

Growling from the gut: co-option of the gastric mill for acoustic communication in ghost crabs

Jennifer R. A. Taylor, Maya S. deVries and Damian O. Elias

Article citation details

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Review timeline

Original submission: 18 May 2019
1st revised submission: 16 July 2019
2nd revised submission: 11 August 2019
Final acceptance: 12 August 2019

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

Review History

RSPB-2019-1161.R0 (Original submission)

Review form: Reviewer 1

Recommendation

Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?

Good

General interest: Is the paper of sufficient general interest?

Acceptable

Quality of the paper: Is the overall quality of the paper suitable?

Excellent

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.

No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?

Yes

Is it clear?

Yes

Is it adequate?

Yes

Do you have any ethical concerns with this paper?

No

Comments to the Author

In this manuscript the authors describe a novel mechanism of sound production in a ghost crab. The manuscript is well-organized and easy to follow. The authors obviously put a lot of effort into characterizing the sound producing mechanism and I was impressed by the use of multiple techniques used to assess this. The data are convincing. The authors suggest (and I think they are correct) that the co-option of the gastric mill for sound production has interesting implications for the evolution of communication systems. Unfortunately, this is where the manuscript seems to fall a bit short. As it is written, it reads more like a functional morphology paper. The authors don't spend much time discussing the evolutionary implications of their finding, and have an overly strong emphasis on crabs. Not only do the authors ignore the larger implications in other diverse taxa, they even fail to acknowledge acoustic communication in other arthropod taxa like snapping shrimp. Related to this, the authors need to provide some additional information for their readers. Specifically, can crabs even hear the acoustic signal? For example, the rattlesnake rattle (mentioned in the ms) evolved as a signal to alert other species. If the crabs are producing the sound in response to a perceived attack (simulated by the researchers), then is this might suggest that the intended receiver is not another crab. The authors do mention that the sounds are produced during agonistic encounters, so the sounds very well could be detected by other crabs. For readers who are not crab specialists, this information would be helpful. Likewise, there are some theoretical and empirical papers discussing how morphological structures can be co-opted for use as part of a complex communication signal in other taxa and these are not discussed. Given my comments on the scope of the implications (as written), I cannot recommend publication in Proc. B. With that said, however, I do think the findings in this paper are extremely interesting. If the authors were willing to expand the scope of their findings, I think this could be an extremely interesting paper. I would be happy to review a new draft of this manuscript framed in a better evolutionary context.

Minor points: (I normally make a ton of comments in my reviews, the fact that I make only two here, point to concise and clear writing by the authors).

Lines 122-124: The experimental design seems not carefully conducted here. The authors state

that “Additional stimuli, including...” Were there other stimuli as well? Did all individuals in the subset experience all the different stimuli? Since the crabs responded, this is a pretty minor point, but a more systematic approach would have been beneficial.

Line 131: where the authors use the term “impulses” I think they mean “pulses”

Review form: Reviewer 2 (John Christy)

Recommendation

Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?

Excellent

General interest: Is the paper of sufficient general interest?

Good

Quality of the paper: Is the overall quality of the paper suitable?

Excellent

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.

No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?

Yes

Is it clear?

Yes

Is it adequate?

Yes

Do you have any ethical concerns with this paper?

No

Comments to the Author

This very well-written paper uses several lines of study and clever techniques to show clearly and for the first time that the ghost crab *Ocypode quadrata* produces sounds when threatened (various stimuli, including other crabs) by scraping one part of its gastric mill against another.

The rasping sounds are like the sounds these crabs, male and female, produce by rubbing a field of ridges and grooves on the palm of their larger claw against a row of tubercles on a basal segment of the same claw. Hence, the two mechanisms appear to produce redundant signals, allowing the crab to continue signaling with the gastric mill while the crab extends its claws to threaten or lunge at a challenger, movements that preclude acoustic signaling with the claw. Such functionally redundant signaling in sequence is unusual, I know of a single case in my own work on visual signaling by fiddler crabs, and another attractive feature of this report. As the authors point out (line 311), food grinding typically is “noisy” yet use of grinding structures to produce signals is known only in a few fish. They suggest, reasonably, that a closer look at noisy grinders may reveal other examples. In short, this is very well-done study of a novel mechanisms for signaling that should be of broad interest to those studying signal evolution. I do have a few comments and suggestions as detailed below by line.

