Life history traits, pace-of-life and dispersal among and within five species of *Trichogramma* wasps: a comparative analysis

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Abstract

Major traits defining the life history of organisms are often not independent from each other, with most of their variation aligning along key axes such as the pace-of-life axis. These axes, along with their potential associations or syndromes with other traits such as dispersal, are however not universal; in particular, support for their presence may be taxon and taxonomic scale-dependent. Knowing about such life-history strategies may be especially important for biological control agents, as these trait syndromes may constrain the ability to optimize production, as well as their efficiency in the field. To understand how life-history traits and dispersal covary in such contexts, we measured these traits in controlled conditions for 28 lines from 5 species of *Trichogramma*, small endoparasitoid wasps frequently used against Lepidoptera pests. We found partial evidence of a pace-of-life axis at the interspecific level: species with higher fecundity also had faster development time. However, faster developing species also were more likely to delay egg-laying, a trait that is usually interpretable as "slow". There was no support for similar covariation patterns at the within-species line level. There was limited variation in dispersal between species and line, and accordingly, we did not detect any correlation between dispersal rates and life-history traits. We discuss how expanding our experimental design by accounting for the density-dependence of both the pace of life and dispersal might reveal a dispersal syndrome in future studies. Overall, our results highlight the importance of exploring covariation at the "right" taxonomic scale, or multiple taxonomic scales, to understand the (co)evolution of life history traits. They also suggest that optimizing all interesting life-history traits for inoculative releases may be difficult in programs using one species.

Keywords: dispersal syndrome; life history strategies; fecundity; intraspecific competition; trait covariation

Introduction

Life history describes the life cycle of an organism, how fast and how much it grows, reproduces, survives, and dies. It is the direct product of a collection of phenotypic traits, called life-history traits (Flatt & Heyland, 2011)**.** Those traits include growth and mortality rates, survival, reproductive investment or even the lifespan, and can be age- or stage-specific. When all life-history traits and the values they can take are combined, many pathways can lead to evolutionary success, resulting in the high diversity of what are called life-history strategies, the covariation through time and space of different traits, found across the tree of life. This high diversity can be observed at multiple taxonomic levels, from the phylum level to within species (Gaillard et al., 1989; Healy et al., 2019; Olsen et al., 2018). Yet, resource limitation means not all strategies are possible: indeed, analyses of life-history traits across taxa and hierarchical levels often reveal that a large part of variation in organisms' life histories can be summarised on a small number of key axes, which often reflect trade-offs between life-history components. It is generally accepted that those life-history-trait correlations arise from trade-offs between allocating a certain amount of acquired resources into one trait or another, with limitations arising from a limited pool of resource to draw from, physiological constraints, and from the influence of the environment one organism is under, resulting in a variety of strategies trying to maximize fitness (Laskowski et al., 2021; Stearns, 2000).

One specific axis has been termed the pace of life and corresponds to a correlation between life-history traits sorting organisms along a fast-slow continuum (Braendle et al., 2011; Stearns, 1983)**.** Many trait combinations can be used to characterize a pace-of-life axis (Gaillard et al., 2016), discriminating low reproduction, long development and long lifespan (slow types) on one side from high reproduction, short development, and short lifespan (fast types) on the other. Pace-of-life axes have been identified in multiple comparative analyses across hierarchical levels (Auer et al., 2018; Healy et al., 2019; Williams et al., 2010) although the traits that cluster to form this axis are not always the same (Bielby et al., 2007). But despite its conceptual appeal and simplicity, the pace-of-life axis should not be assumed as the one unique axis structuring life histories: the proportion of variance explained by such an axis varies between taxa (Healy et al., 2019), and in many cases, alternative axes structuring variation also emerge (Bakewell et al., 2020; Mayhew, 2016; Wright et al., 2020). Moreover, it seems the narrower the taxonomic focus (from tree of life-wide analyses to within-species comparisons), the harder it is to find the presence of a pace of life, and the way life-history variation is structured in one species/taxon cannot always be generalized to others. Adding complexity to life-history trait correlations, the pace-of-life syndrome hypothesis supposes that the pace of life can co-evolve with one or many other phenotypic traits. They can be physiological (Auer et al., 2018; Ricklefs & Wikelski, 2002), behavioural (Réale et al., 2010; Wolf et al., 2007), or associated with other traits like dispersal.

