Peer Community In Evolutionary Biology

Spreading the risk of reproductive failure when the environment is unpredictable and ephemeral

Gabriele Sorci *based on reviews by Thomas Haaland and Zoltan Radai*

A recommendation of:

Bimodal breeding phenology in the Parsley Frog Pelodytes punctatus as a bet-hedging strategy in an unpredictable environment despite strong priority effects

Helene Jourdan-Pineau, Pierre-Andre Crochet, Patrice David *(2022), bioRxiv, 2022.02.24.481784, ver. 5 peer-reviewed and recommended by Peer Community in Evolutionary Biology* **https://doi.org/10.1101/2022.02.24.481784**

Open Access

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Data used for results

- **https://doi.org/10.18167/DVN1/2TOXXV**

Scripts used to obtain or analyze results

- **https://doi.org/10.18167/DVN1/2TOXXV**

Submitted: 28 February 2022, Recommended: 20 August 2022

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Gabriele Sorci (2022) Spreading the risk of reproductive failure when the environment is unpredictable and ephemeral. *Peer Community in Evolutionary Biology, 100147.* **https://doi.org/10.24072/pci.evolbiol.100147**

Recommendation

Many species breed in environments that are unpredictable, for instance in terms of the availability of resources needed to raise the offspring. Organisms might respond to such spatial and temporal unpredictability by adopting plastic responses to adjust their reproductive investment according to perceived cues of environmental quality. Some species such as the amphibians might also face the problem of ephemeral habitats, when the ponds where they breed have a chance of drying up before metamorphosis has occurred. In this case, maximizing long-term fitness might involve a strategy of spreading the risk, even though the reproductive success of a single reproductive bout might be lower. Understanding how animals (and plants) get adapted to stochastic environments is particularly crucial in the current context of rapid environmental changes.

In this article, Jourdan-Pineau et al. report the results of field surveys of the Parsley Frog (*Pelodytes punctatus*) in Southern France. This frog has peculiar breeding phenology with

females breeding in autumn and spring. The authors provide quite an extensive amount of information on the reproductive success of eggs laid in each season and the possible ecological factors accounting for differences between seasons. Although the presence of interspecific competitors and predators does not seem to account for pond-specific reproductive success, the survival of tadpoles hatching from eggs laid in spring is severely impaired when tadpoles from the autumn cohort have managed to survive. This intraspecific competition takes the form of a "priority" effect where tadpoles from the autumn cohort outcompete the smaller larvae from the spring cohort. Given this strong priority effect, one might tentatively predict that females laying in spring should avoid ponds with tadpoles from the autumn cohort. Surprisingly, however, the authors did not find any evidence for such avoidance, which might indicate strong constraints on the availability of ponds where females might possibly lay.

Assuming that each female can indeed lay both in autumn and spring, how is this bimodal phenology maintained? Would not be worthier to allocate all the eggs to the autumn (or the spring) laying season? Eggs laid in autumn and spring have to face different environmental hazards, reducing their hatching success and the probability to produce metamorphs (for instance, tadpoles hatching from eggs laid in autumn have to overwinter which might be a particularly risky phase).

Jourdan-Pineau and coworkers addressed this question by adapting a bet-hedging model that was initially developed to investigate the strategy of allocation into seed dormancy of annual plants (Cohen 1966) to the case of the bimodal phenology of the Parsley Frog. By feeding the model with the parameter values obtained from the field surveys, they found that the two breeding strategies (laying in autumn and in spring) can coexist as long as the probability of breeding success in the autumn cohort is between 20% and 80% (the range of values allowing the coexistence of a bimodal phenology shrinking a little bit when considering that frogs can reproduce 5 times during their lifespan instead of three times).

This paper provides a very nice illustration of the importance of combining approaches (here field monitoring to gather data that can be used to feed models) to understand the evolution of peculiar breeding strategies. Although future work should attempt to gather individual-based data (in addition to population data), this work shows that spreading the risk can be an adaptive strategy in environments characterized by strong stochastic variation.

References

Cohen D (1966) Optimizing reproduction in a randomly varying environment. Journal of Theoretical Biology, 12, 119–129. https://doi.org/10.1016/0022-5193(66)90188-3

Jourdan-Pineau H., Crochet P.-A., David P. (2022) Bimodal breeding phenology in the Parsley Frog Pelodytes punctatus as a bet-hedging strategy in an unpredictable environment despite strong priority effects. bioRxiv, 2022.02.24.481784, ver. 5 peer-reviewed and recommended by Peer Community in Evolutionary Biology. https://doi.org/10.1101/2022.02.24.481784

Reviews

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Evaluation round #2

DOI or URL of the preprint: *https://www.biorxiv.org/content/10.1101/2022.02.24.481784v2*

Version of the preprint: 2

Author's Reply, 12 Aug 2022

Download author's reply
Dear recommender,

Please find attached our reply to the last revision of our manuscript. Our answers are in purple.

