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. 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. Such 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 understanding eco-evolutionary dynamics, as these trait syndromes may constrain trait variation or be correlated with other traits. To understand how life-history traits and effective dispersal covary, we measured these traits in controlled conditions for 28 lines from five species of *Trichogramma*, which are small endoparasitoid wasps frequently used as a biological model in experimental evolution but also in biocontrol 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 interpreted as "slow". There was no support for similar covariation patterns at the within-species line level. There was limited variation in effective dispersal between species and lines, and accordingly, we did not detect any correlation between effective dispersal probability 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 improve our understanding of those traits and how they interact with each other. 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 both reproductive and development traits to maximize the efficiency of biocontrol may be difficult in programs using only 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, and survives. 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 the 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, resulting in a variety of strategies maximizing 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 taxonomic ranks (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 the correlations of life-history traits, 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, including other life-history traits (Clobert et al., 2012), in so-called dispersal syndromes (Ronce, 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 trade-off between competition and colonization where species that are good at colonizing, with high fecundity or dispersal, are in return poor competitors between or among species (e.g. 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). Rather than idiosyncratic correlations between dispersal and specific life-history traits, the pace-of-life syndrome hypothesis suggests dispersal, among others, to be a risky trait linked to the pace of life itself (Cote, Clobert, et al., 2010; Réale et al., 2010). In plants for instance, 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). While many studies found a positive correlation between the pace of life and short-scale movement, like the exploration of a continuous patch, or the activity level within an arena (Gangloff et al., 2017; Lartigue et al., 2022; Rádai et al., 2017), directly transposing short-scale conclusions like exploration or activity, to longer-scale metrics, like dispersal rates or the decision to disperse in discrete landscapes, is not always relevant (Cote, Fogarty, et al., 2010; Harrison et al., 2015; Pennekamp et al., 2019). 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 relationship can impact both 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 axis and then the relationship between the pace of life and effective dispersal in five species of *Trichogramma* wasps. *Trichogramma* (Hymenoptera: Trichogrammatidae) are small (< 1 mm when adult) parasitoids that develop inside the eggs of their hosts, mainly Lepidoptera. They are also model species in ecology and invasion biology studies thanks to their small size, rather short development time (13-15 days, at 22 °C), or also the fact that lines can be either sexual or asexual. The goal of this study is therefore to improve our knowledge of life-history trade-offs specifically in *Trichogramma* for future studies of eco-evolutionary dynamics, but also more generally in insects, which are under-represented in both 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 the difficulty to study and compare insect parasitoids, as their life-history traits are also subject to their host ecology (Mayhew, 2016). Using lab-reared lines belonging to five species of *Trichogramma*, we measured female fecundity, effective dispersal, and development time under experimental conditions, and analysed their line- and species-level covariation between these traits using multivariate Generalized Linear Mixed Models (Careau & Wilson, 2017; Dingemanse & Dochtermann, 2013). While this study is mostly exploratory, we can make some hypotheses: based on previous experiments that analysed trait variation between *Trichogramma* lines (Lartigue et al., 2022), or species (Özder & Kara, 2010), we can expect to observe trade-offs between fecundity and development time at the interline or interspecies level. In addition, as a relationship was found between activity and

fecundity in Lartigue et al. (2022), there is a possibility that one or several life-history traits are linked to effective dispersal in a dispersal syndrome at a species or line level.

Materials and methods

Biological material

Trichogramma are endoparasitoids, which means that females lay their eggs inside their hosts, where the larvae will develop by feeding on the host and ultimately killing it, as opposed to ectoparasitoids, who lay their eggs and develop outside their host. As some of *Trichogramma* hosts are Lepidopteran pest species, several *Trichogramma* species are used as biological control agents, and seem to work rather well (Smith, 1996). For instance, *T. brassicae* is used on a large scale against *Ostrinia nubilalis*, the European corn borer (Mertz et al., 1995), and *T. evanescens*, *T. cacoeciae,* or a mix of the two species can be used against *Cydia pomonella*, an apple pest (Sigsgaard et al., 2017). In addition to their interest as laboratory model species to investigate the pace of life, the identification of correlations between life-history traits in *Trichogramma* could open up new avenues to improve their efficiency as biocontrol agents, through the optimization of their rearing or field performance (Akbari et al., 2012; Consoli et al., 2010).

For this experiment, 32 different lines of *Trichogramma* were originally selected among the collection from the Biological Resource Center (BRC) "Egg Parasitoid Collection"(CRB EP-Coll, Sophia Antipolis; Marchand et al., 2017). We restricted our choice to the only five sexual species where at least three lines were available. Within each species, we selected at random at least three lines per species and up to ten, with a total target of 32 lines for feasibility. Four lines did not correctly synchronize during preparation and could not be used, resulting in 28 lines in the actual experiment (**Table 1**). The Biological Resource Center rears lines on eggs of the Mediterranean flour moth *Ephestia kuehniella* (Lepidoptera: Pyralidae) at 18 °C, 70 % ± 10 % relative humidity, L:D 16:8. Most lines were founded from a single original clutch each, mostly collected between 2013 and 2016 in different parts of France, and one line comes from a crossing of three single-clutch lines made in 2019 (**Supplemental Table S1-1**). With approximately 15 generations per year under those rearing conditions, lines from the BRC collection are expected to have a very low genetic variance at the time of the experiment (as seen for Trichogramma brassicae in the supplemental material of Dahirel, Bertin, Haond, et al., 2021). Little is known about the genetic diversity in the wild, but it is expected to be low as a survey in France and Spain collected only two to three haplotypes for *T. evanescens*, *T. semblidis* and *T. brassicae* (Muru, 2021). After collecting the lines from the BRC, we kept them on *E. kuehniella* eggs at 22 °C, 70 % ± 10 % relative humidity, L:D 16:8 for two to three generations before starting the experiment. 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). Each female used for the experiment was isolated randomly from the rest of the population 24 hours after emerging, as *Trichogramma* start mating as soon as individuals emerge from host eggs (Doyon & Boivin, 2006). Therefore, all females during the experiment were between 24 to 48 hours old.

166 **Table 1:** Summary of the *Trichogramma* species and lines used in the experiment, among the
167 total number of lines available in the BRC at the time.

