, which may or may not be fully shared by different callers. Given that we did observe convergence in the proximity scores for calls from different callers to the same receiver, we think that the failure of the random forest to predict receiver ID independently of caller ID was most likely a result of the small number of calls per receiver. If we had a larger sample size we suspect that we would be able to successfully predict receiver ID independently of caller ID. However, we cannot rule out the possibility that callers exhibit only limited convergence in the calls addressed to the same receiver. We discuss both of these possibilities in the discussion.

I’d also like to see some discussion of further differences between names and these individually



specific calls. While names in humans can also clearly encode information such as context and signaler state, the majority of the variation encodes the identity of the named person. Further, names can be used to discuss the named individuals as a third party. Does your data account for this possibility and could it be affecting your analyses in one way or another?

We have added this discussion to the manuscript (lines 231-237, 267-269). We do not think our analysis would be significantly affected by whether elephants refer to named third parties or not. All the calls we used in our analysis were apparently directed to a single individual in the contexts of trying to reestablish contact with the receiver, greeting the receiver, or providing care to a juvenile receiver. In these contexts, we would typically expect any vocal label in the calls to refer to the receiver of the call, not a third party. If elephants refer to third parties by name, we would expect this to occur more in the context of group “discussions” such as “cadenced” rumbles exchanged between multiple individuals in the context of initiating group movement, or choruses produced in response to a member of the group mating. These types of calls were not included in the present study.

Are there some calls, especially those from bouts of rumbles that were never (or rarely) classified to correct “receiver” or some that were always (or nearly) correctly classified? This would suggest to me that there are calls in the bout that encode the receiver while others do not and instead encode other information. Perhaps those in a bout that are very commonly classified correctly are a better comparison to human names?

Yes, in fact, most calls were either almost always classified correctly or almost never classified correctly (lines 107-108). We have added an analysis to the manuscript that explores the factors influencing the probability of a call being correctly classified. We found that calls produced later in a bout (i.e., with more calls preceding them) were more likely to be classified correctly, although this effect was not particularly strong. We also found that contact calls and caregiving calls were more likely to be predicted correctly than greeting calls, and that calls from adult female callers were more likely to be predicted correctly than calls from juvenile callers (we did not have any recordings of adult male calls in our dataset). This suggests that vocal labels may be more likely to occur in contact and caregiving rumbles and in calls produced by adult females.

What is the likelihood that some of the calls in the dataset are “addressed to” multiple individuals?



We think that very few if any of the calls in our dataset were addressed to multiple individuals, because we only used calls where we were confident that there was a single receiver. For example, greeting displays may involve only two individuals or they may involve many individuals. We only included greeting rumbles where there were only two individuals involved, so there was only one possible receiver (provided we were able to identify which one of the two individuals made the call). For most contact rumbles, we identified the intended receiver because she was the only adult member of the family group who was separated from the caller at the time of the call, and thus was the only likely receiver. This inference made three assumptions that we believe are reasonable: 1) elephants rarely if ever give contact calls to non-family members (supported by McComb et al. 2000), 2) elephants don't use extremely loud contact calls to communicate with family members who are standing very close to them (they are perfectly capable of producing softer calls for close distance communication), and 3) if a single adult female and her dependent calves are lagging behind the rest of the group, any contact calls made by the group will be directed to the adult female and not to her calves.

For a minority of contact calls, there were multiple group members separated from the caller, but only one of them responded to the contact call (by calling back or approaching the caller), and we identified the one individual who responded as the intended receiver. It is possible that some of these contact calls were actually addressed to the whole group rather than to a single individual, even though only one individual responded. However, other contact calls (which we did not include in our analysis) did elicit a response from multiple individuals. Thus, it seems reasonable to conclude that contact calls that elicit a response from multiple individuals are (usually) directed to multiple individuals, while contact calls that only elicit a response from a single individual are (usually) directed to a single individual.

