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Cultural turnover among Galápagos sperm whales

Mauricio Cantor, Hal Whitehead, Shane Gero and Luke Rendell

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Original submission:	11 June 2016
1st revised submission:	19 August 2016
2nd revised submission:	9 September 2016
Final acceptance:	12 September 2016

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

Review History

RSOS-160411.R0 (Original submission)

Review form: Reviewer 1 (Melinda Rekdahl)

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 authors have supplied detailed and important supplementary material to support the paper. I am impressed with the level of detail and clarity of the material supplied.

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)
Dear Authors, This is a very well written paper that contributes valuable information to the body of literature on sperm whale behaviour, communication and culture. I have no objections to this manuscript being published with only very minor edits or suggestions for how it could be improved. The paper is very well written in general and the authors have gone to considerable effort to ensure that there is sufficient information supplied both in the main body of the paper and in the extensive supplementary material section to clearly understand and interpret the results and conclusions of the paper. I feel that this paper contributes important information to the discussion of culture in sperm whale societies and other non-human animals and should be published.

A few minor points to consider:

Overall: The writing is generally very clear, however the constant use of dashes and colons made the introduction in particular a little laborious to read.

Abstract:
Lines 15 and 19 - The coda types in brackets (i.e. Regular, Plus-one). Consider clarifying what these are for those that are not familiar with sperm whale literature by including in the brackets 'coda type' or something to that effect.

Line 15 - When discussing the decline in numbers of the Galapagos populations, it would be helpful for overall clarity in the paper if you make it clear here that there was an apparent shift eastward to other nearby areas.

Line 23 - In the concluding sentence - and this is purely a thought to consider rather than necessarily recommending a revision - while I agree that tracking cultural traits can reveal large-scale population shifts, it is a little unclear how culture, presumably the cultural trait you are talking about, in this case, has influenced the structure and dynamics of animal populations. I can understand that this is the case if culturally mediated foraging preference led to the movement of sperm whales away from the Galapagos (which may apply) but in this case the cultural trait you are tracking is vocal behaviour, which you don't suggest as being the driver for movement away from the area. Therefore the link is not apparent to me in this last sentence and I would just suggest that you clarify your meaning.

Methods:
Line 108: missing 'at' in between from the same group if least 25%...

Supplementary material: method 5, paragraph 1, 4th sentence - coordinated manner not coordinate manner. This paragraph is also a little confusing as it is written. Consider revising with a clearer description of the social structure

Discussion:

Line 234: Perhaps discuss the movement of the galapagos population in a little more depth or refer back to your own study and Figure 1 given this is the basis for your conclusion that

emigration rather than die off or change in composition of the population has led to the shift in population structure as observed.

Figure 1: b) 2013-2014 not 2013-214

Review form: Reviewer 2

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?
I think some of the supplementary materials are not necessary (see comments).

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 paper reports the quite rare event of replacement of sperm whale clans off the Galapagos Islands, which occurred during the last few decades, based on the long term photoID study, and insists the importance of culture in the structuring of populations in these social species. This is the first report of this kind of cultural turnover in mammals other than primates and is of a special value. I recommend this article to be published with minor edits.

The weakness of this article is that the possible causes of this replace are not backed by compelling evidences. To consider the reason of the clan replacement, it should be crucial to know the clan structure in adjacent waters and clan membership of known emigrants. In the first scenario (environmental change), since some whales moved to the coastal areas, the effect of ENSO should be different between Galapagos and coastal areas, where it may be more suitable for one of the emigrate clans. In the second scenario biased clan structure in the coastal areas is unexpected. If the authors have any information on the clan membership of emigrants, it is good to be discussed.

Line 138: The authors used OPTICSxi clustering for the categorical classification of codas and ‘k-means algorithm' should be an error.

Line 203: I do not think the results of PCA are necessary for this paper. The results of PCA are not fully explained and they are not used to draw the conclusion of the paper. Further, the PCA itself is continuous method but listed in the categorical method in figure S2, just for the reason that coda types, results of categorical analyses, are illustrated in the PCA plots.

Line 215: The clan membership of the 6 whales from Gulf of California is not shown in figure 1b, which is referred here or any other information.

Line 249: It is not clear what 'which' points.

Line 275: This scenario does not fully explain why both two clans, one of which showed higher feeding success in ENSO years, disappeared from off Galapagos.

Figure 1: The period of (a) and (b) is the year when IDs obtained off the Galapagos and IDs from all other regions were obtained during 1985 and 2004. Discriminate between those two.

Decision letter (RSOS-160411)

04-Aug-2016

Dear Mr Cantor:

Manuscript ID RSOS-160411 entitled "Cultural turnover among Galápagos sperm whales" which you submitted to Royal Society Open Science, has been reviewed. The comments from reviewers are included at the bottom of this letter.

In view of the criticisms of the reviewers, the manuscript has been rejected in its current form. However, a new manuscript may be submitted which takes into consideration these comments.

Please note that resubmitting your manuscript does not guarantee eventual acceptance, and that your resubmission will be subject to peer review before a decision is made.

You will be unable to make your revisions on the originally submitted version of your manuscript. Instead, revise your manuscript and upload the files via your author centre.

Once you have revised your manuscript, go to https://mc.manuscriptcentral.com/rsos and login to your Author Center. Click on "Manuscripts with Decisions," and then click on "Create a Resubmission" located next to the manuscript number. Then, follow the steps for resubmitting your manuscript.