Dispersal can be described as any movement potentially leading to a flux of genes or individuals across space (Ronce, 2007)**, and is a key component influencing both ecological and evolutionary dynamics,** so much that it is sometimes described as a life-history trait in its own right (Saastamoinen et al., 2018). Dispersal often covaries with other

traits in so-called dispersal syndromes (Ronce, 2012), including other life-history traits (Clobert et al., 2012). Dispersal syndromes have been observed and compared at multiple taxonomic levels, both across (Stevens et al., 2012, 2014) and within species (Jacob et al., 2019). Therefore, it is not surprising that many works have been dedicated to the integration of dispersal along the main life-history axes, and the derivation of ecological and evolutionary implications. This includes for instance the idea of a competition-colonization trade-off where species that are good at colonizing, with high fecundity or dispersal, are in return poor competitors between or among species (Calcagno et al., 2006; Yu & Wilson, 2001), and other studied links between dispersal and fecundity (Bonte & De La Peña, 2009; Crossin et al., 2004; Gu et al., 2006; Karlsson & Johansson, 2008). On another level than a correlation between dispersal and a single life-history trait, the pace-of-life syndrome hypothesis suggests dispersal, among others, to be a risky trait linked to the pace of life (Cote et al., 2010; Réale et al., 2010). In plants, there is a relation between seed dispersal abilities and the fast-slow continuum, where a high capacity to disperse is correlated with faster life histories at the species level (Beckman et al., 2018). Those dispersal-life-history syndromes can lead to different ecological and evolutionary results from when traits are considered as independent. Correlation between traits, but also the strength or shape of this correlation can impact the ecological and evolutionary dynamics of a population (Maharjan et al., 2013; Ochocki et al., 2020).

In that context, we explored first the presence of a pace of life and then its relationship with dispersal rates in five species of *Trichogramma* wasps. *Trichogramma* (Hymenoptera: Trichogrammatidae) are small (< 1 mm when adult) endoparasitoids using insect eggs, mainly Lepidoptera, as hosts. This includes some pest species, which makes them efficient biological control agents. Indeed, *T. brassicae* is commercially available and often used against *Ostrinia nubilalis*, the European corn borer (Mertz et al., 1995), and *T. evanescens* or *T. cacoeciae* against *Cydia pomonella* (Sigsgaard et al., 2017). Understanding how life-history traits vary and covary can have important implications in this system and can help predict the rearing or field performance of biocontrol agents (Akbari et al., 2012; Consoli et al., 2010). *Trichogramma* are also key model species in ecological, physiological, or invasion biology studies thanks to their small size, rather short development time (13-15 days, 22°C), or also the fact that it can be possible to choose sexual or asexual lines. On top of their economic interest, *Trichogramma* are insects, a taxon underexplored in pace of life (but see Blackburn 1991) and pace-of-life syndromes studies (38 invertebrate species vs 141 vertebrates in Royauté et al., 2018). Potential reasons include a lack of data (Bakewell et al., 2020) or peculiar lifestyles, for instance, parasitoids (Mayhew, 2016). Using lab-reared lines belonging to 5 species of *Trichogramma*, we measured fecundity, dispersal, and development time under experimental conditions, and analyzed their line- and species-level covariation using multivariate generalized linear mixed models (Careau & Wilson, 2017; Dingemanse & Dochtermann, 2013). Based on previous experiments on *Trichogramma* that analysed trait variation between lines (Lartigue et al., 2022), or species (Özder & Kara, 2010), we expected to observe trade-offs between the studied traits at the line or species level.

Materials and methods

Biological material

For this experiment, 32 different lines of *Trichogramma* from 5 different species were originally selected. However, 4 lines did not correctly synchronize during preparation and could not be used, resulting in 28 lines: *T. principium* Sugonjaev & Sorokina, 1976 (N_{lines}= 3), *T. evanescens* Westwood, 1833 (N_{lines}= 7), *T. brassicae* Bezdenko, 1968 (N_{lines}= 9), *T. semblidis* (Aurivillius 1898) (N_{lines}= 5) and *T. bourarachae* Pintureau & Babault, 1988 (N_{lines}= 4). All selected lines are sexually reproducing. These lines were selected from the collection of the Biological Resource Centre "Egg Parasitoid Collection"(CRB EP-Coll, Sophia Antipolis; Marchand et al., 2017). Wasps were raised on Mediterranean flour moth *Ephestia kuehniella* (Lepidoptera: Pyralidae) eggs at 22°C, 70% ± 10% relative humidity, L:D 16:8. Host eggs were irradiated with UV for 15 minutes before use; this sterilization method kills the embryo while keeping it viable as a wasp host (St-Onge et al., 2014). Only females isolated 24h after emerging were used in this experiment, under the assumption that all of those females were already mated during that time (Doyon & Boivin, 2006).

