

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

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9

## 10 Abstract

11 Major traits defining the life history of organisms are often not independent from each other,  
12 with most of their variation aligning along key axes such as the pace-of-life axis. ~~These~~We can  
13 define a pace-of-life axis structuring reproduction and development time as a continuum  
14 from less-fecund, longer-developing ‘slow’ types to more-fecund, shorter-developing ‘fast’  
15 types. Such axes, along with their potential associations or syndromes with other traits such  
16 as dispersal, are however not universal; in particular, support for their presence may be  
17 taxon and taxonomic scale-dependent. ~~Knowing~~ about such life-history strategies may be  
18 especially important for ~~biological control agents~~understanding eco-evolutionary dynamics,  
19 as these trait syndromes may constrain ~~the ability to optimize production, as well as their~~  
20 ~~efficiency in the field.~~trait variation or be correlated with other traits. To understand how  
21 life-history traits and effective dispersal covary ~~in such contexts~~, we measured these traits in  
22 controlled conditions for 28 lines from ~~5~~five species of *Trichogramma*, which are small  
23 endoparasitoid wasps frequently used as a biological model in experimental evolution but  
24 also in biocontrol against Lepidoptera pests. We found partial evidence of a pace-of-life axis  
25 at the interspecific level: species with higher fecundity also had faster development time ~~but,~~  
26 However, faster-developing species also were more likely to delay egg-laying. ~~However,~~  
27 ~~there, a trait that is usually interpreted as “slow”.~~ There was no support for similar  
28 covariation patterns at the within-species line level. There was limited variation in effective  
29 dispersal between species and lines, and accordingly, we did not detect any correlation  
30 between effective dispersal ~~rates~~probability and life-history traits. We discuss how  
31 expanding our experimental design by accounting for the density-dependence of both the  
32 pace of life and dispersal might ~~reveal a dispersal syndrome in future studies.~~improve our  
33 understanding of those traits and how they interact with each other. Overall, our results  
34 highlight the importance of exploring covariation at the “right” taxonomic scale, or multiple  
35 taxonomic scales, to understand the (co)evolution of life-history traits. They also suggest  
36 that optimizing ~~all interesting life-history~~both reproductive and development traits ~~for~~  
37 ~~inoculative releases~~to maximize the efficiency of biocontrol may be difficult in programs  
38 using only one species.

39 **Keywords:** dispersal syndrome; life-history strategies; fecundity; intraspecific  
40 competition; trait covariation

41

## 42 Introduction

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

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

82 Dispersal can be described as any movement potentially leading to a flux of genes or  
83 individuals across space (Ronce, 2007), and is a key component influencing both ecological  
84 and evolutionary dynamics, so much that it is sometimes described as a life-history trait in

85 its own right (Saastamoinen et al., 2018). ~~Dispersal often covaries with other traits in so-~~  
86 ~~called dispersal syndromes (Ronce, 2012).~~ Dispersal often covaries with other traits,  
87 including other life-history traits (Clobert et al., 2012), ~~in so-called dispersal syndromes~~  
88 ~~(Ronce, 2012).~~ Dispersal syndromes have been observed and compared at multiple  
89 taxonomic levels, both across (Stevens et al., 2012, 2014) and within species (Jacob et al.,  
90 2019). Therefore, it is not surprising that many works have been dedicated to the integration  
91 of dispersal along the main life-history axes, and the derivation of ecological and evolutionary  
92 implications. This includes, for instance, the idea of a ~~trade-off between~~ competition- ~~and~~  
93 ~~colonization-trade-off~~ where species that are good at colonizing, with high fecundity or  
94 dispersal, are in return poor competitors between or among species (~~Calcagno et al., 2006;~~  
95 ~~Yu & Wilson, 2001~~)(e.g. Calcagno et al., 2006; Yu & Wilson, 2001), and other studied links  
96 between dispersal and fecundity (Bonte & De La Peña, 2009; Crossin et al., 2004; Gu et al.,  
97 2006; Karlsson & Johansson, 2008). ~~On another level~~ Rather than a ~~correlation~~ idiosyncratic  
98 ~~correlations~~ between dispersal and a ~~single~~ specific life-history ~~trait~~ traits, the pace-of-life  
99 syndrome hypothesis suggests dispersal, among others, to be a risky trait linked to the pace  
100 of life (~~Cote et al., 2010; Réale et al., 2010~~). ~~In plants itself~~ (Cote, Clobert, et al., 2010; Réale et  
101 ~~al., 2010~~). ~~In plants for instance~~, there is a relation between seed dispersal abilities and the  
102 fast-slow continuum, where a high capacity to disperse is correlated with faster life histories  
103 at the species level (Beckman et al., 2018). ~~Those dispersal-~~ While many studies found a  
104 ~~positive correlation between the pace of life and short-scale movement, like the exploration~~  
105 ~~of a continuous patch, or the activity level within an arena~~ (Gangloff et al., 2017; Lartigue et  
106 ~~al., 2022; Rádai et al., 2017~~), directly transposing short-scale conclusions like exploration or  
107 ~~activity, to longer-scale metrics, like dispersal rates or the decision to disperse in discrete~~  
108 ~~landscapes, is not always relevant~~ (Cote, Fogarty, et al., 2010; Harrison et al., 2015;  
109 ~~Pennekamp et al., 2019~~). Dispersal/life-history syndromes can lead to different ecological  
110 and evolutionary results from when traits are considered as independent. Correlation  
111 between traits, but also the strength or shape of this ~~correlation~~ relationship can impact both  
112 the ecological and evolutionary dynamics of a population (Maharjan et al., 2013; Ochocki et  
113 al., 2020).