Your resubmitted manuscript should be submitted by 01-Feb-2017. If you are unable to submit by this date please contact the Editorial Office.

We look forward to receiving your resubmission.

Sincerely,
Andrew Dunn
Senior Publishing Editor
Royal Society Open Science

on behalf of
Kevin Padian, Royal Society Open Science
openscience@royalsociety.org

Associate Editor Comments to Author:
Associate Editor: 1
Comments to the Author:
This is an interesting study and provides some evidence for the ability of different clans of sperm whales to range widely over periods of years, perhaps prompted by changing environmental conditions. In that sense, the paper represents a useful contribution to the literature, and if the authors pare it down to focus on that simple conclusion it would be publishable. Overall, however, I find this paper as it stands to be very speculative, and its extended conclusions regarding cultural turnover to be unjustified considering the rather weak survey data on which it is based.

Two clans seen regularly for a few years in the late 1980s suddenly become less frequently sighted, and then disappear from the area in the 1990s. This is followed - though largely much later - by relatively low sighting rates of two different clans in the same area. I have several problems with this.

First, there is the question of sighting effort and detection efficiency: how do the authors know for sure that their survey effort was sufficiently exhaustive to state unequivocally that the Regular and Plus-One clans were not in the Galapagos area at all, and how can they exclude the possibility that they were foraging somewhere just outside the study area? Given the range and nomadic nature of sperm whales, this is an important question.

Second, there is the problem of very patchy effort. The study period of 1985-2014 involved assessment surveys in only eight years, with only one survey in the period 2000-2013. The Regular and Plus-One clans could well have been in the study area during any or all of those years.

Furthermore, there's the issue of the timescale overall, which is pretty short from a whale's perspective. Whales disappearing from an area for long periods is not unusual. On an admittedly smaller spatial scale, right whales were observed in high numbers in Roseway Basin on the Scotian Shelf through the 1980s, then essentially disappeared from that region for ten years beginning in 1993; had you begun surveys there in 1993 and continued them for a decade you would have concluded (incorrectly) that Roseway Basin was completely unimportant for the species. More to the point, the recolonization of Roseway later on by many different individuals did not represent a cultural shift. I know right whales are very different socially from sperm whales, but my point is simply that large whales range extensively in search of food, and when they disappear for a few (or more) years you can't necessarily read too much into it beyond their ability to seek out resources over large spatial and temporal scales.

The first explanation for the supposed turnover hinges upon the idea of the relative success of different foraging strategies within and among clans. This appears to be based upon previous observations of relative foraging success measured only by defecation rates. How reliable is this as a measure? Why are such observations not compromised by the likelihood that whales are often defecating below the surface and out of the sight of the observer? Perhaps this indirectly provides a well-established link between environmental conditions and foraging success, but it seems very weak to me.

The second explanation - regarding a delayed response to whaling - is even more tenuous given the number of observations involved, the question about detection efficiency, and the large gap in effort after 2000.

Minor comments

L 15-16: "Their numbers declined..." This is equivocal because it can mead the abundance of the population itself declined, or that observations of the whales did (i.e. the population size might have remained the same but the whales gradually emigrated out of the study area). Clarify.

L 43-44: The acquisition by humpback whales of a novel feeding strategy - lobtail feeding - did not occur in response to an ecological shift. The whales in question were feeding primarily on sand lance both prior to and after the spread of this feeding behavior.

L 251-253: The comparison with olive baboons doesn't make much sense to me. It's apples and oranges.

L 302: The word "pirate" is probably inappropriate here. Pirate whaling is defined as that occurring by an operation from a country not party to the International Convention for the Regulation of Whaling. Catches made by member states in contravention of the IWC's rules are "illegal" whaling.

Reviewers' Comments to Author:
Reviewer: 1

Comments to the Author(s)
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Figure 1: b) 2013-2014 not 2013-214

Reviewer: 2

Comments to the Author(s)
This paper reports the quite rare event of replacement of sperm whale clans off the Galapagos Islands, which occurred during the last few decades, based on the long term photoID study, and insists the importance of culture in the structuring of populations in these social species. This is the first report of this kind of cultural turnover in mammals other than primates and is of a special value. I recommend this article to be published with minor edits.

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Figure 1: The period of (a) and (b) is the year when IDs obtained off the Galapagos and IDs from all other regions were obtained during 1985 and 2004. Discriminate between those two.

Author's Response to Decision Letter for (RSOS-160411)

See Appendix A.

Decision letter (RSOS-160615)

09-Sep-2016

Dear Mr Cantor

On behalf of the Editor, I am pleased to inform you that your Manuscript RSOS-160615 entitled "Cultural turnover among Galápagos sperm whales" has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the Editor suggestions. Please find the Editor's comments at the end of this email.

The reviewers and Subject Editor have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the comments and revise your manuscript.

• Ethics statement
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:
http://datadryad.org/submit?journalID=RSOS&manu=RSOS-160615

• 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, designed 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.

Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days (i.e. by the 18-Sep-2016). If you do not think you will be able to meet this date please let me know immediately.

To revise your manuscript, log into https://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." You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". You can use this to document any changes you make to the original manuscript. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response to the referees.