Experimental design

We used both single and 2-vial systems to measure lines' life-history traits (Fig. 1). In single vial systems (12 replicates per line), we placed one *Trichogramma* female into a plastic vial (5 cm diameter, 10 cm height) with a non-limiting quantity of irradiated *Ephestia kuehniella* eggs on a paper strip (approximatively 1.4 × 1 cm). This system was used to measure development time and fecundity traits. In 2-vial systems (20 replicates per line), the setup was similar to the previous one, with the exception that a 40cm long plastic tube connected the first vial (where the wasp was deposited) to another one with the same dimensions, also containing a non-limiting quantity of irradiated eggs. This setup allowed us to estimate dispersal rates. While fecundity and development-time data could also be collected in this second setup, we refrained from analysing them here so due to the complexities of accounting for the effects of dispersal and dispersal costs, compared to the 1-vial setup. Females were left in those vials for 48h under standardized conditions: 22°C, 50% relative humidity, L:D 16:8. After 48h, the egg strips were isolated in glass vials (1cm diameter, 4cm height), and kept under the same standardized conditions.

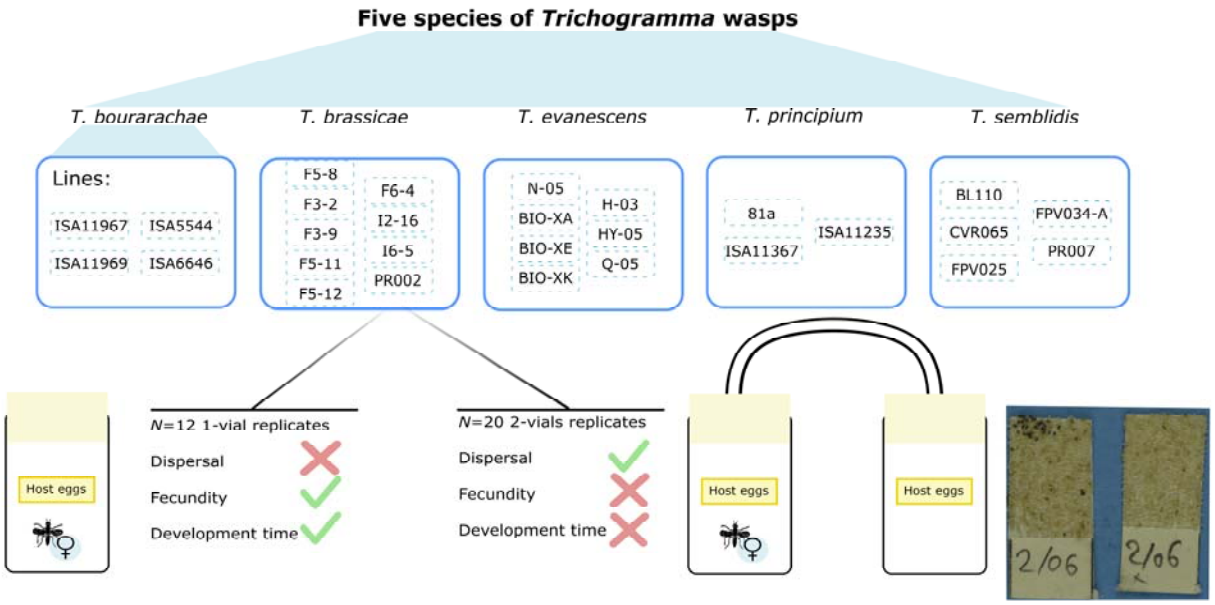

Figure 1: Summary of the experimental design used for measuring fecundity, effective dispersal, and development time. Inset (bottom right): example host egg strips from a 2-vial system; parasitized eggs are darkened and thus easily visible among the off-white unparasitized hosts.

Phenotyping

Fecundity and dispersal

A week after isolation, parasitoid larvae were developed enough to blacken the host egg, allowing the visual identification of successfully parasitized eggs. Egg strips (one for single vial, two for 2-vial systems) were then photographed (resolution: 6 016 × 4 016 pixels, for a real field of view size of around 12 × 8cm) using a Nikon D750 camera (lens: AF-S Micro NIKKOR 60mm f/2.8G ED) fixed above the strips.

Fecundity was measured by manually counting the number of blackened eggs in each picture using ImageJ (Schneider et al., 2012). Even though superparasitism (more than one parasitoid egg laid per host) is frequent for *Trichogramma*, in general only one adult emerges from *E. kuehniella* eggs in the end (Corrigan et al., 1995). In addition, egg retention by refusing to oviposit was previously observed in *T. principium* and *T. brassicae* (Fleury & Boulétreau, 1993; Reznik et al., 2001, 1998). Therefore, it may be present in all of the studied species and may affect fecundity measures in the timeframe of our experiment (see Data analyses).

