Individual, unit and vocal clan level identity cues in sperm whale codas

Shane Gero, Hal Whitehead and Luke Rendell

Article citation details
R. Soc. open sci. 2: 150372.
http://dx.doi.org/10.1098/rsos.150372

Review timeline
Original submission: 27 July 2015
Revised submission: 12 October 2015
Final acceptance: 3 December 2015

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Note: This manuscript was transferred from another Royal Society journal without peer review.

Review History
RSOS-150372.R0 (Original submission)

Review form: Reviewer 1 (Ann Bowles)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Is it clear how to access all supporting data?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
I do not feel qualified to assess the statistics

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Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)
The introduction is a particularly clear summary of the authors’ collective theorizing about sperm whale social communication and its relationship to sperm whale sociality. Although it is more general than the topic of the paper, it is succinct and well-written, and lays the groundwork for the Discussion as well as the Methods and Results.

The authors have put a lot of thought into their analysis based on a large body of previous literature on the same topic. They have examined different aspects of their data using multiple, sometimes similar, statistical procedures. However, the rationale for the steps they took isn’t explicitly laid out, and is particularly difficult to follow because critical information is split out in the electronic supplement and previous papers that used different analysis methods. It would help to have a paragraph at the start of the section, maybe with a diagram, that lays out the strategy for the analysis – the breakdown between categorical and continuous, a summary of the variables were entered into the analyses, the procedures they used for classifying, ordering, clustering, etc. This paragraph/diagram should help readers gain confidence in their approach.

The discussion does not suggest how uncertainties in their methods might affect their conclusions, and this should be included. For example, the range of sample periods/samples among units and individuals is large. Might this have affected their results or blurred the distinctions among some codas by unit/individual?

The authors say they have provided evidence for vocal complexity matching the social complexity of sperm whales. The discussion (beginning on line 269) talks about the importance of understanding how the whales produce and use layers of complexity. However, the authors do not talk about how their findings relate to complexity in other species. In the absence of detail, it is hard to know whether the complexity of sperm whale codas is really directly comparable to other literature on vocal complexity. I know that this paper is not a review of the social complexity hypothesis, but since they have invoked it, I think some additional detail is justified. How would their interpretation of the hypothesis differ, for example, from that of Leuchtenberger et al. (2014), which provides a more traditional terrestrial view of complexity?


Specific Comments (by line number):

9: Something missing or a comma incorrect (….recorded, were....)

30-34: I don’t think the leap from large spatial scale to adaptive pressure for social learning is justified as stated. Pressures of social competition within and across group and species could explain the complexity of cetacean social communication as well or better than habitat structure - remember that social odontocetes must deal with a complex clade of other large, wide ranging, sometimes irascible, and in at least one case predatory, social odontocetes. Great mobility increases the complexities of using the habitat, yes, but any or all of a number of mechanisms could be operating. The last sentence could just as well follow the first.

108: If the classification of click patterns is highly reliable, there should be a statement to that effect with reference(s). If there were ambiguous cases, how were they resolved?

150: Which variants of distance measure (Euclidean, etc.) were tested and how would distance have affected the multivariate similarity if the codas hadn’t been distinctive in the way they
expected? In other words, to what degree was robustness with regard to the distance measure supportive of their results?

164: The observation that the codas did not change significantly over time is mentioned as an aside. However, this invariance is the driving phenomenon behind the degree of individual, unit, etc. specificity they found in their analysis; so, it would make sense to discuss it earlier in the results section, and maybe provide a table or figure about change over time in the codas they studied. This is particularly important given the discussion starting on line 278.

188: A word is missing in this sentence (they also ??? in their usage of coda types..)

229: If the SE values were put in parentheses, the comparison would be clearer.

255: Is there any information about the genetic distances among the units? The population in the area of their study was exploited historically.

269-271: I would add to the list of properties the following: the capacity to produce vocal signals with sufficient stereotypy (not the same as being able to identify them). Their findings suggest that sperm whales must be able to retain an accurate template in memory and to emit sounds using it for very long periods.

278: Make the text about discrimination vs. identification into a separate paragraph.

Figure 2. Something that struck me in this dendrogram: Pinchy was the only F Unit whale that produced a high proportion of 5R1 codas, and yet this is one of the 2 codas uniformly used with high proportion in their clan of Dominican social units. Is there any indication that this whale is special? Say whether the same pattern was found in other units.