When uploading your revised files please make sure that you have:

1) A text file of the manuscript (tex, txt, rtf, docx or doc), references, tables (including captions) and figure captions. Do not upload a PDF as your "Main Document".
2) A separate electronic file of each figure (EPS or print-quality PDF preferred (either format should be produced directly from original creation package), or original software format)
3) Included a 100 word media summary of your paper when requested at submission. Please ensure you have entered correct contact details (email, institution and telephone) in your user account
4) Included the raw data to support the claims made in your paper. You can either include your data as electronic supplementary material or upload to a repository and include the relevant doi within your manuscript
5) Included your supplementary files in a format you are happy with (no line numbers, vancouver referencing, track changes removed etc) as these files will NOT be edited in production

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.

Best wishes
Andrew Dunn
Senior Publishing Editor, Royal Society Open Science

on behalf of Kevin Padian
Subject Editor, Royal Society Open Science
openscience@royalsociety.org

Associate Editor Comments to Author:

The authors are to be commended for the detail and clarity with which they responded to the various reviews of their original manuscript. They have clearly outlined their responses, and by providing both a clean and a marked-up version of the manuscript have made it unusually easy to understand their revision. Would that all authors were this considerate to busy editors...

Overall, I am happy with the revisions made in response to my and the referees' comments. I have a few minor notes, below (referenced by line numbers on the marked-up, track changes manuscript, not the clean version).

21 ff: A little more detail would be helpful here. "...may include large-scale environmental regime shifts favoring clan-specific foraging strategies" for the first part. The term "cascading responses" sounds great, but for the abstract it isn't very informative. I think what you mean is exploitation of a habitat by surviving whales after whaling reduced the local population. Something like "...and a response to heavy whaling in the region involving redistribution of surviving whales into high-quality habitat." In other words, this section needs a little more information on exactly how the two scenarios are potentially manifest.

42-43: Dump the sentence beginning "Take" and modify the next to say "Male humpback whales (Megaptera novaeangliae) sing... etc".

44: Delete "regularly". This implies it has been documented many times, and it actually hasn't.

55: the word is "non-existent" not "inexistent".

70: Do you mean "Within clans"?

260: "span" should read "spanning".

363: I would suggest replacing "hypothetical" with "unclear".

Author's Response to Decision Letter for (RSOS-160615)

See Appendix B.

Appendix A

Manuscript ID: RSOS-160411-R1

Title: Cultural turnover among Galápagos sperm whales

Authors: Mauricio Cantor, Hal Whitehead, Shane Gero, Luke Rendell

To the editorial board at *Royal Society Open Science*

Kevin Padian, Ph.D., Subject Editor

Dear Professor Dr. Padian:

We are very grateful for the interest in our work and the opportunity to review and resubmit the manuscript RSOS-160411.

We appreciate the time invested by the two referees and the associate editor. We are happy they appreciated our question of the importance of culture for the structure and dynamics of animal populations. In particular, we are encouraged by Reviewer 1's statement that our manuscript is "*very well written"* and *"contributes valuable information to the body of literature on sperm whale behaviour, communication and culture*", as well as to Reviewer 2's remark that we present "*the first report of this kind of cultural turnover in mammals*" which is "*of a special value*".

In addition to the positive feedback on the significance of our work, reviewers have provided several thoughtful comments that helped us clarify important points. We reviewed the manuscript thoroughly to address all comments carefully, and paid special attention to the single major issue raised: the speculative interpretations for the cultural turnover. As a result, we now focus better on the observed pattern (the replacement of sperm whale clans), deemphasizing its inferred underlying mechanisms (environmental changes and lagged response to whaling). By better discussing the limitations of our findings and making all the requested adjustments we believe both the presentation and the quality of our manuscript have improved considerably.

We now resubmit a new version of the manuscript RSOS-160411-R1 for your consideration for publication in *Royal Society Open Science*. Below is a point-by-point response letter addressing each comment. For your convenience, we also provide a version of the manuscript with tracked changes.

Thank you for the insightful reviews that improved our work. We hope you will now

find our manuscript suitable for publication.

Yours sincerely,

Mauricio Cantor & co-authors

Department of Biology, Dalhousie University

+1 902 494-3723, mauricio.cantor@dal.ca

COMMENTS BY THE ASSOCIATE EDITOR:

Associate Editor's Comment #1: *This is an interesting study and provides some evidence for the ability of different clans of sperm whales to range widely over periods of years, perhaps prompted by changing environmental conditions. In that sense, the paper represents a useful contribution to the literature, and if the authors pare it down to focus on that simple conclusion it would be publishable.*

Authors' reply: We are very grateful for the editor's positive opinion and appreciate the thoughtful review of our work. We followed all the suggestions provided, in particular focussing on the observed pattern (replacement of sperm whale clans) rather than on speculated underlying mechanisms. Please see below how we addressed each of your comments (note that line numbers refer to the revised version without tracked changes).

Associate Editor's Comment #2: *Overall, however, I find this paper as it stands to be very speculative, and its extended conclusions regarding cultural turnover to be unjustified considering the rather weak survey data on which it is based. Two clans seen regularly for a few years in the late 1980s suddenly become less frequently sighted, and then disappear from the area in the 1990s. This is followed - though largely much later - by relatively low sighting rates of two different clans in the same area. I have several problems with this.*

Authors' reply: The editor's concern is pertinent and stems from the logistical challenges of studying sperm whales at individual levels over large temporal and spatial scales that make our research necessarily patchy over space and time. Although the underlying mechanisms may be speculative, the patterns and contrasts that emerged in our data are strong, indicating very profound changes in how the whales used our study area.