Species	Species authority	Number of lines used (number available in the BRC)
T. bourarachae	Pintureau & Babault, 1988	4 (4)
T. brassicae	Bezdenko, 1968	9 (22)
T. evanescens	Westwood, 1833	7 (21)
T. principium	Sugonjaev & Sorokina, 1976	3 (4)
T. semblidis	(Aurivillius 1898)	5 (5)

168 ## Experimental design

169 We used both single- and two-vial systems to measure life-history traits (**Fig. 1**). In single-
170 vial systems (12 replicates per line), we placed one randomly selected mated *Trichogramma*
171 female between 24 to 48 hours old into a plastic vial (5 cm diameter, 10 cm height). We also
172 added a non-limiting quantity of irradiated *Ephestia kuehniella* eggs on a paper strip
173 (hundreds of host eggs in approximatively 1.4 × 1 cm, see **Supplemental Figure S2-1**). This
174 system was used to measure development time and fecundity traits. In two-vial systems (20
175 replicates per line), the setup was similar to the previous one, with the exception that a see-
176 through 40 cm long plastic pipe (5 mm of internal diameter, large enough for species of less
177 than a millimetre in size) connected the first vial (where the wasp was deposited) to another
178 one with the same dimensions, also containing a non-limiting quantity of irradiated eggs. The
179 ends passed through the centre of the foam plugs without protruding from them. While little
180 is yet known about how females locate host eggs (Consoli et al., 2010), this setup was inspired
181 by previous studies on experimental expansions on *Trichogramma* (Dahirel, Bertin, Calcagno,
182 et al., 2021; Dahirel, Bertin, Haond, et al., 2021) and allowed us to estimate effective dispersal
183 probability in conditions similar to previous experimental expansions. Even though
184 fecundity and development-time data could also be collected in this second setup, we
185 refrained from analysing them here so due to the complexities of accounting for the effects
186 of dispersal and dispersal costs, compared to the single-vial setup. Females were left in those
187 vials for 48 h under standardized conditions: 22 °C, 70 % relative humidity, L:D 16:8. After
188 48 h, the egg strips were isolated in glass vials (1 cm diameter, 4 cm height), and kept under
189 the same standardized conditions. Please note that even if plasticity can be observed in
190 *Trichogramma* (Krishnaraj, 2000; Pinto et al., 1989), we focused our study on the presence
191 or not of a pace-of-life under the standard conditions used in experimental expansions on
192 *Trichogramma*, allowing us to make more direct links between our results in this study and
193 future results in experimental expansions.

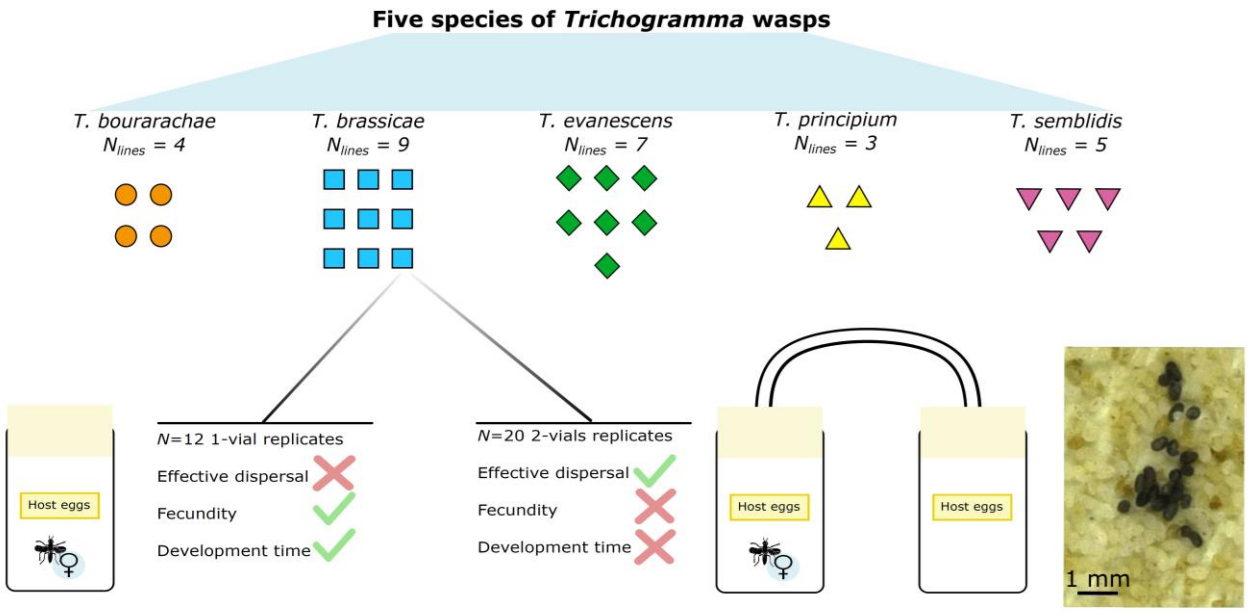

Figure 1: Summary of the experimental design used for measuring fecundity, effective dispersal, and development time. Inset (bottom right): picture of; parasitized host eggs, in black, easily visible among the off-white unparasitized hosts, one week after the experiment.

Phenotyping

For endoparasitoids, the body size is highly dependent on the host size. In our case, 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). Therefore, we assumed that size variance was probably highly limited, with little to no correlations between hind tibia length (one proxy of individual size) and other traits (Pavlík, 1993) and did not measure size.

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 (picture in **Figure 1**). Egg strips (one for single vial, two for two-vial systems) were then photographed (resolution: 6016 × 4016 pixels, for a real field of view size of around 12 × 8 cm) using a Nikon D750 camera (lens: AF-S Micro NIKKOR 60 mm f/2.8 G 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*, it tends to be avoided when an unlimited number of unparasitized eggs are present for single females (in *T. chilonis*, Wang et al., 2016). As in Özder & Kara (2010), the mean fecundity in *Trichogramma* on *E. kuehniella* was at best around a hundred, and each of our host egg strips counted several hundreds of

eggs, we can assume that our study was indeed done in a non-limiting context. Furthermore, in general, only one adult emerges from *E. kuehniella* eggs in the end (Corrigan et al., 1995; Klomp & Teerink, 1966).

Egg retention by refusing to oviposit was previously observed in *T. principium* and *T. brassicae* (Fleury & Boulétreau, 1993; Reznik et al., 2001, 1998). Therefore, egg retention may be present in all of the studied species and may affect fecundity measures in the timeframe of our experiment; see below for how this possibility was accounted for in the context of Data analyses.

In two-vial systems, effective dispersal (i.e. movement between patches leading to actual gene flow) was measured as a binary response, where 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 p.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 two days, because of uncertainty in when precisely eggs were laid during the 48 h window after introduction in the system (see Data analyses for how this is accounted for).

