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**Title:** Evidence for risk-taking behavioural types and potential effects on resource acquisition in a parasitoid wasp

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1           In many animal populations, individuals show consistent behavioural differences  
2 through time and/or across situations (*i.e.* given sets of conditions at one point in time such as  
3 levels of resources) (Sih, Bell, & Johnson, 2004). Moreover, these differences occur in  
4 different contexts, which are functional behavioural categories such as foraging (Sih, Bell, &  
5 Johnson, 2004). When a behavioural trait combines these two characteristics, it is defined as a  
6 personality trait (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). A well-studied  
7 species is the great tit *Parus major*, where some individuals have consistently stronger  
8 exploratory behaviour than others in a novel environment (Dingemanse, Both, Drent, van  
9 Oers, & van Noordwijk, 2002). The individuals thus display behavioural types, meaning that  
10 both strong explorers and superficial explorers can be observed in this species (Sih, Bell, &  
11 Johnson, 2004).. At the population level, suites of behavioural types are sometimes correlated  
12 across situations, forming behavioural syndromes (Sih et al., 2004). In the spider *Philodromus*  
13 *albidus*, boldest individuals were also the most aggressive ones in a foraging context  
14 (Michalko, Košulič, & Řežucha, 2017). Among the personality traits described, risk-taking  
15 behaviours (*i.e.* exploration, activity, aggressiveness and boldness) and their correlations are  
16 particularly well studied because they have major evolutionary and ecological consequences.  
17 They are often heritable (Dingemanse et al., 2002) and linked with fitness components. A  
18 meta-analysis on 37 studies has shown that exploration has a positive effect on survival and  
19 aggressiveness a positive effect on reproductive success, whereas boldness has a positive  
20 effect on reproductive success and a negative effect on survival (Smith & Blumstein, 2008).  
21 Because of their impacts on fitness and on several ecological processes such as dispersal or  
22 population dynamics (Wolf & Weissing, 2012), risk-taking behaviours can thus have broad  
23 implications in major fields of ecology like eco-epidemiology, predator-prey/species  
24 interactions or ecosystem services (Modlmeier, Keiser, Wright, Lichtenstein, & Pruitt, 2015;  
25 Sih, Cote, Evans, Fogarty, & Pruitt, 2012).

26           The correlations observed between risk-taking behaviours and life history traits can be  
27 explained by the Pace-Of-Life Syndrome (hereafter “POLS”) hypothesis (Réale et al., 2010).  
28 Within populations, individuals differ in their life-history strategies along a slow-fast  
29 continuum. “Slow” individuals favour survival to the cost of reproduction, which is thus  
30 delayed, and “fast” ones favour precocious reproduction at a high rate to the cost of survival,  
31 leading to shorter lifespan (Bielby et al., 2007). These differences, maintained because  
32 yielding equal fitness over lifetime, arise from life-history trade-offs in which risk-related  
33 behavioural types can be involved (Biro & Stamps, 2008). Boldness can increase an  
34 individual’s resource acquisition (*i.e.* growth rate) and simultaneously increase its mortality  
35 risk, if foraging in presence of predators for instance (Stamps, 2007). Bold individuals are  
36 thus on the fast side of the continuum. The POLS hypothesis therefore predicts the  
37 coevolution of behavioural and life history traits along a pace-of-life gradient, explaining the  
38 long-term maintenance of consistent between-individual behavioural differences and  
39 behavioural syndromes (Réale et al., 2010).

40           However, there is no clear consensus yet in the literature on the existence of a POLS  
41 integrating behaviour, as shown by a meta-analysis of 179 estimates that found an overall  
42 weak effect size of 0.06 for correlations between behaviours, life-history and physiological  
43 traits (Royauté, Berdal, Garrison, & Dochtermann, 2018). Indeed, some studies have found no  
44 evidence for this hypothesis, with no correlation between behaviours and life history traits in  
45 the house cricket *Acheta domesticus* for instance (Royauté, Greenlee, Baldwin, &  
46 Dochtermann, 2015), and others have showed correlations in contradiction with the POLS.  
47 For instance, in a population of bighorn sheep (*Ovis canadensis*), the boldest males survived  
48 longer than shy ones (Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009), and in a  
49 brown trout (*Salmo trutta*) population, low-explorative behavioural type was associated with a  
50 fast growth rate (Adriaenssens & Johnsson, 2011). The relationship between life-history and

51 behavioural traits may rest on ecological conditions, such as resource distribution or predation  
52 risks, and natural histories of the species (Montiglio et al, 2018). Elucidating the importance  
53 of these factors requires studying a greater number of species in various taxa, both vertebrates  
54 and invertebrates.