Associate Editor's Comment #3: *First, there is the question of sighting effort and detection efficiency: how do the authors know for sure that their survey effort was sufficiently exhaustive to state unequivocally that the Regular and Plus-One clans were not in the Galapagos area at all, and how can they exclude the possibility that they were foraging somewhere just outside the study area? Given the range and nomadic nature of sperm whales, this is an important question.*

Authors' reply: We cannot unequivocally attest that sperm whales from the Regular and Plus-One clans were not present just outside the Galapagos waters. Our recent data (2013-14) allow us to infer presence of sperm whales only within of the Galapagos Marine Reserve

(75 km around the archipelago). However, our sampling effort in these waters yielded sufficient data to show that 1) no individual seen off Galápagos recently were seen in these waters in the past; and 2) the coda repertoires of these new individuals were clearly distinct from the Regular and Plus-One clans present in the early years of the study. We now acknowledge in the revised version that our conclusions are based on data collected within the perimeters of the Galapagos Marine Reserve, and so there are inherent uncertainty regarding the immediate adjacent waters (L230-231: "…we acknowledge the (…) uncertainty regarding presence of whales in waters near the Galápagos…"). However, no sperm whales were detected in our four passages in 2013-2014 to and from the Galapagos region from the north and east.

Associate Editor's Comment #4: *Second, there is the problem of very patchy effort. The study period of 1985-2014 involved assessment surveys in only eight years, with only one survey in the period 2000-2013. The Regular and Plus-One clans could well have been in the study area during any or all of those years.*

Authors' reply: We understand the editor's concern with uneven sampling effort—the reasons being the logistical constraints of surveying a very large area. We have previously acknowledged this limitation (L85-86: "Given the logistical challenges of offshore surveys, sampling was unevenly distributed"). But perhaps the editor misread our figure 1 because the sampling effort is not as patchy as commented. Please note that when our research vessel was not off Galapagos, in most years it was surveying other study areas in the eastern Pacific (Supplementary Table S1). Our effort encompassed 19 (instead of eight) surveyed years in the period of 1985-2014, and six years (instead of one) between 2000-2013. The effort from 2000 on was less consistent for several reasons, including the decline in encounter rates of sperm whales off Galapagos (confirmed by opportunistic surveys carried out by other Galapagos researchers, and not included in our manuscript). We have previously explained this in the caption of figure 2 (L522-523).

We have edited our manuscript now to try and draw conclusions only from the data at hand and clarify that our interpretations on presence of clans are restricted to the surveyed years (L229-231: "Offshore surveys, however, impose several logistical challenges making our sampling effort patchy in time and space (Table S1). We acknowledge the consequent uncertainty regarding presence of whales (…) in unsampled years").

Associate Editor's Comment #5: *Furthermore, there's the issue of the timescale overall, which is pretty short from a whale's perspective. Whales disappearing from an area for long periods is not unusual. On an admittedly smaller spatial scale, right whales were observed in high numbers in Roseway Basin on the Scotian Shelf through the 1980s, then essentially disappeared from that region for ten years beginning in 1993; had you begun surveys there*

in 1993 and continued them for a decade you would have concluded (incorrectly) that Roseway Basin was completely unimportant for the species. More to the point, the recolonization of Roseway later on by many different individuals did not represent a cultural shift. I know right whales are very different socially from sperm whales, but my point is simply that large whales range extensively in search of food, and when they disappear for a few (or more) years you can't necessarily read too much into it beyond their ability to seek out resources over large spatial and temporal scales.

Authors' reply: The temporal scale is important. While a three-decade period is a short window in the lifespan of sperm whales, it still represents a particularly long research endeavor in the context of what researchers have achieved so far. Further, our study spanning less than a generation time makes our point that our results must be driven by movements among areas, rather than changes in clan composition through birth and death, even clearer (L240-243). We agree with the editor that the drivers for the replacement of sperm whales off Galapagos are their ability to seek out resources over large spatial and temporal scales, resembling the right whale example. However, our case is somewhat different. First, we never concluded that the Galapagos was unimportant for sperm whales. Second, by tracking not only presence of individuals, but also their communication repertoires, we showed that current whales using a particular area belong to different cultural groups from the same population. If all the right whales that recolonized the Roseway Basin had a distinct vocal repertoire from those that occupied it before, then it would have been rather noteworthy. As a side note, with the recent results on the cultural transmission of migration routes in southern right whales in mind (Carroll et al. 2015, doi: 10.1038/srep16182) one may not have any a priori reason to discount culture as a factor in the changes of distribution of right whales around Roseway.

Our point is that a local turnover of individual sperm whales also included a replacement of the communication repertoires used in the area. Thus we now follow the reviewer's suggestion and emphasize that the so-called 'cultural turnover' was a consequence of the natural movements of sperm whales in search for resources over large spatiotemporal scales (L255-257: "Therefore, the radical cultural turnover in sperm whale dialects off Galápagos reflected a clan replacement, i.e. a local turnover in whales using the area in consequence of their natural movements over large spatiotemporal scales").