Data analyses

Data were then analysed with Bayesian multivariate multilevel/mixed models, using the brms R package, version 2.17.0 (Bürkner, 2017a), 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).

The multivariate model architecture was made of four connected Generalized Linear Mixed sub-models, one for each response that are effective dispersal, development time, and fecundity divided into two components:

- Effective dispersal (the probability that the female successfully laid eggs in the arrival patch) was modelled with a Bernoulli distribution (with a logit link).
- Development time was modelled with a Log-Normal distribution, often chosen for time-to-event data. Because of the 48 h time period where the female was allowed to reproduce, development times were interval censored (with 48 h wide intervals);
- For fecundity, initial models showed evidence of both potential zero inflation and overdispersion, therefore a Zero-inflated Negative binomial distribution was used. This effectively separates the response variable into two components, “structural zeroes” and counts, each with a valid biological meaning (Blasco-Moreno et al., 2019):
    - On one hand, the zero-inflated part of the distribution, similar to a Bernoulli model, modelled an excess of non-parasitized replicates compared to a

negative binomial model. Given that egg retention is common in *Trichogramma* species, leading to delays in egg-laying of up to several days commonly (Reznik et al., 2001), a biologically plausible reading of these structural zeroes component is the probability of doing retention in the 48 h of the experiment;

- On the other hand, a Negative binomial component (with a log link) was interpreted as the fecundity of individuals that did not perform 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.

We used that model architecture for two multivariate models. We fitted those two models to observe how variance in traits and the covariance between traits are partitioned at the inter- and intra-specific levels. 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 assumed that individuals from two conspecific lines do not resemble each other more than individuals from two randomly selected lines. In both cases, the same predictors were used for all four responses.

The first model included species-level effects as a fixed effect, mostly due to the low number of species studied, and line identity was coded as a random effect, while the second model only included line-level random effects. To account for line-level correlations between the response variables, line-level random effects for the two models were modelled as drawn from a shared variance-covariance matrix (Bürkner, 2017b).

While phylogenetic comparative methods could be used in this context, as some of the variations could be explained by shared ancestry (Felsenstein, 1985), there is no phylogenetic tree available for all lines used we could include (Hadfield & Nakagawa, 2010). Our first model, splitting variation into species and line components is nonetheless similar to the "taxonomic model" suggested in these cases where tree data are absent (Hadfield & Nakagawa, 2010).

The model formulas and the priors used (mostly weakly informative priors based on or modified from McElreath, 2020) are described in detail in **Supplementary Material S3.** The models were run with four 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 and higher development time than *Trichogramma brassicae*, while *T. semblidis* only had a lower development time than *T. bourarachae* but no clear difference in fecundity without retention (**Table 2**, **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 effective dispersal probabilities (**Table 2**, **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**).

Table 2: Mean posterior values and 95 % posterior highest density intervals per species, of single female fecundity in the absence of egg retention, said egg retention probability to occur during the experiment, the development time of the first offspring and effective dispersal probability. For a given trait, two species with no index letters in common are considered to have "significant" pairwise comparison differences.

	T. bourarachae	*T. brassicae*	*T. evanescens*	*T. principium*	*T. semblidis*
Effective dispersal probability	0.09 [a] [0.03; 0.16]	0.14 [a] [0.08; 0.19]	0.11 [a] [0.05 ; 0.17]	0.1 [a] [0.03; 0.18]	0.18 [a] [0.1; 0.27]
Development time	13.3 [a] [12.64; 13.97]	11.79 [b] [11.4; 12.2]	12.47 [ab] [11.94; 12.96]	12.69 [ac] [11.95; 13.42]	11.97 [bc] [11.39; 12.52]
(Fecundity|no retention)	17.42 [a] [12.77; 22.5]	35.24 [b] [27.71 ; 42.7]	24.31 [ac] [18.43 ; 30.49]	20.49 [ac] [13.83 ; 27.71]	30.02 [bc] [21.42 ; 39.2]
Retention probablility	0.17 [a] [0.05 ; 0.32]	0.38 [b] [0.24; 0.51]	0.28 [ab] [0.14; 0.43]	0.32 [ab] [0.13; 0.53]	0.47 [b] [0.27; 0.65]

Correlations between traits at the line level were analysed through the random effect correlation/covariance matrix. In the first model, differences across species were modelled with a fixed effect, so they were not included in random effect correlations, while the second model included both species- and line-level random effects. Therefore, any qualitative difference between the two models can be interpreted as an effect at the species level.

The only detectable correlations among traits were between fecundity without retention and development time (**Table 3, Figure 3**). There was a negative correlation between these two traits at the line level in the model where species effects were not partitioned out (-0.62 [-0.92; -0.28], see **Table 3 bottom**, see also the overall pattern **Figure 3**). However, when looking at the model where species differences are partitioned out into fixed effects (**Table 3 top**), this random effect negative correlation mostly vanishes (-0.22 [-0.76; 0.38]). This reflects the fact that the overall correlation highlighted in **Table 3 top** is mostly driven by between-species differences in both fecundity and development time (see **Figure 2** and species averages in **Figure 3**).