Ann E. Bowles
Senior Research Scientist
Hubbs-SeaWorld Research Institute

Review form: Reviewer 2 (Karen McComb)

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Yes

Are the interpretations and conclusions justified by the results? 
Yes

Is the language acceptable? 
Yes

Is it clear how to access all supporting data? 
Yes

Do you have any ethical concerns with this paper? 
No

Have you any concerns about statistical analyses in this paper? 
No

Recommendation? 
Accept with minor revision (please list in comments)
Comments to the Author(s)

This is a very interesting paper, which uses an impressively extensive dataset to tackle questions about how vocal signals in sperm whales advertise successive levels of social affiliation – specifically clan and social unit membership as well as individual identity. This sort of study is rarely possible in large mammals and by using their unique dataset and powerful analysis methods the authors have been able to break new ground here and their findings should be of wide interest.

My comments for how the manuscript could be improved revolve around clarifying particular arguments and some restructuring to highlight key results – a little work on these aspects would significantly strengthen this interesting manuscript. I hope my suggestions are useful:

1) I think the title could be usefully changed to “Distinctive modes of variation in sperm whale codas reflect social unit membership and vocal clan affiliation as well as individual identity”. This would stress more what is new/unique about the paper.

2) Line 4 “broadest structures” is rather unclear here – change to affiliative structures?

3) Last line of abstract needs some development to say how results support the social complexity hypothesis e.g. …by indicating that selection for advertising identity at different levels of a society may contribute to the evolution of a more complex vocal repertoire.

4) Lines 22/23 describe what your findings support but I’m not sure this view was so widely accepted previously – I think more generally people have thought in terms of selection for social communication increasing as social complexity increases because more messages have to be exchanged. I’d leave out “to discriminate among various tiers of the social structure on lines 22 & 23 and instead add a sentence at the end of the paragraph saying: “This could occur in a number of ways…. …” where you outline this idea to set up your argument?

5) Line 33: Accordingly would be better than As a result here.

6) Line 35 “…the variability of vocal signals would be greatest in cetaceans where…”

7) Line 52/53 Careful of switching from dialect to repertoire – I think the definitions and use of these two terms could be made and kept clearer throughout.

8) Line 73 I suggest “…interpulse interval and therefore size [30,31, see below], …. …

9) Lines 115/116 Rephrase “…number of clicks was measured with both a Euclidian…..using absolute ICI measures as in previous work…”

10) Lines 150/151 – two onlys.

11) Lines 154 – I felt the meat of what you showed got a bit lost in this section and I’d take a key sentence from the legend of Table 1 and have it in the text here. “Mantell test across all units has a null hypothesis that repertoire similarity between recordings of the same days (within unit) is the same as between recordings of different units on different days (between units)… then your very strong results.

12) Line 188 missing word …also ?differ in their…

13) Line 228/9 could be misleading – change to “…units that belong to within-clan units in the Pacific…

14) Para at 245 – very interesting!

15) Lines 278-280 could be clearer on signals versus cues.

16) Last line of conclusion – as with last sentence of abstract need to do more to spell out how it supports the social complexity hypothesis

[Minor - note communication misspelled in keywords]

Best wishes,

Karen McComb
Review form: Reviewer 3 (Yvonnick Le Pendu)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Is it clear how to access all supporting data?
The authors inform (line 325) that the ICI data used in their study will be made available through Dryad upon acceptance for publication. The supplementary material is adequate and clear.

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)
Journal: Royal Society Open Science
Manuscript ID: RSOS-150372
Title: Distinctive modes of variation in sperm whale codas reflect individual identity, social unit membership, and vocal clan affiliation
Authors: Shane Gero, Hal Whitehead, Luke Rendell

The manuscript aims to verify if the hypothesis of social complexity applies to a large marine mammal species, Physeter macrocephalus. To this end, the authors describe the structure of codas issued by the Eastern Caribbean sperm whales and perform discriminant analyzes at the individual and social unity levels. The five years study is based on 4116 codas attributed to nine units of 4 to 12 individuals each. This large amount of raw data and the previous knowledge about the social organization of these units allow the authors to perform several discriminant analyzes and confirm the hypothesis of social complexity in sperm whales. The manuscript provide new and exciting understanding on the social structure of the population of sperm whales from the Eastern Caribbean. The authors demonstrate that the nine units form a single clan because two coda types are dominant in all units for decades. Their results also reveal that certain coda types are only characteristic of one or more social units and that it is possible to discriminate the individuals belonging to the same unit based on the coda types they produce. The manuscript is well written and analyzes are adequate, using powerful statistical reference tools. For all these reasons, I recommend the publication of this manuscript in Royal Society Open Science.

Methodological aspects published in previous articles are always cited in the text. Specific analyzes for this manuscript are fully described in the main text or in the extensive electronic supplemental material. The number of analyzes, figures and tables included in these documents is substantial. Therefore, I suggest the inclusion of a table summarizing all analyzes, each row informing the purpose of the analysis (or the hypothesis tested) and the corresponding figure or table (in the main text or in the ESM).
The following suggestions are mainly minor typographical errors:

Line 3: “hierarchically” instead of “heirarchically”.

L55: “an excess of 70 types” instead of “in excess of 70 types”.