55         Since Kralj-Fišer & Schuett (2014) emphasized the relevance for considering  
56 invertebrate species in the field of animal personality, the initial disequilibrium toward  
57 vertebrates in the number of studies on the POLS hypothesis, and more generally on  
58 personality, has been reduced (Amat, Desouhant, Gomes, Moreau, & Monceau, 2018). The  
59 existence of personality seems widespread in insect species. For instance, the mealworm  
60 beetle *Tenebrio molitor*, a common pest feeding on stored resources, displays a behavioural  
61 syndrome for risk-related behaviours both at the adult and larval stages (Monceau et al.,  
62 2017). In this species, activity, exploration and boldness formed a syndrome along a  
63 continuum from low risk-taking, or “slow”, individuals to high risk-taking, or “fast”,  
64 individuals. These latter are bold, highly active, exploratory and produced more offspring  
65 (Monceau et al., 2017). Variation in behavioural types can have consequences on species  
66 interaction and population dynamics (Sih, Cote, Evans, Fogarty, & Pruitt, 2012), it is  
67 therefore essential to describe the behavioural types in pest species but also in species  
68 regulating their populations, namely biocontrol agents such as parasitoids – arthropods that  
69 kill their hosts during their development. While their capacity to find and parasitize their hosts  
70 or to survive in their environment might depend on behavioural types for traits such as  
71 exploration, activity or boldness, little is known about behavioural syndromes in parasitoid  
72 species, and their potential effects on parasitism efficiency (Modlmeier et al., 2015).  
73 However, when the aim is to select and release successful biocontrol agents, behavioural  
74 types and their relationships with life history traits need and should be considered (Sih et al.,  
75 2012).

77           The aim of this study was to determine, in a parasitoid species, if the two behavioural  
78 traits that are exploration and activity were repeatable, and therefore if the insects exhibit  
79 behavioural types. These two traits are crucial for resource acquisition, since the search for  
80 hosts or food in the environment should depend on the insect exploration behaviour, and  
81 activity is likely linked to the exploitation of a host patch. Then, in the framework of the  
82 POLS hypothesis, we aimed to investigate the links between these behavioural types and  
83 several life history traits related to survival and reproduction, also estimating the parasitism  
84 efficiency of the insects. We thus tackled the three following questions: (1) Do consistent  
85 between-individual differences in exploration and activity exist? (2) Do these behavioural  
86 traits correlate to form a behavioural syndrome? (3) Do the two behavioural traits correlate  
87 with life history traits related to fitness such as longevity, egg load and offspring production  
88 rate? We expected consistent between-individual differences in both exploration and activity,  
89 and we predicted a positive correlation between these two traits, namely a behavioural  
90 syndrome. Finally, we expected behavioural types to covary with longevity and fecundity due  
91 to their involvement in resource acquisition.

## 92 MATERIALS AND METHODS

### 93 *Biological Model and Rearing Conditions*

94 *Venturia canescens* Gravenhorst is a solitary endoparasitoid hymenopteran (Ichneumonidae).  
95 It attacks lepidopteran larvae, mainly Pyralidae (Salt, 1975), in their second to fifth instar  
96 (Harvey & Thompson, 1995). Parasitoid females use a mandibular gland secretion, called  
97 kairomone, released by host larvae when feeding to locate them  
98 (Castelo, Corley, & Desouhant, 2003). During host patch exploitation, *V. canescens* exhibits  
99 several specific behaviours: *antennating* (*i.e.* tapping of the substrate with the antennae),

100 *probing* (*i.e.* searching for hosts in the substrate with the ovipositor), *resting*, *cleaning* and  
101 *cocking* (*i.e.* egg positioning in the ovipositor by an abdomen movement) (Rogers, 1972).  
102 When exploiting a host patch, *V. canescens* moves in a nonlinear way by turning back when  
103 encountering edges of the patch, despite short excursions outside the patch, which increases  
104 the individual angular velocity.

105 We studied *Venturia canescens* arrhenotokous females that live in heterogeneous habitat  
106 (Pelosse, Bernstein, & Desouhant, 2007) and show great genetic variation with high degree of  
107 heterozygosity and allelic richness (Leach, Ferber, Zande, & Beukeboom, 2012), and thereby  
108 are likely to exhibit inter-individual behavioural variation. We used individuals from a strain  
109 established from around 70 wild females trapped near Valence (south of France) during the  
110 summer of 2016. The wasps were kept in the laboratory under controlled conditions (25°C,  
111 60% RH, 12:12 L:D), and maintained in boxes containing organic wheat semolina (*i.e.* food  
112 for host larvae) and *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) larvae as hosts. Adult  
113 wasps were fed *ad libitum* with water-diluted honey (50%), because in natural conditions *V.*  
114 *canescens* use nectar or honeydew as food sources (Desouhant, Lucchetta, Giron, &  
115 Bernstein, 2010).