Minor comments:

First, I apologize for not having the time to review with a fine-toothed comb, as I prefer when reviewing and receiving reviews. These are the few small mistakes I picked up without that.

Line 692 95% confidence intervals, not internals.

Corrected (line 924).

Line 462 – It's unclear what the "focal call" is here.



We have tried to clarify this in the text (lines 614-629).

Line 521 - How old to be considered “adult” female?

For the purposes of the analyses in this paper, we considered a female elephant to be an adult once she was 10 years old (lines 609-611).

Overall, congratulations on an excellent and well-written manuscript!

Thank you!

Reviewer #3 (Remarks to the Author):

This very interesting and thorough study investigates whether the rumble vocalizations of savanna elephants contain individually specific signatures, similar to the use of names in human language, using an observational and experimental approach.

They authors found that the identity of an intended receiver (an individual either separated or approaching the caller) can be successfully predicted based on the acoustic structure of a call, irrespective of callerID and social relationship between recipient and caller. The result indicates that call structure varies by receiver as expected if elephants use vocal labels for other group members. Albeit a proportion larger than expected by chance, interestingly only 20% of calls were classified correctly. However, this may not be surprising given that names are only used in specific contexts in other species, including humans. The authors also found that these vocal labels do not reflect characteristics of the intended recipient’s calls. Combined these results suggest that the vocal labels are not genetically predetermined, nor a result of a particular emotional state (associated with the type of relationship) nor based on imitation but learned arbitrary vocal labels. This is a key similarity to names and the referential nature of human languages, and in contrast to closest analogies to date found in non-human animals, for instance the dolphins and parrots. Yet, the results are ambiguous and the author’s refrained from a definitive conclusion on the role of imitation in the investigated system.

Furthermore, if the vocal labels in savanna elephant rumbles function similarly to names in human language, different callers are expected to use the same vocal label for the same intended recipient. The findings were also ambiguous. While the authors found that calls from different



callers to the same recipient were significantly more similar than calls from different callers to different recipients, they were not able to correctly predict recipient ID based on the call structure of rumbles from different callers.

Lastly, the authors found that recipients reacted more strongly to calls intended for them compared to calls not intended for them, suggesting that elephants recognize the labels and understand that they are being addressed.

The acoustic and statistical approach seems rigorous, and I believe the findings are highly significant and strongly deserve publication. Given the ambiguity of some the results I am concerned that the use of the term “name-like calls” in the title may not be entirely appropriate and overstating the findings.

We acknowledge that elephant vocal labels may differ in some important ways from human names, especially given the ambiguous results about callers sharing labels for the same receiver. We used the term “name-like” rather than “names” to avoid implying that elephant vocal labels function in exactly the same way as human names. We do understand the concern that even “name-like” may imply an unsupported degree of similarity between human and elephant vocal labels. If this is of paramount concern, we would be happy to change to the title to something like “African elephants address one another with individually specific calls”. However, in our view, saying “name-like calls” is less ambiguous than merely saying “individually specific calls”, because the latter may be misinterpreted as referring to calls that are specific to the caller, rather than to the receiver.

Much of the ambiguity may be due to uncertainty in the identification of callers and receivers, inconsistent selection of calls and perhaps inappropriate acoustic parameter selection, all adding potential “noise” to the dataset. I encourage the authors to find ways to remove some of this “noise” to perhaps substantiate the claim that the vocal labels indeed function as “names” that are used consistently across individuals and are not imitated acoustic signatures of the recipients calls.

We have attempted to remove some of the noise in the dataset by only using calls where the receiver ID was known for certain. Unfortunately, some of the ambiguity in our results is likely due to the small average number of calls per receiver and the imbalance in the dataset, which is an inherent limitation of our data.



Below a few more detailed remarks.

Main Text – The manuscript is generally well written. However, the structure of the manuscript with the method section at the end, combined with the very technical writing style, makes it difficult to understand the results and the reading painful at times. I would suggest moving the “Extended Table 1. Hypotheses and predictions tested in this study” from the supplementary material to the main text and refer to the predictions when talking about the respective statistical test and result.

