



The response of interacting species to biotic seasonal cues

Adele Mennerat and Enric Frago based on reviews by Anne Duplouy and 1 anonymous reviewer

A recommendation of:

Tougeron K., Brodeur J., van Baaren J., Renault D. and Le Lann C..

Sex makes them sleepy: host reproductive status induces diapause in a parasitoid population experiencing harsh winters (2019), *bioRxiv*, 371385, ver. 6 peer-reviewed and recommended by Peer Community in Ecology. [10.1101/371385](https://doi.org/10.1101/371385)

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In temperate regions, food abundance and quality vary greatly throughout the year, and the ability of organisms to synchronise their phenology to these changes is a key determinant of their reproductive success. Successful synchronisation requires that cues are perceived prior to change, leaving time for physiological adjustments. But what are the cues used to anticipate seasonal changes? Abiotic factors like temperature and photoperiod are known for their driving role in the phenology of a wide range of plant and animal species [1,2]. Arguably though, biotic cues directly linked to upcoming changes in food abundance could be as important as abiotic factors, but the response of organisms to these cues remains relatively unexplored. Biotic cues may be

particularly important for higher trophic levels because of their tight interaction with the hosts or preys they depend on. In this study Tougeron and colleagues [3] address this topic using interacting insects, namely herbivorous aphids and the parasitic wasps (or parasitoids) that feed on them. The key finding of the study by Tougeron *et al.* [3] is that the host morph in which parasitic wasp larvae develop is a major driver of diapause induction. More importantly, the aphid morph that triggers diapause in the wasp is the one that will lay overwintering eggs in autumn at the onset of harsh winter conditions. Its neatly designed experimental setup also provides evidence that this response may vary across populations as host-dependent diapause induction was only observed in a wasp population that originated from a cold area. As the authors suggests, this may be caused by local adaptation to environmental conditions because, relative to warmer regions, missing the time window to enter diapause in colder regions may have more dramatic consequences. The study also shows that different aphid morphs differ greatly in their chemical composition, and points to particular types of metabolites like sugars and polyols as specific cues for diapause induction. This study provides a nice example of the complexity of biological interactions, and of the importance of phenological synchrony between parasites and their hosts. The authors provide evidence that phenological synchrony is likely to be achieved via chemical cues derived from the host. A similar approach was used to demonstrate that the herbivorous beetle *Leptinotarsa decemlineata* uses plant chemical cues to enter diapause [4]. Beetles fed on plants exposed to pre-wintering conditions entered diapause in higher proportions than those fed on control plants grown at normal conditions. As done by Tougeron *et al.* [3], in [4] the authors associated diapause induction to changes in the composition of metabolites in the plant. In both studies, however, the missing piece is to unveil the particular chemical involved, an answer that may be provided by future experiments. Latitudinal clines in diapause induction have been described in a number of insect species [5]. Correlative studies, in which the phenology of different trophic levels has been monitored, suggest that these clines may in part be governed by lower trophic levels. For example, Phillimore *et al.* [6] explored the relative contribution of temperature and of host plant phenology on adult flight periods of the butterfly *Anthocharis cardamines*. Tougeron *et al.* [3], by using aphids and their associated

parasitoids, take the field further by moving from observational studies to experiments. Besides, aphids are not only a tractable host-parasite system in the laboratory, they are important agricultural pests. Improving our basic knowledge of their ecological interactions may ultimately contribute to improving pest control techniques. The study by Tougeron *et al.* [3] exemplifies the multiple benefits that can be gained from addressing fundamental questions in species that are also directly relevant to society.