#### 116 *Experimental Design Overview*

117 We conducted multiple measurements on *V. canescens* females to estimate the repeatability,  
118 that is the consistency of between-individual differences (Bell, Hankison, & Laskowski,  
119 2009), of exploration and activity, and their possible correlation into a behavioural syndrome.  
120 Furthermore, we aimed to appraise the POLS hypothesis by testing the correlation between  
121 these behavioural traits and several life history traits (offspring production rate, egg load and  
122 longevity).

123 Data collection was organised in five-day sessions. On day 1, in the morning, seven females  
124 were isolated at emergence from rearing boxes, as well as every emerging male. Then the  
125 newly emerged females and males were put together in cages (two males per female;  
126 Van Santen & Schneider, 2002) and left for 180 minutes to allow mating. Each female was  
127 then identified and put individually in a plastic tube (7x3 cm). They were kept in tubes  
128 between experimental trials, and isolated from each other throughout the 5-day session.  
129 Individual storage and experiments were realized under controlled conditions ( $25 \pm 1^\circ\text{C}$ , 60%  
130 RH, 12: 12 L: D) free of host odours.

131 To quantify between-individual variance in behaviour, thus determining whether consistent  
132 inter-individual differences exist, repeated measures of behavioural traits were performed.  
133 From day 1 to day 5, each wasp was tested four times: (i) exploration in the morning and (ii)  
134 activity in the afternoon (Figure 1). The order of turn of females was randomly chosen each  
135 day in each behavioural test. Every evening, the wasps had access to a droplet of honey for 1  
136 hour, and 20  $\mu\text{L}$  of demineralised water throughout the night. This procedure standardised  
137 their physiological state and enhanced their survival throughout the experiments (Desouhant,  
138 Driessen, Amat, & Bernstein, 2005). On day five, once the behavioural tests were over, we  
139 quantified the egg-laying rate of each female (experiment described below). Finally, we  
140 randomly split the females in two groups in order to measure their egg load and longevity (see  
141 description below; Figure 1).

142

143 *Assessing the Repeatability of Two Behavioural Traits in Venturia canescens*

144 *Consistent individual differences in exploration*



145 Exploration is defined as an individual's reaction to a new situation (Réale et al., 2007). We  
146 thus put the insects in a new and non-risky environment containing several obstacles to  
147 measure their exploratory behaviour when confronted with novel objects.

148 The experimental setup consisted of a closed transparent Plexiglas<sup>®</sup> tube with an entrance at  
149 one end (see Figure A1 in the Appendix). *V. canescens* exhibit a positive phototaxis, so a  
150 lamp for binocular magnifier was placed at the other end of the tube, facing the entrance, to  
151 elicit the insect movement (see Figure A1 in the Appendix). Two obstacles were put in the  
152 tube, in a standardised way, to test how exploration behaviour was affected by new objects: a  
153 plasticised yellow funnel and a plasticised orange disc punched by six 1-cm square holes (see  
154 Figure A1 in the Appendix). Their colours were attractive for the insects but not the dark  
155 passages or holes that the insects had to cross through the obstacles (Lucchetta, Bernstein,  
156 Théry, Lazzari, & Desouhant, 2008). Their position was alternated each day to prevent  
157 habituation in the insects. The tube was thus composed of three areas (in front of the first  
158 obstacle, between the two obstacles, behind the second obstacle) and two obstacles (see  
159 Figure A1 in the Appendix) which define five steps to cross for the females.

160 We assessed the insect exploration behaviour by recording the total number of steps (over 5) a  
161 wasp passed in the tube. The test ended after 15 minutes of observation or when the insect  
162 reached the end of the tube. The setup was thoroughly cleaned every four insects.

### 163 *Consistent individual differences in activity*

164 Activity is defined as the general level of activity of an individual in a non-risky and non-  
165 novel situation (Réale et al., 2007). It was assessed by tracking the insect movements on a  
166 host-mimicking patch during five-minute trials. A solution of kairomones was used as a host  
167 odour cue (Castelo et al., 2003). It was obtained by mixing 250 g of 1-month-old host  
168 contaminated semolina with 500 ml of a 50% acetone-50% ethanol solution, then filtering the

169 mix after a 2h30 rest. Every morning, thin veils were soaked with 6 ml of this solution and  
170 dried until solvent evaporation. A host-mimicking patch was built by first covering a Petri®  
171 dish (Ø 55 mm) filled with clean wheat semolina by one of these veils, then putting it in a  
172 larger Petri dish (Ø 90 mm) and filling the surrounding space with clean semolina. A patch  
173 was thus composed of a central area called "kairomone arena" surrounded by an area free of  
174 host odour.

