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Colour dimorphism in labrid fishes as an adaptation to life on coral reefs

J. R. Hodge, F. Santini and P. C. Wainwright

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Review timeline

Original submission:	28 June 2019
1st revised submission:	24 January 2020
2nd revised submission:	1 March 2020
Final acceptance:	2 March 2020

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

Review History

RSPB-2019-1522.R0 (Original submission)

Review form: Reviewer 1

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?
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

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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
The authors take a phylogenetic comparative approach to identify the factors underlying the evolution of colour dimorphism in the Labridae (wrasses and parrotfishes). The results show that colour dimorphism is more prevalent on coral reef habitat, yet contrary to a prevalent idea the effect of habitat (coral reef versus non coral reef) on colour dimorphism is not primarily driven by traits associated with strong sexual selection (lek-like polygyny or diandric protogyny). Selection pressures specific to coral reef habitat (associated with e.g. clear oligotrophic water or structural complexity) appear instead to directly promote the evolution of colour dimorphism, independently of sex allocation and mating system. The results also indicate that labrid terminal phases associated with coral reef habitat are more likely to display blue colors (that are most spectrally contrasting against coral reefs backgrounds) and less likely to display white colors (which are often associated with cryptic coloration through counter-shading and mottled patterns). This suggests that these colors are meant to be conspicuous, at least at short viewing distances. On the other hand, labrids not associated with coral reefs are less likely to have colour-dimorphic heads, bodies and caudal fins but are equally likely to have colour-dimorphic dorsal and anal fins that can either remain folded against the body or extended to signal to conspecifics. This suggests a stronger role of crypsis and predation in non coral reef habitat where turbidity is higher and structurally complexity less important.

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Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions 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?
Excellent

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

Is the length of the paper justified?
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Yes

Is it clear?
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Is it adequate?
N/A

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Comments to the Author
This paper aims to explore the effect of various factors (i.e. sex allocation, mating system and habitat) on the evolution of color dimorphism in a coal reef fish family (Labridae). The authors used a new time-calibrated phylogeny and various phylogenetic comparative methods in order to test their hypotheses.

The topic addressed by this MS is highly interesting for specialists and non-specialists of (coral reef) fishes. Thus, it is a pity that this MS is mainly oriented for « fishy » persons. The great majority of references come from an ichthyological literature and the authors directly start their introduction (Line 35) with their fish group of interests: wrasses and parrotfishes. However we know that various taxonomic groups of animals show color dimorphism such as insects, fishes, snakes, birds,… and there are many works devoted to this topic. So, why do the authors not try to insert their interesting results within the general topic of color dimorphism in the animal kingdom? I highly recommend that the authors put their study in the general perspective of our

understanding of the evolution of color dimorphism by integrating studies conducted on different animal taxa and different methods.

Generally speaking, the methods used are appropriate. However I have to admit that what is tested in the section « Phase- and body-specific selective pressures » appears unclear to me. So I would ask for more explanations but, even more importantly, this section is not really introduced by the authors during the Introduction. That could explain my questioning.

This work could be highly influential and deserve a publication in a top journal like Proceedings B but it still needs works of specifications and broadening in the Introduction/Discussion/Perspectives. Hereafter, I have listed some comments that should be addressed prior to an acceptance for publication.

Specific Comments:

Title:
To my opinion, the title is not appropriate. Indeed, how explain that an extensive number of teleost fishes show color dimorphism when they do not live in coral reef environments. Accordingly, I would suggest a title less generalizing, more adequate like « Life on coral reefs promotes color dimorphism in wrasses and parottfishes (Labridae) » or something very similar.

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Beyond my regrets that the Introduction is too « fish-oriented », I also point out that the term « color dimorphism » is not enough defined in the present MS. Dimorphism in colors can be linked to sex, ontogeny, behavior, habitat, diet… Here, the color dimorphism observed in wrasses and parrotfishes is mainly size-dependent and thus it seems associated with ontogeny and sex-change. Consequently, by using wrasses and parrotfishes, the authors address a specific type of color dimorphism. For example, in coral reef fishes, the type of color dimorphism observed in wrasses and parrotfishes differ from the one of the dusky dottyback Pseudochromis fuscus (e.g. Cortesi et al. 2015, 2016), and the evolutionary forces acting on these types of color dimorphism likely differ. This should be more detailed in the Introduction, by explaining the novelty but also the limits of the system studied along the present MS.