60 You were able to elicit rasping from the gastric mill when the crabs were threatened or approached by objects or other crabs. This suggests that the sounds are aggressive or defensive. Demonstration of signal function, however, requires demonstration of how signal receivers respond to those sounds and some measure of the effect of those responses on the performance of the signaler. I suggest that you emphasize the similarity in the context eliciting rasping by claws and gastric mill consistent with similarity in function, which remains to be shown. In short “dial back” statements on function pending further work.

120 perhaps “Aggression was elicited by...”

123 maybe describe what a Hexbug toy is...?? Not available when my kids were kids. Had to google the name to find out.

128 delete “if” not needed.

Nice methods – like the multiple lines of inquiry.

181 and forward. This section made me think that the sounds you were recording were made by claw rubbing. Yet in the next section you state that the sounds were recorded when the crabs had their claws in a position that would not permit sound production by claw rubbing. Please clarify. Which recordings were from claw rubbing and which were from the gastric mill?

207 - 208 Few readers will know what a meral spread is. You could just say “with their chelipeds spread laterally in a threat display.”

289 A crab in a burrow is in a good position to use its chela to stridulate, since the chela will be folded in front of the crab. Why are you suggesting that they may produce sounds using their gastric mill in this circumstance? Seems unlikely to me, especially because I suspect that the intensity of the sound, and especially the substrate component, will be greater when the claw is used to rasp.

322 *Leptuca musica* and *terpsichores* males “sing” (nearly continuously) to females while they are underground and a female they have attracted by claw waving is at their burrow entrance, using the stridulatory mechanism on their large claws.

Nice study – well done!

John Christy

Video S2 is fantastic. I am a believer!

Decision letter (RSPB-2019-1161.R0)

28-Jun-2019

Dear Miss Taylor:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers’ comments (not including confidential comments to the Editor)

and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

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 Associate Editor, 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. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into <http://mc.manuscriptcentral.com/prsb> 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.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (<https://royalsociety.org/journals/ethics-policies/>). You should pay particular attention to the following:

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If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:

If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

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It is a condition of publication that you make available the data and research materials supporting the results in the article. Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (<https://royalsociety.org/journals/ethics-policies/data-sharing-mining/>). References to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the datasets used should also be fully cited and listed in the references.

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[http://datadryad.org/submit?journalID=RSPB&manu=\(Document not available\)](http://datadryad.org/submit?journalID=RSPB&manu=(Document not available)), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy <http://royalsocietypublishing.org/data-sharing>.

Electronic supplementary material:

All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
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mailto:proceedingsb@royalsociety.org

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Associate Editor, Comments to Author:

We have received two reviews of your manuscript and I am happy to let you know that they were both positive about your study. In particular, both reviewers agree that the described behavior is a fascinating example of the evolution of a redundant signal, they were enthusiastic about the multiple lines of evidence used to assess the behavior and they appreciated the quality and organization of the writing. However, Reviewer 1 had considerable concerns about how the story is presented in terms of the broader scope of animal communication, and these concerns should be addressed before the manuscript can be considered for publication in Proceedings B. In addition, both reviewers requested more information about specific methods and the sensory capabilities of crabs and their potential predators, which would help in illuminating the evolutionary implications of the findings.

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Reviewers' Comments to Author:

Referee: 1

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===

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John Christy

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Author's Response to Decision Letter for (RSPB-2019-1161.R0)

See Appendix A.

RSPB-2019-1161.R1 (Revision)

Review form: Reviewer 1

Recommendation

Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
N/A

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author

I had two primary concerns with the manuscript. The first was that the evolutionary scope needed to be broadened, which I felt would broaden the appeal of the manuscript. The authors have done this. My second, and more important concern, was whether or not the crabs could even hear the acoustic signal. Whether or not the crabs can hear the signal has important evolutionary implications. The authors now provide a citation, indicating that the crabs can indeed hear airborne sounds (very cool!). I'm satisfied with the revisions and I think the authors have a really nice study here.