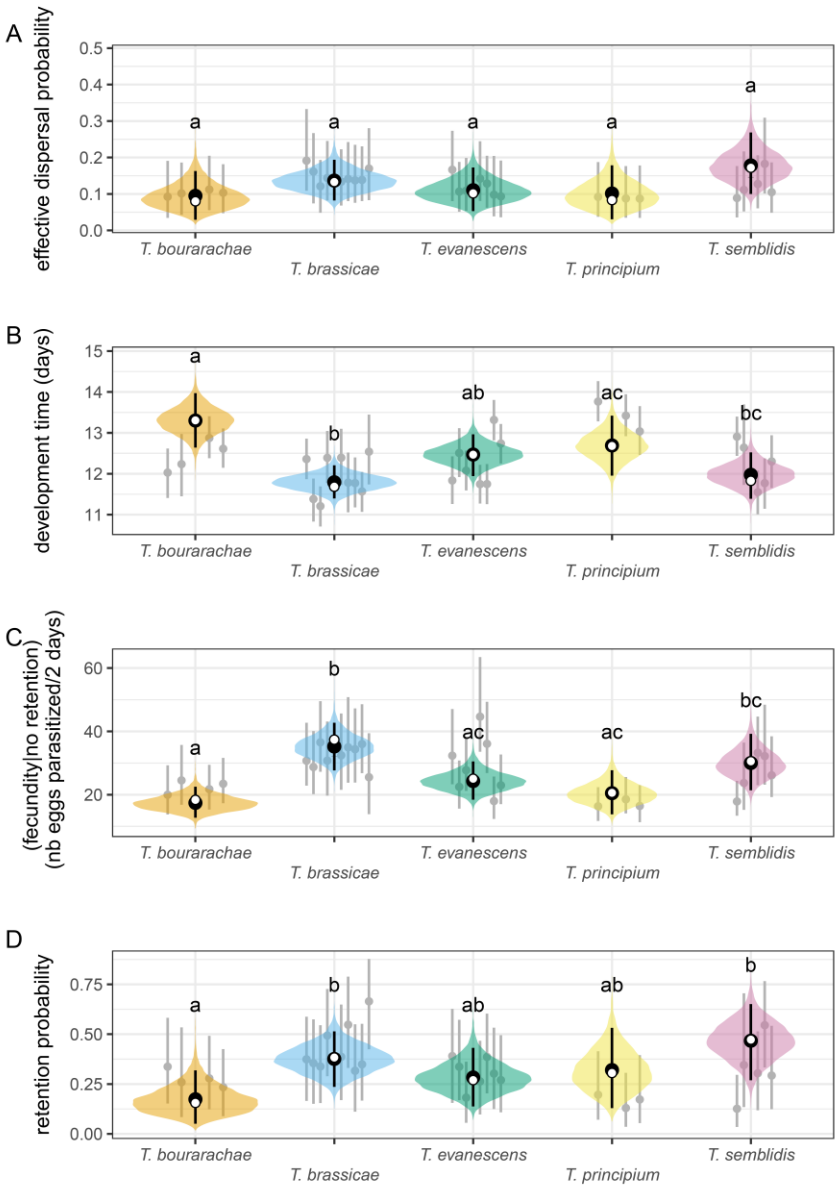

Figure 2: Posterior values as a function of the *Trichogramma* species for A) the probability of effective dispersal, B) the development time in days of the first offspring, C) the number of parasitized eggs for a single female when no retention occurred, and D) the probability for a female to perform egg retention during the experiment. 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 predicted means are 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 zeroes in egg numbers were attributable to retention, and using the midpoint of the 48 h interval for development time).

Table 3: line-level random effect correlations among measured traits, represented by means and 95 % higher posterior density intervals. (top) Between-lines trait correlations, from the partitioned covariance model (species differences are excluded as fixed effects); (bottom) between-lines trait correlations from the model without fixed species effects. Intervals without 0 inside are presented in bold.

	effective dispersal probability	(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]

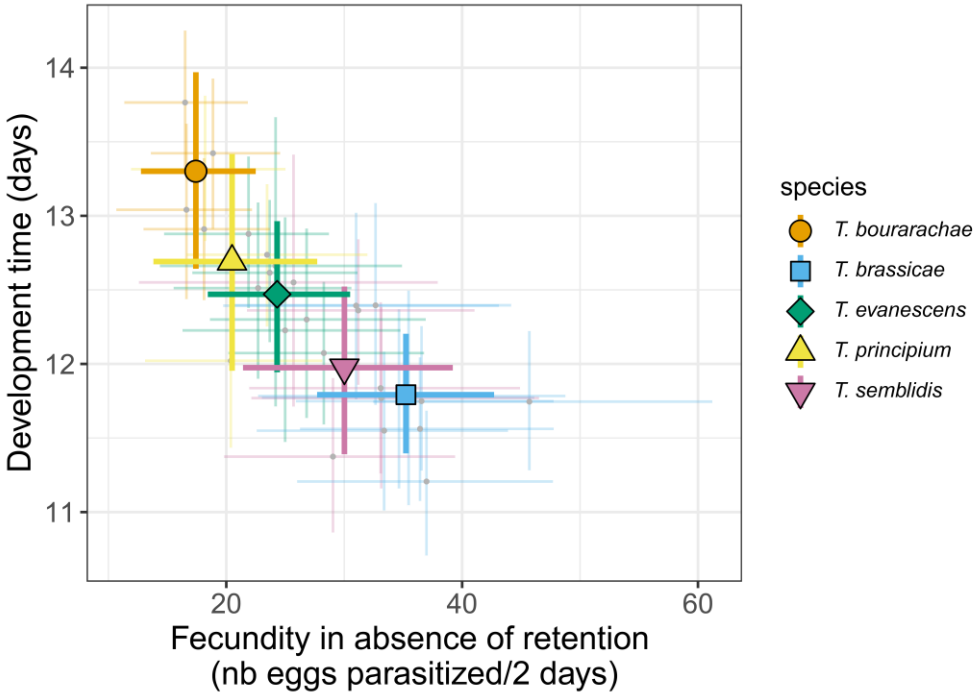

Figure 3: Posterior development time of *Trichogramma* species as a function of posterior fecundity in the absence of egg retention. Coloured crosses represent species 95 % posterior higher posterior density intervals for development time and fecundity, while coloured symbols represent species posterior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

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, Table3**). 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 3**). We note that even if there is no statistically significant correlation when the variance is structured within species and among lines, the sign of this correlation remains negative (**Table 3 top**), following a similar tendency to the interspecific negative correlation observed in **Table 3 bottom**. 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 conclusively at the within-species level is in line with the existing literature, in which consistent pace-of-life axes are considered increasingly difficult to find 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, such as lines or individuals, 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 3**). 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, Table 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 manifesting egg 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 manifesting 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 48 h 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.

No evidence for a syndrome linking effective dispersal probability and the pace of life

Effective dispersal probability varied the least among the four traits measured, with no evidence of between-species or even between-lines differences (**Figure 2**), and values were rather consistent with previous studies (Dahirel, Bertin, Calcagno, et al., 2021). There was also no correlation between effective dispersal and any of the other traits (**Table 3**), meaning that there is no evidence for dispersal/life-history syndromes at the line or species level in our set of *Trichogramma* species. Interestingly, this result on effective dispersal between patches completes previous studies on the activity of *Trichogramma* species. In Wajnberg & Colazza (1998), the authors showed a significant difference in the average area searched within one patch by *T. brassicae* isofemale lines while our results showed no differences in effective dispersal (**Figure 2**). In Reznik & Klyueva (2006), *T. principium* females manifesting egg retention had higher dispersal activity in a continuous environment than females that laid eggs beforehand. This discrepancy may be the result of a focus on different taxonomic levels: Reznik and Klyueva (2006)'s results deal with within-species and within-line covariation, versus between-lines and between-species in the present study. It may also result from differences in experimental designs and metrics used: the dispersal metrics used in Reznik and Klyueva (2006) are based on short-term (less than one day) and short-distance (up to 5 cm) movement on a continuous arena, compared to our experiment (two days and 40 cm between discrete patches). In that case, there may still exist in *Trichogramma* a pace-of-life syndrome linking life history to short-term activity and behaviour, but not effective dispersal. Indeed, correlations between short-term movement activity and life-history traits were also found in *T. evanescens* at the between-line level (Lartigue et al., 2022). While short-term activity metrics in uniform continuous environments are often considered valid proxies of longer-term dispersal between discontinuous patches (Pennekamp et al., 2019), this comparison of our study with the existing literature shows that this is not always the case. Dispersal is extremely context-dependent, including current resource availability (Fronhofer et al., 2018); there is furthermore evidence that correlations between dispersal and other traits can be altered depending on whether individuals disperse from high-resource or low-resource contexts (Cote et al., 2022), but also how density can have an impact on both