We have moved this table to the main text as you suggested, and referred to the predictions by number when discussing each test in the main text.

Data quality - It appears that during data collection callerID, recipientID and behavioral context could not always be discerned with 100% certainty. Ideally, data collection protocols should have provided the opportunity to conduct inter-observer reliability tests, which has not been done or wasn't possible post hoc with the existing datasets. I commend the authors for including the certainty scores as weights into the data analysis. However, to provide some confidence in the data set it would be valuable if the authors could provide some quantification of the scoring certainty (e.g., mean certainty for callerID, proportion of caller identified with 100% certainty etc.). I am wondering why the authors did not include into analysis only data points that were acquired with 100% certainty.

We originally chose to use calls with uncertain ID because we felt that sample size was likely the biggest limiting factor in this study. The random forest method we used is insensitive to a small number of mislabeled cases. However, to further remove some of the uncertainty in our dataset, we have redone all the analyses using only calls with 100% certainty.

The authors made specific choices regarding the selection of calls to be included in the analysis as well as regarding acoustic parameter extraction. Rumbles are typically produced in sequence or as part of an exchange. A standardization of which call to select for analysis among a sequence of calls, for instance consistently choosing the first call in a sequence, may be preferred. It seems the authors selected calls purely based on recording quality. Why didn't the authors select based on certain assumptions regarding when a vocal label would be most likely?

We only used calls from behavioral contexts that we hypothesized a priori would be good candidates for vocal labeling. Contact, greeting, and caregiving rumbles are all frequently

16



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

given to a single, clearly identifiable receiver. We hypothesized that vocal labeling would be particularly beneficial in contact rumbles, as these are usually given when the caller and receiver are out of visual contact, so a vocal label can help clarify whom the caller is attempting to address. In the contexts of greeting and caregiving, vocal labels could help strengthen bonds between the caller and receiver in the same way that calling someone by name in human communication induces positive feelings and increased willingness to cooperate in the receiver (see Discussion section). We specifically excluded from our study calls like “let’s go” rumbles that appear to be addressed to the group at large or calls like protest rumbles where vocal labels seem less likely to be beneficial. Beyond this, there was no way to know which calls were most likely to have a vocal label, so we could not be more selective about which calls to include. We did not limit our dataset to only one call per bout because doing so would have decreased the sample size too much. Instead, we controlled for calling bout in the proximity score ANOVAs by only using pairs of calls that were recorded on different days.

In addition, the authors state that the measured acoustic features may not be the most appropriate. How could the acoustic feature extraction be improved, and could the analysis be conducted based on more suitable parameters?

The best way to improve the acoustic feature extraction would likely be to develop novel features that are tailored to the properties of the elephant vocal tract and auditory system. The time-frequency tradeoff inherent in the Fast Fourier Transform may be especially problematic for low frequency calls such as elephant rumbles, as a long analysis window is required to resolve frequencies in this range, which may smooth over short-time modulations in the fundamental frequency. A hypothetical alternative approach using “instantaneous” frequency might improve time resolution at these low frequencies. It might also be helpful to develop a psychoacoustic frequency scale tailored to the elephant hearing curve, rather than using the mel scale that was designed with the human ear in mind. However, these approaches would require non-trivial innovations that are beyond the scope of this study given current constraints on time and resources.

11. 60 – 75 The definition of the behavioral contexts of the analysed rumbles could be a bit more concise. If I understood correctly, you looked at rumbles produced by elephants when one adult female affiliate had walked away from the group to at least 50m and rumbles produced by elephants when an adult female affiliate returns to the group after having spent time more than

17



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

50m away from the group? The recipient is the adult female separated or reuniting. I suggest revising the text to bring this across more clearly. The current text is a bit convoluted. Please define separation in terms of how long the recipient had been >50m away from the caller, and what counts as an “approach”, particularly in the context of the little greeting.