In 2-vial systems, effective dispersal was measured as a binary response, whether the female has dispersed or not. One female is considered to have successfully dispersed if at least one parasitized egg was found on the strip present in the second plastic vial.

Development time

After taking the pictures for fecundity, each isolated host egg strip was checked every day at around 9:00 a.m., 12:00 a.m., and 4:00 p.m. for the presence of emerged individuals. The development time of one replicate was considered to be the number of days between the female in the plastic vial starting to lay eggs and the emergence of the first offspring. Note that the true time is only known to a precision of 2 days, because of uncertainty in when precisely eggs were laid during the 48h window after introduction in the system (see Data analyses for how this is accounted for).

Data analyses

Data were then analyzed with a Bayesian multivariate multilevel/mixed model, using the brms R package, version 2.17.0 (Bürkner, 2017), a front-end for the Stan language (Stan Development Team, 2022). The code was tested on R versions 4.1.2 to 4.2.0 (R Core Team, 2021). We coded 2 models containing the same three response variables, each with its own sub-model:

- Dispersal was modelled with a Bernoulli model (with a logit link), corresponding to the fact that a female had dispersed or not;
- Development time used a lognormal distribution, often chosen for time-to-event data. Because of the 48h time period where the female was allowed to reproduce, development times were interval censored (with 48h wide intervals);
- For fecundity, initial models showed evidence of potential zero inflation and overdispersion, therefore a zero-inflated negative binomial distribution was used, effectively separating the response variable in two. On one hand, the zero-inflated part of the distribution, similar to a Bernoulli model with a logit link, modelled an excess of non-parasitized replicates, possibly caused by egg retention done by *Trichogramma* species. On the other hand, a negative binomial component (with a log link) was interpreted as individual fecundity without egg retention. From now on, we will use "fecundity without retention" to refer to this fecundity component (i.e. the effectively egg-laying individuals only), and "overall fecundity" will refer to the mean number of eggs laid by all individuals, including those potentially doing retention.

The same predictors were used for all three of the response variables (all four, more accurately, due to the addition of the zero-inflation component). For one model, responses were assumed to vary at two hierarchical levels, "among species" and "among lines within species". Species were considered as a fixed effect, mostly due to the low number of species studied, while line identity was coded as a random effect. To account for line-level correlations between the response variables, line-levels random effects were modelled as a shared variance-covariance matrix. We do not directly include phylogenetic information in this shared-covariance matrix, as there is no phylogenetic tree available including all lines used. The second model is identical, but with no species-fixed effect. While the first model allowed us to observe inter- and intra- species line covariation, the second one let us analyze global line covariation without species partitioning. For convenience in setting

priors, the species-fixed effects in the first model were set as a series of species-specific intercepts, rather than one intercept and species-specific contrasts.

Weakly informative priors were chosen based on, or modified from, McElreath (2020). We used half-Normal ($\mu = 0$, $\sigma = 1$) priors for random effects standard deviations and an LKJ ($\eta = 2$) prior for the random effects correlation matrix. For the fixed-effect intercepts of proportion traits (dispersal and zero-inflation component of fecundity), we used a Normal (0, 1.5) prior (leading to a roughly uniform prior between 0 and 1 when back-transformed from the logit scale to the proportion scale) (McElreath, 2020). For the fixed-effect intercepts of development time and fecundity without retention (both on the log scale), we used Normal (μ, 1) distributions, where μ was based on the log of the median of relevant observed data instead of 0, to assure better scaling (see Data and code availability for details). For the negative binomial component of fecundity, we additionally set a half-Normal (0, 1) prior for the inverse of the shape parameter, which is more amenable to such a generic prior than the shape itself (see Data and code availability for further justification). The models were run with 4 chains during 4500 iterations each, with the first 2000 iterations for each chain used as warmup. This led to good chain convergence and sample size, as checked using the statistics proposed by Vehtari et al (2021). Model outputs were then checked using posterior predictive checks to compare predictions with empirical dataset (as suggested by Gabry et al., 2019). See the "Data and code availability" section, for links to an archived version of the annotated model code.

Results

Trichogramma bourarachae had lower fecundity without retention (mean and 95% posterior highest density interval of 17.42 [12.77; 22.5] parasitized hosts eggs on 2 days) and higher development time (13.3 [12.64; 13.97] days) than *Trichogramma brassicae* (35.24 [27.71; 42.7] parasitized hosts eggs and 11.79 [11.4; 12.2] development days), while *T. semblidis* only had a lower development time than *T. bourarachae* (11.97 [11.39; 12.52] days) (**Figure 2B, C**). There were no other clear species differences (based on 95% intervals of pairwise differences) in fecundity or development time. We did not find any evidence for between-species differences in dispersal rates (**Figure 2A**). *T. brassicae* and *T. semblidis* both had higher egg retention probabilities than *T. bourarachae* (pairwise differences of 0.20 [0.00; 0.40] and 0.29 [0.05; 0.53] respectively, **Figure 2D**).