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M&M:
I am not a supporter of preprints use and associated repositories (e.g. bioRxiv). Accordingly, I am questioning the way how the authors introduce their new time-calibrated phylogeny of Labridae (line 137). We can obtain details on phylogenetic inference and divergence time estimation via a preprint version of another paper from the same authors (Hodge et al. 2019). I think that this work is probably under review in another journal. If the preprint is not accepted for publication shortly, I suggest that all the details about the production of phylogenetic hypotheses should be provided as Supplementary Materials in the present paper.

Results and Discussion:
Table S4, providing results from models comparisons, should be part of the main text. This table

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Lines 307-322. I would suggest the authors avoid too much interpretation about camouflage and conspicuousness of colors in coral reef fishes because a color may be good for camouflage or communication depending on the background they are viewed against; and reef fishes use a combination of color and behavior to regulate their conspicuousness and crypsis. The authors should stay on more general statements, commenting that the behaviors of small fishes (mainly driven by the avoidance of predators) differ from the ones of large fish (mainly driven by reproductive success) and this could sustain an ontogenetic color dimorphism. This suggestion could also help for a rewriting of the conclusions (especially lines 328-331).

In addition to these considerations, I am also questioning if the number of color dimorphic species could be linked to the total number of species in one environment. Knowing that, in the marine realm, coral reefs house one of the highest numbers of fish species; it could explain why fishes developed a so large repertoire of signals including sex dimorphism in order to improve communication in a « crowded » environment. This argument could certainly be added in the Discussion.

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Coral reefs are often connected to other coastal systems like seagrass beds and mangroves, and many fish species like parrotfishes moves from one system to another during their ontogeny or even during nycthemeral cycles. How do the authors deal with this and classify these species? Could it have an impact on results and related conclusions?

References
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Hodge JR, Santini F, Wainwright PC. 2019 Correlated evolution of sex allocation and mating system in wrasses and parrotfishes. bioRxiv , 665638.

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Review form: Reviewer 3

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?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
Yes

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

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Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
No

Do you have any ethical concerns with this paper?
No

Comments to the Author
This study investigates the evolution of colour polymorphism in marine fishes. While studies that explore the role of sexual selection and life-history strategies in the maintenance of colour polymorphism are frequent, studies that investigate the significance of respective habitat while controlling for sexual selection and life-history hypotheses are scarce. To this end this work makes a neat contribution. The authors use phylogenetic comparative analysis to show that parrotfishes and wrasses exclusive to coral reefs are the most colour dimorphic, but surprisingly, the effect of habitat is not influenced by traits associated with strong sexual selection. This suggests that environment dependent interactions take place in addition to sexual selection to facilitate colour polymorphism. Authors remark that habitat-specific selection promotes the colour variation in the colour-dimorphic fishes, rather than it would be an outcome of sexual selection alone. The work is well written with respect to its strengths.

Detailed comments:

Page 6, Line 93 (also in the methods in the trait-data compilation section, lines 110-115): Was the quantification of colour dimorphism done subjectively? To me this seems fine, because it is not purpose of this paper to make full scale image analysis, but it must be stated. It would be important to add this detail as scoring may also be also done objectively quantifying the colour traits from the image data in which case describing this must be included.

Page 7, Line 121: What was the component loading and eigenvalue of the first component if this was used? This would indicate how well it represents the focal traits.

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Page 13, Lines 283-292: I do not entirely follow this: 'white hues are commonly featured in cryptic coloration like countershading and mottled patterning'. Do authors mean that in their data white 'hues' were seemingly associated with countershading and/or mottled patterning, or that more generally speaking in fishes white is considered as serving camouflage purpose? This has a bearing to the conclusion 'wrasses and parrotfishes on coral reefs are more likely to lose a component of cryptic coloration and gain more conspicuous colours, opposing the idea that brightly coloured fishes appear less conspicuous when viewed against a coral reef background', and I feel this would need more reassurance. The reason for my concern is that the visibility depends on many things including the irradiance in the medium, spectral reflectance of the object and its background as well as psychophysiological constraints of the viewer (as authors do discuss). However, I am not sure if white in aquatic environment necessarily has to be linked to camouflage. As it is the juveniles that are whiter, why it not could not be related to some life-history related physiological constraint? Further, some colours that appear conspicuous to us may be concealing when viewed in their natural visual scene (e.g. green colour against coral, which is not mentioned here, does this mean the fishes considered here are never green - the supplementary notes blue-green). I do not necessarily disagree with the conclusions, but the claim for 'white hues' serving camouflage function in juveniles and to gain more conspicuous colours would need to be more carefully stated.

Page 13, Lines 307-309: Authors say 'despite our results showing that terminal phase fishes on coral reefs display colours that contrast against the background', but has this to be the case as conspicuousness against the viewing background was not measured? Were certain colour combinations simply assumed to be more contrasting against the background?