175 Before each behavioural test, a new patch was placed in a Plexiglas® box (34x18x12 cm)  
176 under a camera connected to a computer. The five-minute trial began just after the wasp was  
177 carefully placed in the middle of the patch. We recorded manually five behaviours  
178 (*antennating, probing, cocking, resting, cleaning*) through an event recorder (Ethovision,  
179 Noldus®) when the insect was on the "kairomone arena". The software also calculated  
180 classical variables used to characterize activity (see below Statistical Analyses section): mean  
181 speed, mean angular velocity, total distance moved and total movement duration, while the  
182 focal insect was on the patch. The room was ventilated between every female.

### 183 *Appraising the POLS Hypothesis in Venturia canescens: Measures of Life History Traits*

184 To appraise the existence of a POLS in *Venturia canescens*, we measured three life history  
185 traits on the female wasps to evaluate their correlation with the individual behavioural types.

#### 186 *Offspring production rate*

187 The offspring production rate of each female was quantified in a complex environment, where  
188 access to the resources that are host and food patches should depend on her behavioural type,  
189 that is the degree of exploratory and activity behaviours expressed by the insect through the  
190 whole duration of the experiment. The context of this experiment (food and patch searching  
191 plus host handling) was different from the contexts of the exploration and activity tests (light

192 and kairomone stimuli, respectively), ensuring that no artificial correlation between  
193 behavioural and life history traits would be due to the experimental procedure.

194 The experimental setup was a Lego<sup>®</sup>-made labyrinth (25.5 x 25.5 cm) containing three host  
195 patches where the females could lay eggs and a food patch, placed in a standardised way  
196 (see Figure A2 in the Appendix). Five gaps were created in the inside walls to allow the  
197 insects to move through the labyrinth; there were also four more gaps which, associated with  
198 a fan, allowed host kairomone and food odours to spread throughout the setup (see Figure A2  
199 in the Appendix). The host patches consisted of three third-instar larvae in a Petri<sup>®</sup> dish (Ø 35  
200 mm) filled with semolina and covered by a veil; patches were prepared 8 days before the test  
201 to make sure their kairomone concentration was high enough. A food patch was prepared by  
202 putting 1 ml of diluted honey (50%) in a Petri<sup>®</sup> dish (Ø 35 mm). The honey was dyed blue so  
203 we could easily determine if the focal insect ate or not by looking at the colour of its abdomen  
204 at the end of the test (see also Desouhant et al., 2005).

205 Each female was left in the labyrinth setup for 40 minutes. After 40 minutes, the host patches  
206 were identified by the female identity, kept in the rearing room until emergence to count the  
207 offspring. We also checked whether a female ate by looking at the colour of its abdomen.

#### 208 *Quantification of egg load and longevity*

209 At the end of the experiment measuring their offspring production rate, the females were  
210 randomly split in two groups (Figure 1). The wasps assigned to group 1 were frozen (-20°C)  
211 and dissected to estimate their egg load. Their ovaries were removed and the number of eggs  
212 counted under a microscope. The females assigned to group 2 were kept in their tubes with 20  
213 µL of diluted honey (50%), maintained under controlled conditions in the rearing room and  
214 checked daily in the morning and in the evening until death to determine their longevity in  
215 days. Finally, we also conducted size measurements on the females of both groups. The left

216 hind tibia of each female was removed, placed under a binocular magnifier coupled with a  
217 camera and a picture was taken. The tibia length, index of adult body size (Harvey & Vet,  
218 1997), was then measured using the software Motic Images Plus 2.0.

### 219 *Ethical Note*

220 The authors declare that the experiments comply with the current laws of the country (France)  
221 in which they were performed, and were carried out in accordance with University Lyon 1  
222 procedures for ethical animal experimentation.

### 223 *Statistical Analyses*

224 Statistical analyses were realized with R 3.3.2 (R Core Team, 2016). Individuals that died  
225 before performing at least three trials for a behavioural trait were discarded from the analysis  
226 ( $N = 9$  for exploration and  $N = 7$  for activity). The numbers of individuals for each test are  
227 given in the Results section.

### 228 *Consistent individual differences in exploration and activity*

229 To investigate consistent individual differences (*i.e.* repeatabilities) in exploration and activity  
230 behaviours, we used mixed models that estimate both within and among individual variances  
231 for Gaussian or non-Gaussian data (Nakagawa & Schielzeth, 2010).

232 The total number of steps passed in the tube followed a bimodal distribution (see Figure A3 in  
233 the Appendix), we thus defined the exploration score as a binary variable. Each day,  
234 individuals that passed two steps or less were given the score of “0”, and individuals that  
235 passed three steps or more were given the score of “1”. We then built a binomial generalised  
236 linear mixed model (GLMM) with logit link using the *lme4* package (Bates, Mächler, Bolker,  
237 & Walker, 2014), including female identity as a random effect (Female) and the day of  
238 measure as a fixed effect (Day). We thus assessed the variance explained by the random

239 factor, and calculated the repeatability ( $R$ ) of the exploration score on the logit-link scale  
240 (Nakagawa & Schielzeth, 2010).