We have tried to clarify this language in the text (lines 54-59).

1. 92 Why did you chose random forest classification? Would it make sense to try additional alternative classification methods to see if classification accuracy can be improved? Would an unsupervised classification (e.g., model based cluster analyses) based solely on the acoustic features be suitable?

We chose random forest for a few reasons. It is relatively insensitive to a small number of mislabeled calls, and requires less training data than certain other types of classifiers such as deep neural networks. Moreover, random forest has the advantage of providing in-built proximity scores. Because the proximity scores are derived from the tree structure of the random forest, they provide a measure of call similarity in terms of the features most relevant to predicting receiver ID, which makes them superior to alternative distance measures based directly on the acoustic features. Moreover, because the forest aggregates the process of data splitting across many trees that are trained on different subsets of calls and acoustic features, the proximity scores represent a fine-scale measure of call similarity that generalizes across multiple scenarios used for call classification. As such, the analyses of proximity scores are likely more informative about call structure than the results of the classifier itself.

11. 106 - 118 “correlation” between caller and recipient ID. I think this would be easier to understand if you could add a sentence explaining what you mean by “correlation” and add a prediction. This is explained more concisely in the methods section and I recommend moving some of the verbiage from the methods to the main text.

We have moved some of the language from the methods section here to clarify this (lines 87-89).

11. 119 You really need to include additional verbiage to explain the different tests you performed here. The table with predictions would help.

We have moved the table to the main text and referred to the hypotheses and predictions in the main text as you suggested.



l. 237 Above you mention acoustic features that predict receiver ID. Aren't those candidate parameters that encode receiver ID?

It is true that the variable importance scores provide a measure of which acoustic features in our dataset were most informative for predicting receiver ID. However, we are not confident that the acoustic features we measured necessarily capture all of the relevant variation in the calls (see above). Thus, it is difficult to conclude that the top acoustic features in our dataset are the acoustic features that encode receiver ID. It may be that they only partially or indirectly reflect the acoustic parameters that actually carry this information. Unfortunately we are still not able to reconstruct a vocal label from the acoustic features we measured.

l. 246 Are there specific parallels in the social system/cognition between these species which would point towards convergent evolutionary drivers? The manuscript would benefit from a deeper discussion on functions and drivers behind the use of names and/or vocal learning.

We have added this to the Discussion (lines 278-282).

Decision Letter, first revision:

6th March 2024

*Please ensure you delete the link to your author homepage in this e-mail if you wish to forward it to your co-authors.

Dear Dr Pardo,

Your manuscript entitled "African elephants address one another with individually specific name-like calls" has now been seen by three reviewers, whose comments are attached. While the reviewers are mostly happy with the revision, reviewer 1 has noticed a new technical issue that they apologise for not having identified in the previous round of review, but which has only become apparent to them on studying the revised SI and Extended Data figures. They ask that you repeat your analysis without subjects M6 and M6.99 to check that they are not driving a disproportionate part of the results.

We will therefore need to see your responses to the criticisms raised, along with a revised manuscript, before we can reach a final decision regarding publication.

We therefore invite you to revise your manuscript taking into account all reviewer and editor comments. Please highlight all changes in the manuscript text file.

19



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

We are committed to providing a fair and constructive peer-review process. Do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

When revising your manuscript:

- * Include a "Response to reviewers" document detailing, point-by-point, how you addressed each reviewer comment. If no action was taken to address a point, you must provide a compelling argument. This response will be sent back to the reviewers along with the revised manuscript.
- * If you have not done so already please begin to revise your manuscript so that it conforms to our Article format instructions at <http://www.nature.com/natecolevol/info/final-submission>. Refer also to any guidelines provided in this letter.
- * Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

Please use the link below to submit your revised manuscript and related files:

[REDACTED]

Note: This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

We hope to receive your revised manuscript within four to eight weeks. If you cannot send it within this time, please let us know. We will be happy to consider your revision so long as nothing similar has been accepted for publication at Nature Ecology & Evolution or published elsewhere.