Figure 3: I suggest adding initial and terminal phase labels into the figure panels a and b, although they are specified in the figure legends.

Decision letter (RSPB-2019-1522.R0)

25-Jul-2019

Dear Dr Hodge:

I am writing to inform you that your manuscript RSPB-2019-1522 entitled "Colour dimorphism in fishes as an adaptation to life on coral reefs" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

To upload a resubmitted manuscript, 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 Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely,
Professor Gary Carvalho
mailto: proceedingsb@royalsociety.org

Associate Editor

Comments to Author:
This manuscript has now been seen by three expert reviewers in the field. They all agree that this manuscript has merit and will make a nice addition to Proceedings B. However, there a few issues that need to be addressed before the manuscript can be accepted. Mainly, the references and taxonomic scope of the Introduction should be expanded upon and all reviewer comments must be specifically addressed. I look forward to seeing a revised version of this paper.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
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Specific Comments:

Title:
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References
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Author's Response to Decision Letter for (RSPB-2019-1522.R0)

See Appendix A.

RSPB-2020-0167.R0

Review form: Reviewer 2

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?
Good

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

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
The authors have addressed all my previous comments and those from the two other reviewers. They made a great job, especially by broadening their introduction. Looking forward for seeing this very interesting paper in a forthcoming issue of Proceedings B.

Decision letter (RSPB-2020-0167.R0)

24-Feb-2020

Dear Dr Hodge

I am pleased to inform you that your Review manuscript RSPB-2020-0167 entitled "Colour dimorphism in labrid fishes as an adaptation to life on coral reefs" has been accepted for publication in Proceedings B.

The referee(s) do not recommend any further changes. Therefore, please proof-read your

manuscript carefully and upload your final files for publication. 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 me know immediately.

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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. Please see: https://royalsociety.org/journals/authors/author-guidelines/

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

Sincerely,
Professor Gary Carvalho
mailto:proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
Dear Authors,

Your paper has now been reassessed by a past reviewer and myself. Both of us find the manuscript much improved and commend the authors on a fine job of answering all the reviewer queries and comments. Specifically, in my opinion, revisions such as 1) the expanded description of the study system section and statistical methods (nicely explained here and in the recent 'In press' paper associated with it), and 2) broadening the taxonomic scope of the background information as well as the implications of the actual results have further enhanced the readability of the manuscript for a general journal like Proc B. We thank the authors for submitting their paper here and wish them the best with final revisions.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
The authors have addressed all my previous comments and those from the two other reviewers. They made a great job, especially by broadening their introduction. Looking forward for seeing this very interesting paper in a forthcoming issue of Proceedings B.

Decision letter (RSPB-2020-0167.R1)

02-Mar-2020

Dear Dr Hodge

I am pleased to inform you that your manuscript entitled "Colour dimorphism in labrid fishes as an adaptation to life on coral reefs" 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.

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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

Dear Professor Carvalho,

We are pleased to resubmit a revised version of manuscript RSPB-2019-1522 “Colour dimorphism in labrid fishes as an adaptation to life on coral reefs”. We appreciate the time and careful attention you, the associate editor and three anonymous reviewers have given to our manuscript, and we were pleased that there was consensus regarding the paper’s merit, broad interest and high scientific standard.

The reviewers and associate editor also agreed that the initial submission required modifications. The most substantial concerns pertained to broadening the taxonomic scope of the Introduction and references cited. We have expanded the beginning of the introduction to this end. The revised manuscript is 4,111 words, 535 words longer than the original submission, which was 3,576 words (not including references). The references have also increased from 50 to 80.

We feel that the comments and suggestions we received have substantially improved the manuscript, particularly with regard to its broader applicability. We hope you find the revised manuscript suitable for publication.

Sincerely,

The authors

25-Jul-2019

Dear Dr Hodge:

I am writing to inform you that your manuscript RSPB-2019-1522 entitled "Colour dimorphism in fishes as an adaptation to life on coral reefs" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A ‘response to referees’ document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
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Sincerely,

Professor Gary Carvalho
mailto: proceedingsb@royalsociety.org

Associate Editor

Comments to Author:
This manuscript has now been seen by three expert reviewers in the field. They all agree that this manuscript has merit and will make a nice addition to Proceedings B. However, there a few issues that need to be addressed before the manuscript can be accepted. Mainly, the references and taxonomic scope of the Introduction should be expanded upon and all reviewer comments must be specifically addressed. I look forward to seeing a revised version of this paper.