114 In that context, we explored first the presence of a ~~pace-of life and then its relationship~~  
115 ~~with dispersal rates in five species of Trichogramma wasps.~~ *Trichogramma*  
116 (Hymenoptera: Trichogrammatidae) are small (< 1 mm when adult) endoparasitoids using  
117 insect eggs, mainly Lepidoptera, as hosts. This includes some pest species, which makes them  
118 efficient biological control agents. Indeed, *T. brassicae* is commercially available and often  
119 ~~used-of-life axis and then the relationship between the pace of life and effective dispersal in~~  
120 ~~five species of Trichogramma wasps.~~ *Trichogramma* (Hymenoptera: Trichogrammatidae) are  
121 ~~small (< 1 mm when adult) parasitoids that develop inside the eggs of their hosts, mainly~~  
122 ~~Lepidoptera. They are also model species in ecology and invasion biology studies thanks to~~  
123 ~~their small size, rather short development time (13-15 days, at 22 °C), or also the fact that~~  
124 ~~lines can be either sexual or asexual. The goal of this study is therefore to improve our~~  
125 ~~knowledge of life-history trade-offs specifically in Trichogramma for future studies of eco-~~  
126 ~~evolutionary dynamics, but also more generally in insects, which are under-represented in~~  
127 ~~both pace-of- against Ostrinia nubilalis, the European corn borer (Mertz et al., 1995), and T.~~  
128 ~~evanescens or T. cacoeciae against Cydia pomonella (Sigsgaard et al., 2017).~~ Understanding  
129 how life-history traits vary and covary can have important implications in this system and

130 can help predict the rearing or field performance of biocontrol agents (Akbari et al., 2012;  
131 Consoli et al., 2010). *Trichogramma* are also key model species in ecological, physiological, or  
132 invasion biology studies thanks to their small size, rather short development time (13–15  
133 days, 22°C), or also the fact that it can be possible to choose sexual or asexual lines. On top of  
134 their economic interest, *Trichogramma* are insects, a taxon underexplored in pace of life (but  
135 see Blackburn 1991) and pace-of-life syndromes studies (38 invertebrate species vs 141  
136 vertebrates in Royauté et al., 2018). Potential reasons include a lack of data (Bakewell et al.,  
137 2020) or peculiar lifestyles, for instance, parasitoids the difficulty to study and compare insect  
138 parasitoids, as their life-history traits are also subject to their host ecology (Mayhew, 2016).  
139 Using lab-reared lines belonging to 5 five species of *Trichogramma*, we measured female  
140 fecundity, effective dispersal, and development time under experimental conditions, and  
141 analyzed analysed their line- and species-level covariation between these traits using  
142 multivariate generalized linear mixed models Generalized Linear Mixed Models (Careau &  
143 Wilson, 2017; Dingemanse & Dochtermann, 2013). Based While this study is mostly  
144 exploratory, we can make some hypotheses: based on previous experiments on  
145 *Trichogramma* that analysed trait variation between *Trichogramma* lines (Lartigue et al.,  
146 2022), or species (Özder & Kara, 2010), we expected to observe trade-offs between the  
147 studied traits at the line or species can expect to observe trade-offs between fecundity and  
148 development time at the interline or interspecies level. In addition, as a relationship was  
149 found between activity and fecundity in Lartigue et al. (2022), there is a possibility that one  
150 or several life-history traits are linked to effective dispersal in a dispersal syndrome at a  
151 species or line level.

## 152 Materials and methods

### 153 Biological material

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

166 For this experiment, 32 different lines of *Trichogramma* from 5 different species were  
167 originally selected. However, 4 lines did not correctly synchronize during preparation and  
168 could not be used, resulting in 28 lines: *T. principium* Sugonjaev & Sorokina, 1976 ( $N_{\text{lines}}=3$ ),  
169 *T. evanescens* Westwood, 1833 ( $N_{\text{lines}}=7$ ), *T. brassicae* Bezdenko, 1968 ( $N_{\text{lines}}=9$ ), *T. semblidis*  
170 (*Aurivillius* 1898) ( $N_{\text{lines}}=5$ ) and *T. bourarachae* Pintureau & Babault, 1988 ( $N_{\text{lines}}=4$ ). All  
171 selected lines are sexually reproducing. These lines were selected from among the collection

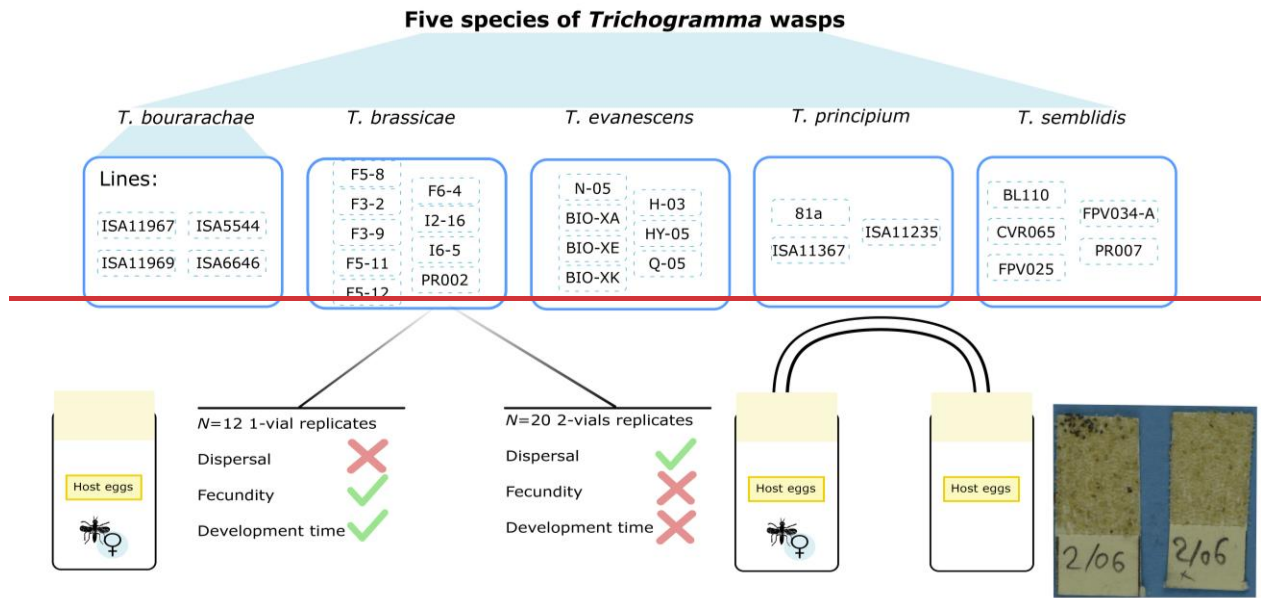
~~offrom~~ the Biological Resource ~~Centre~~Center (BRC) “Egg Parasitoid Collection” (CRB EP-Coll, Sophia Antipolis; Marchand et al., 2017). ~~Wasps were raised on Mediterranean flour moth *Ephestia kuehniella* (Lepidoptera: Pyralidae) eggs at 22°C, 70% ± 10% relative humidity, L:D 16:8. We restricted 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). 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. 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.~~