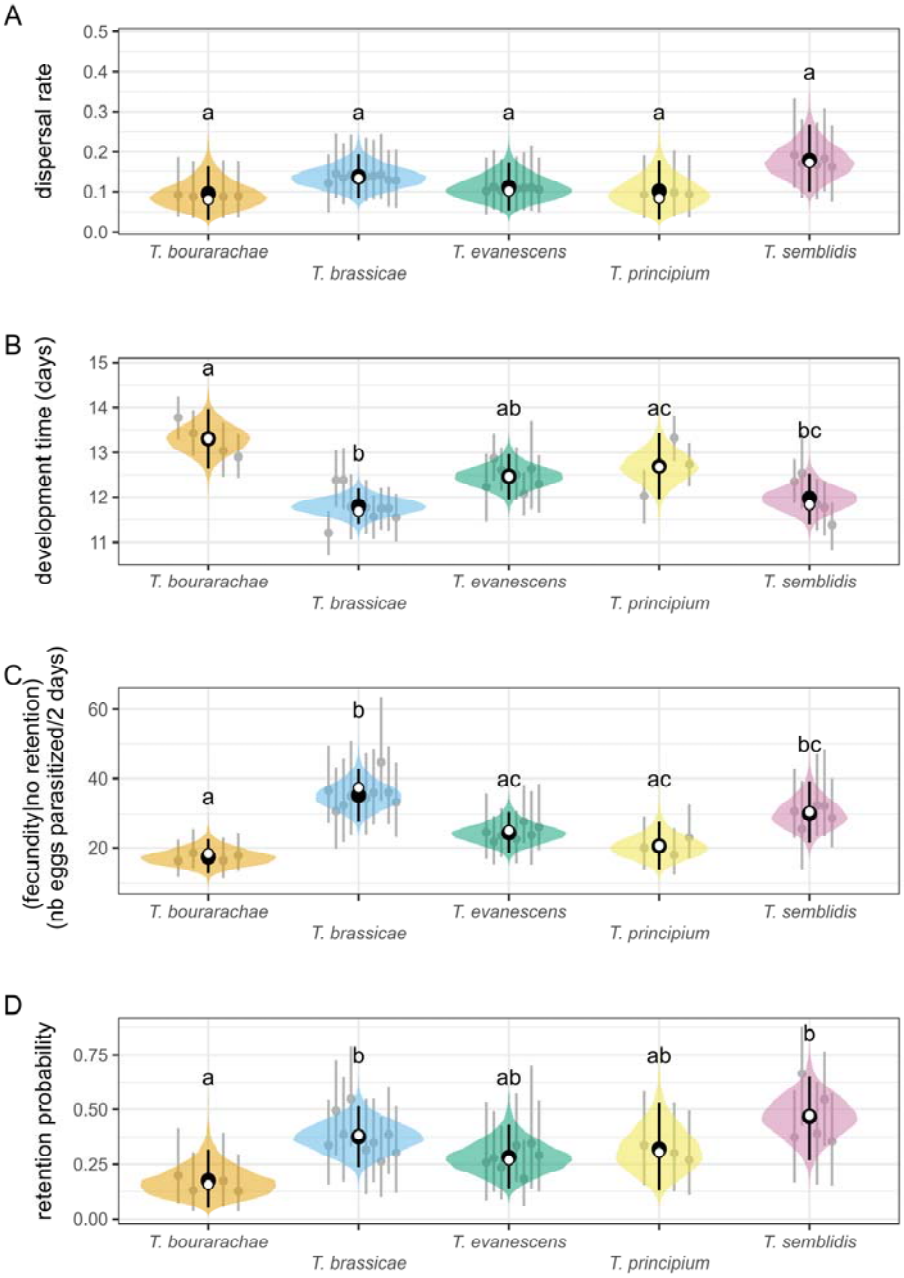

Figure 2: Posterior trait values as a function of the *Trichogramma* species. 95% posterior highest density intervals per line for each species are displayed in grey. Black dots represent posterior means, and bars the 95% intervals, while the posterior density distributions of fixed (species) effect only predicted means is coloured depending on the species. For a given trait, two species with no index letters in common are considered to have "significant" pairwise comparison differences (i.e. the 95% highest density interval of the difference does not include 0). White dots represent observed means per species, presented for illustrative purposes only (as they are calculated assuming all observed

255 zeroes in egg numbers were attributable to retention, and using the midpoint of the 48h
256 interval for development time).

