



The relationship between dispersal and pace-of-life at different scales

Jacques Deere based on peer reviews by *Mélanie Thierry* and 1 anonymous reviewer

Chloé Guicharnaud, Géraldine Groussier, Erwan Beranger, Laurent Lamy, Elodie Vercken, Maxime Dahirel (2023) Life-history traits, pace of life and dispersal among and within five species of *Trichogramma* wasps: a comparative analysis. bioRxiv, ver. 3, peer-reviewed and recommended by Peer Community in Zoology.

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The sorting of organisms along a fast-slow continuum through correlations between life history traits is a long-standing framework (Stearns 1983) and corresponds to the pace-of-life axis. This axis represents the variation in a continuum of life-history strategies, from fast-reproducing short-lived species to slow-reproducing long-lived species. The pace-of-life axis has been the focus of much research largely in mammals, birds, reptiles and plants but less so in invertebrates (Salguero-Gómez et al. 2016; Araya-Ajoy et al. 2018; Healy et al. 2019; Bakewell et al. 2020). Outcomes from this research have highlighted variation across taxa on this axis and mixed support for, and against, patterns expected of the pace-of-life continuum. Given this, a greater understanding of the variation of the pace-of-life across-, and within, taxa are needed. Indeed, Guicharnaud et al. (2023) highlight several points regarding our broader understanding of pace-of-life. In general, invertebrates are poorly represented, the variation of pace-of-life across taxonomic scales is less well understood and the relationship between pace-of-life and dispersal, a key life history, requires more attention. Here, Guicharnaud et al. (2023) provide a first attempt at addressing the relationship between dispersal and pace-of-life at different scales.

The authors, under controlled conditions, investigated how life-history traits and effective dispersal covary for 28 lines from five species of endoparasitoid wasps from the genus *Trichogramma*. At the species level negative correlations were found between development time and fecundity, matching pace-of-life axis predictions. Although this correlation was not found to be significant among lines, within species, a similar pattern of a negative correlation was observed. This outcome matches previous findings that consistent pace-of-life axes become more difficult to find at lower taxonomic levels. Unlike the other life-history traits measured,

effective dispersal showed no evidence of differences between species or between lines. The authors also found no correlation between effective dispersal and other-life history traits which suggests no dispersal/life-history syndromes in the species investigated. One aspect that was not assessed was the impact of density dependence on pace-of-life and effective dispersal, largely as this was a first step in assessing relationship of dispersal with pace-of-life at different scales. However, the authors do acknowledge the importance of future studies incorporating density dependence and that such studies could potentially lead to more generalizable understanding of pace-of-life and dispersal within *Trichogramma*.

A pleasant addition was the link to potential implications for biocontrol. This addition showed an awareness by the authors of how insights into pace-of-life can have an applied component. The results of the study highlighted that selecting for specific lines of a species, to maximise a trait of interest at the cost of another, may not be as effective as selecting different species when implementing biocontrol. This is especially important as often single, established species used in biocontrol are favoured without consideration of the potential of other species which can lead to more efficient biocontrol.

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Reviews

Evaluation round #2

DOI or URL of the preprint: <https://doi.org/10.1101/2023.01.24.525360>
Version of the preprint: 2

Authors' reply, 06 June 2023

Dear Dr Jacques Deere,

Thank you for all the new suggestions to improve our manuscript. All of the proposed changes were added in the latest version.

We additionally identified two minor editing errors in the Acknowledgements (one species name not in italics L.483 and an excess space L.488), along with a minor coding issue that led to errors in some of the line-level posteriors for Figure 2 (the grey dots and lines). This was an issue limited to this plot code only and had no effect whatsoever on any of our results and interpretation and is now corrected.

Kind regards,

Chloé Guicharnaud, in behalf of the authors.

Decision by Jacques Deere, posted 01 June 2023, validated 05 June 2023

Manuscript revision

Dear Chloé and authors

The revised manuscript was assessed by myself, and I am satisfied that you have addressed the comments raised by both reviewers. There are only some minor changes that I would suggest before the manuscript can be fully recommended.

Line 114: "Potential reasons include..." the statement as it is does not make it completely obvious to what the 'reasons' are refereeing to. Possibly: "Potential reasons for this under-representation include..."

Line 118: "...and analysed their..." should read "...and analysed the..."

Line 133: "...and seem to work rather well" the use of 'seem' suggests that this is more of an observation than an actual assessment. If this is based on an observation only then this needs to be stated otherwise replace the word 'seem': Possibly "...and have shown to work well..."

Line 154: *Trichogramma brassicae* should be italicized.

Line 185: "...them here so due to the..." remove 'so'.

Line 260: "...probability of doing retention...!" should read "...probability of retention..."

Line 267: "We used that model architecture..." and "We fitted those two models..." sounds a bit clunky and may cause confusion given the complexity of the statistics used. Possibly "We used the model architecture described above for two multivariate models. The two multivariate models were fitted..."

With kind regards,

Jacques Deere

Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.1101/2023.01.24.525360>

Version of the preprint: 1

Authors' reply, 04 May 2023

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Decision by Jacques Deere, posted 16 March 2023, validated 16 March 2023

Manuscript revision

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

Reviewed by anonymous reviewer 1, 07 March 2023

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.

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?

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.

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.

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.

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).

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.

Minor edits

Abs L18 - 'five' rather than 5?

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

L29 - why 'interesting'?

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

Intro

Why is the first sentence or two in each paragraph in bold?

L36 'how much it dies' reads oddly. Dies needs to be moved out of that construction.

L45 need 'the' before variation.

L51 'one organism is under' is rather odd. It works if you just delete those words.

L51 probably just drop 'trying' too.

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.

L59 I'm not sure that 'hierarchical levels' is clear.

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

L94 what about 'shape of this relationship' rather than correlation?

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'.

L100 Just because they attack the eggs of pests doesn't automatically make them 'efficient'.

L102 why 'or'; are both species used?

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.

L107 surely 'at 22'

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

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'

L112 five rather than 5.

Method

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?

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

L124 hard space after T. will stop breaking over end of line

L135 'lines' isn't needed

L136 how are the single females selected? Is there an age that can be applied to them?

L138/140 inconsistency in use of a space between value and units. 10cm and 10 cm.

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?

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

L176 I think noon is pm

L186 two rather than 2

L190 I think lognormal should be hyphenated

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

L218/220/224/227 I wouldn't give normal an upper case, but would give Gaussian.

Results

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

Fig 2 it would be conventional to at least mention the panels in the figure legend.

L264 missing upper case start to sentence?

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

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

Discussion

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.

L317 'did retention' sounds odd

L320 same for 'doing egg retention'

L364 'and' rather than 'but'?

Reviewed by **Mélanie Thierry**, 27 February 2023

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.

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.

Abstract:

- line 10: briefly define the pace-of-life axis
- line 17: which contexts?

Introduction:

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

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

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

Materials and methods:

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.

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

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.

- lines 132-133: why did you isolate them if you want mated females?
- line 137: how many eggs is a non-limiting quantity? Density of hosts might be important for parasitoid behavior

- 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?

- 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.

- 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.

- line 168: what may be present?

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

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

- 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.

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

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

Discussion:

- lines 283-286: not clear

- line 300: what do you call lower levels?

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

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