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

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

202 **Experimental design**

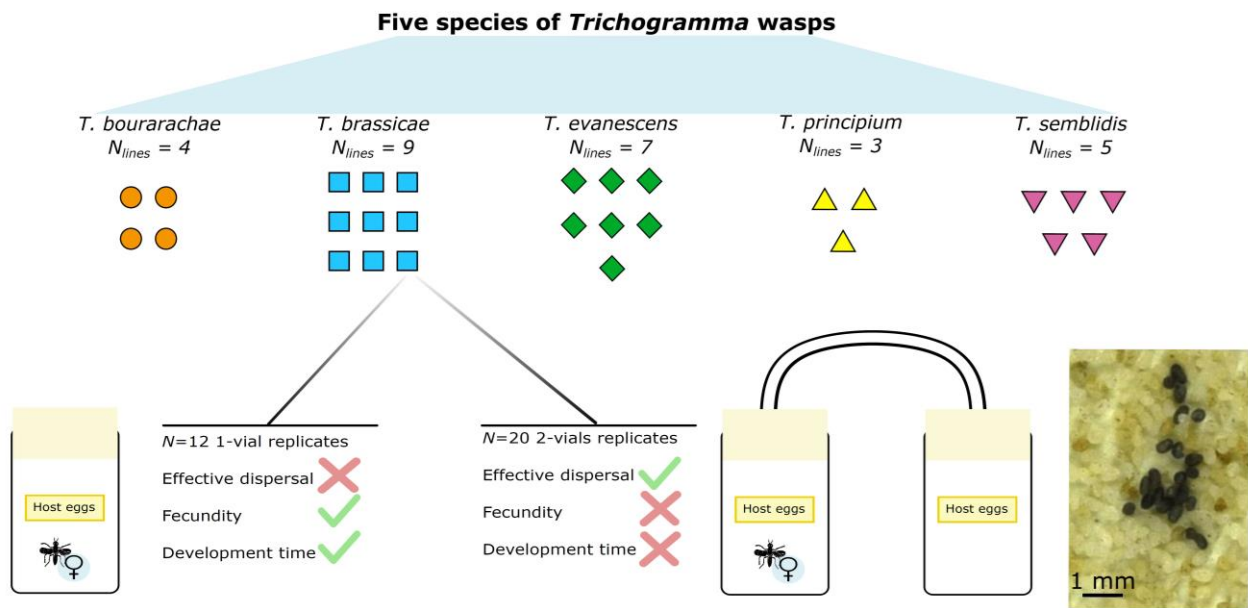
203 We used both single and 2-vial systems to measure lines' life-history traits (Fig. 1). In single  
 204 vial systems (12 replicates per line), we placed one *Trichogramma* female into a plastic vial  
 205 (5 cm diameter, 10 cm height) with a non-limiting quantity of irradiated *Ephestia kuehniella*  
 206 eggs on a paper strip (approximately 1.4 × 1 cm). This system was used to measure  
 207 development time and fecundity traits. In 2-vial systems (20 replicates per line), the setup  
 208 was similar to the previous one, with the exception that a 40cm long plastic tube connected  
 209 the first vial (where the wasp was deposited) to another one with the same dimensions, also  
 210 containing a non-limiting quantity of irradiated eggs. This setup allowed us to estimate  
 211 dispersal rates. While fecundity and development-time data could also be collected in this  
 212 second setup, we refrained from analysing them here so due to the complexities of accounting  
 213 for the effects of dispersal and dispersal costs, compared to the 1-vial setup. Females were  
 214 left in those vials for 48h under standardized conditions: 22°C, 50% relative humidity, L:D  
 215 16:8. After 48h, the egg strips were isolated in glass vials (1cm diameter, 4cm height), and  
 216 kept under the same standardized conditions.



219

220 We used both single- and two-vial systems to measure life-history traits (Fig. 1). In single-  
 221 vial systems (12 replicates per line), we placed one randomly selected mated *Trichogramma*  
 222 female between 24 to 48 hours old into a plastic vial (5 cm diameter, 10 cm height). We also  
 223 added a non-limiting quantity of irradiated *Ephestia kuehniella* eggs on a paper strip  
 224 (hundreds of host eggs in approximately 1.4 × 1 cm, see Supplemental Figure S2-1). This

225 system was used to measure development time and fecundity traits. In two-vial systems (20  
 226 replicates per line), the setup was similar to the previous one, with the exception that a see-  
 227 through 40 cm long plastic pipe (5 mm of internal diameter, large enough for species of less  
 228 than a millimetre in size) connected the first vial (where the wasp was deposited) to another  
 229 one with the same dimensions, also containing a non-limiting quantity of irradiated eggs. The  
 230 ends passed through the centre of the foam plugs without protruding from them. While little  
 231 is yet known about how females locate host eggs (Consoli et al., 2010), this setup was inspired  
 232 by previous studies on experimental expansions on *Trichogramma* (Dahirel, Bertin, Calcagno,  
 233 et al., 2021; Dahirel, Bertin, Haond, et al., 2021) and allowed us to estimate effective dispersal  
 234 probability in conditions similar to previous experimental expansions. Even though  
 235 fecundity and development-time data could also be collected in this second setup, we  
 236 refrained from analysing them here so due to the complexities of accounting for the effects  
 237 of dispersal and dispersal costs, compared to the single-vial setup. Females were left in those  
 238 vials for 48 h under standardized conditions: 22 °C, 70 % relative humidity, L:D 16:8. After  
 239 48 h, the egg strips were isolated in glass vials (1 cm diameter, 4 cm height), and kept under  
 240 the same standardized conditions. Please note that even if plasticity can be observed in  
 241 *Trichogramma* (Krishnaraj, 2000; Pinto et al., 1989), we focused our study on the presence  
 242 or not of a pace-of-life under the standard conditions used in experimental expansions on  
 243 *Trichogramma*, allowing us to make more direct links between our results in this study and  
 244 future results in experimental expansions.



245 **Figure 1:** Summary of the experimental design used for measuring fecundity, effective  
 246 dispersal, and development time. Inset (bottom right): example host egg strips from a 2-vial  
 247 system picture of; parasitized host eggs are darkened and thus, in black, easily visible among  
 248 the off-white unparasitized hosts, one week after the experiment.  
 249



## 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~~ ~~6016 × 4016~~ pixels, for a real field of view size of around ~~12 × 8 cm × 8 cm~~) using a Nikon D750 camera (lens: AF-S Micro NIKKOR ~~60mm~~ ~~60 mm~~ f/2.8 ~~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*, 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).~~

. 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, ~~whether the female has dispersed or not~~. ~~One~~ newhere 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.