Decision letter (RSPB-2019-1161.R1)

07-Aug-2019

Dear Miss Taylor

I am pleased to inform you that your manuscript RSPB-2019-1161.R1 entitled "Growling from the

gut: co-option of the gastric mill for acoustic communication in ghost crabs" has been accepted for publication in Proceedings B.

The referee and associate editor have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to these comments and revise your manuscript. 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. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into <https://mc.manuscriptcentral.com/prsb> 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. 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 referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

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- 1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".
- 2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.
- 3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

5) Data accessibility section and data citation

It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository.

In order to ensure effective and robust dissemination and appropriate credit to authors the

dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:

- DNA sequences: Genbank accessions F234391-F234402
- Phylogenetic data: TreeBASE accession number S9123
- Final DNA sequence assembly uploaded as online supplemental material
- Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311

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If you wish to submit your data to Dryad (<http://datadryad.org/>) and have not already done so you can submit your data via this link

[http://datadryad.org/submit?journalID=RSPB&manu=\(Document not available\)](http://datadryad.org/submit?journalID=RSPB&manu=(Document%20not%20available)) which will take you to your unique entry in the Dryad repository. If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

Please see <https://royalsociety.org/journals/ethics-policies/data-sharing-mining/> for more details.

6) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit <https://royalsociety.org/journals/authors/author-guidelines/>.

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

Sincerely,
Victoria Braithwaite

Professor V A Braithwaite
Editor, Proceedings B
<mailto:proceedingsb@royalsociety.org>

Associate Editor, Comments to Author:

Thank you for addressing the reviewer feedback in your revised manuscript. I am pleased to inform you that your revision of MS RSPB-2019-1161 is very close to being acceptable for publication in Proceedings B. We ask for one minor revision. The first line of the final paragraph (lines 346-347) states that "Functionally redundant signaling is known to occur in the visual courtship displays of animals, but not in acoustic communication systems." This statement requires supporting references. Please provide these in a revised manuscript. This second revision will not be sent out for further review but will be checked by our Editorial staff to make sure that the paper is suitable to be sent to Production.

=====

Reviewer Comments to Author:

Referee: 1

I had two primary concerns with the manuscript. The first was that the evolutionary scope needed to be broadened, which I felt would broaden the appeal of the manuscript. The authors have done this. My second, and more important concern, was whether or not the crabs could even hear the acoustic signal. Whether or not the crabs can hear the signal has important evolutionary implications. The authors now provide a citation, indicating that the crabs can indeed hear airborne sounds (very cool!). I'm satisfied with the revisions and I think the authors have a really nice study here.

Author's Response to Decision Letter for (RSPB-2019-1161.R1)

See Appendix B.

Decision letter (RSPB-2019-1161.R2)

12-Aug-2019

Dear Miss Taylor

I am pleased to inform you that your manuscript entitled "Growling from the gut: co-option of the gastric mill for acoustic communication in ghost crabs" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

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All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,

Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

Response to Referees

*Please note that our responses are in bold blue font following each of the referees' comments. The manuscript showing all edits in "Track changes" follows our response to referees.

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Associate Editor, Comments to Author:

We have received two reviews of your manuscript and I am happy to let you know that they were both positive about your study. In particular, both reviewers agree that the described behavior is a fascinating example of the evolution of a redundant signal, they were enthusiastic about the multiple lines of evidence used to assess the behavior and they appreciated the quality and organization of the writing. However, Reviewer 1 had considerable concerns about how the story is presented in terms of the broader scope of animal communication, and these concerns should be addressed before the manuscript can be considered for publication in Proceedings B. In addition, both reviewers requested more information about specific methods and the sensory capabilities of crabs and their potential predators, which would help in illuminating the evolutionary implications of the findings.

