

Dear Dr Jacques Deere,

Please find along this reply a revised version of the manuscript entitled “Life-history traits, pace of life and dispersal among and within five species of Trichogramma wasps: a comparative analysis”. We have carefully read all comments and suggestions from you and the reviewers, and tried our best to address them, both in this new version of the manuscript and within this reply. We hope that this revised version will be to your satisfaction.

Yours sincerely,

Chloé Guicharnaud, on behalf of the authors

---

### **ANSWERS TO COMMENTS FROM THE RECOMMENDER**

*Dear Chloé and authors*

*After reading the manuscript and the assessment of the two reviewers, several points were raised that need to be addressed and which I believe will improve the quality of the manuscript. One point I would like to highlight, and on which I agree with both reviewers, is that of how dispersal is assessed and discussed. This point is central to the manuscript and requires clarity. I suggest revision of the manuscript in which the authors need to carefully address the reviewers' comments.*

*With kind regards,*

*Jacques Deere*

**Response:** We would like to thank the recommender for accepting to look at our manuscript. We did our best to address all the points raised by the reviewers, among them the issue of dispersal. All responses are detailed below reviewers' comments.

### **ANSWERS TO COMMENTS FROM ANONYMOUS REVIEWER**

*R1-1: This is a very detailed study of fecundity and other life-history information in many lines of five species from the same genus of parasitoids. The experiments are clearly described and well controlled and the complex statistical analysis is carried out in a clear way with scripts available on GitHub.*

**Response:** We thank the anonymous reviewer for this positive assessment of our study and how it was presented and hope that our revised version did answer all of their comments.

*R1-2: What's striking to me is that there are so many lines investigated, but little between-line variation that can be at all ascribed to any trade-offs. The authors seem to be suggesting at one point that if far more lines were used the effect would be revealed. That might be true, but it really suggests that if there is a within-species effect looking at available lines then it might be quite weak. Given the importance of lines for this investigation there was surprisingly little information about them. How have they been reared and maintained? How different are the accessions, where collected, how many foundresses and how long have they been in captivity? The main outcome of all that is that a long time in lab rearing conditions will tend to lead to evolution to the lab conditions and much of the wild population variation will be*

*lost. I've not reared these species, but there is often a distinct genetic bottleneck as lines become selected to the lab conditions. Is there any information on the genetic variation in the lab lines? ... And how it compares to genetic variation in wild populations?*

**Response:** Details about where and when lines were sampled were added in **Supplemental Table S1-1**. Most of them were sampled between 2013 and 2016 in France, with one line sampled in 1975, and another one being the result of crossing three lines for a previous experiment in 2019 (Lartigue et al., 2022). Some lines were provided by a biocontrol firm and their precise sampling location is confidential, only the collection year and whether they were sampled in France or Europe can be disclosed.

As for the genetic variance, with approximately 15 generations per year in rearing conditions (18 °C, 70 % ± 10 % relative humidity, L:D 16:8), and originating from one sampled founder clutch (also the case for all parent lines of the hybrid from Lartigue et al (2022)), lines have a very low genetic variation, as seen in Supplemental Figure S1.1 in Dahirel et al. (2021). There is little information regarding genetic diversity in the wild, but it is supposed to be low as a large survey in France and Spain collected only two to three haplotypes for *T. evanescens*, *T. semblidis* and *T. brassicae* (Muru, 2021). (L.147-157).

*R1-3: On L302 plasticity is mentioned. That's what I was also thinking and given the constant conditions there is no scope to see what plasticity the lines have. Furthermore, the lab condition selection - presumably constant temp, high density, will tend to select out plasticity anyway.*

**Response:** Indeed, the phenotypic plasticity of the lines would be interesting to study knowing that previous studies observed significant plasticity in *Trichogramma* (Krishnaraj, 2000; Pinto et al., 1989). However, the experimentation was not designed to study plasticity, as we focused our study on the presence or not of a pace-of-life under standard conditions used in experimental expansions on *Trichogramma* allowing us to make more direct links between our results in this study with different expansion dynamics later. This justification was added in the manuscript L.189-193.