434 dispersal behaviour and its evolution (Bitume et al., 2013; Clobert et al., 2009; Poethke et al.,
435 2016; Poethke & Hovestadt, 2002).

436 *The potential implications of context-dependence and especially density-dependence*

437 Building on this point, our study ignored this potential for context dependence, as every
438 female tested for a given trait was tested under the same low-density conditions (alone in the
439 experimental design with a non-limiting host supply). Dispersal syndromes (Bonte & Dahirel,
440 2017; Cote et al., 2022; Ronce, 2012) and also pace-of-life syndromes can be context-
441 dependent. Behavioural types can be dependent of the dispersal status and predation risks
442 (Bell & Sih, 2007; Cote, Clobert, et al., 2010). Pace-of-life syndromes and/or their constituent
443 traits may also depend on resource acquisition through plastic responses (Laskowski et al.,
444 2021; Montiglio et al., 2018) or quality. In *Trichogramma* for instance, host egg species and
445 quality can influence life-history traits (Paul et al., 1981), and we used a substitution host in
446 the present study. Recent works suggest that population density and density fluctuations, in
447 particular, may also play a key role in shaping the presence of a pace of life in the first place
448 (Wright et al., 2020) and its association with behaviours: fast individuals may have a higher
449 reproductive rate in low-density contexts, but their lower intra-specific competition is a
450 disadvantage when close to the carrying capacity of an environment, and therefore are more
451 likely to disperse to escape to lower densities where this competition is lessened (Wright et
452 al., 2019). This interaction between the pace of life and density may interact with the overall
453 density dependence of dispersal (Clobert et al., 2009; Harman et al., 2020), altering
454 syndromes linking dispersal and life history. Given that there is evidence for dispersal and/or
455 fecundity being density-dependent in several *Trichogramma* species (*T. brassicae*; Dahirel,
456 Bertin, Calcagno, et al., 2021; *Trichogramma achaeae*, *T. chilonis* and *T. euproctidis*, Zboralski
457 et al., 2016), further studies including density dependence may lead to more generalizable
458 insights about pace of life and dispersal in *Trichogramma*.

459 *Implications for biocontrol improvement and perspectives*

460 While studies on trade-offs (Bennett et al., 2002; Reznik & Klyueva, 2006; Zboralski et al.,
461 2016) or pace-of-life syndromes (Lartigue et al., 2022) already existed in small biocontrol
462 agents including *Trichogramma*, our results provide new insights on between-species
463 comparisons and the taxonomic scales at which trait variation is important. Some species like
464 *T. evanescens*, *T. cacoeciae* (Sigsgaard et al., 2017) or *T. brassicae* (Özder & Kara, 2010) are
465 already well used as biocontrol agents. In that context, a choice might be needed between
466 maximizing one trait or a set of traits of interest at the expense of the others. For
467 *Trichogramma*, while having fast-developing and high-fecundity individuals can be beneficial
468 to quick intervention and a higher number of host eggs parasitized, they are reared and
469 released mainly at high densities, (Consoli et al., 2010) densities for which individuals with
470 longer development time might fare better against the intra-species competition (Wright et
471 al., 2019). For inoculative releases, where a small population of biocontrol agents in the area
472 of interest must establish itself and reach higher densities in further generations, both
473 fecundity and competitive abilities are to be favoured for efficiency (Smith, 1996). Our results
474 suggest that for some purposes, selecting different species might actually be more successful
475 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.

References

Agrawal, A. A. (2020). A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology*, *101*. https://doi.org/10.1002/ecy.2924

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

Auer, S. K., Dick, C. A., Metcalfe, N. B., & Reznick, D. N. (2018). Metabolic rate evolves rapidly and in parallel with the pace of life history. *Nature Communications*, *9*(1), 9–14. https://doi.org/10.1038/s41467-017-02514-z

Bakewell, A. T., Davis, K. E., Freckleton, R. P., Isaac, N. J. B., & Mayhew, P. J. (2020). Comparing life histories across taxonomic groups in multiple dimensions: How mammal-like are insects? *The American Naturalist*, *195*(1), 70–81. https://doi.org/10.1086/706195

Beckman, N. G., Bullock, J. M., & Salguero-Gómez, R. (2018). High dispersal ability is related to fast life-history strategies. *Journal of Ecology*, *106*(4), 1349–1362. https://doi.org/10.1111/1365-2745.12989

Bell, A. M., & Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, *10*(9), 828–834. https://doi.org/10.1111/j.1461-0248.2007.01081.x

Bennett, D. M., Reynolds, K. T., Thomson, L. J., & Hoffmann, A. A. (2002). Individual level trade-offs and artifacts in the egg parasitoid *Trichogramma carverae* (Hymenoptera: Trichogrammatidae). *Annals of the Entomological Society of America*, *95*(6), 695–700. https://doi.org/10.1603/0013-8746(2002)095[0695:ILTOAA]2.0.CO;2

Bielby, J., Mace, G. M., Bininda-Emonds, O. R. P., Cardillo, M., Gittleman, J. L., Jones, K. E., Orme, C. D. L., & Purvis, A. (2007). The fast-slow continuum in mammalian life history: An empirical reevaluation. *The American Naturalist*, *169*(6), 748–757. https://doi.org/10.1086/516847

Bitume, E. V., Bonte, D., Ronce, O., Bach, F., Flaven, E., Olivieri, I., & Nieberding, C. M. (2013). Density and genetic relatedness increase dispersal distance in a subsocial organism. *Ecology Letters*, *16*(4), 430–437. https://doi.org/10.1111/ele.12057