Associate Editor's Comment #6: *The first explanation for the supposed turnover hinges upon the idea of the relative success of different foraging strategies within and among clans. This appears to be based upon previous observations of relative foraging success measured only by defecation rates. How reliable is this as a measure? Why are such observations not compromised by the likelihood that whales are often defecating below the surface and out of the sight of the observer? Perhaps this indirectly provides a well-established link between environmental conditions and foraging success, but it seems very weak to me.*

Authors' reply: Defecation rates is by now a well-established method for foraging success in the sperm whale literature (e.g. Whitehead et al. 1989, Smith & Whitehead 1993, Whitehead 1996, Jaquet & Whitehead 1999, Marcoux et al. 2007, Whitehead & Rendell 2004). It has been repeatedly argued that this measure is useful (see above references, and especially Jaquet & Whitehead 1999 Aquatic Mammals 25.1, for a consideration of the usefulness of this method).

The methodological details are available in these references, and we briefly describe here. Whenever the vessel was suitably placed after the photo-identification attempt, we checked each 'fluke-print' (a visible pattern on the water surface left by an individual whale after diving) to record whether or not it defecated (indicated by the presence of a brown patch in the water). The defecation rate was then calculated as the number of defecations observed divided by number of fluke-prints examined. Sperm whales usually defecate at surface, when preparing for a foraging dive; by following whales from hour to days, one can rarely miss a defecation at the surface. While they may defecate below the surface or out of sight, by standardizing the data collection as described above, we are confident that our metric is valid. We acknowledge the method is indirect—one does not measure feeding success *per se*, but proportion of times whales defecated. However, its underlying assumption is simple and very reasonable: what comes out must have gone in, in similar proportions.

Alternatively, acoustic cues of foraging could be used, as echolocation clicks followed by rapid-click buzzes ('creaks') suggest food consumption (e.g. Miller et al. 2004). However, this method has three major limitations: 1) if sounds are recorded by hydrophone arrays, one cannot identify the forager (and then assign it to a clan); 2) if modern computer tags (e.g. D-tags) are used, the problem becomes the sample size (since this technology is still expensive and laborious to employ); 3) the data would, at best, provide another indirect measure of feeding success. Thus, for our study spanning decades of research there are no better alternative measures of foraging success than defecation rates.

Associate Editor's Comment #7: *The second explanation - regarding a delayed response to whaling - is even more tenuous given the number of observations involved, the question about detection efficiency, and the large gap in effort after 2000.*

Authors' reply: We agree with the editor that our explanations are necessarily speculative at this point. We have rephrased parts of our discussion to 1) be clear about the limitations of our sampling and data (L229-232); 2) acknowledge that our scenarios are hypothetical, tentative explanations for the observed pattern (L277-278: "While our data show a clear shift in Galápagos sperm whale dialects, the underlying mechanisms for the large-scale displacement of clans are necessarily speculative"; L343-344: "The changes in sperm whale acoustic repertoires off Galápagos are clear, but the ultimate causes of this cultural turnover remain hypothetical"). We believe that being upfront about these two points will help readers to focus on the pattern our data shows (replacement of clans) rather than the hypothesized

drivers for this pattern (environmental changes and responses to whaling).

Associate Editor's Comment #8: *L 15-16: "Their numbers declined..." This is equivocal because it can mead the abundance of the population itself declined, or that observations of the whales did (i.e. the population size might have remained the same but the whales gradually emigrated out of the study area). Clarify.*

Authors' reply: The editor is correct. We meant to say that the observations of whales in our study area declined rather than the population itself. We removed the ambiguity by rephrasing the excerpt to "Their occurrence in the area declined through the 1990's…" (L16).

Associate Editor's Comment #9: *L 43-44: The acquisition by humpback whales of a novel feeding strategy - lobtail feeding - did not occur in response to an ecological shift. The whales in question were feeding primarily on sand lance both prior to and after the spread of this feeding behavior.*

Authors' reply: Since our point is the transmission of the strategy, we now omitted the phrase "in response to an ecological shift" (L44).

Associate Editor's Comment #10: *L 251-253: The comparison with olive baboons doesn't make much sense to me. It's apples and oranges.*

Authors' reply: We understand the editor's concern with our comparison and removed this reference.

Associate Editor's Comment #11: *L 302: The word "pirate" is probably inappropriate here. Pirate whaling is defined as that occurring by an operation from a country not party to the International Convention for the Regulation of Whaling. Catches made by member states in contravention of the IWC's rules are "illegal" whaling.*

Authors' reply: We are referring in particular to the Olympic Challenger, which was pirate whaling by this definition.

COMMENTS BY THE REVIEWER 1:

Comment #1 by Reviewer#1: *Dear Authors, This is a very well written paper that contributes valuable information to the body of literature on sperm whale behaviour, communication and culture. I have no objections to this manuscript being published with only very minor edits or suggestions for how it could be improved. The paper is very well written in general and the authors have gone to considerable effort to ensure that there is sufficient information supplied both in the main body of the paper and in the extensive supplementary material section to clearly understand and interpret the results and conclusions of the paper. I feel that this paper contributes important information to the discussion of culture in sperm whale societies and other non-human animals and should be published.*

Authors' reply: We appreciate the positive feedback highlighting the strong points and novelty of our manuscript. We are happy that the reviewer found our question relevant and the presentation of our work appropriate. Please see below how we acknowledged each of your comments on the revised version of the manuscript. Note that line numbers refer to the version without tracked changes.

Comment #2 by Reviewer#1: *A few minor points to consider: Overall: The writing is generally very clear, however the constant use of dashes and colons made the introduction in particular a little laborious to read.*

Authors' reply: We thank the reviewer for the suggestion to improve readability. As suggested, we reduced the number of dashes and colons throughout the text (e.g. L48-50, 57, 281, 313).