*R1-4: There is a clear between-species effect in life history trade-off. So I'm now wondering about the actual size of the species and their delivered eggs - can't be the same for all of them. Often life-history trade-offs manifest as a change in size (of eggs and/or adults), at least in Drosophila which I'm more familiar with.*

**Response:** For endoparasitoids, the body size is highly dependent on the host size. As all species were maintained and experimented using *E. kuehniella* as host eggs, which are small enough to allow only one viable descendent (Corrigan et al., 1995) and were provided in high enough quantity to avoid superparasitism (as multiple eggs within one host might affect the viable descendent size), size variance is probably highly limited, with little to no correlations between hind tibia length (one proxy of individual size) and other traits as showed in Pavlík (1993). This justification on why size was not analysed was added in the revised manuscript L.199-205.

*R1-5: I agree that the 'dispersal' assessed in the study is quite different to that discussed on L346 - sounds like the Reznik study is more like 'choosiness' than dispersal and that might behave quite differently in these conditions.*

**Response:** We thank the reviewer for pointing out the differences between the two studies and support the review MT-24 made by the second reviewer. We modified our approach by using the results from the Reznik study to complete our result and rewrote this paragraph to better fit this new approach. (L.415-425)

*R1-6: Around L350 you discuss context dependence with a focus on resource availability, but don't really cover density dependence. Models of dispersal going back more than 20 years have shown that density-dependent dispersal is really easy to evolve and a very strong effect (models of Travis, Poethke, Hovestadt).*

**Response:** Indeed, both this paragraph and the next one are general discussions about condition dependence. While the end of this paragraph is about resource dependence, the next one focuses on density dependence. We rewrote the reviewed manuscript to add a clear link between those two paragraphs. (L.433-435)

*R1-7: The final conclusion that releasing several species as a biocontrol seems reasonable and does follow from the results. Might have been better to set up the introduction more with that in mind rather than the strong focus on 'pace of life' variation within species.*

**Response:** We thank the reviewer for the positive view on the biocontrol conclusion. We kept the applied aspect of our results as a perspective and rewrote the introduction to refocus our study on exploring between species trait variations and their relationship on top of the between-lines variation already mentioned. (L.116-124)

*R1-8: L18 - 'five' rather than 5?*

*R1-28: L112 five rather than 5.*

*R1-38: L186 two rather than 2*

**Response to R1-8, R1-28 and R1-38:** We thank the reviewer for pointing this error on how to correctly write numbers. All instances were corrected in the reviewed manuscript.

*R1-9: L19 - 'used against' might not be clear that it's biocontrol even though that was mentioned a few lines earlier.*

**Response:** While this abstract section was rewritten to be more pace-of-life focused, we clarified our sentence by adding that *Trichogramma* are small endoparasitoid wasps frequently used in biocontrol against Lepidoptera pests. (L.21-22)

*R1-10: L29 - why 'interesting'?*

**Response:** For inoculative releases, biocontrol agents need to establish a self-sustained population in the area treated. Therefore, traits such as high reproduction and resistance to competition (which can be observed through a longer development time) are to be optimized to end with a successful establishment with a population at a high enough density to still act as an effective biocontrol agent. We removed the imprecise term 'interesting' and the mention of inoculative releases in the reviewed abstract. (L. 32-34)

*R1-11: L30 - 'inoculative releases' is probably too much biocontrol jargon and needs a little explanation.*

**Response:** While rewording our manuscript for review R1-11, we removed the mention of inoculative releases, now only present in the last paragraph of the Discussion. We added that inoculative releases are where a small population of biocontrol agents in the area of interest must establish themselves and reach higher densities in further generations. (L.473-475)

Intro

*R1-12: Why is the first sentence or two in each paragraph in bold?*

**Response:** This is a stylistic remainder of the writing process. This formatting has been removed from the revised version.

*R1-13: L36 'how much it .... dies' reads oddly. Dies needs to be moved out of that construction.*  
**Response:** We did as suggested and removed Dies from the sentence. (L.40)

*R1-14: L45 need 'the' before variation.*

**Response:** We did as suggested and added “the” before the variation on L.49

*R1-15: L51 'one organism is under' is rather odd. It works if you just delete those words.*

*R1-16: L51 probably just drop 'trying' too.*

**Response to R1-15 and R1-16:** We did as suggested and removed those words from the sentence, replacing “trying to maximize fitness” with “maximizing fitness”. (L.54-55)

*R1-17: L55 I think you're following the rules of hyphenation when 'pace of life' is being used as an adjective, but it's important to be consistent with hyphenation in pace-of-life / pace of life when it appears so many times in the text.*

**Response:** We thank the reviewer for pointing out the need to be very careful in the reviewed manuscript as to when to use hyphens