## 288 *Development time*

289 After taking the pictures for fecundity, each isolated host egg strip was checked every day at  
290 around 9:00-a.m., 12:00-a.p.m., and 4:00-p.m. for the presence of emerged individuals. The  
291 development time of one replicate was considered to be the number of days between the  
292 female in the plastic vial starting to lay eggs and the emergence of the first offspring. Note  
293 that the true time is only known to a precision of 2two days, because of uncertainty in when  
294 precisely eggs were laid during the 48h48 h window after introduction in the system (see  
295 Data analyses for how this is accounted for).

## 296 *Data analyses*

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

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

- 305 • Effective dispersal (the probability that the female successfully laid eggs in the arrival  
306 patch) was modelled with a Bernoulli ~~model~~distribution (with a logit link);  
307 ~~corresponding to the fact that a female had dispersed or not;~~
- 308 • Development time ~~used a lognormal~~was modelled with a Log-Normal distribution,  
309 often chosen for time-to-event data. Because of the 48h48 h time period where the  
310 female was allowed to reproduce, development times were interval censored (with  
311 48h48 h wide intervals);
- 312 • For fecundity, initial models showed evidence of both potential zero inflation and  
313 overdispersion, therefore a zero~~Zero~~-inflated negative~~Negative~~binomial distribution  
314 was used. This effectively separating~~separates~~ the response variable into  
315 two~~components~~, “structural zeroes” and counts, each with a valid biological meaning  
316 (Blasco-Moreno et al., 2019):
  - 317 — On one hand, the zero-inflated part of the distribution, similar to a Bernoulli  
318 ~~model~~with a logit link, modelled an excess of non-parasitized replicates;  
319 ~~possibly caused by~~ compared to a negative binomial model. Given that egg  
320 retention ~~done by~~is common in Trichogramma species, leading to delays in  
321 egg-laying of up to several days commonly (Reznik et al., 2001), a biologically  
322 plausible reading of these structural zeroes component is the probability of  
323 doing retention in the 48 h of the experiment;
  - 324 — On the other hand, a ~~negative~~Negative binomial component (with a log link)  
325 was interpreted as ~~individual~~the fecundity ~~without~~of individuals that did not  
326 perform egg retention. From now on, we will use “fecundity without retention”  
327 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 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,

The first model included species”. Species were considered -level effects as a fixed effect, mostly due to the low number of species studied, while 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. We do not directly include (Bürkner, 2017b).

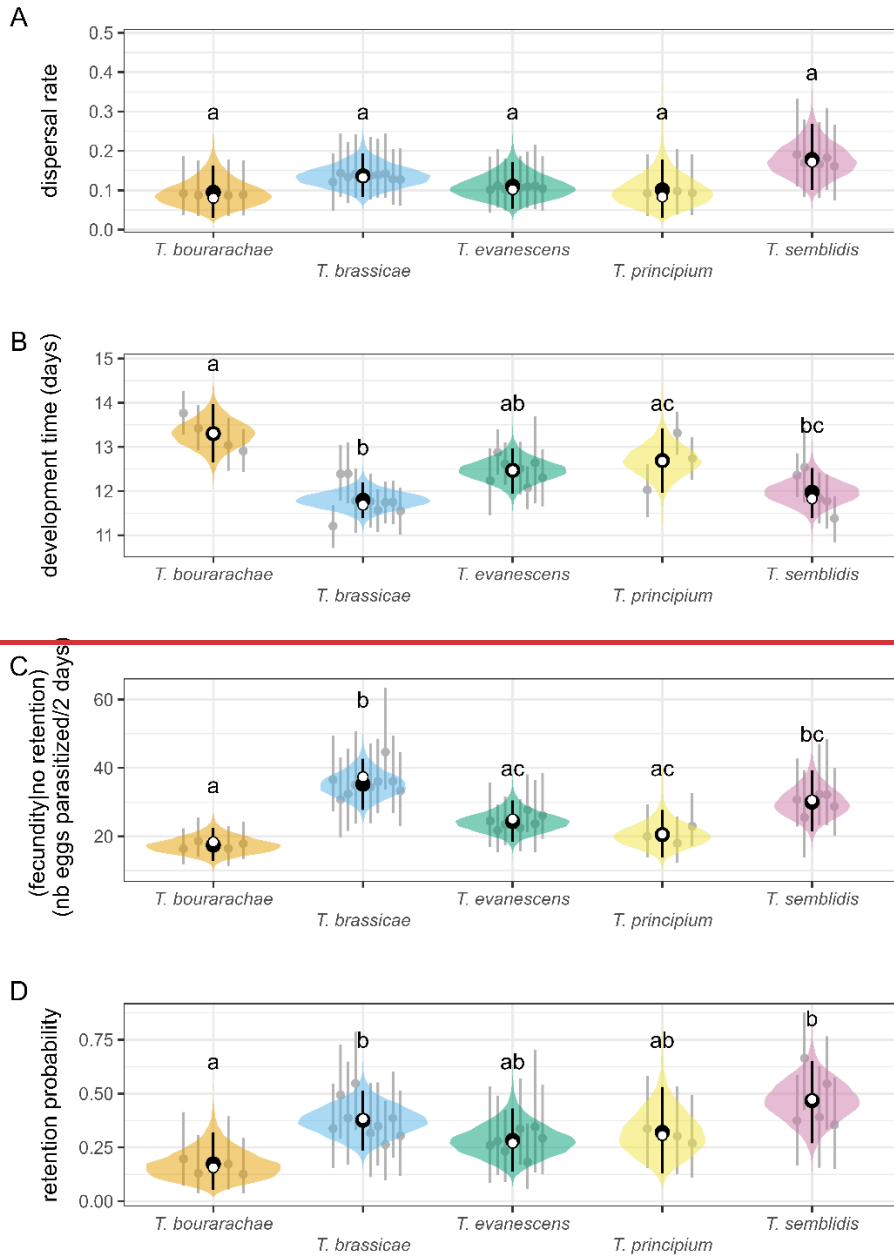
While phylogenetic information in this comparative methods could be used in this context, as some of the variations could be explained by shared-covariance matrix, as ancestry (Felsenstein, 1985), there is no phylogenetic tree available including all lines used. The second model is identical, but with no species-fixed effect. While the first model allowed us to observe inter- and intra- for all lines used we could include (Hadfield & Nakagawa, 2010). Our first model, splitting variation into 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 and line components is nonetheless similar to the “taxonomic model” suggested in these cases where tree data are absent (Hadfield & Nakagawa, 2010).