L70: You need to explain that ESM stand for Electronic Supplementary Material at first instance.

L82 and ESM: How many “first few minutes”?

L133 and ESM: Verify the phrasing: “which Antunes et al. 53 found varied between individuals”.

L151: delete only (already in L150)

L170: Table S5 do not present “standardized discriminant coefficient and variance explained”.

You may refer to tables S10-S12.

L216 “from 1 to 5” instead of “from 1 and 5”?

L354-530: The first letter of each word of some titles of journal articles are capitalized (e.g. references 5, 26, 61) while others are not; The word DOI is sometimes repeated (e.g. references 5, 18, 64); the complete DOI number is repeated (reference 70); use instead of Use (reference 8); delete space after Data (reference 43).

Line 539, tables S2 and S6: explain b letter does it mean basal similarity?

Table 2: Explain what does the last column (%) stand for?

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L565-567: “On 8 days...Unit Days)”. This long sentence is difficult to understand.

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Supplementary material:

Page 1: “three platforms: a dedicated 12m” instead of “three platforms: platforms a dedicated 12m”; “in the 2007 and 2009 seasons, we used” instead of “in the 2007 and 2009, we used”; Delete the word “recent” since the cited analyses (reference 4) were published in 2006

Page 3: You may provide a value and a citation for “over relatively short ranges”; Tables S3-S5: I suggest to inform the number of days of recording of each individual for each year.

Figures S3 and S4 title: Delete “Letters denote age class (A – Adult, C – Calf)” if they do not appear on the figures.

Figure S3 title: “All notations are as in Figure 1” instead of “All notations are as in Figure 1 in text”

Tables S10-S12 titles: inform what ICI1 to ICI4 stand for in the tables.

Page 20: "References" instead of “Refernces”

Decision letter (RSOS-150372)

29-Sep-2015

Dear Dr Gero,

The editors assigned to your paper ("Distinctive modes of variation in sperm whale codas reflect individual identity, social unit membership, and vocal clan affiliation") has now received comments from reviewers. We would like you to revise your paper in accordance with the referee and Subject Editor suggestions which can be found below (not including confidential reports to the Editor). Please note this decision does not guarantee eventual acceptance.

Please submit a copy of your revised paper within three weeks (i.e. by the 22-Oct-2015). If we do not hear from you within this time then it will be assumed that the paper has been withdrawn. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office in advance. We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Editors, your
manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers.

To revise your manuscript, log into http://mc.manuscriptcentral.com/rsos and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. Revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you must respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". Please use this to document how you have responded to the comments, and the adjustments you have made. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response.

In addition to addressing all of the reviewers' and editor's comments please also ensure that your revised manuscript contains the following sections as appropriate before the reference list:

• Ethics statement (if applicable)
If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

• Data accessibility
It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

If you wish to submit your supporting data or code to Dryad (http://datadryad.org/), or modify your current submission to dryad, please use the following link:

• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.

• Authors’ contributions
All submissions, other than those with a single author, must include an Authors’ Contributions section which individually lists the specific contribution of each author. The list of Authors should meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:
AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out
the statistical analyses; EF collected field data; GH conceived of the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements
Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement
Please list the source of funding for each author.

Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Yours sincerely,
Emilie Aime
Senior Publishing Editor, Royal Society Open Science
openscience@royalsociety.org

Associate Editor's comments (Dr Sean Rands):
Associate Editor: 1

Comments to the Author:
Three reviewers have commented in detail on your manuscript. Please could you address their recommendations.

Reviewers' Comments to Author:
Reviewer: 1

Comments to the Author(s)
Journal: Royal Society Open Science
Manuscript ID: RSOS-150372
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Ann E. Bowles
Senior Research Scientist
Hubbs-SeaWorld Research Institute

Reviewer: 3

Comments to the Author(s)

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16) Last line of conclusion – as with last sentence of abstract need to do more to spell out how it supports the social complexity hypothesis

[Minor - note communication misspelled in keywords]

Best wishes,

Karen McComb
Author's Response to Decision Letter for (RSOS-150372)

See Appendix A.

RSOS-150372.R1 (Revision)

Review form: Reviewer 1 (Karen McComb)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Is it clear how to access all supporting data?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept as is

Comments to the Author(s)
I am very happy with the revised manuscript - and the authors are to be commended for their very careful responses to my comments and those of the other referees. This paper will be a very interesting addition to the literature and a great manuscript for Open Science.

Best wishes,

Karen McComb

Review form: Reviewer 2 (Yvonnick Le Pendu)

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes
Is it clear how to access all supporting data?
Yes (The ICI data used in this study will be made available through Dryad upon acceptance for publication).
Yes, supplementary material is adequate and clear.