*R1-18: L59 I'm not sure that 'hierarchical levels' is clear.*

**Response:** We changed ‘hierarchical levels’ by “taxonomic ranks” in the reviewed manuscript to be more precise about the subjects of the comparative analyses cited in the manuscript. (L.62)

*R1-19: L84 comp-col trade offs are much older than that. Levins and Culver in 1971 at least and probably before that.*

**Response:** this part of the text is not written from a historical perspective; therefore our citation process here reflects more recent theoretical-relevant studies than landmark older papers. We slightly changed the citation by adding ‘e.g.’ to specify that these are only two papers among many others. (L.86)

*R1-20: L94 what about 'shape of this relationship' rather than correlation?*

**Response:** The sentence was slightly changed to replace correlation by relationship (L.101)

*R1-21: L99 This includes some pest species could be clearer. How about 'Some hosts are pest species' or run on from the previous sentence with '... including some pest species'.*

**Response:** A couple of sentences on Trichogramma, including the one from which the suggestion comes, were moved at the beginning of the Biological section of Material and Method (L.131-132), in response to the review MT-6, suggesting that the last paragraph of the introduction might be too descriptive

*R1-22: L100 Just because they attack the eggs of pests doesn't automatically make them 'efficient'.*

**Response:** As for R1-21, the sentence was relocated, and we changed it to say that as Trichogramma species can use pest eggs as hosts, they were chosen as biological agents, and work rather well (Smith, 1996). (L.132-133)

*R&-23: L102 why 'or'; are both species used?*

**Response:** Indeed, in this study, Sigsgaard et al used either *T. principium*, *T. cacoeciae* or a mix of both. We did change our manuscript to add this information. (L.135-136)

*R1-24: L103 the sentence starting on this line is fine, but it seems to be out of place and does not follow from the previous sentence.*

**Response:** This sentence is now in the first paragraph of Material and Method, and was modified to add a link with the previous sentence by saying that given the relative importance of *Trichogramma* as a biocontrol agent, this study could help us suggest new ideas for improving their role in biocontrol, as understanding how life-history traits vary and covary can have important implications in rearing and field performance (Akbari et al., 2012; Consoli et al., 2010). (L.136-140)

*R1-25: L107 surely 'at 22'*

**Response:** We corrected this mistake as suggested. (L.109)

*R1-26: L108 probably better to say something like 'Insects are under-represented in pace of life studies'*

**Response:** We slightly modified the phrasing of this sentence as suggested in this comment. By saying that the goal of this study is to develop our knowledge of insects, under-represented in both pace-of-life and pace-of-life syndromes studies. (L112-113)

*R1-27: L111 'peculiar' seems an odd way to put it, especially when parasitoids are a quarter of all insects. Something like 'parasitoids are more difficult to study'*

**Response:** We modified the sentence as suggested by the reviewer to clarify. Peculiar referred to the different life-cycle of parasitoids as they interact closely with their host ecology (Mayhew, 2016), making studies and comparisons with other species difficult. (L.115-116)

## Method

*R1-29: How were the lines chosen? Is that just the total that was available? If so, could you give an idea of how those were chosen?*

**Response:** We chose lines from a catalogue of lines available, and restricted our search, for feasibility reasons, to a maximum of 32 sexually reproducing lines from the only 5 species (among 14 species, for a total of over 100 lines) where at least 3 lines were available for statistical power. Those details were added to the manuscript. (L. 143-145)

*R1-30: What about a table for the information in L123-126 - it's not easy to read as prose.*

**Response:** As suggested, each species' name, authority, and number of lines are now in **Table 1**. (L.166)

*R1-31: L124 hard space after T. will stop breaking over end of line*

**Response:** We thank the reviewer for this formatting tip we were not aware of, and added a hard space in species names.

*R1-32: L135 'lines' isn't needed*

**Response:** 'lines' was removed in the revised version as suggested L.169

*R1-33: L136 how are the single females selected? Is there an age that can be applied to them?*

**Response:** Single healthy females were selected at random in the population. Females were between 24 to 48 hours old. That information was added to the manuscript. (L.161-164; L.170-171)

*R1-34: L138/140 inconsistency in use of a space between value and units. 10cm and 10 cm.*

**Response:** We modified the manuscript to stay consistent by adding spaces between all values and units, according to the International System of Units.