Comment #3 by Reviewer#1: *Abstract: Lines 15 and 19 - The coda types in brackets (i.e. Regular, Plus-one). Consider clarifying what these are for those that are not familiar with sperm whale literature by including in the brackets 'coda type' or something to that effect.*

Authors' reply: Thank you for the suggestion to improve the clarity of our text. These are the names of the vocal clans. We reworded the two excerpts to make it clear (L14, 19: … "whales from two clans (called Regular and Plus-One)… two other clans (called Short and Four-Plus)…")

Comment #4 by Reviewer#1: *Line 15 - When discussing the decline in numbers of the Galapagos populations, it would be helpful for overall clarity in the paper if you make it clear here that there was an apparent shift eastward to other nearby areas.*

Authors' reply: Thank you for the suggestion. We now rephrased this sentence to read "…re-sighting rates were low, with no matches with the Galápagos 1985-1999 population, suggesting an eastward shift to coastal areas" (L18-19).

Comment #5 by Reviewer#1: *Line 23 - In the concluding sentence - and this is purely a thought to consider rather than necessarily recommending a revision - while I agree that tracking cultural traits can reveal large-scale population shifts, it is a little unclear how culture, presumably the cultural trait you are talking about, in this case, has influenced the structure and dynamics of animal populations. I can understand that this is the case if culturally mediated foraging preference led to the movement of sperm whales away from the Galapagos (which may apply) but in this case the cultural trait you are tracking is vocal behaviour, which you don't suggest as being the driver for movement away from the area. Therefore the link is not apparent to me in this last sentence and I would just suggest that you clarify your meaning.*

Authors' reply: The reviewer is correct: the cultural trait we tracked (vocal behaviour) is unlikely to have directly driven the movement away from Galápagos. Since our findings indicate that cultural vocal clans are long-lasting structures of the sperm whale society, we meant to say that although whales move over very large areas they keep their clan membership. Therefore, a large-scale and somewhat collective movement of cultural groups would reflect population shifts. We elaborate this point in the second last paragraph of the discussion (L322-332), and agree that the link in the abstract was unclear. Therefore, to improve clarity we now transferred these ideas from the concluding paragraph to the discussion (L332-335), and rephrased the abstract to read "Long-lasting clan membership illustrates how culture can be bound up in the structure and dynamics of animal populations and how tracking cultural traits can reveal large-scale population shifts" (L24-26).

Comment #6 by Reviewer#1: *Methods: Line 108: missing 'at' in between from the same group if least 25%...*

Authors' reply: Corrected (L107).

Comment #7 by Reviewer#1: *Supplementary material: method 5, paragraph 1, 4th sentence - coordinated manner not coordinate manner. This paragraph is also a little confusing as it is written. Consider revising with a clearer description of the social structure*

Authors' reply: Thank you for the attentive review. We corrected the typo and rephrased this entire paragraph to clarify the description of the social structure as follows: "Sperm whale societies contain multiple social levels [4,13]. The fundamental one is the nearly-permanent social unit, defined as sets of individuals that live and move together for long periods, from several months to several years [14]. Social units form temporary groups among themselves, defining sets of animals that move together in a coordinated manner for periods of few hours to few days [4]. These groups are formed among social units of the same vocal clan [2], defined by sets of social units with high similarity in their coda repertoires [2]."

Comment #8 by Reviewer#1: *Discussion: Line 234: Perhaps discuss the movement of the Galapagos population in a little more depth or refer back to your own study and Figure 1 given this is the basis for your conclusion that emigration rather than die off or change in composition of the population has led to the shift in population structure as observed.*

Authors' reply: We followed the reviewer's suggestion and now refer back to our study, to a 2003 study, and to our figure 1a on the photo-identification matchings that illustrate movements of individuals from Galapagos to coastal waters (L237-238). We also rephrased parts of this paragraph to better organize the 4 reasons that made us conclude that emigration is the main underling mechanism for the clan replacement (L235-246: "There are four lines of evidence that support emigration out of Galápagos, rather than changes in the composition of the clans themselves, as the most likely mechanism for the local decline in sperm whale sightings. First, there were several re-identifications of Galápagos groups and clans off northern Chile and Gulf of California (figure 1a, see also [20, 31]) evidencing that sperm whales do move long distances. Second, sperm whales seem not change their clan membership, or if so, only very rarely [24]. Third, sperm whales are slow-reproducing, long-living animals [24] and the last three decades is a relatively short window in their life span during which no high mortality was evident [22]; all of these make death and birth very unlikely the drivers of the replacement of individuals off Galápagos. Finally, errors in individual identification cannot be a major factor because marks used to photo-identify animals rarely change [32]...").

Comment #9 by Reviewer#1: *Figure 1: b) 2013-2014 not 2013-214*

Authors' reply: Corrected (L514).

COMMENTS BY THE REVIEWER 2:

Comment #1 by Reviewer#2: *This paper reports the quite rare event of replacement of sperm whale clans off the Galapagos Islands, which occurred during the last few decades, based on the long term photoID study, and insists the importance of culture in the structuring of populations in these social species. This is the first report of this kind of cultural turnover in mammals other than primates and is of a special value. I recommend this article to be published with minor edits.*

Authors' reply: We very grateful for the reviewer's opinion on the novelty and relevance of our work, as well as for the attentive review that helped us to improve the presentation of our findings. We addressed all the comments and incorporated all suggestions in the revised version as detailed below. Please note that line numbers refer to the version without tracked changes.