257 The only detectable line-level trait correlation, whether within life-history traits or between
258 life-history traits and dispersal, was a negative correlation between females' fecundity
259 without retention and development time (-0.62 [-0.92; -0.28]), and only when between-
260 species differences were included in the estimation (see **Table 1 bottom**, **Figure 3**). This
261 random effect negative correlation disappeared when co-variation was partitioned between
262 species (fixed effects) and line levels (random effects) (-0.22 [-0.76; 0.38], **Table 1 top**).

263 **Table 1:** line-level random effect correlations among measured traits, represented by
264 means and 95% higher posterior density intervals. (top) between-lines trait correlations,
265 from the partitioned covariance model (species differences are excluded as fixed effects);
266 (bottom) between-lines trait correlations from the model without fixed species effects.
267 Intervals without 0 inside are presented in bold.

	Dispersal rate	(Fecundity|no retention)	Retention probability
Within-species, among-line correlations (after excluding between-species differences as fixed effects)			
(Fecundity|no retention)	0.04 [-0.66; 0.72]		
Retention probability	0.04 [-0.65; 0.73]	-0.22 [-0.85; 0.4]	
Development time	0.12 [-0.58; 0.79]	-0.22 [-0.76; 0.38]	0.2 [-0.37; 0.71]
Overall among-line correlations, inclusive of between-species differences			
(Fecundity|no retention)	0.19 [-0.46; 0.82]		
Retention probability	0.15 [-0.52; 0.81]	0.08 [-0.48; 0.61]	
Development time	-0.08 [-0.71; 0.59]	**-0.62 [-0.92; -0.28]**	-0.17 [-0.64; 0.31]

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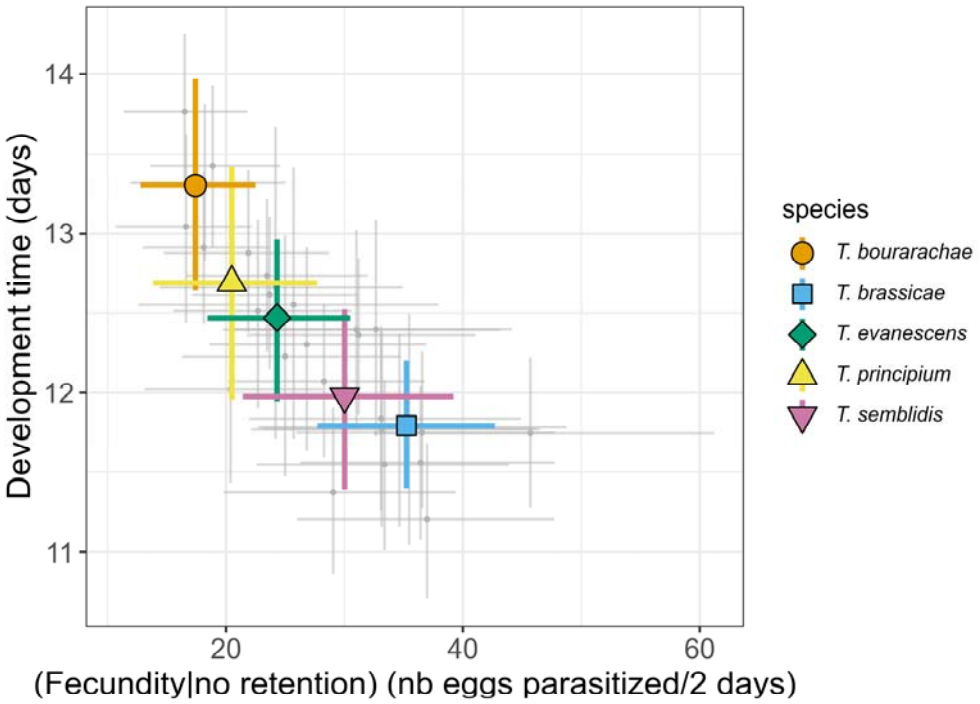

Figure 3: Posterior development time of *Trichogramma* species as a function of posterior fecundity in the absence of egg retention. Coloured crosses represent species 95% posterior higher posterior density intervals for development time and fecundity, while coloured symbols represent species posterior means; line-level posterior means and 95% intervals are displayed in grey.