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept as is

Comments to the Author(s)
The authors dis a cautious revision of their manuscript that attend all my requests and suggestions. The Figure S1 is clear and helpful. I recommend to publish this version of the manuscript.

Decision letter (RSOS-150372.R1)

03-Dec-2015

Dear Dr Gero,

I am pleased to inform you that your manuscript entitled "Individual, unit, and vocal clan level identity cues in sperm whale codas" is now accepted for publication in Royal Society Open Science.

We hope to send you a proof of your article soon. Please contact the production office (openscience_proofs@royalsociety.org) if you have any queries regarding these.

Royal Society Open Science operates under a continuous publication model (http://bit.ly/cpFAQ). Your article will be published straight into the next open issue and this will be the final version of the paper. As such, it can be cited immediately by other researchers. As the issue version of your paper will be the only version to be published I would advise you to check your proofs thoroughly as changes cannot be made once the paper is published.

In order to raise the profile of your paper once it is published, we can send through a PDF of your paper to selected colleagues. If you wish to take advantage of this, please reply to this email with the name and email addresses of up to 10 people who you feel would wish to read your article.

On behalf of the Editors of Royal Society Open Science, we look forward to your continued contributions to the Journal.

Best wishes,
Ms Emilie Aime
emilie.aime@royalsociety.org
http://rsos.royalsocietypublishing.org/
Dear Dr. Aimé, Dr. Rands and our reviewers,

We are grateful for the opportunity to resubmit to Royal Society Open Science. These reviews were a chance for us to improve our work based on thoughtful comments from respected members of our fields, but also proof that an open system for reviews yields critical yet constructive comments and we support RSOS in this endeavour.

Please accept this revised manuscript for your consideration. Below we address the reviewers’ comments on the original manuscript # RSOS-150372. We hope that you will find that these revisions are to your satisfaction and that this manuscript merits publication.

Sincerely,

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Reviewer 1: Unnamed

Reviewer 1 highlighted how our long-term “previous knowledge of social organization” and “large amount of raw data” allow us to “provide new and exciting understanding on the social structure of the population of sperm whales from the Eastern Caribbean” and “confirm the hypothesis of social complexity in sperm whales” through a “well written” manuscript. They conclude by recommending publication.

Their main comment suggests the inclusion of a figure or table summarizing our complex multi-staged analysis. This comment was echoed by Dr. Bowles and Dr. McComb and we have included Fig S1 in the ESM to clarify our analytical process.

We thank reviewer 1 for such a positive and thorough review which identified several typographical errors and sentence structure improvements.

Reviewer 1 Specific comments:

Line 3: “hierarchically” instead of “heirarchically”. 
Corrected
L55: “an excess of 70 types” instead of “in excess of 70 types”?
We have reworded this sentence to make clear we do mean “greater than” 70 coda type quantitatively and not that there is an excessive amount of types – but both are true to some extent.
L70: You need to explain that ESM stand for Electronic Supplementary Material at first instance. Corrected
L82 and ESM: How many “first few minutes”? We have now indicated in the ESM that the range of duration of recordings is between 2 – 18 minutes after fluke up.
L85: “the library of echolocation click IPIs” is hardly understandable: cite the ESM (page 2 and 3). We now refer the reader to the detailed methods in the ESM as requested
L133 and ESM: Verify the phrasing: “which Antunes et al. 53 found varied between individuals”. Our intent here is to show that early work done by Antunes et al on a very small subset of data suggested that the 5R type codas showed variation among individuals. We have reworded to clarify.
L151: delete only (already in L150)
Deleted
L170: Table S5 do not present “standardized discriminant coefficient and variance explained”. You may refer to tables S10-S12. Thank you for catching this, we reordered the ESM just prior to submission. It now refers to table S10 where the 4 click coda coefficients are located.
L216 “from 1 to 5” instead of “from 1 and 5”? Corrected
L354-530: The first letter of each word of some titles of journal articles are capitalized (e.g. references 5, 26, 61) while others are not; The word DOI is sometimes repeated (e.g. references 5, 18, 64); the complete DOI number is repeated (reference 70); use instead of Use (reference 8); delete space after Data (reference 43). These have been addressed and we have made a thorough pass through the remaining references. Line 539, tables S2 and S6: explain b letter does it mean basal similarity? Yes, this indicates basal similarity for the level of analysis. We have replaced the abbreviation with basal similarity in full
Table 2: Explain what does the last column (%) stand for? This is simply a proportion of the randomized datasets which have a greater than observed correct classification for the DFA when discriminating units or individuals. It was meant to help the reader determine the degree to which the random and observed datasets are different given that correct classification may be biased due to imbalances in the sample sizes between the groups being discriminated (i.e. the expectation under random assignment for n groups is not simply 1/n if the sample sizes are not equal). It is not a statistical test and perhaps confuses the reader more than it helps. We have removed it and clarified the table captions in regards to the difference between randomized and observed data DFA classifications. We have also moved further detail about randomization and the reasoning behind it from the ESM to the methods in the main text.
L551: “Euclidean” instead of “Eulidean” Corrected
L565-567: “On 8 days...Unit Days)”. This long sentence is difficult to understand. We have reworded to clarify.
L585: (Figure 1, line 36): the 86 value (5R1 for F unit) should not be shaded since 86/1107<0.1 and “Shaded numbers indicate predominant coda types which made up at least 10% of the unit’s coda production”. Thanks for catching that, this was a copy and paste error in Adobe Illustrator.