Comment #2 by Reviewer#2: *The weakness of this article is that the possible causes of this replace are not backed by compelling evidences. To consider the reason of the clan replacement, it should be crucial to know the clan structure in adjacent waters and clan membership of known emigrants. In the first scenario (environmental change), since some whales moved to the coastal areas, the effect of ENSO should be different between Galapagos and coastal areas, where it may be more suitable for one of the emigrate clans. In the second scenario biased clan structure in the coastal areas is unexpected. If the authors have any information on the clan membership of emigrants, it is good to be discussed.*

Authors' reply: We understand the reviewer's concern with the uncertainty about the causes of the replacement of sperm whale clans. The reviewer's rationale to expect different clans in coastal waters given both of our hypothesized scenarios makes sense. There is some information on this in Rendell and Whitehead (2003). While groups from the Galapagos clans were found inshore (e.g. off mainland Ecuador, and northern Chile), they were found in different proportions. We now state this fact in L237-238 ("…there were several re-identifications of Galápagos groups and clans off northern Chile and Gulf of California…"). Unfortunately, there is not much more available information. Thus we now rephrase other parts of the manuscript to acknowledge more clearly the limitations of our data (L229-232) and to focus on the observed pattern (clan replacement) rather than its hypothesized drivers (L277-278: "While our data show a clear shift in Galápagos sperm whale dialects, the underlying mechanisms for the large-scale displacement of clans are necessarily speculative"; L343-344: "The changes in sperm whale acoustic repertoires off Galápagos are

clear, but the ultimate causes of this cultural turnover remain hypothetical").

Comment #3 by Reviewer#2: *Line 138: The authors used OPTICSxi clustering for the categorical classification of codas and 'k-means algorithm' should be an error.*

Authors' reply: We apologize for the lack of clarity on our text. We meant to say that the k-means algorithm was used in the original classification of clans by Rendell & Whitehead (2003), not in the current manuscript. We removed ambiguity by rephrasing this excerpt (L135-139: "The original partition of vocal repertoires into clans ([14], Supplementary Methods 5) used hierarchical clustering analyses based on the continuous multivariate similarities of standardized ICIs of codas, and the k-means algorithm to categorize codas into types [14]. Here we used the updated methods for comparing repertoires described above to re-analyze this data set together with the repertoires recorded off Galápagos in 2013 and 2014").

Comment #4 by Reviewer#2: *Line 203: I do not think the results of PCA are necessary for this paper. The results of PCA are not fully explained and they are not used to draw the conclusion of the paper. Further, the PCA itself is continuous method but listed in the categorical method in figure S2, just for the reason that coda types, results of categorical analyses, are illustrated in the PCA plots.*

Authors' reply: The reviewer is correct in that we do use PCA in an unconventional way. In this context, we are not really conducting an "analysis" per se, but simply using the principal components to reduce the dimensionality of the data. This allows for a clearer illustration of the results of the classification derived by the OPTICSxi algorithm. When codas are 8 clicks long, for example, the real data has 7 dimensions (7 absolute inter-click interval values which quantitatively define the coda). However, it would be impossible to plot these in any way which would allow the reader to observe and determine if the clustering completed by OPTICSxi yielded a valid result. The reviewer is correct in that we do not really draw conclusions from the PCA, but simply use it to reduce the dimensionality for illustrative purposes and thereby allow the reader to deduce for themselves if they feel that OPTICSxi has done an acceptable job in categorizing the data into valid clusters. In this way, the principal component plots were meant only to provide a visual cross-validation of the different use of coda types among clans (abbreviated in the contingency table of figure 3b). In figure S6, we label codas by type (as derived by OPTICSxi using shape of the icon) and by clan (color) for all codas retained after categorical analysis. In figure S7 we present all coda sampled, including those regarded as 'noise' by the OPTICSxi algorithm and label them by categorical type (color). We believe this information is important to illustrate the distinctness of the clusters which define the coda types, demonstrate the data retained and excluded from the categorical analysis, and support our main results presented (figure 3).

Therefore, feel strongly that they should be available for the interested reader in the supplement. We have improved the captions of figures S1, S6 and S7 to describe the above; and edited the main Results section (L202-203: "The patterns seen in the clustering analysis agreed with the distribution of coda types per clan in the multivariate space…")

Comment #5 by Reviewer#2: *Line 215: The clan membership of the 6 whales from Gulf of California is not shown in figure 1b, which is referred here or any other information.*

Authors' reply: The reviewer is correct. Our reference to the figure 1b was intended to show the photo-identification matches between Galapagos and Gulf of California, not the clan membership that is presented in the figure 3a. We rephrase this sentence to make our point clearer (L244-245: "the 6 whales seen in 2003 in the Gulf of California (figure 1 b) were found to be members of the Four-Plus clan in 2013 off Galápagos (figure 3 a).").

Comment #6 by Reviewer#2: *Line 249: It is not clear what 'which' points.*

Authors' reply: We meant to refer to "coda types with longer pauses at the end". We rephrased this excerpt to read "The groups recorded off Tonga and in the western Caribbean contained dominant codas with longer pauses at the end (e.g. Tonga: 4+1+1; Caribbean: 1+3+1, 5+1, 6I, 10I). These coda types may explain the tendency for Tonga and Caribbean groups to cluster with the Plus-One clan in our analysis." (L201-202).