Nature Ecology & Evolution is committed to improving transparency in authorship. As part of our efforts in this direction, we are now requesting that all authors identified as 'corresponding author' on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with their account on the Manuscript Tracking System (MTS), prior to acceptance. ORCID helps the scientific community achieve unambiguous attribution of all scholarly contributions. You can create and link your ORCID from the home page of the MTS by clicking on 'Modify my Springer Nature account'. For more information please visit www.springernature.com/orcid.

Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

[REDACTED]

20



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

Reviewers' comments:

Reviewer #1 (Remarks to the Author):

The manuscript is greatly improved. I have one remaining concern. Looking at the newly provided table S1 and Extended Figure 1, we observe that subjects M6 and M6.99 drive a significant (maybe disproportionate) part of the result. Please repeat the analysis without these two subjects. If these two subjects have a disproportionate effect, this needs some discussion.

Reviewer #2 (Remarks to the Author):

I commend the authors for their thorough and satisfying responses to all of my concerns. I have no outstanding concerns and recommend this manuscript for publication.

Reviewer #3 (Remarks to the Author):

I believe the authors have completed a thorough revision of the analysis and the manuscript. I can recommend the manuscript for publication.

*****END*****

Author Rebuttal, first revision:

Response to reviewers

Reviewer #1 (Remarks to the Author):

The manuscript is greatly improved. I have one remaining concern. Looking at the newly provided table S1 and Extended Figure 1, we observe that subjects M6 and M6.99 drive a significant (maybe disproportionate) part of the result. Please repeat the analysis without these two subjects. If these two subjects have a disproportionate effect, this needs some discussion.



We have repeated the analyses without these two subjects, and the results are qualitatively the same as before. We have included the details of the new results in the Supplementary Information. We have also added a statement to the Discussion in the main manuscript (lines 195-198) indicating that removing these two subjects did not change the results, so the results are unlikely to be driven by a few highly influential individuals.

Reviewer #2 (Remarks to the Author):

I commend the authors for their thorough and satisfying responses to all of my concerns. I have no outstanding concerns and recommend this manuscript for publication.

Reviewer #3 (Remarks to the Author):

I believe the authors have completed a thorough revision of the analysis and the manuscript. I can recommend the manuscript for publication.

Decision Letter, second revision:

13th March 2024

Dear Dr. Pardo,

Thank you for submitting your revised manuscript "African elephants address one another with individually specific name-like calls" (NATECOLEVOL-23102495B). It has now been seen again by the original reviewers and their comments are below. The reviewers find that the paper has improved in revision, and therefore we'll be happy in principle to publish it in Nature Ecology & Evolution, pending minor revisions to comply with our editorial and formatting guidelines.

If the current version of your manuscript is in a PDF format, please email us a copy of the file in an editable format (Microsoft Word or LaTeX)-- we can not proceed with PDFs at this stage.

We are now performing detailed checks on your paper and will send you a checklist detailing our editorial and formatting requirements in about a week. Please do not upload the final materials and make any revisions until you receive this additional information from us.

Thank you again for your interest in Nature Ecology & Evolution. Please do not hesitate to contact me

22



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

if you have any questions.

Sincerely,
[REDACTED]

Reviewer #1 (Remarks to the Author):

The authors addressed all my concerns. The authors produced a beautiful piece of work. Congratulations.

Our ref: NATECOLEVOL-23102495B

25th March 2024

Dear Dr. Pardo,

Thank you for your patience as we've prepared the guidelines for final submission of your Nature Ecology & Evolution manuscript, "African elephants address one another with individually specific name-like calls" (NATECOLEVOL-23102495B). Please carefully follow the step-by-step instructions provided in the attached file, and add a response in each row of the table to indicate the changes that you have made. Please also check and comment on any additional marked-up edits we have proposed within the text. Ensuring that each point is addressed will help to ensure that your revised manuscript can be swiftly handed over to our production team.