Blackburn, T. M. (1991). Evidence for a `fast-slow' continuum of life-history traits among parasitoid Hymenoptera. *Functional Ecology*, *5*(1), 65–74. https://doi.org/10.2307/2389556

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

Bonte, D., & Dahirel, M. (2017). Dispersal: A central and independent trait in life history. *Oikos*, *126*(4), 472–479. https://doi.org/10.1111/oik.03801

Bonte, D., & De La Peña, E. (2009). Evolution of body condition-dependent dispersal in metapopulations. *Journal of Evolutionary Biology*, *22*(6), 1242–1251. https://doi.org/10.1111/j.1420-9101.2009.01737.x

Braendle, C., Heyland, A., & Flatt, T. (2011). Integrating mechanistic and evolutionary analysis of life history variation. In T. Flatt & A. Heyland (Eds.), *Mechanisms of Life History Evolution* (pp. 3–10). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199568765.001.0001

Bürkner, P.-C. (2017a). **brms**: An *R* package for Bayesian multilevel models using *Stan*. *Journal of Statistical Software*, *80*(1), 1–28. https://doi.org/10.18637/jss.v080.i01

Bürkner, P.-C. (2017b). *Advanced bayesian multilevel modeling with the R package* ***brms*** (arXiv:1705.11123). arXiv. http://arxiv.org/abs/1705.11123

Calcagno, V., Mouquet, N., Jarne, P., & David, P. (2006). Coexistence in a metacommunity: The competition–colonization trade-off is not dead. *Ecology Letters*, *9*(8), 897–907. https://doi.org/10.1111/j.1461-0248.2006.00930.x

549 Careau, V., & Wilson, R. S. (2017). Of uberfleas and krakens: Detecting trade-offs using
550 mixed models. *Integrative and Comparative Biology*, *57*(2), 362–371.
551 https://doi.org/10.1093/icb/icx015
552 Clobert, J., Baguette, M., Benton, T. G., & Bullock, J. M. (Eds.). (2012). *Dispersal ecology and*
553 *evolution* (1st ed). Oxford University Press.
554 https://doi.org/10.1093/acprof:oso/9780199608898.001.0001
555 Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal,
556 heterogeneity in animal dispersal syndromes and the dynamics of spatially
557 structured populations. *Ecology Letters*, *12*(3), 197–209.
558 https://doi.org/10.1111/j.1461-0248.2008.01267.x
559 Consoli, F. L., Parra, J. R. P., & Zucchi, R. A. (Eds.). (2010). *Egg parasitoids in agroecosystems*
560 *with emphasis on* Trichogramma. Springer Netherlands.
561 https://doi.org/10.1007/978-1-4020-9110-0
562 Corrigan, J. E., Laing, J. E., & Zubricky, J. S. (1995). Effects of parasitoid to host ratio and time
563 of day of parasitism on development and emergence of *Trichogramma minutum*
564 (Hymenoptera: Trichogrammatidae) parasitizing eggs of *Ephestia kuehniella*
565 (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America*, *88*(6), 773–
566 780. https://doi.org/10.1093/aesa/88.6.773
567 Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal:
568 Characterization, ontogeny and consequences for spatially structured populations.
569 *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560),
570 4065–4076. https://doi.org/10.1098/rstb.2010.0176

Cote, J., Dahirel, M., Schtickzelle, N., Altermatt, F., Ansart, A., Blanchet, S., Chaine, A. S., De Laender, F., De Raedt, J., Haegeman, B., Jacob, S., Kaltz, O., Laurent, E., Little, C. J., Madec, L., Manzi, F., Masier, S., Pellerin, F., Pennekamp, F., … Legrand, D. (2022). Dispersal syndromes in challenging environments: A cross-species experiment. *Ecology Letters*, *25*, 2675–2687. https://doi.org/10.1111/ele.14124

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T., & Sih, A. (2010). Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society B: Biological Sciences*, *277*(1687), 1571–1579. https://doi.org/10.1098/rspb.2009.2128

Crossin, G. T., Hinch, S. G., Farrell, A. P., Higgs, D. A., Lotto, A. G., Oakes, J. D., & Healey, M. C. (2004). Energetics and morphology of sockeye salmon: Effects of upriver migratory distance and elevation. *Journal of Fish Biology*, *65*(3), 788–810. https://doi.org/10.1111/j.0022-1112.2004.00486.x

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

592 Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in
593 behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39–
594 54. https://doi.org/10.1111/1365-2656.12013
595 Doyon, J., & Boivin, G. (2006). Impact of the timing of male emergence on mating capacity of
596 males in *Trichogramma evanescens* Westwood. *BioControl*, *51*(6), 703–713.
597 https://doi.org/10.1007/s10526-006-9001-0
598 Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*,
599 *125*(1), 1–15. https://doi.org/10.1086/284325
600 Flatt, T., & Heyland, A. (Eds.). (2011). *Mechanisms of life history evolution: The genetics and*
601 *physiology of life history traits and trade-offs*. Oxford University Press.
602 https://doi.org/10.1093/acprof:oso/9780199568765.001.0001
603 Fleury, F., & Boulétreau, M. (1993). Effects of temporary host deprivation on the
604 reproductive potential of *Trichogramma brassicae*. *Entomologia Experimentalis et*
605 *Applicata*, *68*(3), 203–210. https://doi.org/10.1111/j.1570-7458.1993.tb01705.x
606 Fronhofer, E. A., Legrand, D., Altermatt, F., Ansart, A., Blanchet, S., Bonte, D., Chaine, A.,
607 Dahirel, M., De Laender, F., De Raedt, J., di Gesu, L., Jacob, S., Kaltz, O., Laurent, E.,
608 Little, C. J., Madec, L., Manzi, F., Masier, S., Pellerin, F., … Cote, J. (2018). Bottom-up
609 and top-down control of dispersal across major organismal groups. *Nature Ecology &*
610 *Evolution*, *2*(12), 1859–1863. https://doi.org/10.1038/s41559-018-0686-0
611 Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in
612 Bayesian workflow. *Journal of the Royal Statistical Society: Series A (Statistics in*
613 *Society)*, *182*(2), 389–402. https://doi.org/10.1111/rssa.12378