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 ( $\mu, 1$ ) distributions, where  $\mu$  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 4The 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

371 iterations for each chain used as warmup. This led to good chain convergence and sample  
372 size, as checked using the statistics proposed by Vehtari et al (2021). Model outputs were  
373 then checked using posterior predictive checks to compare predictions with empirical  
374 dataset (as suggested by Gabry et al., 2019). See the “Data and code availability” section, for  
375 links to an archived version of the annotated model code.

## 376 Results

377 *Trichogramma bourarachae* had lower fecundity without retention (~~mean and 95% posterior~~  
378 ~~highest density interval of 17.42 [12.77; 22.5] parasitized hosts eggs on 2 days~~) and higher  
379 development time (~~13.3 [12.64; 13.97] days~~) than *Trichogramma brassicae* (~~35.24 [27.71;~~  
380 ~~42.7] parasitized hosts eggs and 11.79 [11.4; 12.2] development days~~), while *T. semblidis*  
381 only had a lower development time than *T. bourarachae* (~~11.97 [11.39; 12.52] days~~) (~~but no~~  
382 ~~clear difference in fecundity without retention (Table 2, Figure 2B, C)~~). There were no other  
383 clear species differences (based on 95% intervals of pairwise differences) in fecundity or  
384 development time. We did not find any evidence for between-species differences in effective  
385 dispersal ~~rates (probabilities (Table 2, Figure 2A))~~. *T. brassicae* and *T. semblidis* both had  
386 higher egg retention probabilities than *T. bourarachae* (pairwise differences of 0.20 [0.00;  
387 0.40] and 0.29 [0.05; 0.53] respectively, **Figure 2D**).



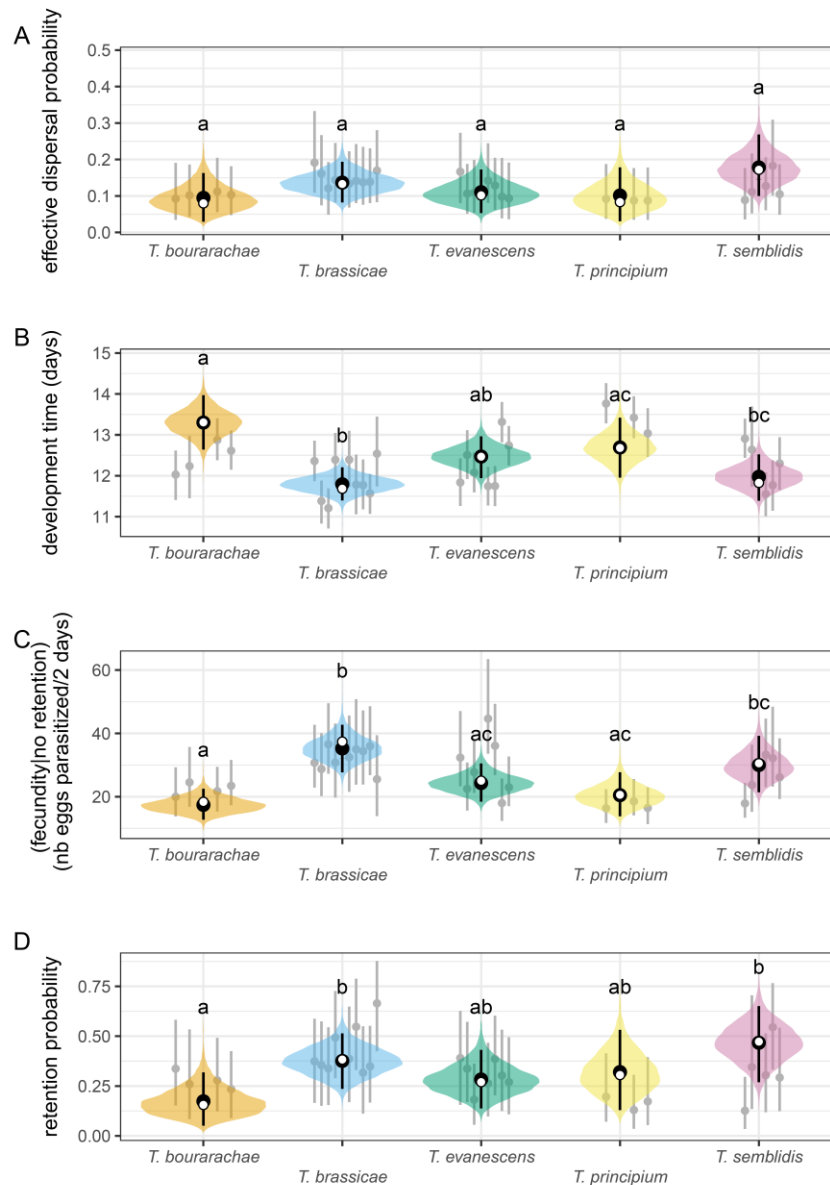
388 —  
 389 **FigureTable 2:** Posterior trait Mean posterior values as a function of the *Trichogramma*  
 390 species and 95% posterior highest density intervals per line for each species are displayed,  
 391 of single female fecundity in grey. Black dots represent posterior means, and bars the absence  
 392 of egg retention, said egg retention probability to occur during the 95% intervals,  
 393 while experiment, the posterior density distributions of fixed (species) effect only predicted  
 394 means is coloured depending on development time of the species first offspring and effective  
 395 dispersal probability. For a given trait, two species with no index letters in common are  
 396 considered to have “significant” pairwise comparison differences (i.e. the 95.

*T. bourarachae*    *T. brassicae*    *T. evanescens*    *T. principium*    *T. semblidis*

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

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

402 The only detectable correlations among traits were between fecundity without retention and  
403 development time (Table 3, Figure 3). There was a negative correlation between these two  
404 traits at the line level in the model where species effects were not partitioned out (-0.62 [-  
405 0.92; -0.28], see Table 3 bottom, see also the overall pattern Figure 3). However, when  
406 looking at the model where species differences are partitioned out into fixed effects (Table  
407 3 top), this random effect negative correlation mostly vanishes (-0.22 [-0.76; 0.38]). This  
408 reflects the fact that the overall correlation highlighted in Table 3 top is mostly driven by  
409 between-species differences in both fecundity and development time (see Figure 2 and  
410 species averages in Figure 3).