Discussion

Identification of one interspecific Pace-of-Life axis in Trichogramma

We found a negative between-line correlation between development time and fecundity in this subset of five *Trichogramma* species, with high fecundity without retention, fast development time on one side, and low fecundity, slow development on the other (Figures 2, 3, Table1). This correlation, which matches the classical pace-of-life axis (Healy et al., 2019) is mainly or only due to species-level differences: species with higher fecundity also had faster development times (**Figures 2, 3**), and the line-level correlation vanishes when species differences are partitioned out (**Table 1**). We note that although there is no clear support for a non-zero correlation between lines within each species, the sign of this correlation remains negative (**Table 2 top**), as in the between-species case. More data may be needed to determine whether within-species patterns result from a true absence of correlation or limited power (given we had 28 lines; Dingemanse & Dochtermann, 2013). Having relatively similar patterns of interspecific and intraspecific correlation may result from close genetic correlations between development time and fecundity in *Trichogramma*, through pleiotropy or other strong genetic architecture, constraining the evolution of this trade-off among lines and species (Peiman & Robinson, 2017). It is also possible that at the metabolic level, resource acquisition and allocation may

favour longer development times at the expense of fecundity or the opposite (Agrawal, 2020; Jørgensen & Fiksen, 2006; Stearns, 2000). The fact that a pace of life was found at the between-species level but not the within-species level is in line with the existing literature, in which it is increasingly difficult to find consistent pace-of-life axes as the taxonomic level narrows down, possibly due to scale-dependent mechanisms (Agrawal, 2020; Simons, 2002). Correlations at the species level act over a longer macroevolutionary timescale, where divergent positions on the pace-of-life axis of each species may represent long-term trade-offs and selection pressure over a wider environmental range than at lower levels, like lines. For lower levels, traits may be more responsive to direct environment variation through phenotypic plasticity, and a shorter evolutionary timescale may lead to lower variation range compared to a higher level (Siefert et al., 2015).

However, this pace-of-life finding is based on splitting fecundity into what we interpret as egg retention and fecundity without retention components. While a significant negative correlation with development was found on the latter component of overall fecundity, results are more complex for retention probabilities. Indeed, there is no evidence for the line-level correlation between egg retention and other life-history traits (**Table 1**). Furthermore, at the species level, faster species (lower development time and higher fecundity in the absence of retention) were also the species with the highest retention probabilities (**Figure 2**). If we interpret retention rates as a trade-off between present reproduction and future opportunities, then high retention can be seen as a "slow" trait; its association with "faster" life history traits may then appear paradoxical. It might be that fecundity in the absence of retention and retention probabilities are not actually separate traits, and that the trait correlations described above derive from their "artificial" separation by the statistical model. However, previous studies indicate that in *T. principium*, except for prolonged periods of egg-retention, individuals that did retention had similar fecundities in their first days of actual egg-laying and similar lifetime fecundities than individuals that did not (Reznik et al., 2001, 1998). Still in *T. principium*, there are indications that individuals doing egg retention have longer mean lifespans than individuals that immediately oviposit (Reznik et al., 2003; Reznik & Vaghina, 2007). These results support the idea that egg retention is a separate trait, interpretable as a mark of delayed reproduction (thus typically "slow" life history) rather than merely a component of reduced reproduction. While the pace of life remains an important and valuable structuring pattern in life histories, our results would agree with other studies showing that, deviations from naïve expectations, where all traits should be either "slow" or "fast", can be frequent (Bielby et al., 2007; Wright et al., 2020). In Wright et al (2020), their eco-evolutionary model presented possibly unexpected but existing life-history strategies, like "slow" adult reproduction alongside "fast" offspring survival (that the authors likened to an oak tree life history) or the opposite (represented by mayflies). However, because egg-laying was restricted to a 48h window in our experiment, we cannot yet confirm this interpretation. Further studies measuring lifetime reproductive success, longevity or the way reproductive effort is spread throughout the lifetime may shed more light on the way life history is structured in *Trichogramma* wasps.