Supplementary material:
Page 1: “three platforms: a dedicated 12m” instead of “three platforms: platforms a dedicated 12m”; “in the 2007 and 2009 seasons, we used” instead of “in the 2007 and 2009, we used”; Corrected
Delete the word “recent” since the cited analyses (reference 4) were published in 2006 Corrected
Page 3: You may provide a value and a citation for “over relatively short ranges”;
We have rephrased the section in the ESM as:
“Clusters were small [Mean = 1.75 individuals, SD=1.24, 16], and generally hundreds to thousands of meters apart. Thus only members of the photoidentified cluster were within a few hundred metres of the hydrophone and therefore recorded, given that codas are only audible through hydrophones that are near the surface over a few hundred metres (SG unpublished).”

Tables S3-S5: I suggest to inform the number of days of recording of each individual for each year.
We have added a row with number of recording days.

Figures S3 and S4 title: Delete “Letters denote age class (A – Adult, C – Calf)” if they do not appear on the figures.
The have been added to the figures to clarify age class.
Figure S3 title: “All notations are as in Figure 1” instead of “All notations are as in Figure 1 in text”
Corrected

Tables S10-S12 titles: inform what ICI1 to ICI4 stand for in the tables.
We have added “Inter-click intervals (ICI) are numbered from first to last in the coda.” to the table caption.

Page 20: “References” instead of “Refernces”
Corrected

Reviewer 2: Ann E. Bowles

Dear Dr. Bowles,

Thank you for your very constructive insights. We feel that your suggestions have improved both the clarity in which we present our results the breadth with which we discuss them. Please find below the details of how each of your comments were addressed in the new manuscript.

The introduction is a particularly clear summary of the authors’ collective theorizing about sperm whale social communication and its relationship to sperm whale sociality. Although it is more general than the topic of the paper, it is succinct and well-written, and lays the groundwork for the Discussion as well as the Methods and Results.

Thank you.

The authors have put a lot of thought into their analysis based on a large body of previous literature on the same topic. They have examined different aspects of their data using multiple, sometimes similar, statistical procedures. However, the rationale for the steps they took isn’t explicitly laid out, and is particularly difficult to follow because critical information is split out in the electronic supplement and previous papers that used different analysis methods. It would help to have a paragraph at the start of the section, maybe with a diagram, that lays out the strategy for the analysis – the breakdown between categorical and continuous, a summary of the variables were entered into the analyses, the procedures they used for classifying, ordering, clustering, etc. This paragraph/diagram should help readers gain confidence in their approach.

Reviewer 1 and Dr. McComb also pick up on this. We have tried to use both innovative new methods while also ensuring that our assumptions and parameter choices do not affect the analysis. This inevitably leads what should be a linear narrative our “what we did” to have both branching points and repeats as we retest with differing inputs. We struggled with how to best present all the varied analyses while not losing the reader. Nonetheless, we felt that presenting the results from multiple methods and parameter choices made
the case for our results stronger. We have attempted to both our analytical approach in text and have included a new figure in the ESM which we hope clarifies our choices and methodological approach.

The discussion does not suggest how uncertainties in their methods might affect their conclusions, and this should be included. For example, the range of sample periods/samples among units and individuals is large. Might this have affected their results or blurred the distinctions among some codas by unit/individual?

Based on the discovery curves presented in the ESM we felt that at the level of the coda types recorded, we have sampled both individuals and units well. Our statistical tests strongly suggest that the differences between repertoires are likely not the result of sampling. Furthermore, we have tried to account for differences in sample size with respect to the discrimination results by comparing our results with the percent correct of randomized data as we describe in the main test and ESM. In addition, we have used several different methods to address the same question in terms of distance metrics, ICI measures, and by using categorical and continuous similarity measures – all which support the same results. One can always say that sampling could have affected the results, but we feel we have addressed this diligently. Lastly, it is important to note that Antunes et al.’s [ref 53 in main text] earlier work indicated that the 5R codas varied among individuals, while the 1+1+3 did not, with data from one unit, and this larger dataset across multiple units confirms these findings. This suggests that under sampling likely would not affect our conclusions. We have added: “Antunes et al.’s [15] preliminary work indicated that the 5R codas varied among individuals, while the 1+1+3 did not, using data from one unit, and this larger dataset across multiple units confirms these findings. This suggests that our conclusions are likely robust to under sampling.” to the section of the ESM with the discovery curves which discusses sample sizes.