Response: Thank you for your evaluation of our manuscript. We have addressed the individual reviewers' comments below.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
The authors take a phylogenetic comparative approach to identify the factors underlying the evolution of colour dimorphism in the Labridae (wrasses and parrotfishes). The results show that colour dimorphism is more prevalent on coral reef habitat, yet contrary to a prevalent idea the effect of habitat (coral reef versus non coral reef) on colour dimorphism is not primarily driven by traits associated with strong sexual selection (lek-like polygyny or diandric protogyny). Selection pressures specific to coral reef habitat (associated with e.g. clear oligotrophic water or structural complexity) appear instead to directly promote the evolution of colour dimorphism, independently of sex allocation and mating system. The results also indicate that labrid terminal phases associated with coral reef habitat are more likely to display blue colors (that are most spectrally contrasting against coral reefs backgrounds) and less likely to display white colors (which are often associated with cryptic coloration through counter-shading and mottled patterns). This suggests that these colors are meant to be conspicuous, at least at short viewing distances. On the other hand, labrids not associated with coral reefs are less likely to have colour-dimorphic heads, bodies and caudal fins but are equally likely to have colour-dimorphic dorsal and anal fins that can either remain folded against the body or extended to signal to conspecifics. This suggests a stronger role of crypsis and predation in non coral reef habitat where turbidity is higher and structurally complexity less important.

The study is competent and well-written, and the statistical analyses appear appropriate. The results are somewhat counter-intuitive and will be of interest to the broad Proceedings B audience. I have only relatively minor comments. The first one is that the study is limited and specific to the Labridae. This should be reflected in the title (replace "fishes" by "labrid fishes" or similar), abstract (replace "fishes" by "labrid fishes" or similar in the last sentence) and conclusion (replace "marine fishes" by "labrid fishes" or similar in the first sentence).

Response: We thank the reviewer for their thoughtful assessment of our manuscript and for suggesting that we focus more specifically on our study group in the title, abstract and conclusion. We have changed "fishes/marine fishes" to "labrid fishes" in all three places following the reviewer's suggestion (Line 2; Line 27; Line 368).

My second comment would be that non coral reef habitat is a very broad category. I found myself wondering whether this category could be subdivided (into e.g. seagrass, rocky reefs or pelagic habitat) to refine the analyses.

Response: Yes this is true – 'non coral reef' is a broad category. Our decision to not subdivide this (and the 'coral reef associated' category) is based on two points of justification: 1) previous predictions regarding the habitat factors that influence the evolution of colour dimorphism in labrid fishes have focused almost entirely on the effect of coral reefs, and we wanted to quantitatively evaluate these predictions; and 2) it can become more difficult to fit evolutionary models to trait data as the number of predictor trait categories increases. This is because as the number of categories increases, sample size (i.e. the number of replicate independent evolutionary transitions to that character state) decreases.

Furthermore, if we had included more habitat categories and were able to fit evolutionary models to the data with confidence, distinguishing the effects of each habitat category on the continuous trait (in this case colour dimorphism) would also be more difficult with a greater number of categories. For example, if one is interested in the effect of a predictor trait with two categories (on a continuous trait) and you fit a series of evolutionary models, and the best-fit model shows multiple peaks you can be confident that those two discrete trait categories drive separation in the continuous trait toward discrete optimal values. However, when the predictor has more than two categories it can be more difficult to determine which of those categories is driving the 'multi-peakness' of the model.

In this case, our predictor traits all included a spectrum of associated selection thought to influence the evolution of colour dimorphism, which we decided to discretise into three categories. Doing so was a compromise that allowed us to both fit evolutionary models and understand the results with confidence, and to capture and quantify the spectrum of selection of each of the predictor traits.

Finally it is important to point out that color dimorphism was scored manually, which implies that it is limited and specific to the human visual system and perception. Statements about what is conspicuous or cryptic should ideally take into account the visual environment and the visual system of the fishes.

Response: We acknowledge that this an accurate statement – our scoring of color dimorphism was done from the perspective of human vision, which is not identical to the color sensitivity of labrid fishes (which itself may vary somewhat among species). We have added several sentences to the first paragraph of the Methods section discussing the limitations of our quantification of colour dimorphism (Lines 142-149). Our statements about the conspicuous or cryptic nature of different pigment-based colours (in the Results and Discussion) are based on research that has more carefully considered the effects of the visual environment and the fish visual system (Cheney et al. 2009; Marshall 2000).

References

Cheney K, Grutter AS, Blomberg SP, Marshall NJ. 2009 Blue and yellow signal cleaning behavior in coral reef fishes. *Curr. Biol.* 19, 1283–1287.