****We would like to start working on your revised paper, with all of the requested files and forms, as soon as possible (preferably within two weeks). Please get in contact with us immediately if you anticipate it taking more than two weeks to submit these revised files.****

When you upload your final materials, please include a point-by-point response to any remaining reviewer comments.

If you have not done so already, please alert us to any related manuscripts from your group that are under consideration or in press at other journals, or are being written up for submission to other journals (see: <https://www.nature.com/nature-research/editorial-policies/plagiarism#policy-on-duplicate-publication> for details).

In recognition of the time and expertise our reviewers provide to Nature Ecology & Evolution's editorial

23



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

process, we would like to formally acknowledge their contribution to the external peer review of your manuscript entitled "African elephants address one another with individually specific name-like calls". For those reviewers who give their assent, we will be publishing their names alongside the published article.

Nature Ecology & Evolution offers a Transparent Peer Review option for new original research manuscripts submitted after December 1st, 2019. As part of this initiative, we encourage our authors to support increased transparency into the peer review process by agreeing to have the reviewer comments, author rebuttal letters, and editorial decision letters published as a Supplementary item. When you submit your final files please clearly state in your cover letter whether or not you would like to participate in this initiative. Please note that failure to state your preference will result in delays in accepting your manuscript for publication.

Cover suggestions

We welcome submissions of artwork for consideration for our cover. For more information, please see our [guide for cover artwork](#).

If your image is selected, we may also use it on the journal website as a banner image, and may need to make artistic alterations to fit our journal style.

Please submit your suggestions, clearly labeled, along with your final files. We'll be in touch if more information is needed.

Nature Ecology & Evolution has now transitioned to a unified Rights Collection system which will allow our Author Services team to quickly and easily collect the rights and permissions required to publish your work. Approximately 10 days after your paper is formally accepted, you will receive an email in providing you with a link to complete the grant of rights. If your paper is eligible for Open Access, our Author Services team will also be in touch regarding any additional information that may be required to arrange payment for your article.

Please note that *Nature Ecology & Evolution* is a Transformative Journal (TJ). Authors may publish their research with us through the traditional subscription access route or make their paper immediately open access through payment of an article-processing charge (APC). Authors will not be required to make a final decision about access to their article until it has been accepted. [Find out more about Transformative Journals](#)

Authors may need to take specific actions to achieve [compliance](#) with funder and institutional open access mandates. If your research is supported by a funder that requires immediate open access (e.g. according to [Plan S principles](#)) then you should select the gold OA route, and we will direct you to the compliant route where possible. For authors selecting the subscription publication route, the journal's standard licensing terms will need to be accepted, including [a href="https://www.nature.com/nature-portfolio/editorial-policies/self-archiving-and-license-to-publish"](https://www.nature.com/nature-portfolio/editorial-policies/self-archiving-and-license-to-publish). Those licensing terms will supersede any other terms that the author or any third party may

24



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

assert apply to any version of the manuscript.

For information regarding our different publishing models please see our [Transformative Journals](#) page. If you have any questions about costs, Open Access requirements, or our legal forms, please contact ASJournals@springernature.com.

Please use the following link for uploading these materials:

[REDACTED]

If you have any further questions, please feel free to contact me.

[REDACTED]

Reviewer #1:

Remarks to the Author:

The authors addressed all my concerns. The authors produced a beautiful piece of work. Congratulations.

Final Decision Letter:

22nd April 2024

Dear Dr Pardo,

We are pleased to inform you that your Article entitled "African elephants address one another with individually specific name-like calls", has now been accepted for publication in Nature Ecology & Evolution.

Over the next few weeks, your paper will be copyedited to ensure that it conforms to Nature Ecology and Evolution style. Once your paper is typeset, you will receive an email with a link to choose the appropriate publishing options for your paper and our Author Services team will be in touch regarding any additional information that may be required

After the grant of rights is completed, you will receive a link to your electronic proof via email with a request to make any corrections within 48 hours. If, when you receive your proof, you cannot meet this deadline, please inform us at rjsproduction@springernature.com immediately.