241 To get an integrative measure of activity, we first ran a Principal Component Analysis (PCA)  
242 (package *ade4*; Dray & Dufour, 2007) on the five variables recorded during the activity  
243 experiments: mean speed, mean angular velocity, total distance moved, total movement  
244 duration, and the cumulated duration of *probing* and *antennating* weighted by the time spent  
245 on the “kairomone arena”. We handled these two behaviours together because they are both  
246 directly involved in host searching in *V. canescens* (Rogers, 1972). We then used the  
247 individual coordinates on the first and second principal components (PC1 and PC2  
248 representing 33.8% and 26.7% of total variance respectively) of this PCA to assign two  
249 activity scores to each individual. The total distance moved, mean speed and, to a lesser  
250 extent, total movement duration contributed mainly to PC1 (see Figure A4 and Table A1 in  
251 the Appendix), so the matching activity score 1, hereafter “movement activity”, represented  
252 the general level of insect movement during trial. The mean angular velocity and the total  
253 duration of *probing* plus *antennating* contributed mostly to PC2 (see Figure A4 and Table A1  
254 in the Appendix), so the matching activity score 2, hereafter “exploitation activity”,  
255 represented the exploitation intensity of a host-mimicking patch, a high score corresponding  
256 to a high level of patch exploitation activity. The two activity scores followed a Gaussian  
257 distribution, so we fitted a linear mixed model (LMM) for each score with the female identity  
258 as a random effect (Female), the day of measure and the kairomone solution used to mimic a  
259 host patch (because we had to prepare some additional solution during experiments; factor S1  
260 vs. S2) as fixed effects (Day and Solution) and their interaction (Day:Solution) in the models.

261 We estimated the repeatabilities of exploration, movement activity and patch exploitation  
262 activity with the package *rptR* (Stoffel, Nakagawa, & Schielzeth, 2017). We tested the  
263 statistical significance of repeatability estimates using likelihood ratio tests (LRTs) over one

264 degree of freedom, and obtained their 95% confidence intervals with parametric bootstrapping  
265 (Nakagawa & Schielzeth, 2010). For the exploration score model (non-Gaussian data),  
266 statistical significance of the fixed effect was tested with a LRT combined to parametric  
267 bootstrapping to obtain a more accurate p-value (Bolker et al., 2009; Faraway, 2006, p. 175).  
268 For movement activity and patch exploitation activity models, statistical significance of fixed  
269 effects was based on F-statistic.

#### 270 *Correlations between behavioural traits: testing the presence of a behavioural syndrome*

271 When two behavioural traits hold significant between-individual variation, we decomposed  
272 their phenotypic correlation into between- and within-individual correlations in order to test  
273 for a behavioural syndrome, defined as a nonzero between-individual correlation  
274 (Dingemanse & Dochtermann, 2013). We built two bivariate GLMMs (package *MCMCglmm*;  
275 Hadfield, 2010) to partition the phenotypic correlation and estimate the between-individual  
276 correlation between exploration and movement activity, and between exploration and patch  
277 exploitation activity. These models had Gaussian and binomial error structures, and we fitted  
278 the female identity (Female) as random effect and the day of measure (Day) as fixed effect.  
279 The between-individual correlation was considered significant if its 95% credibility interval  
280 (equivalent to confidence interval) did not overlap zero.

#### 281 *Correlations between behavioural traits and life history traits*

282 We considered three life history traits: offspring production rate, which is the total number of  
283 offspring emerging from the hosts provided in the 40-minute trial in the “labyrinth” setup, egg  
284 load and longevity. As exploration and both movement and patch exploitation activities were  
285 not structured in a behavioural syndrome (see Results), we subsequently calculated the  
286 individual mean score for each of the three behavioural traits, using all the repeats available  
287 for each individual. The mean behavioural scores were fitted in generalised linear models

288 (GLM) to assess their correlation with life history traits. We built Poisson models with log  
289 link for count data, correcting for over-dispersion if needed, that had offspring production rate  
290 and egg load as responses, and the mean behavioural scores of exploration, movement activity  
291 and patch exploitation activity, as well as tibia length, as explanatory variables. To test the  
292 relationship between longevity and mean behavioural scores, we built two Cox proportional  
293 hazards models with the mean behavioural scores and tibia length as explanatory variables,  
294 using the package *survival* (Therneau, 2015).

## 295 RESULTS

### 296 *Consistent Individual Differences Exploration and Activity*

297 *Venturia canescens* exhibit consistent between individual differences in exploration (Table 1),  
298 with between individual variation explaining 10% of the behavioural variance after  
299 controlling for the effects of the day of measure and type of solution (Table 1).