Marshall NJ. 2000 Communication and camouflage with the same 'bright' colours in reef fishes. *Philos. Trans. R. Soc. B* 355, 1243–1248.

Line 176 replace "sub-sampled" by "sub-sample".

Response: Thank you for pointing out this typo. We have corrected it (Line 216).

Referee: 2

Comments to the Author(s)
This paper aims to explore the effect of various factors (i.e. sex allocation, mating system and habitat) on the evolution of color dimorphism in a coal reef fish family (Labridae). The authors used a new time-calibrated phylogeny and various phylogenetic comparative methods in order to test their hypotheses.

The topic addressed by this MS is highly interesting for specialists and non-specialists of (coral reef) fishes. Thus, it is a pity that this MS is mainly oriented for « fishy » persons. The great majority of references come from an ichthyological literature and the authors directly start their introduction (Line 35) with their fish group of interests: wrasses and parrotfishes. However we know that various taxonomic groups of animals show color dimorphism such as insects, fishes, snakes, birds,… and there are many works devoted to this topic. So, why do the authors not try to insert their interesting results within the general topic of color dimorphism in the animal kingdom? I highly recommend that the authors put their study in the general perspective of our understanding of the evolution of color dimorphism by integrating studies conducted on different animal taxa and different methods.

Response: We thank the reviewer for their positive comments regarding the interest that our manuscript would expect from the broad readership of PRS, and for encouraging us to extend our work into the broader topic of colour dimorphism by integrating studies on other animal taxa. Following this advice, we expanded the beginning of the introduction with three new paragraphs (Lines 33-69), and revised the remainder of the introduction to retain our specific predictions.

Generally speaking, the methods used are appropriate. However I have to admit that what is tested in the section « Phase- and body-specific selective pressures » appears unclear to me. So I would ask for more explanations but, even more importantly, this section is not really introduced by the authors during the Introduction. That could explain my questioning.

Response: Thank you for pointing this out. In expanding the introduction, we have included examples of how selection (Lines 55-57) and development (Lines 64-67) may impact the sexes/phases differently. We also now include more background explaining how habitat structural complexity may influence the evolution of visual signals through its effects on signal transmission and predation vulnerability (Lines 49-55), and we more broadly introduce the impacts of predator-mediated selection on the evolution of colour dimorphism.

This work could be highly influential and deserve a publication in a top journal like Proceedings B but it still needs works of specifications and broadening in the Introduction/Discussion/Perspectives. Hereafter, I have listed some comments that should be addressed prior to an acceptance for publication.

Response: Thank you for encouraging us to broaden the perspectives presented in the paper. We have strived to achieve this level of broad appeal and perspective primarily with substantial changes to the Introduction. We hope these changes reach the level sought by this the referee.

Specific Comments:

Title:
To my opinion, the title is not appropriate. Indeed, how explain that an extensive number of teleost fishes show color dimorphism when they do not live in coral reef environments. Accordingly, I would suggest a title less generalizing, more adequate like « Life on coral reefs promotes color dimorphism in wrasses and parottfishes (Labridae) » or something very similar.

Response: We changed the title to make it more specific to labrid fishes.

Introduction:
Beyond my regrets that the Introduction is too « fish-oriented », I also point out that the term « color dimorphism » is not enough defined in the present MS. Dimorphism in colors can be linked to sex, ontogeny, behavior, habitat, diet… Here, the color dimorphism observed in wrasses and parrotfishes is mainly size-dependent and thus it seems associated with ontogeny and sex-change. Consequently, by using wrasses and parrotfishes, the authors address a specific type of color dimorphism. For example, in coral reef fishes, the type of color dimorphism observed in wrasses and parrotfishes differ from the one of the dusky dottyback Pseudochromis fuscus (e.g. Cortesi et al. 2015, 2016), and the evolutionary forces acting on these types of color dimorphism likely differ. This should be more detailed in the Introduction, by explaining the novelty but also the limits of the system studied along the present MS.

Response: We agree with the gist of this comment and our revised introduction now includes a section on ontogenetic colour change. We highlight the taxonomic extent to which this phenomenon is recorded to address the novelty and limitations of our study system.

Even if we can retrieve some information from Figure 1, I would suggest that the authors provide some statistics about the occurence of color dimorphism in Labridae. At the end of the MS, we still do not know the fraction (%) of wrasses and parrotfishes showing color dimorphism. This absolute information would be interesting for future comparative analyses and would be useful in the current Discussion.