Due to the importance of these deadlines, we ask you please us know now whether you will be difficult to contact over the next month. If this is the case, we ask you provide us with the contact information (email, phone and fax) of someone who will be able to check the proofs on your behalf, and who will

25



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

be available to address any last-minute problems. Once your paper has been scheduled for online publication, the Nature press office will be in touch to confirm the details.

Acceptance of your manuscript is conditional on all authors' agreement with our publication policies (see www.nature.com/authors/policies/index.html). In particular your manuscript must not be published elsewhere and there must be no announcement of the work to any media outlet until the publication date (the day on which it is uploaded onto our web site).

Please note that *Nature Ecology & Evolution* is a Transformative Journal (TJ). Authors may publish their research with us through the traditional subscription access route or make their paper immediately open access through payment of an article-processing charge (APC). Authors will not be required to make a final decision about access to their article until it has been accepted. [Find out more about Transformative Journals](#)

Authors may need to take specific actions to achieve [compliance](#) with funder and institutional open access mandates. If your research is supported by a funder that requires immediate open access (e.g. according to [Plan S principles](#)) then you should select the gold OA route, and we will direct you to the compliant route where possible. For authors selecting the subscription publication route, the journal's standard licensing terms will need to be accepted, including [a href="https://www.nature.com/nature-portfolio/editorial-policies/self-archiving-and-license-to-publish"](https://www.nature.com/nature-portfolio/editorial-policies/self-archiving-and-license-to-publish). Those licensing terms will supersede any other terms that the author or any third party may assert apply to any version of the manuscript.

In approximately 10 business days you will receive an email with a link to choose the appropriate publishing options for your paper and our Author Services team will be in touch regarding any additional information that may be required.

If you have any questions about our publishing options, costs, Open Access requirements, or our legal forms, please contact ASJournals@springernature.com

An online order form for reprints of your paper is available at <https://www.nature.com/reprints/author-reprints.html>. All co-authors, authors' institutions and authors' funding agencies can order reprints using the form appropriate to their geographical region.

We welcome the submission of potential cover material (including a short caption of around 40 words) related to your manuscript; suggestions should be sent to Nature Ecology & Evolution as electronic files (the image should be 300 dpi at 210 x 297 mm in either TIFF or JPEG format). Please note that such pictures should be selected more for their aesthetic appeal than for their scientific content, and that colour images work better than black and white or grayscale images. Please do not try to design a cover with the Nature Ecology & Evolution logo etc., and please do not submit composites of images related to your work. I am sure you will understand that we cannot make any promise as to whether any of your suggestions might be selected for the cover of the journal.

You can now use a single sign-on for all your accounts, view the status of all your manuscript submissions and reviews, access usage statistics for your published articles and download a record of

26



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

your refereeing activity for the Nature journals.

To assist our authors in disseminating their research to the broader community, our SharedIt initiative provides you with a unique shareable link that will allow anyone (with or without a subscription) to read the published article. Recipients of the link with a subscription will also be able to download and print the PDF.

You can generate the link yourself when you receive your article DOI by entering it here: <http://authors.springernature.com/share>.

Yours sincerely,

[REDACTED]

P.S. Click on the following link if you would like to recommend Nature Ecology & Evolution to your librarian <http://www.nature.com/subscriptions/recommend.html#forms>

** Visit the Springer Nature Editorial and Publishing website at www.springernature.com/editorial-and-publishing-jobs for more information about our career opportunities. If you have any questions please click [here](#).**



Open Access This file is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. In the cases where the authors are anonymous, such as is the case for the reports of anonymous peer reviewers, author attribution should be to 'Anonymous Referee' followed by a clear attribution to the source work. The images or other third party material in this file are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.