References

- [1] Tauber, M. J., Tauber, C. A., and Masaki, S. (1986). *Seasonal Adaptations of Insects*. Oxford, New York: Oxford University Press. [2] Bradshaw, W. E., and Holzapfel, C. M. (2007). Evolution of Animal Photoperiodism. *Annual Review of Ecology, Evolution, and Systematics*, 38(1), 1–25. doi: [10.1146/annurev.ecolsys.37.091305.110115](https://doi.org/10.1146/annurev.ecolsys.37.091305.110115) [3] Tougeron, K., Brodeur, J., Baaren, J. van, Renault, D., and Lann, C. L. (2019b). Sex makes them sleepy: host reproductive status induces diapause in a parasitoid population experiencing harsh winters. *bioRxiv*, 371385, ver. 6 peer-reviewed and recommended by PCI Ecology. doi: [10.1101/371385](https://doi.org/10.1101/371385) [4] Izzo, V. M., Armstrong, J., Hawthorne, D., and Chen, Y. (2014). Time of the season: the effect of host photoperiodism on diapause induction in an insect herbivore, *Leptinotarsa decemlineata*. *Ecological Entomology*, 39(1), 75–82. doi: [10.1111/een.12066](https://doi.org/10.1111/een.12066) [5] Hut Roelof A., Paolucci Silvia, Dor Roi, Kyriacou Charalambos P., and Daan Serge. (2013). Latitudinal clines: an evolutionary view on biological rhythms. *Proceedings of the Royal Society B: Biological Sciences*, 280(1765), 20130433. doi: [10.1098/rspb.2013.0433](https://doi.org/10.1098/rspb.2013.0433) [6] Phillimore, A. B., Stålhandske, S., Smithers, R. J., and Bernard, R. (2012). Dissecting the Contributions of Plasticity and Local Adaptation to the Phenology of a Butterfly and Its Host Plants. *The American Naturalist*, 180(5), 655–670. doi: [10.1086/667893](https://doi.org/10.1086/667893)

Revision round #2

2019-04-23

Dear K. Tougeron and co-authors,

We have now read your revised manuscript, as well as your answer to reviewers. Congratulations for all the work done addressing the reviewers' suggestions and questions, and for a neat and thorough experimental study. We are willing to recommend your preprint, but before we do this, could you please consider the following suggestions for edits and upload a new version of your preprint?

Thanks in advance, Best regards, Adele Mennerat & Enric Frago.

L46: trait expression (remove hyphen) L59: across time -> over time L74: contributes to maintain -> contributes to maintaining L75: reproductive cycle (remove hyphen) L91: detangled -> disentangled L124: the mild winter area (add "the") L125: diapause-inducing cues (add hyphen) L126: and to the relative occurrence L127: respective area of origin -> respective areas of origin L134: origins -> origin L135: , which (comma before which) L142: half of the grandparent was -> either "half of the grandparent generation" or "half of the grandparents" L143: , it is thus likely... -> . It is thus likely... (break sentence in two) L144: fava bean -> fava beans L166: allows to measuring -> allows to measure L272: summed up among -> summed up within L297: in some female's brood -> in some broods L325: lines may be confounded -> lines may be overlapping? L363: one species needs to synchronize its life cycle -> species need to synchronize their life cycle L380: within each female's offspring -> across broods of individual females (?) L381: in a lower extent -> to a lower extent L382: the response of diapause inducing cues -> the response to diapause-inducing cues L423: comma before which L430: the importance of each cue at inducing diapause -> importance for diapause induction (?) L432: parasitoid's response -> the response of parasitoids L481: glycerol, a cryoprotective compound (add comma)

Preprint DOI: [10.1101/371385](https://doi.org/10.1101/371385)

Author's reply:

Dear recommenders,

Thank you for accepting our article pending minor revisions. We have made the requested changes on the manuscript.

Best, Kevin Tougeron

[Download author's reply \(PDF file\)](#)

Revision round #1

2018-10-22

Dear authors,

We have now received two reviews for your preprint, and would like to apologize for the long delay. It was very difficult to get reviewers during the summer. Based on the reviews and our own reading, we find this preprint mostly interesting and well written. The study is carefully designed, and its main asset lies in the fact that several factors are tested simultaneously (harsh/mild climate at the site of origin, host morph, and seasonal abiotic conditions).

As you will see however, the reviewers raise a number of points that, if addressed, can further improve the quality of your manuscript. We would therefore like you to revise your manuscript.

As suggested by one of the reviewers, we believe that you don't have real replicates in terms of populations originating from harsh/mild winters as a single population from each condition was used. As suggested by reviewer 2 this issue is not likely to invalidate your findings, but this has to be carefully discussed in your manuscript.

We would like to raise your attention on many other comments made by reviewer 2, we find them really useful, particularly those concerning the genetic variation in plasticity in diapause induction and the potential inference of reaction

norms in the insects studied. Adding this aspect(s) to your study would further increase both its quality and relevance.

We also think that the title and abstract should more explicitly state that diapause levels vary mainly between harsh and mild winter areas, and that diapause induction in oviparous hosts is observed in the harsh winter area only. This would not make your abstract any weaker; on the contrary, the two findings make more sense when taken together. The abstract and some parts of the introduction sections are a bit too technical, we believe that writing some parts of the manuscript using less field-specific jargon would help your manuscript to be read by non-experts on the field.