Response: We found this a very helpful suggestion. We added a new column to what is now Table S2 summarising the proportion of body regions scored 'colour dimorphic' for each species in our dataset. We also added summary statistics to the methods section describing how many species we scored as completely colour dimorphic, somewhat colour dimorphic, and not colour dimorphic (Lines 150-152; Lines 169-171).

Above, I have introduced my concern regarding the section « Phase- and body-specific selective pressures » from the M&M but, even more importantly, the results collected through the associated analyses are not adequately introduced. The authors do not present their expectations related to this section during the Introduction. Moreover, this part is not listed within the main objectives of the present study (lines 101-106).

Response: In the expanded introduction we include justification for exploring whether selection impacts the sexes/phases differently (Lines 55-57; 64-67). We also explain how habitat structural complexity may influence the evolution of visual signals through its effects on predation vulnerability (Lines 49-55). Finally, we added a 3rd objective to the end of the introduction describing our tests of phase- and body-specific selective pressures (Line 132-133).

M&M:
I am not a supporter of preprints use and associated repositories (e.g. bioRxiv). Accordingly, I am questioning the way how the authors introduce their new time-calibrated phylogeny of Labridae (line 137). We can obtain details on phylogenetic inference and divergence time estimation via a preprint version of another paper from the same authors (Hodge et al. 2019). I think that this work is probably under review in another journal. If the preprint is not accepted for publication shortly, I suggest that all the details about the production of phylogenetic hypotheses should be provided as Supplementary Materials in the present paper.

Response: You are correct that the preprint paper presenting the details of the phylogenetic analyses was under review at the time of submission. It has now been accepted for publication in *The American Naturalist* and is currently in press. As such we have modified the citation and refrained from adding details of the phylogenetic analyses to this paper.

Results and Discussion:
Table S4, providing results from models comparisons, should be part of the main text. This table is an essential part of the results. It is unclear to me if Table S3 provides the 95% confidence intervals for the best-fit model parameters using bootstrapping procedures. If yes, that should more clearly stated. Moreover, it looks wrong that table S3 is cited/used before table S4. First, provide the results of model comparisons (i.e. contents of table S4) and then provide the results from simulations using the best model retained. This is a more logical flow.

Response: Thank you for this suggestion. We moved Table S4 to the main text (now Table 2). Table S3 (now Table S4) does provide the 95% confidence intervals for the best fit model parameters estimated from bootstrapping. We added a statement about this (and the estimates of statistical power) to the table caption. The reason Table S3 was cited before S4 in the original manuscript is because Table S3 provides the results of evolutionary models fit to each predictor (habitat, mating system, sex allocation) separately; whereas Table S4 provides the overall comparison of models fit to all three predictors. We added 'separately' to the methods (Line 224) and to the caption of now Table S4 to clarify this.

Lines 277-292. What about the effect of ontogenetic habitat shifts on these results? A lot of reef fishes experienced habitat shifts during growth (e.g. McCormick & Makey 1997, Lecchini & Galzin 2005) and this could explain, at least partially, a part the these results. Such an ecological point of view should be added in the Discussion.

Response: We agree that many reef fishes experience an ontogenetic habitat shift. Our habitat classifications encompass this. Species that shift ontogenetically to coral reef habitat were classified as 'coral reef associated'. Because such shifts are accounted for by our data classification it is unclear how they could further explain our results. Species that spend their whole lives only on coral reefs are the most colour dimorphic, while species that spend all or part of their lives on coral reefs and in other habitats are less so, and species that are not associated with coral reefs at any point in their lives are the least colour dimorphic.

Lines 307-322. I would suggest the authors avoid too much interpretation about camouflage and conspicuousness of colors in coral reef fishes because a color may be good for camouflage or communication depending on the background they are viewed against; and reef fishes use a combination of color and behavior to regulate their conspicuousness and crypsis. The authors should stay on more general statements, commenting that the behaviors of small fishes (mainly driven by the avoidance of predators) differ from the ones of large fish (mainly driven by reproductive success) and this could sustain an ontogenetic color dimorphism. This suggestion could also help for a rewriting of the conclusions (especially lines 328-331).

Response: We agree that whether a colour is effective in camouflage or communication depends on the background. The statements we make about the conspicuous or cryptic nature of different colours are based on research that has more carefully considered the effects of the visual environment and the fish visual system (Cheney et al. 2009; Marshall 2000). The scope of our research was too broad to consider the many ways in which ephemeral behaviours can regulate conspicuousness and crypsis. It is likely true that small fish are at greater risk of predation than larger fish, however, in our study size is also indicative of colour phase, and we focus our discussion there.

References

Cheney K, Grutter AS, Blomberg SP, Marshall NJ. 2009 Blue and yellow signal cleaning behavior in coral reef fishes. *Curr. Biol.* 19, 1283–1287.