300

301 Females thus expressed different behavioural types. Some individuals, like female 87 that  
302 obtained four exploration scores of “1” on the four days of measure (Figure 2), were  
303 consistently more exploratory, whereas some individuals, like females 15 and 96 that obtained  
304 four exploration scores of “0” on the four days of measure (Figure 2), were consistently less  
305 exploratory. We also observed that the day of measure had an influence on the exploration  
306 score (Table 1). But despite this day-to-day variation, the individual rank differences  
307 remained constant.

308 Female wasps also differed consistently in activity, both in movement activity and patch  
309 exploitation activity, given that the repeatabilities of the two scores were significantly  
310 different from zero (Table 1; Figure 3). These consistent individual differences in movement

311 activity and patch exploitation activity explained 34% and 32% of the total behavioural  
312 variance, respectively (Table 1). We detected a significant interaction between the predictors  
313 Day and Solution for the movement activity, as well as a significant effect of each predictor  
314 separately (Table 1). The movement activity was lower with the solution S1 than with the  
315 solution S2, and it decreased with time with both solutions, yet decreasing faster for solution  
316 S1 (Figure 4). We also observed that patch exploitation activity decreased with time, but there  
317 was only a tendency for an effect of the kairomone solution used, and no significant  
318 interaction between the two predictors (Table 1).

319

#### 320 *Existence of a Behavioural Syndrome Involving Exploration and Activity in V. canescens*

321 We did not find evidence for the existence of a behavioural syndrome in *V. canescens*. The  
322 between-individual correlations between exploration and movement activity, and between  
323 exploration and patch exploitation activity were both non-significant (Table 2). If we adopt a  
324 more restrictive method, using only the behavioural traits measured at the same time and not  
325 all the repeats for each trait (Dingemanse & Dochtermann, 2013), the result was qualitatively  
326 unchanged.

327

328

#### 329 *Appraisal of a POLS in V. canescens: Correlations between Behavioural and Life History*

##### 330 *Traits*

331 We found no significant relationships between the three life history traits studied and the  
332 individual behavioural types (Table 3). We did not test the feeding activity of the insects  
333 because it showed little variability.



334

335

## 336 DISCUSSION

337 Our results showed consistent individual differences, thus behavioural types, in  
338 exploration and both movement activity and patch exploitation activity in *V. canescens*.  
339 Assuming that these traits increase resource acquisition at the expense of survival, the POLS  
340 hypothesis predicted on one hand positive correlations between individual's exploration and  
341 activity types and their egg load and offspring production rate, and on the other hand a  
342 negative correlation between these behavioural traits and longevity. However, in our  
343 laboratory experiment, behavioural types in *Venturia canescens* neither correlated to each  
344 other to form a syndrome, nor correlated to the life history traits tested.

345 The repeatability ( $R$ ) value of exploration is low in *V. canescens* (about 0.10) and goes  
346 along with a p-value close to the significance threshold of 0.05. This might be due to the  
347 binary variable used as the exploration score, which was required by the bimodal distribution  
348 of data (see Figure A3 in the Appendix). It may have masked some of the between-individual  
349 variability, leading to a decrease in statistical power. However, similar  $R$  values have been  
350 found in other species such as the field cricket *Gryllus campestris* (two behavioural traits  
351 measuring boldness with  $R = 0.114$  and  $R = 0.160$ ; Niemelä, Lattenkamp, & Dingemanse,  
352 2015) or the fairy-wren *Malurus cyaneus* (activity:  $R = 0.14$ ; boldness:  $R = 0.10$ ; Hall et al.,  
353 2015). Moreover, low  $R$  values between 0.08 and 0.15 represent 10.7% of the repeatability  
354 estimates reported in 114 personality studies on 13 different behavioural traits (Bell et al.,  
355 2009). Concerning activity, consistent between-individual differences have been described in  
356 other insect species as well (firebug *Pyrrhocoris apterus* Gyuris, Feró, & Barta, 2012;  
357 mealworm beetle *Tenebrio molitor* Monceau et al., 2017). The repeatability values of both  
358 movement activity and patch exploitation activity in *V. canescens* (respectively 0.34 and 0.32)

359 match the average repeatability of behaviour reported in a meta-analysis on 114 studies  
360 representing 98 animal species (0.37; Bell et al., 2009). However, one can expect some  
361 behaviours to be less repeatable than others because they are more sensitive to environmental  
362 conditions for instance (Bell et al., 2009). Finding host resources in the field is challenging  
363 due to the heterogeneity of the environment and the complexity of cues animals have to deal  
364 with. To locate hosts, parasitoids do rely on various stimuli from the environment, chemical,  
365 visual or vibrational. This may lead to a high flexibility of exploration, explaining its low  
366 value of repeatability.