Please also state the sample sizes more explicitly and report your statistical results in a summary table (including also some information on the random effects). You will see that the reviewers' opinions differ on Figure 3. We would suggest you to keep the PCA plots (both detailed and per metabolite category), but to move the contributions of variables to Supplementary materials, as this would allow you to increase the legend size and readability. Could you also specify somewhere in your manuscript - or supplementary material - whether the patterns found in each of the two repeated experiments were consistent with each other?

Additional requirements of the managing board

We ask you to carefully verify that your manuscript complies with the following requirements (indicated in the 'How does it work?' section and in the code of conduct) and to modify your manuscript accordingly: -Data must be available to readers after recommendation, either in the text or through an open data repository such as Zenodo, Dryad or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data. -Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) must be available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be

reused. -Details on experimental procedures must be available to readers in the text or as appendices. -Authors must have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." This disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: "XY is one of the PCI Evol Biol recommenders."

Preprint DOI: [10.1101/371385](https://doi.org/10.1101/371385)

Reviewed by [Anne Duplouy](#), 2018-08-22 13:20

Tougeron and colleagues provide here an interesting study on how higher trophic levels may adjust to abiotic conditions and to the phenology and phenotype or their host. Using the predator-prey interaction between the parasitoid wasp *Aphidius ervi* and the aphid *Acyrtosiphon pisum*, they show that abiotic factors (aka: temperature and photoperiod) remain the main signal for the induction of diapause in the parasitoid wasp. However, they also show that in contrast with French specimens, the Canadian specimens of *A. ervi* more often enter diapause when parasitizing the sexual morph of their aphid host, than when parasitizing the asexual aphids. The authors explain that in Canada, winters are harsher than in France and the sexual morph often only occurs just before the fall/winter season. Therefore the local parasitoid would have evolved to use the aphid morph as a cue for the induction of its diapause. Finally, Tougeron and colleagues provide the metabolite contents of both sexual and asexual morphs of the aphid host, and show that the sexual morph specimens are more rich in polyols and sugar, which are potential resources that the parasitoid could use for the induction of and survival during the diapause period. This is a nice read and it is well written, with also some nice figures provided to ease both the understanding of the method and the results. I just suggest some minor things that the authors might want to consider before publication.

Consider providing the reader with an idea of the endosymbionts that inhabit your insect species. Do you believe each aphid clone carries the same symbiotic

load? This could have important implication as endosymbionts have been show to affect many aspect of host-parasitoid interaction, including increased host resistance to parasitoid (Vorburger et al), but also increased host susceptibility to parasitoids (van Nouhuys et al.)

I may have missed it but why did you not provide the metabolite content of the aphids from the 17C temperature treatment? Do you think they would have differ?

L39: I think it is not clear from your abstract that the pattern described is only observed in Canada, where the wasp species has evolved under harsher conditions, and not in France. L155: 'the parasitoid does not parasitize the male aphids': Any idea why? Could this be added to the study? do the males show a different metabolite profile? are they too small to support the full development of a wasp? L164: I would provide the total number of aphid offered for parasitization per female wasp ($N_{total}=X$) I would think 48 right? Fig1: I really think this figure is well-done. L218: Does this include the control viviparous too? If not why? Table1: Do you mean 'Figure 3'? instead of 'Figure 1' - Also: did you identify each of those metabolite in both viviparous and oviparous aphids? if not I would suggest to provide a table with the content of each morph separated. If yes: Do nothing. L.262: I would actually start this results section by bringing forward that the origin of the parasitoid had a major effect, with Canadian ones parasitizing much more than French specimens, because it is really the first thing that shows from your figure2. L.270: Provide the range for the low level diapause in Canadian population at 20C, as you have done for previous results. Figure2: I would provide a better description of the graph, with the meaning of the box and whiskers. 95% confidence intervals?? Also in the legend: add 'Naturally' experiencing harsh/mild winter, so the reader does understand these are the natural conditions, not the lab conditions that you are mentioning. L:276: remove the extra bracket L.289: Do you mean variation in metabolite content between specimens of the 2 morphs? Figure 3: Add the % value for your confidence ellipse in the legend. Add 'Metabilites' under the lower panels, and define the Dim-1 and Dim-2 in the legend.

Reviewed by anonymous reviewer, 2018-10-05 17:40

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Author's reply:

Dear recommenders,

Thanks for letting us the opportunity to revise our manuscript. We apologize for the delay. Please find attached our answer to both reviewers.

Regards, The authors

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