Marshall NJ. 2000 Communication and camouflage with the same 'bright' colours in reef fishes. *Philos. Trans. R. Soc. B* 355, 1243–1248.

In addition to these considerations, I am also questioning if the number of color dimorphic species could be linked to the total number of species in one environment. Knowing that, in the marine realm, coral reefs house one of the highest numbers of fish species; it could explain why fishes developed a so large repertoire of signals including sex dimorphism in order to improve communication in a « crowded » environment. This argument could certainly be added in the Discussion.

Response: Great question, we plan to address it with data on species richness in the occurrence range of each species and using this dataset in a future manuscript. We feel that the topics of this manuscript deserve separate attention and ask to save discussion of the utility of sexual signalling in a crowded environment for our forthcoming manuscript.

Table 1

Coral reefs are often connected to other coastal systems like seagrass beds and mangroves, and many fish species like parrotfishes moves from one system to another during their ontogeny or even during nycthemeral cycles. How do the authors deal with this and classify these species? Could it have an impact on results and related conclusions?

Response: Species that move between coral reefs and other non-coral reef adjacent environments were classified as 'coral reef associated'. Because these phenomena are already incorporated in our classifications they are also reflected in the results.

References

Cortesi, F., Feeney, W.E., Ferrari, M.C.O., Waldie, P.A., Phillips, G.A.C., McClure, E.C., Sköld, H.N., Salzburger, W., Marshall, N.J., and Cheney, K.L. (2015). Phenotypic plasticity confers multiple fitness benefits to a mimic. Current Biology 25, 949-954.

Cortesi, F., Musilová, Z., Stieb, S.M., Hart, N.S., Siebeck, U.E., Cheney, K.L., Salzburger, W., and Marshall, J. (2016). From crypsis to mimicry: Changes in colour and the configuration of the visual system during ontogenetic habitat transitions in a coral reef fish. Journal of Experimental Biology 219, 2545-2558.

Hodge JR, Santini F, Wainwright PC. 2019 Correlated evolution of sex allocation and mating system in wrasses and parrotfishes. bioRxiv , 665638.

Lecchini D, Galzin R (2005) Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). Marine Biology 147:47-58.

McCormick MI, Makey LJ (1997) Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. Marine Ecology-Progress Series 153:247-257.

Referee: 3

Comments to the Author(s)
This study investigates the evolution of colour polymorphism in marine fishes. While studies that explore the role of sexual selection and life-history strategies in the maintenance of colour polymorphism are frequent, studies that investigate the significance of respective habitat while controlling for sexual selection and life-history hypotheses are scarce. To this end this work makes a neat contribution. The authors use phylogenetic comparative analysis to show that parrotfishes and wrasses exclusive to coral reefs are the most colour dimorphic, but surprisingly, the effect of habitat is not influenced by traits associated with strong sexual selection. This suggests that environment dependent interactions take place in addition to sexual selection to facilitate colour polymorphism. Authors remark that habitat-specific selection promotes the colour variation in the colour-dimorphic fishes, rather than it would be an outcome of sexual selection alone. The work is well written with respect to its strengths.

Response: We thank the reviewer for their positive comments and attention to the writing of our manuscript.

Detailed comments:

Page 6, Line 93 (also in the methods in the trait-data compilation section, lines 110-115): Was the quantification of colour dimorphism done subjectively? To me this seems fine, because it is not purpose of this paper to make full scale image analysis, but it must be stated. It would be important to add this detail as scoring may also be also done objectively quantifying the colour traits from the image data in which case describing this must be included.

Response: Yes, quantification of colour dimorphism was done subjectively. We have expanded the first paragraph of the Methods section to describe our method in more detail, including findings of other studies that have addressed the utility of human-perceived scoring coloration in comparative studies (Lines 142-149).

Page 7, Line 121: What was the component loading and eigenvalue of the first component if this was used? This would indicate how well it represents the focal traits.

Response: We added detail about the cumulative percentage of deviance explained by the first two principal component axes (Lines 156-157; the output of the logistic PCA doesn't separate % deviance for the first and second PCs). We also added a supplemental table that includes the variable loadings on the first two PC axes (Line 158 and supplemental material).

Page 13, Line 283: 'white hues' - I suggest caution when using this wording in the following sentences. White is often not considered to have as its own colour or hue (i.e. having its own typical wavelength) as opposed to blue and green which do have distinct chromatic hues, because sensation of white appearance arises from achromatic brightness variation. For example, least saturated colours appear almost white.