*R1-35: L140 more detail on the tube needed. What's the internal diameter? Is the end of the tube flush with one of the walls of the rearing vial? Is it clear?*

**Response:** We used a clear pipe with an internal diameter of 0.5 cm, going through vials foam caps, without protruding from it. Details were added to the experimental design section. (L.175-179)

*R1-36: Fig 1 might be better to have a zoomed in picture of eggs to see the darkened ones more clearly.*

**Response:** The picture of darkened eggs was added, taking the place of the picture of host egg strips (**Figure 1**). We also modified the figure as suggested by the second reviewer in comment MT-8 by removing line details (as described in R1-1), now in **Supplemental Table S1-1**.

*R1-37: L176 I think noon is pm*

*R1-39: L190 I think lognormal should be hyphenated*

**Response to R1-37 and R1-39:** We thank the reviewer for those misspellings and corrected them with Log-Normal in the revised version, as noted in McElreath (2020). (L.248)

*R1-40: L209-210 I suggest a reference to this way of treating the random line effect*

**Response:** We modelled line-level random effects as a variance-covariance matrix as suggested in Bürkner (2017). The reference was added in the revised manuscript. (L.278)

*R1-41: L218/220/224/227 I wouldn't give normal an upper case, but would give Gaussian.*

**Response:** We follow the notation in McElreath (2020) for Normal in uppercase.

## Results

*R1-42: The basic mean and variation numbers could be in a table which would make the text easier to read.*

**Response:** Posterior mean values and 95% posterior highest density intervals per species were compiled in the new table (**Table 2**).

*R1-43: Fig 2 it would be conventional to at least mention the panels in the figure legend.*

**Response:** We thank the reviewer for pointing out the missed information in the figure legend. We modified the legend according to the review. (L.322-325)

*R1-44: L264 missing upper case start to sentence?*

**Response:** We corrected this error. (L.335)

*R1-45: Fig 3 could the line-level information be coded by species? Perhaps using the same colour but with low alpha?*

*R1-46: Fig 3 x axis label is not very helpful. Better to give a simpler label with an explanation in the figure legend.*

**Response to R1-45 and R1-46:** We considered the different points to improve **Figure 3** and made the changes proposed. Line-level information is now of the same colour as their species,

and the x axis label, formerly “(fecundity/no retention) (nb eggs parasitized/2 days)” is now labelled “fecundity in absence of retention (nb eggs parasitized/2 days)”.

Discussion

*R1-47: L287 - it's not clear to me whether the 'given we had 28 lines' means it's a large number or a small number and how that relates to the given reference.*

**Response:** In Dingemanse & Dochtermann (2013), their simulations showed that having 28 lines might not have enough statistical power when looking for a weak correlation signal (as the “residual” line-level correlations might be once species effects are removed). This sentence was removed from the revised manuscript as it was indeed not very clear and did not lead to more discussion.

*R1-48: L317 'did retention' sounds odd*

*R1-49: L320 same for 'doing egg retention'*

**Response to R1-48 and R1-49:** We changed “individuals that did egg retention” to “individuals manifesting egg retention” in both scenarios L.388 and L.390.

*R1-50: L364 'and' rather than 'but'?*

**Response:** We replaced ‘but’ by ‘and’ as suggested by the reviewer L.440.

#### **ANSWERS TO COMMENTS FROM MÉLANIE THIERRY**

*MT-1: This study explores the covariation between life-history traits of Trichogramma species. The authors used an experimental approach in laboratory with several lines for each species. The number of lines, species and replicates used make the results convincing. However, few parts are not clear enough and additional data could be provided to make the results more appealing.*

**Response:** We thank the reviewer for pointing out the parts that needed to be cleared and did our best to rewrite and develop all of them. While it would indeed be highly interesting to add more data, it was out of the scope so we decided to keep the results and analyses as they are, for reasons described below, but we did modify our manuscript to better fit.

*MT-2: Something you should be careful with throughout the manuscript is when talking about dispersal rates and dispersal syndromes. What you observed was the decision to immigrate of a single female parasitoid and not a dispersal rate. This term should be changed through. For dispersal syndromes you should look at traits of the parasitoids that disperse rather than traits of the whole line or species. More detailed recommendations and comments bellow.*

**Response:** We thank the reviewer for those words of caution. Dispersal is a complex subject and can have multiple slightly different definitions based on the researcher's background and what is studied. We decided to use the classical definition found in (Ronce, 2007): Dispersal corresponds to any movement *potentially* leading to gene flow. As our measure only counted disperser females that laid eggs in the arrival patch, we were indeed more accurately looking at *effective* dispersal (as there was gene flow by laying eggs). All instances of dispersal rate were replaced by effective dispersal probability in the revised version of the manuscript, be it at lines or species level.