367         Determining the evolutionary and ecological consequences of behavioural types  
368 requires investigating their link with life history traits and their impacts on organism fitness.  
369 In *Venturia canescens*, exploration and activity are involved in food, mate and especially host  
370 searching. In the field host are scattered and concealed inside dried fruits (Driessen &  
371 Bernstein, 1999), we hence expect that the more the female is explorative, the higher its  
372 ability to find host aggregates, leading to a positive correlation between exploration and  
373 fecundity. While on the host patches, activity of females' likely influence their patch  
374 residence time which is positively correlated with fitness in parasitoids (van Alphen,  
375 Bernstein, & Driessen, 2003). However, both exploration in search for host patches and  
376 exploitation of host on the patch are physiologically costly, thereby reducing survival. We  
377 hence expected a correlation between these behavioural traits and the three life history traits  
378 tested. More precisely, we expected a positive correlation between risk-taking behaviours and  
379 fecundity investment represented by egg load and offspring production rate, but a negative  
380 correlation between risk-taking behaviour and longevity. However, under laboratory  
381 conditions, our data did not show such relationship. However, absence of correlation at  
382 phenotypic level does not mean that correlations cannot occur at genetic level. In the  
383 Mediterranean field cricket (*Gryllus bimaculeatus*), correlation patterns of behavioural and

384 life history traits at phenotypic and genetic levels differed, which is probably due to a  
385 masking effect of the environment (Santostefano, Wilson, Niemelä, & Dingemanse, 2017).  
386 The authors found genetic relationships between exploration and aggression with lifespan but  
387 these behaviours did not mediate the life-history trade-off between development time and  
388 lifespan (Santostefano et al., 2017).

389         Our experimental design and metric choice may have prevented us to detect an  
390 existing POLS in *V. canescens*. In fact, the POLS hypothesis predicts equal lifetime fitness  
391 between slow and fast strategies, which explains their coexistence. However, in our  
392 experiment, we measured the offspring production rate of individuals on a short time scale  
393 relative to their lifetime. *V. canescens* can indeed live more than two weeks in the laboratory  
394 if well-fed (Desouhant et al., 2005). A repeated measure of offspring production rate across  
395 the lifespan of the insects would have been relevant to test the correlation of lifetime  
396 reproductive success with behaviours in the POLS framework (Dammhahn, Dingemanse,  
397 Niemelä, & Réale, 2018; Niemelä & Dingemanse, 2018). Moreover, the POLS hypothesis is  
398 based on trade-offs between growth, reproduction and survival (Biro & Stamps, 2008), or  
399 more broadly on the trade-off between current and future reproduction (Dammhahn et al.,  
400 2018). Ecological conditions, and especially the variation in resource acquisition, can thereby  
401 influence the detection of this trade-off hence the existence of a slow-fast continuum in a  
402 population (Montiglio, Dammhahn, Dubuc Messier, & Réale, 2018). Our laboratory  
403 experiment, with *ad libitum* food and no predation, may thus have weakened the strength of  
404 correlations between life history traits and behavioural types. This was observed in the spider  
405 *Latrodectus hesperus*, where the resources available during development influenced life-  
406 history strategies and the individual consistency of associated behaviours such as foraging and  
407 web building (DiRienzo & Montiglio, 2016). Nevertheless, in our study the favourable  
408 conditions were necessary for the insects to survive long enough and thus perform all the

409 behavioural tests, and to avoid state-dependent behavioural responses in terms of foraging  
410 (Castelo et al., 2003) and patch exploitation (Lucchetta, Desouhant, Wajnberg, & Bernstein,  
411 2007).

412 Even though no relationship was found between exploratory behaviour and offspring  
413 production rate in our experiment, the existence of behavioural types likely influences female  
414 capacities to find and exploit host aggregates, thus their fitness, due to the concealment of  
415 hosts in the wild. These host patches are relatively rare and homogeneously distributed in  
416 natural habitats (Pelosse et al., 2007). Dispersal has been shown to be positively correlated to  
417 exploration in numerous species such as in great tit (Dingemanse, Both, van Noordwijk,  
418 Rutten, & Drent, 2003), we can thus suppose that the most explorative and active *V.*  
419 *canescens* females may have a higher probability of finding hosts and food in a natural  
420 context than less explorative ones, leading to a selection for the more explorative individuals.  
421 However, we observed behavioural type variability in our population of arrhenotokous *V.*  
422 *canescens*. In natural habitats like orchards, the wasps experience fluctuating environmental  
423 conditions, hence varying selection pressures. This variability of behavioural types might  
424 therefore be selected for. Indeed, populations displaying various behavioural types seem less  
425 vulnerable to environmental changes (Wolf & Weissing, 2012).