335 *No evidence for a syndrome linking dispersal rates and pace-of-life*

336 **Dispersal rate varied the least among the four traits measured, with no evidence of**
337 **between-species or even between-lines differences (Figure 2).** There was also no
338 correlation between dispersal and any of the other traits (**Table 1**), meaning that there is
339 no evidence for dispersal-life history syndromes in our set of *Trichogramma* species.
340 Interestingly, this result contradicts a previous study in *T. principium*, in which females
341 manifesting egg retention had higher dispersal rates than females that laid eggs beforehand
342 (Reznik & Klyueva, 2006). This discrepancy may be the result of a focus on different
343 taxonomic levels: Reznik and Klyueva (2006)'s results deal with within-species and within-
344 line covariation, versus between-lines and between-species in the present study. It may also
345 result from differences in experimental designs and metrics used: the dispersal metrics
346 used in Reznik and Klyueva (2006) are based on short-term (<1 day) and short-distance
347 (up to 5 cm) movement compared to our experiment (2 days and 40 cm). In that case, there
348 may still exist in *Trichogramma* a pace-of-life syndrome linking life history to short-term
349 activity and behaviour, but not dispersal. Indeed, correlations between short-term
350 movement behaviour and life-history traits were also found in *T. evanescens* at the
351 between-line level (Lartigue et al., 2022). Finally, we allowed both dispersal and oviposition
352 to occur at the same time, while Reznik and Klyueva (2006) and Lartigue et al. (2022)'s
353 setups were based on measuring dispersal/movement in the absence of hosts and
354 presenting hosts to the wasps at another time. Dispersal is extremely context-dependent,
355 including to current resource availability (Fronhofer et al., 2018); there is furthermore
356 evidence that syndromes linking dispersal to other traits can be altered depending on
357 whether individuals disperse from high-resource or low-resource contexts (Cote et al.,
358 2022).

359 *The potential implications of context-dependence and especially density-dependence for this*
360 *syndrome*

361 **Building on this point, our study was indeed context-independent, with every female**
362 **tested for a given trait being tested under the same low-density conditions (alone in**
363 **the experimental design with a non-limiting host supply).** Dispersal syndromes (Bonte
364 & Dahirel, 2017; Cote et al., 2022; Ronce, 2012) but also pace-of-life syndromes can be
365 context-dependent. Behavioural types can be dependent of the dispersal status and
366 predation risks (Bell & Sih, 2007; Cote et al., 2010). Pace-of-life syndromes and/or their
367 constituent traits may also depend on resource acquisition through plastic responses
368 (Laskowski et al., 2021; Montiglio et al., 2018) or quality. In *Trichogramma* for instance,
369 host egg species and quality can influence life-history traits (Paul et al., 1981), and we used
370 a substitution host in the present study. Recent works suggest that population density and
371 density fluctuations in particular may also play a key role in shaping the presence of a pace
372 of life in the first place (Wright et al., 2020) and its association with behaviours: fast
373 individuals may have a higher reproductive rate in low-density contexts, but their lower
374 intra-specific competition is a disadvantage when close to the carrying capacity of an
375 environment, and therefore are more likely to disperse to escape to lower densities where
376 this competition is lessened (Wright et al., 2019). This interaction between the pace of life
377 and density may interact with the overall density-dependence of dispersal (Clobert et al.,

2009; Harman et al., 2020), altering syndromes linking dispersal and life history. Given that there is evidence for dispersal and fecundity both being density-dependent in several *Trichogramma* species (*T. brassicae*; Dahirel et al., 2021; *Trichogramma achaeae*, *T. chilonis* and *T. euproctidis*, Zboralski et al., 2016), further studies including density-dependence may lead to more generalizable insights about pace of life and dispersal in *Trichogramma*.

Implications for biocontrol improvement and perspectives

While studies on trade-offs (Bennett et al., 2002; Reznik & Klyueva, 2006; Zboralski et al., 2016) **or pace-of-life syndromes** (Lartigue et al., 2022) **already existed in small biocontrol agents including *Trichogramma*, our results provide new insights on between-species comparisons and the taxonomic scales at which trait variation is important.** Some species like *T. evanescens*, *T. cacoeciae* (Sigsgaard et al., 2017) or *T. brassicae* (Özder & Kara, 2010) are already well used as biocontrol agents. In that context, a choice might be needed between maximizing one trait or a set of traits of interest at the expense of the others. For *Trichogramma*, while having fast-developing and high-fecundity individuals can be beneficial to quick intervention and a higher number of host eggs parasitized, they are reared and released mainly at high densities, (Consoli et al., 2010) densities for which individuals with longer development time might fare better against the intra-species competition (Wright et al., 2019). For inoculative releases, both fecundity and competitive abilities are to be favoured for efficiency (Smith, 1996). Our results suggest that for some purposes, selecting different species might actually be more successful than attempting to select specific lines within one already used species.

Data availability

Data and R code to reproduce all analyses presented in this manuscript are available on GitHub (https://github.com/CGuicharnaud/Trichogramma_POL_dispersal_2023) and archived in Zenodo (https://doi.org/10.5281/zenodo.7544901).

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Author contributions

CG, GG, EV and MD designed the experiment. Lines rearing was done by LL and CG, while CG, GG, EB, LL and EV conducted the experiments in the lab. CG and LL collected data; CG and MD analysed the data. CG wrote the first draft; all authors were able to read, edit, and approve the manuscript.

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