411  
 412 **Figure 2:** Posterior values as a function of the *Trichogramma* species for A) the probability  
 413 of effective dispersal, B) the development time in days of the first offspring, C) the number of  
 414 parasitized eggs for a single female when no retention occurred, and D) the probability for a  
 415 female to perform egg retention during the experiment. 95 % posterior highest density  
 416 intervals per line for each species are displayed in grey. Black dots represent posterior means  
 417 and bars the 95 % intervals, while the posterior density distributions of fixed (species) effect  
 418 predicted means are coloured depending on the species. For a given trait, two species with  
 419 no index letters in common are considered to have “significant” pairwise comparison  
 420 differences (i.e. the 95 % highest density interval of the difference does not include 0). White  
 421 dots represent observed means per species, presented for illustrative purposes only (as they  
 422 are calculated assuming all observed zeroes in egg numbers were attributable to retention,  
 423 and using the midpoint of the ~~48h~~48 h interval for development time).

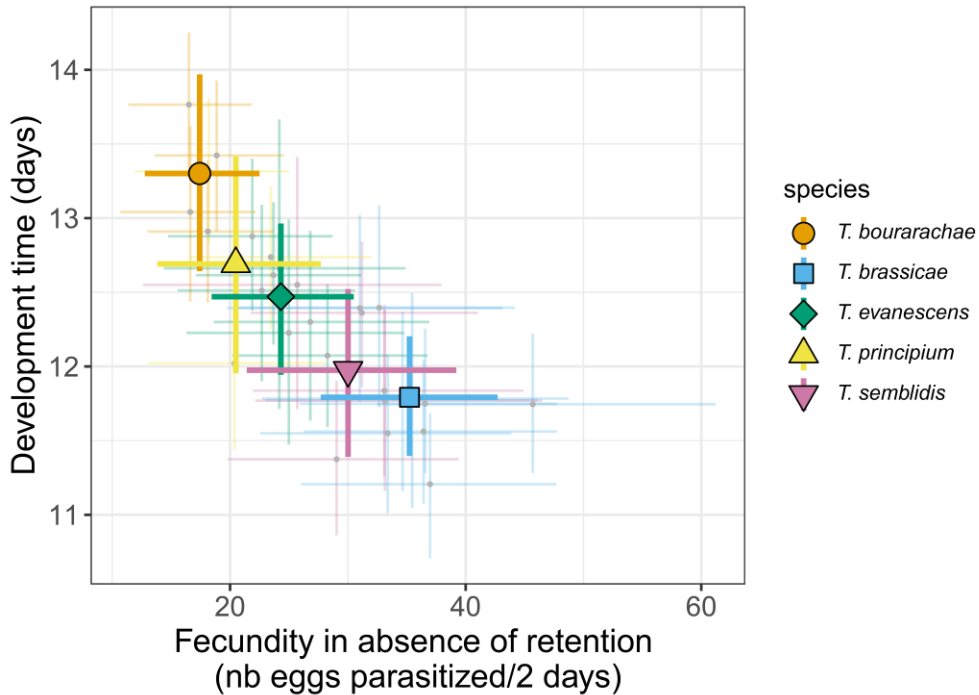
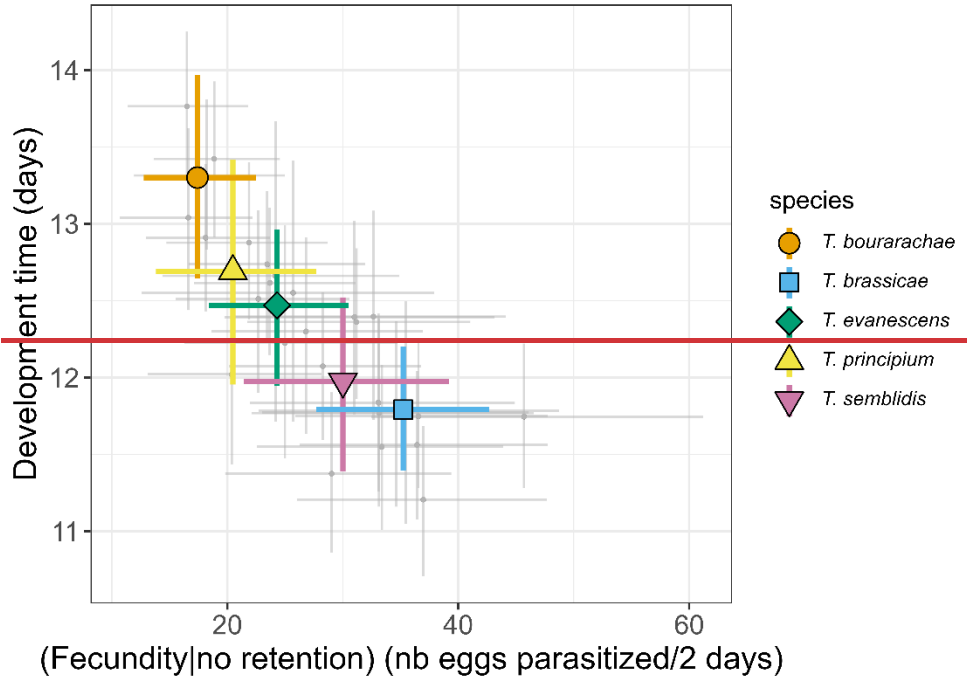
424 ~~The only detectable line-level trait correlation, whether within life-history traits or between~~  
 425 ~~life-history traits and dispersal, was a negative correlation between females' fecundity~~  
 426 ~~without retention and development time (-0.62 [-0.92; -0.28]), and only when between-~~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

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

	<u>Dispersal rate</u> <u>probability</u>	<u>effective dispersal</u> (Fecundity no retention)	Retention probability
<b>Within-species, among-line correlations (after excluding between-species differences as fixed effects)</b>			
(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]
<b>Overall among-line correlations, inclusive of between-species differences</b>			
(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]	<b>-0.62 [-0.92; -0.28]</b>	-0.17 [-0.64; 0.31]

435





**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 grey the colour of their corresponding species but more transparent.