614 Gaillard, J.-M., Lemaître, J.-F., Berger, V., Bonenfant, C., Devillard, S., Douhard, M., Gamelon,
615 M., Plard, F., & Lebreton, J.-D. (2016). Life histories, axes of variation in. In
616 *Encyclopedia of Evolutionary Biology* (pp. 312–323). Elsevier.
617 https://doi.org/10.1016/B978-0-12-800049-6.00085-8
618 Gaillard, J.-M., Pontier, D., Allainé, D., Lebreton, J. D., Trouvilliez, J., Clobert, J., & Allaine, D.
619 (1989). An analysis of demographic tactics in birds and mammals. *Oikos*, *56*(1), 59–
620 76. https://doi.org/10.2307/3566088
621 Gangloff, E. J., Chow, M., Leos-Barajas, V., Hynes, S., Hobbs, B., & Sparkman, A. M. (2017).
622 Integrating behaviour into the pace-of-life continuum: Divergent levels of activity
623 and information gathering in fast- and slow-living snakes. *Behavioural Processes*,
624 *142*, 156–163. https://doi.org/10.1016/j.beproc.2017.06.006
625 Gu, H., Hughes, J., & Dorn, S. (2006). Trade-off between mobility and fitness in *Cydia*
626 *pomonella* L. (Lepidoptera: Tortricidae). *Ecological Entomology*, *31*(1), 68–74.
627 https://doi.org/10.1111/j.0307-6946.2006.00761.x
628 Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for comparative
629 biology: Phylogenies, taxonomies and multi-trait models for continuous and
630 categorical characters. *Journal of Evolutionary Biology*, *23*(3), 494–508.
631 https://doi.org/10.1111/j.1420-9101.2009.01915.x
632 Harman, R. R., Goddard, J., Shivaji, R., & Cronin, J. T. (2020). Frequency of occurrence and
633 population-dynamic consequences of different forms of density-dependent
634 emigration. *The American Naturalist*, *195*(5), 851–867.
635 https://doi.org/10.1086/708156

Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Patterson, D. A., Cooke, S. J., & Power, M. (2015). Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). *Behavioral Ecology*, *26*(2), 483–492. https://doi.org/10.1093/beheco/aru216

Healy, K., Ezard, T. H. G., Jones, O. R., Salguero-Gómez, R., & Buckley, Y. M. (2019). Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. *Nature Ecology & Evolution*, *3*(8), 1217–1224. https://doi.org/10.1038/s41559-019-0938-7

Jacob, S., Chaine, A. S., Huet, M., Clobert, J., & Legrand, D. (2019). Variability in dispersal syndromes is a key driver of metapopulation dynamics in experimental microcosms. *The American Naturalist*, *194*(5), 613–626. https://doi.org/10.1086/705410

Jørgensen, C., & Fiksen, Ø. (2006). State-dependent energy allocation in cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(1), 186–199. https://doi.org/10.1139/f05-209

Karlsson, B., & Johansson, A. (2008). Seasonal polyphenism and developmental trade-offs between flight ability and egg laying in a pierid butterfly. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1647), 2131–2136. https://doi.org/10.1098/rspb.2008.0404

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

Laskowski, K. L., Moiron, M., & Niemelä, P. T. (2021). Integrating behavior in life-history theory: Allocation versus acquisition? *Trends in Ecology & Evolution*, *36*(2), 132–138. https://doi.org/10.1016/j.tree.2020.10.017

Maharjan, R., Nilsson, S., Sung, J., Haynes, K., Beardmore, R. E., Hurst, L. D., Ferenci, T., & Gudelj, I. (2013). The form of a trade-off determines the response to competition. *Ecology Letters*, *16*(10), 1267–1276. https://doi.org/10.1111/ele.12159

Marchand, A., Sellier, N., Warot, S., Ion-Scotta, M., Ris, N., & Groussier-Bout, G. (2017). Formalisation d'un centre de ressources biologiques dédié aux parasitoïdes oophages: CRB Ep-Coll. *Cahiers des Techniques de l'INRA*, *Numéro spécial « Entomologie Appliquée »*, 48–57.

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.

Mertz, B. P., Calvin, D. D., & Ridgwayl, R. L. (1995). Field assessment of *Trichograrnma brassicae* (Hymenoptera: Trichogrammatidae) and *Bacillus thuringiensis* for control of *Ostrinia nubilalis* (Lepidoptera: Pyralidae) in sweet corn. *Journal of Economic Entomology*, *88*(6), 1616–1625. https://doi.org/doi:10.1093/jee/88.6.1616

Montiglio, P.-O., Dammhahn, M., Dubuc Messier, G., & Réale, D. (2018). The pace-of-life syndrome revisited: The role of ecological conditions and natural history on the slow-fast continuum. *Behavioral Ecology and Sociobiology*, *72*(7), 116. https://doi.org/10.1007/s00265-018-2526-2

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

Ochocki, B. M., Saltz, J. B., & Miller, T. E. X. (2020). Demography-dispersal trait correlations modify the eco-evolutionary dynamics of range expansion. *The American Naturalist*, *195*(2), 231–246. https://doi.org/10.1086/706904

Olsen, Z., McDonald, D., & Bumguardner, B. (2018). Intraspecific variation in life history strategies and implications for management: A case study of black drum (*Pogonias cromis*) in the Upper Laguna Madre, Texas USA. *Fisheries Research*, *207*, 55–62. https://doi.org/10.1016/j.fishres.2018.06.009

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

Paul, A. V., Dass, R., & Parshad, B. (1981). Influence of different hosts on parasitism by *Trichogramma chilonis* Ishii and *T. exiguum* Pinto and Platner (Hymenoptera: Trichogrammatidae)1,2. *Zeitschrift Für Angewandte Entomologie*, *92*(1–5), 160–164. https://doi.org/10.1111/j.1439-0418.1981.tb01664.x

Pavlík, 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

Pennekamp, F., Clobert, J., & Schtickzelle, N. (2019). The interplay between movement, morphology and dispersal in *Tetrahymena* ciliates. *PeerJ*, *7*, e8197. https://doi.org/10.7717/peerj.8197

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

Poethke, H. J., & Hovestadt, T. (2002). Evolution of density–and patch–size–dependent dispersal rates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1491), 637–645. https://doi.org/10.1098/rspb.2001.1936

Poethke, H. J., Kubisch, A., Mitesser, O., & Hovestadt, T. (2016). The evolution of density-dependent dispersal under limited information. *Ecological Modelling*, *338*, 1–10. https://doi.org/10.1016/j.ecolmodel.2016.07.020

R Core Team. (2021). *R: A language and environment for statistical computing* (4.1.2). R Foundation for Statistical Computing. https://www.R-project.org/

Rádai, Z., Kiss, B., & Barta, Z. (2017). Pace of life and behaviour: Rapid development is linked with increased activity and voracity in the wolf spider *Pardosa agrestis*. *Animal Behaviour*, *126*, 145–151. https://doi.org/10.1016/j.anbehav.2017.02.004

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Reznik, S. Y., & Klyueva, N. Z. (2006). Egg retention and dispersal activity in the parasitoid wasp, *Trichogramma principium*. *Journal of Insect Science*, *6*(16). https://doi.org/10.1673/2006_06_16.1

Reznik, S. Ya., Umarova, T. Ya., & Voinovich, N. D. (2003). Egg retention in *Trichogramma* (Hymenoptera: Chalcidoidea: Trichogrammatidae): Learning or diapause? *Acta Societatis Zoologicae Bohemicae*, *67*, 25–33.