On behalf of all coauthors,

Hélène Jourdan-Pineau

Decision by Gabriele Sorci, 29 Jul 2022

We could only get one review from the referees who read the first version of the manuscript. As you can see, the referee is very happy with the revision but there are still some typos and minor corrections that have been done. I'll be very pleased to recommend this preprint once these minor corrections are done.

Reviewed by Thomas Haaland, 23 Jun 2022

Thank you for your edits and thorough responses to my previous comments! The revised version is a really nice and clear paper. I now only have some very minor edits, mostly to the new bits of text added.

Line numbers referred to the cleaned manuscript version (i.e., on bioRxiv from 20. June).

Line 23, 111, 418, 425: Don't capitalize "p" in parsley frog. Most places you use get it right, but be consistent.

Line 512: "priority effect is" -> "priority effects are".

Line 516: Should "of" be changed to "if" or "whether"?.

Line 520: "dye-off" -> "die-off".

Line 522 and 526 both start with "Last,". Maybe the Line 522 one could instead be "Additionally", or "Furthermore". Also, "Lastly" is better than "Last" in this usage.

Line 530: After "parameters", add comma and "and": "...range of parameters, and these uncertainties..."

Line 531: "parsley frog" -> "the parsley frog", "parsley frogs", or (if you don't want to generalize that much) "these parsley frogs" or "parsley frogs in southern France"... Also, missing "s": "consitute" -> "consitutes". And missing "a": "bet-hedging strategy" -> "a bet-hedging strategy".

Evaluation round #1

DOI or URL of the preprint: *https://doi.org/10.1101/2022.02.24.481784*

Version of the preprint: 1

Author's Reply, 20 Jun 2022

Download author's replyDownload tracked changes file
Dear Reviewers,

We want to thank you for your very interesting and useful comments that helped us improve our manuscript entitled "Bimodal breeding phenology in the parsley frog Pelodytes punctatus as a bet-hedging strategy in an unpredictable environment despite strong priority effects."

Please find attached a revised version of our manuscript We took into account all suggestions proposed: all changes and answers to the reviewers are in the reply file (answers in purple, text cited in italics). We hope that this revised version will suit to PCI Journal.

Sincerely yours,

On behalf of all authors, Hélène Jourdan-Pineau

Decision by Gabriele Sorci, 17 Mar 2022

Both referees agreed that this is an intersting work. However, they also suggested that some revision is needed in order to improve the clarity of the manuscript. In particular, they thought that more details should be provided on the rationale underlying the definition and use of the reproductive indeces, the structure of the statistical models, the meaning of selection gradient in this context, etc. They also did a terrific job in spotting the typos and mispelling. I am looking forward to seeing the revised version of this nice piece of work.

Reviewed by Thomas Haaland, 14 Mar 2022

General comments:

This is a really nice study that aims to quantify and explain a puzzling phenological pattern, and it has an elegant mix of empirical and theoretical work that I enjoy a lot. It is well written overall with a good structure, good motivation, and nice discussion. Most of my comments are quite detailed, as there is just a little bit of grammar/punctuation that isn't very tidy – I hope you don't mind me nitpicking on this. Otherwise I just miss a little bit more clarity on the derivation of the bet-hedging model, as well as clarifying the many various metrics and indeces that you measure (as you will see in my line-by-line comments below)… just make sure that everything is consistent, and actually necessary! It is a bit easy as a reader to get lost. However, once these small things are addressed, I have no hesitation to recommend this preprint for PCI Evol Biol. Thanks for an enjoyable read and a very cool study!

Specific comments:
Line 23: Should "…breeds from autumn to spring" be changed to "…breeds both in autumn and spring"?

Line 51: You give the definition of bet-hedging in the following sentence, line 53-54, so I might move the ending of this sentence, "a strategy known as bet-hedging", to the end of that next sentence instead. The current sentence (line 50-51) is already quite long with several subclauses - and only gives an example of a bet-hedging strategy, not the definition.

Line 57: Change "genotypic" -> "genotype"

Line 65: Change "dormancy seeds" -> "dormant seeds"

Line 67: Could add a citation to Graham et al. 2014 (http://dx.doi.org/10.1098/rspb.2014.0706) here, perhaps the most convincing example of experimental evolution of bet hedging in my opinion.

Line 79: Missing plural s: "partitioning brood" -> "partitioning broods"

Line 89: Missing plural s: "insect" -> "insects".

Line 114: Remove word "than": "it thus prefers seasonally flooded habitats to large permanent water bodies".

Line 121: Change "in altitude" -> "at higher altitudes"

Line 123: Change word order: "Adults have thus to" -> "Adults thus have to"

Line 125: Missing plural s: "tadpoles"

Line 139-140: I'm not sure this parenthesis is adding anything. Could be removed.

Line 161: Add starting parenthesis before 2001? Or remove the closing parenthesis?

Line 167: Add missing s, remove comma and change word order: "In only 2% of the larval cohorts produced were small larvae observed…"

Line 168: Perhaps remove "Note that", since you haven't actually shown any data yet (referred to a figure/table), so we (the reader) can't note anything.