As for dispersal syndrome, we added a sentence in L.124-126 to clarify that this study will not be focused on individual-level dispersal syndromes but rather on line- and species-level

syndromes (as seen in e.g. (Dahirel et al., 2015; Peiman & Robinson, 2017; Ronce, 2012; Stevens et al., 2010, 2013). We rewrote our manuscript to be more explicit in the definition and level of dispersal syndrome studied.

Abstract:

*MT-3: line 10: briefly define the pace-of-life axis*

**Response:** We can define a pace-of-life axis structuring reproduction and development time as a continuum from less-fecund, longer-developing ‘slow’ types to more-fecund, shorter-developing ‘fast’ types. This sentence was added in the manuscript L. 11-14

*MT-4: line 17: which contexts?*

**Response:** We were referring to the production and efficiency in the field of biocontrol agents. This sentence does not exist anymore as the reviewed manuscript is now more pace-of-life centred.

Introduction:

*MT-5: It would be good to add a short definition of what a parasitoid is for readers that might not be familiar with them.*

**Response:** We added that endoparasitoid, lay their eggs inside of their hosts, as opposed to ectoparasitoids, and the larvae feed on the host, eventually killing it. (L.129-130)

*MT-6: I am missing some hypotheses you want to test with this study. The end of the introduction sounds too descriptive.*

**Response:** We rewrote the last paragraph of the introduction in the hope to be less descriptive, but as the main goal of this study was to make an assessment of the inter- and intra- specific traits variances and their structure, we must keep in mind that it will inevitably be a little descriptive. The only major hypotheses we had was that it should exist a pace of life between life-history traits, at the species or line level, and at least one of those traits might be correlated with effective dispersal (L.120-126). Some of the descriptions on *Trichogramma* were relocated at the start of the ‘biological material’ section to lighten the paragraph. (L.129-140)

*MT-7: line 102: what are the crops *Cydia pomonella* attacks?*

**Response:** *Cydia pomonella* is an apple pest. We added these details in the manuscript at the start of the ‘biological material’ section. (L-136)

Materials and methods:

*MT-8: Figure 1 needs to be improved. The details of species and lines might not be needed. The picture at the bottom right would be better in supplement material than on this figure.*

**Response:** We thank the reviewer for suggesting improvements to **Figure 1**. We did move the picture in Supplemental Material (**Supplemental Figure S2-1**) and replaced it with zoomed parasitized eggs as suggested in R1-36. Details on lines were replaced by the number of lines per species and symbols consistent with later figures, while the names and other details as presented in R1-2 are now in **Supplemental Table S1-1**.

*MT-9: Information on how these species locate their hosts could be important when talking about decision to disperse or not.*



**Response:** Little is known about how females specifically locate host eggs, but there are speculations that the sex-pheromones, scales or directly eggs of hosts may play a role (Consoli et al., 2010). While the effective dispersal observed seems low, it does correspond to effective dispersal values observed in other experiments (Dahirel, Bertin, Calcagno, et al., 2021). We added this information about locating hosts in the manuscript in the ‘experimental design’ section of Material and Method (L.179-180) and the consistent value on L.406-408

*MT-10: Why did you not look at parasitism rate? Did you rear the insects or only looked at the number of blacken eggs over the total number of host eggs? This could be an important information in addition to your fecundity measurement, especially in relation to dispersal decisions.*

**Response:** Since we worked with non-limiting host eggs, the parasitism rate (% of total hosts) is meaningless in itself, as opposed to the number of eggs parasitised. Only the number of blackened eggs was taken. Eggs were kept until the first descendent emerged for development time measures, but not reared further.

*MT-11: lines 132-133: why did you isolate them if you want mated females?*

**Response:** We isolated females 24 h after the population emerged. As *Trichogramma* mate right after emerging, waiting 24 h was enough to be mostly assured to have mated females for our study (Doyon & Boivin, 2006). We reworded the sentence in the reviewed manuscript. (L.161-164)

*MT-12: line 137: how many eggs is a non-limiting quantity? Density of hosts might be important for parasitoid behavior*

**Response:** We assume egg supply to be non-limiting based on previous studies where females tend to lay no more than around a hundred eggs in their lifetime under the best conditions (Özder & Kara, 2010), and each of our host egg strips contained several hundreds of eggs, but the precise number is unknown. The non-limiting aspect was supported by the fact that no stripes were entirely parasitized in the experiment. We added that information to the Methods (L.216-218)