Reznik, S. Ya., & Vaghina, N. P. (2007). Effect of photoperiod on parasitization by *Trichogramma principium* (Hymenoptera: Trichogrammatidae). *European Journal of Entomology*, *104*(4), 705–713. https://doi.org/10.14411/eje.2007.089

Reznik, S. Ya., Voinovich, N. D., & Umarova, T. Ya. (1998). Egg retention in the presence of a host in *Trichogramma* females. *Journal of Applied Entomology*, *122*(1–5), 555–559. https://doi.org/10.1111/j.1439-0418.1998.tb01544.x

Reznik, Voinovich, & Umarova. (2001). Long-term egg retention and parasitization in *Trichogramma principum* (Hym., Trichogrammatidae). *Journal of Applied Entomology*, *125*(4), 169–175. https://doi.org/10.1046/j.1439-0418.2001.00535.x

Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends in Ecology & Evolution*, *17*(10), 462–468. https://doi.org/10.1016/S0169-5347(02)02578-8

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.

Royauté, R., Berdal, M. A., Garrison, C. R., & Dochtermann, N. A. (2018). Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behavioral Ecology and Sociobiology*, *72*(3), 64. https://doi.org/10.1007/s00265-018-2472-z

Saastamoinen, M., Bocedi, G., Cote, J., Legrand, D., Guillaume, F., Wheat, C. W., Fronhofer, E. A., Garcia, C., Henry, R., Husby, A., Baguette, M., Bonte, D., Coulon, A., Kokko, H., Matthysen, E., Niitepõld, K., Nonaka, E., Stevens, V. M., Travis, J. M. J., … del Mar Delgado, M. (2018). Genetics of dispersal. *Biological Reviews*, *93*(1), 574–599. https://doi.org/10.1111/brv.12356

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., L. Dantas, V., Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*(12), 1406–1419. https://doi.org/10.1111/ele.12508

Sigsgaard, L., Herz, A., Korsgaard, M., & Wührer, B. (2017). Mass release of *Trichogramma evanescens* and *T. cacoeciae* can reduce damage by the apple codling moth *Cydia pomonella* in organic orchards under pheromone disruption. *Insects*, *8*(2), 41. https://doi.org/10.3390/insects8020041

Simons, A. M. (2002). The continuity of microevolution and macroevolution. *Journal of Evolutionary Biology*, *15*(5), 688–701. https://doi.org/10.1046/j.1420-9101.2002.00437.x

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

Stan Development Team. (2022). *Stan modeling language users guide and reference manual* (2.28.1). http://mc-stan.org/

Stearns, S. C. (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, *41*(2), 173–187. https://doi.org/10.2307/3544261

Stearns, S. C. (2000). Life history evolution: Successes, limitations, and prospects. *Naturwissenschaften*, *87*(11), 476–486. https://doi.org/10.1007/s001140050763

Stevens, V. M., Trochet, A., Van Dyck, H., Clobert, J., & Baguette, M. (2012). How is dispersal integrated in life histories: A quantitative analysis using butterflies: Dispersal life-history correlates. *Ecology Letters*, *15*(1), 74–86. https://doi.org/10.1111/j.1461-0248.2011.01709.x

Stevens, V. M., Whitmee, S., Le Galliard, J.-F., Clobert, J., Böhning-Gaese, K., Bonte, D., Brändle, M., Matthias Dehling, D., Hof, C., Trochet, A., & Baguette, M. (2014). A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecology Letters*, *17*(8), 1039–1052. https://doi.org/10.1111/ele.12303

St-Onge, M., Cormier, D., Todorova, S., & Lucas, É. (2014). Comparison of *Ephestia kuehniella* eggs sterilization methods for *Trichogramma* rearing. *Biological Control*, *70*, 73–77. https://doi.org/10.1016/j.biocontrol.2013.12.006

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., & Bürkner, P.-C. (2021). Rank-normalization, folding, and localization: An improved R̂ for assessing convergence of MCMC (with discussion). *Bayesian Analysis*, *16*(2), 667–718. https://doi.org/10.1214/20-BA1221

Wajnberg, E., & Colazza, S. (1998). Genetic variability in the area searched by a parasitic wasp: Analysis from automatic video tracking of the walking path. *Journal of Insect Physiology*, *44*(5–6), 437–444. https://doi.org/10.1016/S0022-1910(98)00032-8

Wang, D., Lü, L., He, Y., Shi, Q., Tu, C., & Gu, J. (2016). Mate choice and host discrimination behavior of the parasitoid *Trichogramma chilonis*. *Bulletin of Entomological Research*, *106*(4), 530–537. https://doi.org/10.1017/S0007485316000225

Williams, J. B., Miller, R. A., Harper, J. M., & Wiersma, P. (2010). Functional linkages for the pace of life, life-history, and environment in birds. *Integrative and Comparative Biology*, *50*(5), 855–868. https://doi.org/10.1093/icb/icq024

Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *447*(7144), 581–584. https://doi.org/10.1038/nature05835

Wright, J., Bolstad, G. H., Araya-Ajoy, Y. G., & Dingemanse, N. J. (2019). Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. *Biological Reviews*, *94*(1), 230–247. https://doi.org/10.1111/brv.12451

Wright, J., Solbu, E. B., & Engen, S. (2020). Contrasting patterns of density-dependent selection at different life stages can create more than one fast–slow axis of life-history variation. *Ecology and Evolution*, *10*(6), 3068–3078. https://doi.org/10.1002/ece3.6122

Yu, D. W., & Wilson, H. B. (2001). The competition-colonization trade-off is dead; long live the competition-colonization trade-off. *The American Naturalist*, *158*(1), 49–63. https://doi.org/10.1086/320865

Zboralski, A., Vilarelle, M., Colombel, E., Tabone, E., & Vercken, E. (2016). Density-dependent dispersal in biological control agents: A reflexion on the side-effects of mass-rearing conditions. *BioControl*, *61*(1), 13–22. https://doi.org/10.1007/s10526-015-9696-x