We have broadened the scope of our discussion on animal communication by adding more examples of co-option in the introduction (lines 50-51), a new paragraph on the breadth of sound production mechanisms across lineages (lines 312-322), and a few lines addressing the implications of our findings in the last paragraph (lines 348-355).

We inserted all of the additional requested information regarding specific methods (detailed in the point by point responses below).

We also added information on signal reception in crabs and potential predators. Specifically, we mention how the frequency of the gastric stridulation acoustic signal is within the frequency range of hearing of the two primary predators of ghost crabs as well as conspecifics (lines 290-292).

=====

Reviewers' Comments to Author:

Referee: 1

In this manuscript the authors describe a novel mechanism of sound production in a ghost crab. The manuscript is well-organized and easy to follow. The authors obviously put a lot of effort into characterizing the sound producing mechanism and I was impressed by the use of multiple techniques used to assess this. The data are convincing. The authors suggest (and I think they are correct) that the co-option of the gastric mill for sound production has interesting implications for the evolution of communication systems. Unfortunately, this is where the manuscript seems to fall a bit short. As it is written, it reads more like a functional morphology

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We expanded the scope of our discussion on acoustic communication by adding more examples of co-option in the introduction (lines 50-51), a new paragraph on the breadth of sound production mechanisms across lineages, including arthropods (lines 312-322), and a few lines addressing the implications of our findings in the last paragraph (lines 348-355).

Related to this, the authors need to provide some additional information for their readers. Specifically, can crabs even hear the acoustic signal? For example, the rattlesnake rattle (mentioned in the ms) evolved as a signal to alert other species. If the crabs are producing the sound in response to a perceived attack (simulated by the researchers), then this might suggest that the intended receiver is not another crab. The authors do mention that the sounds are produced during agonistic encounters, so the sounds very well could be detected by other crabs. For readers who are not crab specialists, this information would be helpful.

Good point. We added information on signal reception in crabs and potential predators. Specifically, we mention how the frequency of the gastric stridulation acoustic signal is within the frequency range of hearing of two primary predators of ghost crabs as well as conspecifics (lines 290-292).

Likewise, there are some theoretical and empirical papers discussing how morphological structures can be co-opted for use as part of a complex communication signal in other taxa and these are not discussed.

As we expanded the scope of our discussion (described above), we included several new citations of papers on the co-option of structures for communication signals in other taxa (lines 50-51, 312-322).

Given my comments on the scope of the implications (as written), I cannot recommend publication in Proc. B. With that said, however, I do think the findings in this paper are extremely interesting. If the authors were willing to expand the scope of their findings, I think this could be an extremely interesting paper. I would be happy to review a new draft of this manuscript framed in a better evolutionary context.

Minor points: (I normally make a ton of comments in my reviews, the fact that I make only two here, point to concise and clear writing by the authors).

Lines 122-124: The experimental design seems not carefully conducted here. The authors state that "Additional stimuli, including..." Were there other stimuli as well? Did all individuals in the subset experience all the different stimuli? Since the crabs responded, this is a pretty minor point, but a more systematic approach would have been beneficial.

We added more information and a better description to clarify this component of the study. The 4 stimuli listed were the only ones tested. Each crab was exposed to all 4 stimuli, in random order, over the course of 4 days (1 stimulus per day). See lines 123-126.

Line 131: where the authors use the term “impulses” I think they mean “pulses”

This has been corrected accordingly. See line 133.

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Referee: 2

This very well-written paper uses several lines of study and clever techniques to show clearly and for the first time that the ghost crab *Ocypode quadrata* produces sounds when threatened (various stimuli, including other crabs) by scraping one part of its gastric mill against another. The rasping sounds are like the sounds these crabs, male and female, produce by rubbing a field of ridges and grooves on the palm of their larger claw against a row of tubercles on a basal segment of the same claw. Hence, the two mechanisms appear to produce redundant signals, allowing the crab to continue signaling with the gastric mill while the crab extends its claws to threaten or lunge at a challenger, movements that preclude acoustic signaling with the claw. Such functionally redundant signaling in sequence is unusual, I know of a single case in my own work on visual signaling by fiddler crabs, and another attractive feature of this report. As the authors point out (line 311), food grinding typically is “noisy” yet use of grinding structures to produce signals is known only in a few fish. They suggest, reasonably, that a closer look at noisy grinders may reveal other examples. In short, this is very well-done study of a novel mechanisms for signaling that should be of broad interest to those studying signal evolution. I do have a few comments and suggestions as detailed below by line.