*MT-13: lines 140 and 146: are 40 cm long tube and 48h relevant to observe dispersal decisions in these species? Did you choose these based on previous studies on your system?*

**Response:** Indeed, we chose those numbers according to previous experiments (Dahirel, Bertin, Calcagno, et al., 2021), to be the closest to protocols used in experimental range expansion conditions, as our results in this study will later be used in such context. We added that the design was inspired by this study in the manuscript. (L.179-183)

*MT-14: lines 143-145: it would actually be interesting to look at traits of parasitoids that did not disperse versus parasitoids that did. That way you could talk about dispersal syndromes if you find significant differences between dispersers and residents.*

**Response:** We thank the reviewer for insightful suggestions, and will do as suggested in further studies on dispersal syndromes at the individual level. There were many reasons for not looking at traits on dispersers separately in that specific study, mainly because there were not enough dispersers to have high statistical power, but also because as mentioned in previous comments we wanted to look at the potential dispersal syndrome at a line/species level, where our analyses as presented are enough.

*MT-15: lines 164-168: in your study you only had one female parasitoid at a time. In this case, mechanisms of avoidance of superparasitism are quite different. In some solitary parasitoid*

*species, a single female may lay more than one egg in a single host, potentially to overwhelm host immune system.*

**Response:** In *Trichogramma* species, it was shown by Wang et al in 2016 that single females tend to avoid superparasitism when possible and lay eggs on unparasitized host eggs. As we worked with a non-limiting number of host eggs, there is a very low possibility of superparasitism. Moreover, *Ephestia kuehniella* is small enough to only permit the viable development of only one descendent per egg (Klomp & Teerink, 1966). We added this information to the reviewed manuscript. (L.213-220)

*MT-16: line 168: what may be present?*

**Response:** In this setting, we referred to egg retention. We clarified our sentence in the new version of the manuscript. (L.2242-224)

*MT-17: lines 171- 173: you cannot talk about dispersal rate with your experiment.*

**Response:** We thank the reviewer for pointing out this shortcoming and we changed the dispersal rate by the effective dispersal probability thorough the reviewed manuscript as detailed in MT-2.

*MT-18: line 186: explain what are the two different models here.*

**Response:** We reworded most of the Data analyses section to be clearer in our model description. The fact that there are two main models is now only mentioned after describing the three sub-models for each response variable. Then, we described that “We coded those two models to observe how variance in traits and the covariance between traits are partitioned at the inter- and intra-specific level. The first model incorporated both line and species-level effects, structuring the variance into intra- and inter-specific levels. The second model only had line effects as predictors, and therefore assumes that individuals from two conspecific lines do not resemble each other more than individuals from two randomly selected lines”. Those sentences were added to the reviewed version. (L.267-273)

*MT-19: lines 193-203: I am not familiar with this method to look at egg retention. Where does it come from? A reference would be welcome to make the method convincing.*

**Response:** There is no standard way to look at egg retention per se, and most of the studies on the topic simply looked at whether wasps laid eggs or not within a given time frame in a binary way (e.g. Carey et al., 2021). However, zero-inflated models are actually a standard way to model data with an excess of structural zeroes, like our fecundity data, especially when these zeroes may have a biological interpretation (Blasco-Moreno et al., 2019), which they would in a system where some individuals lay eggs and some do not, as in *Trichogramma*. We did clarify this method in the reviewed version of the manuscript. (L.251-260)

*MT-20: lines 204-216: this part is not clear to me.*

**Response:** This paragraph was about how the two main models were coded to observe how variance in traits is partitioned at the inter- and intra-specific level, and better described now in the paragraph presented in MT-18. As for line-level correlations, we specified in our code (through a variance-covariance matrix) that each response variable line-level random effects were correlated with one another. However, even if there is the possibility that some of this variation might be attributed to a common ancestor, also known as phylogenetic bias (Felsenstein, 1985), there was no phylogenetic tree available including all lines we used to include in this shared covariance matrix and account for the phylogenetic signal (Hadfield & Nakagawa, 2010). We hope that the newer version of the Data analyses section is clearer

(L.274-284). More detailed description of the model was added in **Supplementary Material S3**.

*MT-21: line 208: why not nesting lines within species for the random factor?*

**Response:** As there were only five species, it was not enough to treat species as a random factor, and especially not to estimate species-level between traits as random-effect correlations, as we would have needed to do. It is not an issue as the species/lines interaction effect is accounted for in our formula, as there was no repetition of line names between different species.