## 444 Discussion

### 445 *Identification of one interspecific Pace-of-Life axis in Trichogramma*

446 We found a negative between-line correlation between development time and fecundity in  
447 this subset of five *Trichogramma* species, with high fecundity without retention, fast  
448 development time on one side, and low fecundity, slow development on the other (**Figures**  
449 **2, 3, Table1Table3**). This correlation, which matches the classical pace-of-life axis (Healy et  
450 al., 2019) is mainly or only due to species-level differences: species with higher fecundity also  
451 had faster development times (**Figures 2, 3**), and the line-level correlation vanishes when  
452 species differences are partitioned out (**Table 1**). ~~We note that although there is no clear~~  
453 ~~support for a non-zero correlation between lines within each species, the sign of this~~  
454 ~~correlation remains negative (Table 2 top), as in the between-species case. More data may~~  
455 ~~be needed to determine whether within-species patterns result from a true absence of~~  
456 ~~correlation or limited power (given we had 28 lines; Dingemanse & Dochtermann, 2013).3).~~  
457 We note that even if there is no statistically significant correlation when the variance is  
458 structured within species and among lines, the sign of this correlation remains negative  
459 (Table 3 top), following a similar tendency to the interspecific negative correlation observed  
460 in Table 3 bottom. Having relatively similar patterns of interspecific and intraspecific  
461 correlation may result from close genetic correlations between development time and  
462 fecundity in *Trichogramma*, through pleiotropy or other strong genetic architecture,  
463 constraining the evolution of this trade-off among lines and species (Peiman & Robinson,  
464 2017). It is also possible that at the metabolic level, resource acquisition and allocation may  
465 favour longer development times at the expense of fecundity or the opposite (Agrawal, 2020;  
466 Jørgensen & Fiksen, 2006; Stearns, 2000). The fact that a pace of life was found at the  
467 between-species level but not conclusively at the within-species level is in line with the  
468 existing literature, in which it is inconsistent pace-of-life axes are considered increasingly  
469 difficult to find ~~consistent pace-of-life axes~~ as the taxonomic level narrows down, possibly  
470 due to scale-dependent mechanisms (Agrawal, 2020; Simons, 2002). Correlations at the  
471 species level act over a longer macroevolutionary timescale, where divergent positions on  
472 the pace-of-life axis of each species may represent long-term trade-offs and selection  
473 pressure over a wider environmental range than at lower levels, like lines. For lower levels,  
474 such as lines or individuals, traits may be more responsive to direct environment variation  
475 through phenotypic plasticity, and a shorter evolutionary timescale may lead to lower  
476 variation range compared to a higher level (Siefert et al., 2015).

477 However, this pace-of-life finding is based on splitting fecundity into what we interpret as  
478 egg retention and fecundity without retention components. While a significant negative  
479 correlation with development was found on the latter component of overall fecundity, results  
480 are more complex for retention probabilities. Indeed, there is no evidence for the line-level  
481 correlation between egg retention and other life-history traits (**Table 1**). ~~However, the~~  
482 ~~situation may be different3).~~ Furthermore, at the species level, faster species (lower  
483 development time and higher fecundity in the absence of retention) were also the species  
484 with the highest retention probabilities (**Figure 2, Table 2**). If we interpret retention rates  
485 as a trade-off between present reproduction and future opportunities, then high retention  
486 can be seen as a “slow” trait ~~and observed species-level differences as fully compatible; its~~

487 ~~association with our interspecific pace-of-“faster” life framework. However, because egg-~~  
488 ~~laying was restricted to a 48h window history traits may then appear paradoxical. It might be~~  
489 ~~that fecundity in our experiment, we cannot yet confirm this interpretation, as we were the~~  
490 ~~absence of retention and retention probabilities are not able to measure lifetime~~  
491 ~~reproductive success, longevity or the way reproductive effort is spread throughout actually~~  
492 ~~separate traits, and that the lifetime. Nonetheless, trait correlations described above derive~~  
493 ~~from their “artificial” separation by the statistical model. However, previous studies indicate~~  
494 ~~that in *T.-principium*, except for prolonged periods of egg-retention, individuals that~~  
495 ~~did manifesting egg retention had similar fecundities in their first days of actual egg-laying~~  
496 ~~and similar lifetime fecundities than individuals that did not (Reznik et al., 2001,~~  
497 ~~1998)(Reznik et al., 2001, 1998). Still in *T.-principium*, there are indications that individuals~~  
498 ~~doing manifesting egg retention have longer mean lifespans than individuals that~~  
499 ~~immediately oviposit (Reznik et al., 2003; Reznik & Vaghina, 2007). This would support our~~  
500 ~~idea that egg retention is a mark of delayed reproduction (thus “slow” life history) rather~~  
501 ~~than merely reduced reproduction, and further support our choice of treating retention and~~  
502 ~~actual fecundity as separate traits, that may be controlled through different pathways or~~  
503 ~~mechanisms. These results support the idea that egg retention is a separate trait,~~  
504 ~~interpretable as a mark of delayed reproduction (thus typically “slow” life history) rather~~  
505 ~~than merely a component of reduced reproduction. While the pace of life remains an~~  
506 ~~important and valuable structuring pattern in life histories, our results would agree with~~  
507 ~~other studies showing that deviations from naïve expectations, where all traits should be~~  
508 ~~either “slow” or “fast”, can be frequent (Bielby et al., 2007; Wright et al., 2020). In Wright et~~  
509 ~~al (2020), their eco-evolutionary model presented possibly unexpected but existing life-~~  
510 ~~history strategies, like “slow” adult reproduction alongside “fast” offspring survival (that the~~  
511 ~~authors likened to an oak tree life history) or the opposite (represented by mayflies).~~  
512 ~~However, because egg-laying was restricted to a 48 h window in our experiment, we cannot~~  
513 ~~yet confirm this interpretation. Further studies measuring lifetime reproductive success,~~  
514 ~~longevity or the way reproductive effort is spread throughout the lifetime may shed more~~  
515 ~~light on the way life history is structured in *Trichogramma* wasps.~~

516 *No evidence for a syndrome linking effective dispersal rates probability and the pace-of-life*

517 ~~**Dispersal rate** Effective dispersal probability varied the least among the four traits~~  
518 ~~measured, with no evidence of between-species or even between-lines differences (**Figure**~~  
519 ~~**2**). There was also no correlation between dispersal and any of the other traits (**Table 1**),~~  
520 ~~meaning that there is no evidence for dispersal life history syndromes in our set of~~  
521 ~~*Trichogramma* species. Interestingly, this result contradicts a previous study in *T. principium*,~~  
522 ~~in which females manifesting egg retention had higher dispersal rates than females that laid~~  
523 ~~eggs beforehand (Reznik & Klyueva, 2006).), and values were rather consistent with previous~~  
524 ~~studies (Dahirel, Bertin, Calcagno, et al., 2021). There was also no correlation between~~  
525 ~~effective dispersal and any of the other traits (**Table 3**), meaning that there is no evidence~~  
526 ~~for dispersal/life-history syndromes at the line or species level in our set of *Trichogramma*~~  
527 ~~species. Interestingly, this result on effective dispersal between patches completes previous~~  
528 ~~studies on the activity of *Trichogramma* species. In Wajnberg & Colazza (1998), the authors~~  
529 ~~showed a significant difference in the average area searched within one patch by *T. brassicae*~~  
530 ~~isofemale lines while our results showed no differences in effective dispersal (**Figure 2**). In~~