60 You were able to elicit rasping from the gastric mill when the crabs were threatened or approached by objects or other crabs. This suggests that the sounds are aggressive or defensive. Demonstration of signal function, however, requires demonstration of how signal receivers respond to those sounds and some measure of the effect of those responses on the performance of the signaler. I suggest that you emphasize the similarity in the context eliciting rasping by claws and gastric mill consistent with similarity in function, which remains to be shown. In short “dial back” statements on function pending further work.

We dialed back our statements on function throughout the manuscript as suggested. See for example lines 60-61.

120 perhaps “Aggression was elicited by...”

This has been corrected accordingly. See line 121.

123 maybe describe what a Hexbug toy is...?? Not available when my kids were kids. Had to google the name to find out.

We defined this as “a remote control robotic toy (Hexbug spider)” to offer a better description of these pretty nifty toys (which unfortunately a crab destroyed). See line 125.

128 delete “if” not needed.

This deletion has been made. See line 130.

Nice methods – like the multiple lines of inquiry.

181 and forward. This section made me think that the sounds you were recording were made by claw rubbing. Yet in the next section you state that the sounds were recorded when the crabs had their claws in a position that would not permit sound production by claw rubbing. Please clarify. Which recordings were from claw rubbing and which were from the gastric mill?

We did not analyze any stridulation by the claw mechanism. To eliminate this confusion, we specified on line 184 and lines 200-201 that the sounds heard and analyzed were produced by the hypothesized gastric mechanism.

207 - 208 Few readers will know what a meral spread is. You could just say “with their chelipeds spread laterally in a threat display.”

Thanks for this suggestion. We replaced “meral spread” with the more clear description you offered. See line 210-211.

289 A crab in a burrow is in a good position to use its chela to stridulate, since the chela will be folded in front of the crab. Why are you suggesting that they may produce sounds using their gastric mill in this circumstance? Seems unlikely to me, especially because I suspect that the intensity of the sound, and especially the substrate component, will be greater when the claw is used to rasp.

We offered this as a possibility simply because the mechanism used while in the burrow is not seen and the sound signal is similar. But this is highly speculative and you are likely right about the use of the claws, so we deleted this statement. See line 294-295.

322 *Leptuca musica* and *terpsichores* males “sing” (nearly continuously) to females while they are underground and a female they have attracted by claw waving is at their burrow entrance, using the stridulatory mechanism on their large claws.

Thank you for pointing this out. We corrected the sentence to include that stridulation is also used by some male fiddler crabs for courtship. See line 340-341.

Nice study – well done!

John Christy

Video S2 is fantastic. I am a believer!

Thank you!

Appendix B

Response to Referees

Associate Editor, Comments to Author:

Thank you for addressing the reviewer feedback in your revised manuscript. I am pleased to inform you that your revision of MS RSPB-2019-1161 is very close to being acceptable for publication in Proceedings B. We ask for one minor revision. The first line of the final paragraph (lines 346-347) states that “Functionally redundant signaling is known to occur in the visual courtship displays of animals, but not in acoustic communication systems.” This statement requires supporting references. Please provide these in a revised manuscript. This second revision will not be sent out for further review but will be checked by our Editorial staff to make sure that the paper is suitable to be sent to Production.

Thank you. We are elated that our manuscript has been accepted. We modified the sentence on lines 346-347 slightly to better clarify our point and we added the only known reference that supports this statement.

The sentence now reads

Sequential, functionally redundant signaling is known to occur in the visual courtship displays of one group of animals (fiddler crabs) (57), but we know of no examples in acoustic communication systems.