Discussion:

*MT-22: lines 283-286: not clear*

**Response:** In this sentence, we wanted to point out that, even if the correlations between lines within species are not statistically significant, we tend to have a negative correlation between fecundity and development time, like the significant negative correlation seen at the between-species level. We tried to clarify the sentence in the newest manuscript. (L.355-358)

*MT-23: line 300: what do you call lower levels?*

**Response:** Lower levels refer to all levels found under species, here line-level for example. We clarified the sentence in the new manuscript and removed the term lower level by 'line or even individual levels'. (L.371-372)

*MT-24: lines 342-344: why did you not look at that to compare your results with Reznik and Klyueva's ones?*

**Response:** We reworded this paragraph to present our study as a complement to the study of Reznik and Klueva. While they talked about the activity within one continuous patch, we wanted to explore long-distance dispersal between discrete patches, as its correlation with the pace of life is less proven and less studied in *Trichogramma*. (L.415-425)

*MT-25: lines 361-363: how can it be context-independent if you only work with one context?*

**Response:** Our experiment was context-independent in the sense that, as every measure were indeed done in the same conditions, our result cannot be explained by a difference in context, be it rearing condition, density or other environmental values. As this might indeed be confusing, we tried to clarify this sentence in the revised manuscript. (L.437-439)

## **REFERENCES**

Akbari, F., Askarianzadeh, A., Zamani, A. A., & Hosseinpour, M. H. (2012). Biological characteristics of three *Trichogramma* species on the eggs of diamondback moth (*Plutella xylostella* L.). *Archives Of Phytopathology And Plant Protection*, 45(19), 2364–2368. <https://doi.org/10.1080/03235408.2012.727325>

Blasco-Moreno, A., Pérez-Casany, M., Puig, P., Morante, M., & Castells, E. (2019). What does a zero mean? Understanding false, random and structural zeros in ecology.

*Methods in Ecology and Evolution*, 10(7), 949–959. <https://doi.org/10.1111/2041-210X.13185>

Bürkner, P.-C. (2017). *Advanced bayesian multilevel modeling with the R package brms*

(arXiv:1705.11123). arXiv. <http://arxiv.org/abs/1705.11123>

Carey, M. P., Von Biela, V. R., Dunker, A., Keith, K. D., Schelske, M., Lean, C., &

Zimmerman, C. E. (2021). Egg retention of high-latitude sockeye salmon

(*Oncorhynchus nerka*) in the Pilgrim River, Alaska, during the Pacific marine heatwave of 2014–2016. *Polar Biology*, 44(8), 1643–1654.

<https://doi.org/10.1007/s00300-021-02902-8>

Consoli, F. L., Parra, J. R. P., & Zucchi, R. A. (Eds.). (2010). *Egg parasitoids in agroecosystems with emphasis on Trichogramma*. Springer Netherlands.

<https://doi.org/10.1007/978-1-4020-9110-0>

Corrigan, J. E., Laing, J. E., & Zubricky, J. S. (1995). Effects of parasitoid to host ratio and time of day of parasitism on development and emergence of *Trichogramma minutum*

(Hymenoptera: Trichogrammatidae) parasitizing eggs of *Ephestia kuehniella*

(Lepidoptera: Pyralidae). *Annals of the Entomological Society of America*, 88(6), 773–780. <https://doi.org/10.1093/aesa/88.6.773>

Dahirel, M., Bertin, A., Calcagno, V., Duraj, C., Fellous, S., Groussier, G., Lombaert, E.,

Mailleret, L., Marchand, A., & Vercken, E. (2021). Landscape connectivity alters the evolution of density-dependent dispersal during pushed range expansions. *BioRxiv*,

*Peer Reviewed by Peer Community in Evolutionary Biology*.

<https://doi.org/10.1101/2021.03.03.433752>

Dahirel, M., Bertin, A., Haond, M., Blin, A., Lombaert, E., Calcagno, V., Fellous, S.,

Mailleret, L., & Vercken, E. (2021). Shifts from pulled to pushed range expansions

caused by reductions in connectedness. *Oikos*. <https://doi.org/10.1111/oik.08278>