531 Reznik & Klyueva (2006), *T. principium* females manifesting egg retention had higher  
532 dispersal activity in a continuous environment than females that laid eggs beforehand. This  
533 discrepancy may be the result of a focus on different taxonomic levels: Reznik and Klyueva  
534 (2006)'s results deal with within-species and within-line covariation, versus between-lines  
535 and between-species in the present study. It may also result from differences in experimental  
536 designs and metrics used: the dispersal metrics used in Reznik and Klyueva (2006) are based  
537 on short-term (~~1~~less than one day) and short-distance (up to 5-cm) movement on a  
538 continuous arena, compared to our experiment (two days and 40-cm between discrete  
539 patches). In that case, there may still exist in *Trichogramma* a pace-of-life syndrome linking  
540 life history to short-term activity and behaviour, but not effective dispersal. Indeed,  
541 correlations between short-term movement behaviouractivity and life-history traits were  
542 also found in *T. evanescens* at the between-line level (Lartigue et al., 2022). ~~Finally, we~~  
543 ~~allowed both~~While short-term activity metrics in uniform continuous environments are  
544 often considered valid proxies of longer-term dispersal ~~and oviposition to occur at the same~~  
545 ~~time, while Reznik and Klyueva~~between discontinuous patches (2006) and Lartigue et al.  
546 ~~(2022)'s setups were based on measuring dispersal/movement in the absence of hosts and~~  
547 ~~presenting hosts to the wasps at another time.~~(Pennekamp et al., 2019), this comparison of  
548 our study with the existing literature shows that this is not always the case. Dispersal is  
549 extremely context-dependent, including ~~to~~ current resource availability (Fronhofer et al.,  
550 2018); there is furthermore evidence that syndromes linkingcorrelations between dispersal  
551 ~~to~~and other traits can be altered depending on whether individuals disperse from high-  
552 resource or low-resource contexts ~~(Cote et al., 2022)~~(Cote et al., 2022), but also how density  
553 can have an impact on both dispersal behaviour and its evolution (Bitume et al., 2013; Clobert  
554 et al., 2009; Poethke et al., 2016; Poethke & Hovestadt, 2002).

555 *The potential implications of context-dependence and especially density-dependence for this*  
556 *syndrome*

557 Building on this point, our study ~~was indeed~~ ignored this potential for context-  
558 independent, with dependence, as every female tested for a given trait ~~being~~was tested  
559 under the same low-density conditions (alone in the experimental design with a non-limiting  
560 host supply). Dispersal syndromes (Bonte & Doherty, 2017; Cote et al., 2022; Ronce, 2012)  
561 ~~but~~and also pace-of-life syndromes can be context-dependent. Behavioural types can be  
562 dependent of the dispersal status and predation risks ~~(Bell & Sih, 2007; Cote et al., 2010)~~(Bell  
563 & Sih, 2007; Cote, Clobert, et al., 2010). Pace-of-life syndromes and/or their constituent traits  
564 may also depend on resource acquisition through plastic responses (Laskowski et al., 2021;  
565 Montiglio et al., 2018) or quality. In *Trichogramma* for instance, host egg species and quality  
566 can influence life-history traits (Paul et al., 1981), and we used a substitution host in the  
567 present study. Recent works suggest that population density and density fluctuations, in  
568 particular, may also play a key role in shaping the presence of a pace of life in the first place  
569 (Wright et al., 2020) and its association with behaviours: fast individuals may have a higher  
570 reproductive rate in low-density contexts, but their lower intra-specific competition is a  
571 disadvantage when close to the carrying capacity of an environment, and therefore are more  
572 likely to disperse to escape to lower densities where this competition is lessened (Wright et  
573 al., 2019). This interaction between the pace of life and density may interact with the overall  
574 density-dependence of dispersal (Clobert et al., 2009; Harman et al., 2020), altering

575 syndromes linking dispersal and life history. Given that there is evidence for dispersal and/or  
576 fecundity ~~both~~ being density-dependent in several *Trichogramma* species (~~*T. brassicae*;~~  
577 ~~Dahirel et al., 2021; *Trichogramma achaeae*, *T. chilonis* and *T. euproctidis*, Zboralski et al.,~~  
578 ~~2016)~~(*T. brassicae*; Dahirel, Bertin, Calcagno, et al., 2021; *Trichogramma achaeae*, *T. chilonis*  
579 ~~and *T. euproctidis*, Zboralski et al., 2016~~), further studies including density-dependence may  
580 lead to more generalizable insights about pace of life and dispersal in *Trichogramma*.

### 581 *Implications for biocontrol improvement and perspectives*

582 While studies on trade-offs (Bennett et al., 2002; Reznik & Klyueva, 2006; Zboralski et al.,  
583 2016) or pace-of-life syndromes (Lartigue et al., 2022) already existed in small biocontrol  
584 agents including *Trichogramma*, our results provide new insights on between-species  
585 comparisons and the taxonomic scales at which trait variation is important. Some species like  
586 *T. evanescens*, *T. cacoeciae* (Sigsgaard et al., 2017) or *T. brassicae* (Özder & Kara, 2010) are  
587 already well used as biocontrol agents. In that context, a choice might be needed between  
588 maximizing one trait or a set of traits of interest at the expense of the others. For  
589 *Trichogramma*, while having fast-developing and high-fecundity individuals can be beneficial  
590 to quick intervention and a higher number of host eggs parasitized, they are reared and  
591 released mainly at high densities, (Consoli et al., 2010) densities for which individuals with  
592 longer development time might fare better against the intra-species competition (Wright et  
593 al., 2019). ~~For inoculative releases~~For inoculative releases, where a small population of  
594 biocontrol agents in the area of interest must establish itself and reach higher densities in  
595 further generations, both fecundity and competitive abilities are to be favoured for efficiency  
596 (Smith, 1996). Our results suggest that for some purposes, selecting different species might  
597 actually be more successful than attempting to select specific lines within one already used  
598 species.

### 599 **Data availability**

600 Data and R code to reproduce all analyses presented in this manuscript are available on  
601 GitHub ([https://github.com/CGuicharnaud/Trichogramma\\_POL\\_dispersal\\_2023](https://github.com/CGuicharnaud/Trichogramma_POL_dispersal_2023)) and  
602 archived in Zenodo (<https://doi.org/10.5281/zenodo.7544901>).

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613 **Author contributions**

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

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