Line 193-198: I'm having a hard time following what these different ratios that you're describing are. If hatch rate is #tadpoles/#eggs, and survival form egg to metamorph is #metamorphs/#eggs, and you claim that you calculate "survival during larval stage as the product of the two former ratios", then somehow survival becomes (#tadpoles * #metamorphs) / #eggs^2 ?? What exactly do you define as the larval stage? Does survival during sarval stage just be #metamorphs/#tadpoles?

Line 251: Here and elsewhere the formatting of references is a bit weird. I guess it should say "This model was primarily inspired by Cohen (1966, reviewed by Seger and Brockman 1987)." Initials haven't been used elsewhere, and place parentheses only around the year when author names are part of the text.

Line 254: Add comma after "environmental conditions".

Line 264: Remove space between "below" and closing parenthesis.

Line 280: I didn't understand how this selection gradient was arrived at. Could you add some derivation, or at least a bit of written explanation to guide the reader from the expressions on the previous page to this result?

Line 320: The different measures of breeding success and survival rates continues to confuse me. Aside from the sheer number of these measures being calculated, some confusion about the terms used to describe the stages of the life cycle just makes this a lot to keep track of. There is: hatching success (% of breeding events producing at least one larva), hatch rate (#tadpoles/#eggs), breeding success (% of breeding events producing at least one metamorph), survival until metamorphosis (#metamorphs/#eggs), and larval survival (uncertain). It's fine that there are many, just make sure they are clearly defined and used consistenly throughout.

Line 346: Add missing s, remove word "the": "Finally, the figure 5 summarize" -> "Finally, figure 5 summarizes".

Line 348-349: This last sentence is too vague to be helpful. How exactly does it illustrate the quasi-exclusion between the two cohorts? Either add some more detail (what features of the figure or lack thereof can we look at to see this?), or remove the sentence. If keeping it, change illustrated -> illustrates.

Line 355: Shouldn't the reference to Figure 4 here be Figure 6?

Line 364: Remove extra opening parenthesis. Your reference manager probably has an option that lets you "add prefix" to a reference, so the "but see" can be inside the auto-generated reference.

Line 370: Remove extra closing parenthesis.

Line 383: Remove "compared to our study area" on line 383? You can add "our study area in" on line 384, making it (also add missing s in "makes"): "It is thus possible that increased competition for Pelodytes punctatus larvae in autumn and winter makes the autumn niche less favourable in northeastern Spain compare to our study area in southern France…"

Line 395: Remove extra opening and closing parenthesis. The "e.g." can be added as a prefix :)

Line 399: Add comma after "(Baradun & Reyer 1997)".

Line 407: Remove extra "*perezi*"? Or is it to specify subspecies, in which case the comma between the *perezi*s can be removed.

Line 410: hypothesized -> hypothesize.

Line 422: Change words: "predates" -> "depredate". And "predaceous" -> "predatory"

Line 424: Add missing s: priority effects.

Line 425: described on some -> described in some.

Line 428: Add missing s: …also affects the larval survival.

Line 431: Add missing s: microorganisms.

Line 450: Remove extra parentheses around reference? And add comma before "e.g.".

Line 451-453: Do you know which of these two possibilities it is? You don't have individual-level data, right? What is the interval between breeding attempts for females? Would she both in autumn and that same spring?

Line 461: Remove "Poethke et al." inside parenthesis. Your reference manager might have an option to "suppress author"? Which will only insert "(2016)".

Line 466: Perhaps add "($0 < c < 1$)" after "mixed breeding strategy".

Line 469 & 470: Also here adding the symbols used for the metrics is useful – make it "(q=0.43)" and "(c=0.57)".

Line 489: This Haaland et al. reference isn't 2020 biorXiv, but now out in J Evol Biol 2021, so can update here and in the reference list. doi:10.1111/jeb.13788

Line 491: Remove extra space before the comma.

Line 492: Use suppress author again to just make it read "…by Rádai (2020)."

Line 495: The shift from the previous paragraph to this conclusion is very unexpected. Perhaps add something to the beginning of the sentence like "In conclusion, …"?

Line 730 (legend Fig. 6): Change ("solid black line)" to "(black lines)". Both the lines show the optimal strategies. Also, about using "Evolutionarily stable strategy": is this in fact an ESS model? I can't quite tell how you arrive at your selection gradient, or even how the given selection gradient produces the "optimal strategy". Although it's straightforward to just optimize the equation on line 276 over c – is this what you do? If so, what do we use the selection gradient for? As you can tell from my confusion, some more explanation either here, or better at the end of the methods and results, would help.

Line 732: Where did the numbers 4.7% and 3.8% for autumn tadpoles and spring tadpoles come from – have we been shown these elsewhere? I can't see for example from Fig. 4 how the 3.8 number is arrived at. And shouldn't autumn tadpole survival be lower than that of spring tadpoles (in absence of older competitors) because of the risk of a bad winter?

Reviewed by Zoltan Radai, 14 Mar 2022

Download the review