- Dahirel, M., Olivier, E., Guiller, A., Martin, M.-C., Madec, L., & Ansart, A. (2015). Movement propensity and ability correlate with ecological specialization in European land snails: Comparative analysis of a dispersal syndrome. *Journal of Animal Ecology*, *84*(1), 228–238. <https://doi.org/10.1111/1365-2656.12276>
- Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39–54. <https://doi.org/10.1111/1365-2656.12013>
- Doyon, J., & Boivin, G. (2006). Impact of the timing of male emergence on mating capacity of males in *Trichogramma evanescens* Westwood. *BioControl*, *51*(6), 703–713. <https://doi.org/10.1007/s10526-006-9001-0>
- Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, *125*(1), 1–15. <https://doi.org/10.1086/284325>
- Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, *23*(3), 494–508. <https://doi.org/10.1111/j.1420-9101.2009.01915.x>
- Klomp, H., & Teerink, B. J. (1966). The significance of oviposition rates in the egg parasite, *Trichogramma embryophagum* Htg. *Archives Néerlandaises de Zoologie*, *17*(3), 350–375. <https://doi.org/10.1163/036551667X00065>
- Krishnaraj, R. (2000). *Phenotypic plasticity of Trichogramma minutum riley (kymenoptera: Trichogrammatidae) and its implications for mass rearing* [University of Toronto]. <https://hdl.handle.net/1807/14378>
- Lartigue, S., Yalaoui, M., Belliard, J., Caravel, C., Jeandroz, L., Groussier, G., Calcagno, V., Louâpre, P., Dechaume-Moncharmont, F., Malausa, T., & Moreau, J. (2022). Consistent variations in personality traits and their potential for genetic improvement

- in biocontrol agents: *Trichogramma evanescens* as a case study. *Evolutionary Applications*, 15(10), 1565–1579. <https://doi.org/10.1111/eva.13329>
- Mayhew, P. J. (2016). Comparing parasitoid life histories. *Entomologia Experimentalis et Applicata*, 159(2), 147–162. <https://doi.org/10.1111/eea.12411>
- McElreath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and Stan* (2nd ed.). Taylor and Francis, CRC Press.
- Muru, D. (2021). *Magic bullet or shot in the dark? Potential and limits of biological control for experimental ecology* [Université Côte d'Azur]. <https://theses.hal.science/tel-03272503>
- Özder, N., & Kara, G. (2010). Comparative biology and life tables of *Trichogramma cacoeciae*, *T. brassicae* and *T. evanescens* (Hymenoptera: Trichogrammatidae) with *Ephestia kuehniella* and *Cadra cautella* (Lepidoptera: Pyralidae) as hosts at three constant temperatures. *Biocontrol Science and Technology*, 20(3), 245–255. <https://doi.org/10.1080/09583150903497880>
- Pavlik, J. (1993). The size of the female and quality assessment of mass-reared *Trichogramma* spp. *Entomologia Experimentalis et Applicata*, 66(2), 171–177. <https://doi.org/10.1111/j.1570-7458.1993.tb00705.x>
- Peiman, K. S., & Robinson, B. W. (2017). Comparative analyses of phenotypic trait covariation within and among populations. *The American Naturalist*, 190(4), 451–468. <https://doi.org/10.1086/693482>
- Pinto, J. D., Velten, R. K., Platner, G. R., & Oatman, E. R. (1989). Phenotypic plasticity and taxonomic characters in *Trichogramma* (hymenoptera: Trichogrammatidae). *Annals of the Entomological Society of America*, 82(4), 414–425. <https://doi.org/10.1093/aesa/82.4.414>

- Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics*, 38(1), 231–253.  
<https://doi.org/10.1146/annurev.ecolsys.38.091206.095611>
- Ronce, O. (2012). Dispersal syndromes. In J. Clobert, M. Baguette, T. G. Benton, & J. M. Bullock (Eds.), *Dispersal Ecology and Evolution* (1st ed, pp. 119–138). Oxford University Press.
- Smith, S. M. (1996). Biological control with *Trichogramma*: Advances, successes, and potential of their use. *Annual Review of Entomology*, 41(1), 375–406.  
<https://doi.org/10.1146/annurev.en.41.010196.002111>
- Stevens, V. M., Trochet, A., Blanchet, S., Moulherat, S., Clobert, J., & Baguette, M. (2013). Dispersal syndromes and the use of life-histories to predict dispersal. *Evolutionary Applications*, 6(4), 630–642. <https://doi.org/10.1111/eva.12049>
- Stevens, V. M., Turlure, C., & Baguette, M. (2010). A meta-analysis of dispersal in butterflies. *Biological Reviews*, 85, 625–642. <https://doi.org/10.1111/j.1469-185X.2009.00119.x>