The authors say they have provided evidence for vocal complexity matching the social complexity of sperm whales. The discussion (beginning on line 269) talks about the importance of understanding how the whales produce and use layers of complexity. However, the authors do not talk about how their findings relate to complexity in other species. In the absence of detail, it is hard to know whether the complexity of sperm whale codas is really directly comparable to other literature on vocal complexity. I know that this paper is not a review of the social complexity hypothesis, but since they have invoked it, I think some additional detail is justified. How would their interpretation of the hypothesis differ, for example, from that of Leuchtenberger et al. (2014), which provides a more traditional terrestrial view of complexity?


Thanks for sharing this really interesting paper of which we were not aware (we have added the citation in our introduction). Leuchtenberger et al. in addition to describing the repertoire of the giant otter in more detail than previous work also correlate group size with repertoire size among mustelids. Their classical interpretation of the social complexity hypothesis proposes that species with complex social structure (quantified as group size in their analysis) should present a more sophisticated communication system (quantified as number of call types in their analysis), “which is necessary to deal with a wider range of social interactions in different behavioural contexts.”

In place of the perspective that simple diversity of call types indicates complexity (like Leuchtenegerger et al) here we consider complexity in terms of signals delivering a diversity of cues with functionally usable information related to multiple levels of social structure – “which [are] necessary to deal with a wider range of social interactions”. We take the hypothesis deeper in demonstrating that not only do sperm whales have a complex multi-levelled social structure (previously defined by both increasing group size and the modular, multileveled organization), but that they have the accordingly sophisticated communication (quantified by both number of call types but also the variation within types), to deal with the specific social interactions at
various levels of their social structure. We connect the specific structures which create the social complexity with their expected signal diversity. This is not just a correlation between the two, it is a demonstration that the expected signals a sperm whale would need to address the specifics types of social interactions they may encounter do in fact exist.

We have reworded the introduction as requested by a similar comment by Dr. McComb and added to the discussion on lines 282-286 to highlight these points.

Specific Comments (by line number):

9: Something missing or a comma incorrect (....recorded, were....)
We have reworded and split into two sentences

30-34: I don’t think the leap from large spatial scale to adaptive pressure for social learning is justified as stated. Pressures of social competition within and across group and species could explain the complexity of cetacean social communication as well or better than habitat structure - remember that social odontocetes must deal with a complex clade of other large, wide ranging, sometimes irascible, and in at least one case predatory, social odontocetes. Great mobility increases the complexities of using the habitat, yes, but any or all of a number of mechanisms could be operating. The last sentence could just as well follow the first.

We meant that ecological variability is a pressure for culture, and the modelling suggests it as cited. But, social variability, as you, point out is also an issue (which is considered in reference 17 in more detail than we can here). Our focus on environment was intended to highlight why marine species are important when looking at the social complexity hypothesis (implicit is the social variability) as they provide a dramatic contrast in ecology compared to terrestrial species. To clarify, we have rephrased the last sentence.

108: If the classification of click patterns is highly reliable, there should be a statement to that effect with reference(s). If there were ambiguous cases, how were they resolved?
This the main reason for our new methodological approach in using OPTICS rather than k-means clustering. OPTICS allows for codas that are outliers or located in sparse areas between dense clusters to be labelled as noise, rather than being forced into clusters. This creates a scenario in which classification of click patterns is highly conservative (all codas included in a cluster – i.e. a Type – are very similar to each other), and ambiguous codas were removed from the categorical analysis as ‘noise’. This is explained in our “Justification for the use of OPTICS over previously used k-means methods” in the ESM and more briefly in text. We have attempted to clarify these points in both locations and we provide a reference to the advantages of OPTICS over k-means in the ESM.

150: Which variants of distance measure (Euclidean, etc.) were tested and how would distance have affected the multivariate similarity if the codas hadn’t been distinctive in the way they expected? In other words, to what degree was robustness with regard to the distance measure supportive of their results?

In our analysis, we used two measures of ICI to quantify the ICIs within codas (absolute timing and standardized by duration) and two distance metrics to quantify continuous similarity between codas (Euclidean and Infinity-norm). By demonstrating that the results are robust to changing our methods support our conclusions by eliminating the possibility that our methodological choices lead to our results.

ICI measures:
How we define a coda quantitatively in order to apply the analytical measures of similarity is determined by a choice of the measure. Previous work has demonstrated that using absolute ICI timing over standardized
timing, so including information regarding both the rhythm and tempo of a coda, preserves more useful information (e.g. Antunes et al.). As a result, we provide the absolute ICI results in the main text and the standardized in the ESM.