Response: Thank you for this suggestion. We changed the wording of this part of the sentence to clarify that leucophores appear white because they scatter light (not because they produce a characteristic wavelength, as implied by the word hue; Lines 279-280). We also replaced the use of 'white hues' with 'white' throughout (Lines 324, 326).

Page 13, Lines 283-292: I do not entirely follow this: 'white hues are commonly featured in cryptic coloration like countershading and mottled patterning'. Do authors mean that in their data white 'hues' were seemingly associated with countershading and/or mottled patterning, or that more generally speaking in fishes white is considered as serving camouflage purpose? This has a bearing to the conclusion 'wrasses and parrotfishes on coral reefs are more likely to lose a component of cryptic coloration and gain more conspicuous colours, opposing the idea that brightly coloured fishes appear less conspicuous when viewed against a coral reef background', and I feel this would need more reassurance. The reason for my concern is that the visibility depends on many things including the irradiance in the medium, spectral reflectance of the object and its background as well as psychophysiological constraints of the viewer (as authors do discuss). However, I am not sure if white in aquatic environment necessarily has to be linked to camouflage. As it is the juveniles that are whiter, why it not could not be related to some life-history related physiological constraint? Further, some colours that appear conspicuous to us may be concealing when viewed in their natural visual scene (e.g. green colour against coral, which is not mentioned here, does this mean the fishes considered here are never green - the supplementary notes blue-green). I do not necessarily disagree with the conclusions, but the claim for 'white hues' serving camouflage function in juveniles and to gain more conspicuous colours would need to be more carefully stated.

Response: Both – in our data white was associated with countershading and/or mottled patterning AND more generally speaking these two types of colour-patterning serve camouflage purposes. We agree that white doesn't necessarily have to be linked to camouflage, but because it is present in the aforementioned types of colour-patterning in our dataset we concluded that upon transition to the terminal phase, wrasses and parrotfishes lose white, which they otherwise exhibit as a part of their cryptic or camouflage colour patterning when in the initial phase. We have added more detail to clarify our line of reasoning on this point (Lines 327-329).

Physiological constraints could play a role in the expression of colour and consequently the magnitude of colour dimorphism of wrasses and parrotfishes. There are many avenues for further study in this area, including how physiological constraints interact with selection pressures imposed by predation.

Yes, we agree that some colours that appear conspicuous to us are in fact concealing when viewed against their natural backgrounds. The statements we make about the conspicuous or cryptic nature of different colours (in the Results and Discussion) are based on research that has more carefully considered the effects of the visual environment and the fish visual system (Cheney et al. 2009; Marshall 2000).

References

Cheney K, Grutter AS, Blomberg SP, Marshall NJ. 2009 Blue and yellow signal cleaning behavior in coral reef fishes. *Curr. Biol.* 19, 1283–1287.

Marshall NJ. 2000 Communication and camouflage with the same 'bright' colours in reef fishes. *Philos. Trans. R. Soc. B* 355, 1243–1248.

Page 13, Lines 307-309: Authors say 'despite our results showing that terminal phase fishes on coral reefs display colours that contrast against the background', but has this to be the case as conspicuousness against the viewing background was not measured? Were certain colour combinations simply assumed to be more contrasting against the background?

Response: Yes, certain colours (e.g. blue) have been shown to more contrasting against coral reef backgrounds (Cheney et al. 2009; Marshall 2000) – as we state in Lines 329-330.

While we did not measure background contrast directly in this study, the authors of the studies we reference did.

Figure 3: I suggest adding initial and terminal phase labels into the figure panels a and b, although they are specified in the figure legends.

Response: Thank you for this suggestion. We trialled adding labels to the photographs to indicate initial and terminal phases; however, the labels impede the image of the fish in some cases. As such we decided not to add labels directly to the images.

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Abstract: Conspicuous colouration displayed by animals that express sexual colour dimorphism is generally explained as an adaptation to sexual selection, yet the interactions and relative effects of selective forces influencing colour dimorphism are largely unknown. Qualitatively, colour dimorphism appears more pronounced in marine fishes that live on coral reefs where traits associated with strong sexual selection are purportedly more common. Using phylogenetic comparative analysis, we show that wrasses and parrotfishes exclusive to coral reefs are the most colour-dimorphic, but surprisingly, the effect of habitat is not influenced by traits associated with strong sexual selection. Rather, habitat-specific selective forces, including clear water and structural refuge promote the evolution of pronounced colour dimorphism that manifests colours less likely to be displayed in other habitats. Our results demonstrate that environmental conditions ultimately shape the selective forces underlying the evolution of conspicuous colouration in colour-dimorphic fishes.
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