Comment #7 by Reviewer#2: *Line 275: This scenario does not fully explain why both two clans, one of which showed higher feeding success in ENSO years, disappeared from off Galapagos.*

Authors' reply: We believe the reviewer's concern stems from the lack of clarity in our original text. The reviewer is correct in saying that the two clans have different feeding successes during the ENSO years. However, in these years the feeding success was drastically reduced for both clans, as shown in reference [17] (Whitehead & Rendell 2004). Therefore, our main argument in this scenario is that both original clans left the area because both foraging strategies became inefficient during these less productive years. We now clarify our scenario in two ways. First, we explain that in ENSO years both clan strategies performed poorly (L294-297: "In years of normal temperatures, the foraging strategy of the Regular clan outperforms the Plus-One; whereas in the warmer, less productive ENSO years the foraging successes of both clans is reduced considerably but the Plus-One's strategy becomes more efficient than the Regular's [17]."). Second, we explain that our argument assumes that whales from different clans (be it the original Regular or Plus-Ones, or the new Short or Four-Plus) would experience the low food availability differently because clans may

conserve their different foraging strategies (L300-305: "This assumed cultural inertia of foraging strategy—not uncommon in marine mammals [43,44]—implies that large-scale movement is favored over remaining in a changing habitat and adapting to the new conditions. This [scenario] may explain both why the original clans left and why the new immigrants are from different clans, but implies that changes to the ecosystem around Galápagos [37-39] are perceived differently by sperm whales from different clans.")

Comment #8 by Reviewer#2: *Figure 1: The period of (a) and (b) is the year when IDs obtained off the Galapagos and IDs from all other regions were obtained during 1985 and 2004. Discriminate between those two.*

Authors' reply: Done (L513-514).

Appendix B

Manuscript ID: RSOS-160615

Title: Cultural turnover among Galápagos sperm whales

Authors: Mauricio Cantor, Hal Whitehead, Shane Gero, Luke Rendell

To the editorial board at *Royal Society Open Science*

Kevin Padian, Ph.D., Subject Editor

Andrew Dunn, Senior Publishing Editor

Dear Professor Padian and Dr. Dunn:

We are very happy that the Associate Editor has recommended publication of manuscript RSOS-160615. Thank you very much for the interest on our work.

We appreciate the time invested in another review round, which helped us clarify minor issues. We addressed all comments, as indicated in our point-by-point response letter, and now resubmit the final version of our manuscript along with its data and high-quality figure files. We also double-checked and/or updated all the following sections as requested: Ethics statement, Data accessibility, Competing interests, Authors' contributions, Acknowledgements, and Funding statement.

Thank you for accepting our manuscript for publication in *Royal Society Open Science*, and for the excellent editorial service provided.

Yours sincerely,

Mauricio Cantor & co-authors

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ASSOCIATE EDITOR COMMENTS:

Comment #1 by Associate Editor: *The authors are to be commended for the detail and clarity with which they responded to the various reviews of their original manuscript. They have clearly outlined their responses, and by providing both a clean and a marked-up version of the manuscript have made it unusually easy to understand their revision. Would that all authors were this considerate to busy editors...*

Authors' reply: We are grateful for the opportunity to revise and resubmit our manuscript and appreciate very much the positive feedback.

Comment #2 by Associate Editor: *Overall, I am happy with the revisions made in response to my and the referees' comments. I have a few minor notes, below (referenced by line numbers on the marked-up, track changes manuscript, not the clean version).*

Authors' reply: We are happy that the editor felt we addressed all previous comments adequately, and now accepted all the last minor suggestions. Please note that line numbers refer to the final version, without tracked changes.

Comment #3 by Associate Editor: *21 ff: A little more detail would be helpful here. "...may include large-scale environmental regime shifts favoring clan-specific foraging strategies" for the first part. The term "cascading responses" sounds great, but for the abstract it isn't very informative. I think what you mean is exploitation of a habitat by surviving whales after whaling reduced the local population. Something like "...and a response to heavy whaling in the region involving redistribution of surviving whales into high-quality habitat." In other words, this section needs a little more information on exactly how the two scenarios are potentially manifest.*

Authors' reply: Thank you for the suggestion to improve the readability of our abstract. We now clarified this excerpt your suggested (L20-23: "The mechanisms behind this cultural turnover may include large-scale environmental regime shifts favouring clan-specific foraging strategies, and a response to heavy whaling in the region involving redistribution of surviving whales into high-quality habitats".)

Comment #4 by Associate Editor: *42-43: Dump the sentence beginning "Take" and modify the next to say "Male humpback whales (Megaptera novaeangliae) sing... etc".*

Authors' reply: Done (L41-42: "Male humpback whales (*Megaptera novaeangliae*) sing a continuously evolving population-specific song…").

Comment #5 by Associate Editor: *44: Delete "regularly". This implies it has been documented many times, and it actually hasn't.*

Authors' reply: Deleted (L43).

Comment #6 by Associate Editor: *55: the word is "non-existent" not "inexistent".*

Authors' reply: Corrected (L53).

Comment #7 by Associate Editor: *70: Do you mean "Within clans"?*

Authors' reply: No. The original sentence is correct: mitochondrial DNA is very similar among clans.

Comment #8 by Associate Editor: *260: "span" should read "spanning".*

Authors' reply: Corrected (L251).

Comment #9 by Associate Editor: *363: I would suggest replacing "hypothetical" with "unclear".*

Authors' reply: Replaced (L344).