Distance metrics and Similarity:
Once we have quantified the codas, we needed a similarity measure between two codas. In the continuous method, we are essentially measuring a multivariate distance between two points, and then inverting it to provide a similarity measure. There are a large number of ways to do this. Euclidean distances are often seen as a default when the different variables are in the same units (as they are in our case), while infinity-norm has been the one chosen in previous work on codas.

Mixing Measures and Metrics:
In the main text, we present the results from the absolute ICIs using a Euclidean distance metric in the continuous measure of similarity. In the ESM, we present those results using standardized ICIs and an Infinity-norm distance. In reality, we also tested the two other combinations: absolute ICIs with infinity-norm distance and Standardized ICIs with Euclidean distances. We also changed the value for the basal similarity from 1 – 0.001 with no variation in overall patterns. We felt that for publication, we would simplify as much as possible (only reporting two of the four parallel analyses and including only basal similarity of 0.001 – the most fine resolution comparison), while still highlighting that our methods produce results which are robust to variation in the choices we made during analysis.

Should Dr. Bowles or the editor feel that there is a need to extend the discussion and definition of these measures and metrics in the ESM we would be happy to do so, but we do not feel that it is really within the scope of the paper or that it would improve the comprehension of the reader by diving even deeper into the mechanics of the multivariate statistics used given that all three reviewers already feel the description of the analyses is complex. Furthermore, each of these are discussed at length in both methods and experimental papers in the past which we reference. Lastly, we hope that the new figure in the ESM (FIG S1) and the changes in the methods section text have clarified this issue.

164: The observation that the codas did not change significantly over time is mentioned as an aside. However, this invariance is the driving phenomenon behind the degree of individual, unit, etc. specificity they found in their analysis; so, it would make sense to discuss it earlier in the results section, and maybe provide a table or figure about change over time in the codas they studied. This is particularly important given the discussion starting on line 278.

On line 164 (now line 184), we stated that the unit level repertoires do not change significantly across the 6 year study. We provide a table of statistics (Table S7) in the ESM (referenced in main text) to show the similarity between years of the repertoires of units and individualss. Variation in the structure of particular coda types across years within coda types (c.f. Deecke et al 2000 Dialect change in resident killer whales: implications for vocal learning and cultural transmission. Anim. Behav. 60, 629–638.) is not within the scope of this analysis.

188: A word is missing in this sentence (they also ??? in their usage of coda types..)
We have clarified this sentence

229: If the SE values were put in parentheses, the comparison would be clearer.
We have reworded the sentence to clarify.

255: Is there any information about the genetic distances among the units? The population in the area of their study was exploited historically.
We are currently undertaking the genetic analysis that will allow us to examine kinship within and between units. Unfortunately, these data are not currently available to supplement this analysis. As for exploitation, modern mechanized whaling did not target sperm whales in the western tropical North Atlantic and thus will have had minimal impact on the social units of females living in the Caribbean; however they were subject to the traditional "open-boat" hunts in the 18th and 19th centuries.

269-271: I would add to the list of properties the following: the capacity to produce vocal signals with sufficient stereotypy (not the same as being able to identify them). Their findings suggest that sperm whales must be able to retain an accurate template in memory and to emit sounds using it for very long periods.

We have added the required stereotype in this section and we do make a point in our conclusions that the 1+1+3 coda provides a remarkable example maintaining high levels of conformity in behaviour across large numbers of individuals that are not continuously associated

278: Make the text about discrimination vs. identification into a separate paragraph.

Corrected

Figure 2. Something that struck me in this dendrogram: Pinchy was the only F Unit whale that produced a high proportion of 5R1 codas, and yet this is one of the 2 codas uniformly used with high proportion in their clan of Dominican social units. Is there any indication that this whale is special? Say whether the same pattern was found in other units.

In the other units, there are several animals which produce 5R1 as >10% of their production (see the ESM). Such patterns are interesting. Our current work tries to help understand by looking at possible syntax and ordering of coda types, patterns of type use across social and behavioural contexts, and perhaps most specific to your observation, vocal dominance – do certain animals consistently lead vocal exchanges or produce an unexpected proportion of codas? Pinchy has been a mother for the majority of our study, with a juvenile male leaving the unit when she gave birth to her next son. She has also been a primary babysitter for another female in her unit.

Reviewer 3: Karen McComb

Dear Dr. McComb,

I really appreciate your enthusiasm for the manuscript and your positive feedback. We hope that you feel we have addressed all of your specific comments and improved the manuscript to a level that you would recommend publication.

This is a very interesting paper, which uses an impressively extensive dataset to tackle questions about how vocal signals in sperm whales advertise successive levels of social affiliation – specifically clan and social unit membership as well as individual identity. This sort of study is rarely possible in large mammals and by using their unique dataset and powerful analysis methods the authors have been able to break new ground here and their findings should be of wide interest.

Thank you.

1) I think the title could be usefully changed to “Distinctive modes of variation in sperm whale codas reflect social unit membership and vocal clan affiliation as well as individual identity”. This would stress more what is new/unique about the paper.
It is true that the most distinctive new results are at the unit level, but the results at the other levels are important too, and the comparison between them is arguably most significant. Thus we have provided a shorter, clearer variant of our original title that treats individual, unit and clan variation as similarly significant by listing them in the order of the social hierarchy.

2) Line 4 “broadest structures” is rather unclear here – change to affiliative structures?
   We have reworded as “Sperm whales have a hierarchically-structured society in which the largest affiliative structures, the vocal clans, are marked on ocean-basin scales by culturally-transmitted dialects of acoustic signals known as ‘codas’.” We feel this highlights both your point about affiliation and ours about clans being the largest/highest structure in their society.

3) Last line of abstract needs some development to say how results support the social complexity hypothesis e.g. ...by indicating that selection for advertising identity at different levels of a society may contribute to the evolution of a more complex vocal repertoire.
   We have flipped the last two lines in the abstract and reworded slightly though out to make this point, while still keeping it under 200 words.

4) Lines 22/23 describe what your findings support but I’m not sure this view was so widely accepted previously – I think more generally people have thought in terms of selection for social communication increasing as social complexity increases because more messages have to be exchanged. I’d leave out “to discriminate among various tiers of the social structure on lines 22 & 23 and instead add a sentence at the end of the paragraph saying: “This could occur in a number of ways… ...” where you outline this idea to set up your argument?
   We have reworded the first paragraph to fit better with the classical interpretation of the hypothesis, but note that in some respects we have taken testing this hypothesis to a deeper level by highlighting the implicit assumption underlying the hypothesis; that there must be functional usage of these additional “messages”. We connect the specific structures which create the social complexity with their expected signal diversity. We now make this point in the discussion.

5) Line 33: Accordingly would be better than As a result here.
   Changed

6) Line 35 “…the variability of vocal signals would be greatest in cetaceans where...”
   We have added “in cetaceans”.

7) Line 52/53 Careful of switching from dialect to repertoire – I think the definitions and use of these two terms could be made and kept clear throughout.
   We ascribe to the distinction of a dialect put forward by Conner (1982 Dialects versus geographic variation in mammalian vocalizations. Anim. Behav. 30, 297–298) for mammals based on Nottenbohm (1969 The song of the chingolo, Zonotrichia capensis, in Argentina: description and evaluation of a system of dialects. Condor, 71, 299-315.). Dialects refer to distinctions between communities which are overlapping or neighbouring and have the potential to interbreed. We use “repertoire” simply as the collection of calls made by a unit or individual. In this case, the geographic variation of repertoires in the Atlantic and the multiple sympatric dialects among clans in the Pacific. We only use the term dialect in the introduction in this paragraph and once in the discussion to state we have not found evidence of sympatric dialects in the Caribbean; throughout the rest of the manuscript we use the term repertoire. We did reword one sentence here to clarify this.
8) Line 73 I suggest “…interpulse interval and therefore size [30,31, see below], …

   Changed to fit your suggestion

9) Lines 115/116 Rephrase”…number of clicks was measured with both a Euclidian….using absolute ICI measures as in previous work…”

   Reworded

10) Lines 150/151 – two onlys.

    Fixed

11) Lines 154 – I felt the meat of what you showed got a bit lost in this section and I’d take a key sentence from the legend of Table 1 and have it in the text here. “Mantell test across all units has a null hypothesis that repertoire similarity between recordings of the same days (within unit) is the same as between recordings of different units on different days (between units)... then your very strong results.

    We have added the details of the Mantel tests here and in the individuals’ results and presented the test statistics and p-values in the text.

12) Line 188 missing word ...also ?differ in their...

    Corrected

13) Line 228/9 could be misleading – change to …units that belong to within-clan units in the Pacific...

    We are very sorry, but we are not sure what you'd would like changed here. This sentence points out that the repertoire similarity between units in the Caribbean is higher than that of unit repertoires for members of the same vocal clan in the Pacific; and therefore that all these Caribbean units belong to a single clan. We have reworded in an attempt to clarify.

14) Para at 245 – very interesting!

    We think so too! Glad we are not the only ones!

15) Lines 278-280 could be clearer on signals versus cues.

    We have added “The existence of cues does not imply that selection has acted on those cues to produce unambiguous, recognizable identity signals” to clarify.

16) Last line of conclusion – as with last sentence of abstract need to do more to spell out how it supports the social complexity hypothesis

    We’ve added as suggested

17) [Minor - note communication misspelled in keywords]

    Corrected