426 Behavioural types have been found in various insect species, and our study shows that  
427 these also exist in parasitoids such as *Venturia canescens*. Because insects might be pests or  
428 provide ecosystem services, such as pollination or pest management (*e.g.* with parasitoid  
429 species), and because behavioural types might be involved in species interactions, population  
430 dynamics or response to novel environment (Sih et al., 2012), studying parasitoid personality  
431 may influence ecosystem management policies in biocontrol of pest species. Some studies  
432 have already shown the effect of different behavioural types on biocontrol agent efficacy, for  
433 instance the impact of the activity level of the spider *Trochosa ruricola* on herbivorous insect

434 communities (Keiser, Snyder, Carson, & Pruitt, 2015). However, further experiments would  
435 be needed to measure parasitism efficiency in relation to behavioural types at larger spatial  
436 and temporal scales, for instance through measurements of the life time reproductive success.  
437 These experiments would allow choosing efficient biocontrol agents and optimizing their  
438 impact on pest control. Simultaneously, field experiments comparing the parasitism efficiency  
439 of populations displaying a single behavioural type *versus* populations with a mixture of  
440 behavioural types would be needed to determine the importance of intraspecific behavioural  
441 variation to pest management (Royauté & Pruitt, 2015).

442

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620 Table 1. Repeatability *R* of the three behavioural traits tested (exploration, movement activity, patch exploitation  
 621 activity) with its standard error (SE), 95% confidence interval (*CI*) and P-value (*P*).

| <b>Trait</b>                       | <b>N</b> | <b>Random effect</b> |                    |          | <b>Fixed effects</b> |                     |          |
|------------------------------------|----------|----------------------|--------------------|----------|----------------------|---------------------|----------|
|                                    |          | <i>R</i><br>(SE)     | <i>CI</i><br>(95%) | <i>P</i> | $\chi^2_3$           |                     | <i>P</i> |
| <b>Exploration</b>                 | 55       | 0.103<br>(0.069)     | [0 , 0.259]        | 0.049    |                      |                     |          |
| Day                                |          |                      |                    |          | 11.502               |                     | 0.009    |
|                                    |          |                      |                    |          | <i>F</i>             | <i>NUMdf, DENdf</i> | <i>P</i> |
| <b>Movement activity</b>           | 57       | 0.342<br>(0.075)     | [0.197 , 0.486]    | <0.001   |                      |                     |          |
| Day                                |          |                      |                    |          | 11.530               | 3, 159.20           | <0.001   |
| Solution                           |          |                      |                    |          | 14.304               | 1, 54.85            | <0.001   |
| Day:Solution                       |          |                      |                    |          | 5.065                | 3, 159.20           | 0.002    |
| <b>Patch Exploitation activity</b> | 57       | 0.321<br>(0.075)     | [0.164 , 0.458]    | <0.001   |                      |                     |          |
| Day                                |          |                      |                    |          | 23.202               | 3, 159.29           | <0.001   |
| Solution                           |          |                      |                    |          | 3.427                | 1, 54.84            | 0.07     |
| Day:Solution                       |          |                      |                    |          | 1.186                | 3, 159.26           | 0.317    |

622 The table also shows the effects of two fixed predictors: the day of measure (Day; for exploration, movement  
 623 and patch exploitation) and the kairomone solution used (Solution) along with their interaction (Day:Solution)  
 624 for movement and patch exploitation activities only. *NUMdf* and *DENdf* stand for numerator degrees of freedom  
 625 and denominator degrees of freedom respectively. These results were obtained from GLMMs (for exploration)  
 626 and LMMs (for movement and patch exploitation).

627

628 Table 2. Between-individual correlations between exploration, movement activity and patch exploitation  
629 activity.

| <b>Trait 1</b> | <b>Trait 2</b>              | <b>Between-individual correlation [HPD 95%]</b> |
|----------------|-----------------------------|---|
| Exploration    | Movement activity           | 0.119 [-0.422 , 0.694]                          |
| Exploration    | Patch exploitation activity | -0.123 [-0.651 , 0.414]                         |

630 These correlations were obtained with bivariate mixed models ( $N = 53$  individuals for each model) and the table  
631 shows, for each correlation, its 95% credibility interval (HPD). A correlation is non-significant when its HPD  
632 overlaps zero.

633  
634

635 Table 3. Relationships between life history and behavioural traits.

|  | <i>N</i> | <i>F</i>            | <i>NUMdf,</i><br><i>DENdf</i> | <i>P</i> |
|--|----------|---------------------|-------------------------------|----------|
| <b>Egg load</b> ~ Exploration                          | 25       | 0.026               | 1, 24                         | 0.873    |
| <b>Egg load</b> ~ Movement activity+                   | 27       | 0.13                | 1,26                          | 0.722    |
| Patch exploitation activity                            |          | 0.064               | 1,26                          | 0.803    |
| <b>Offspring production rate</b> ~ Exploration         | 52       | 0.917               | 1, 51                         | 0.410    |
| <b>Offspring production rate</b> ~ Movement activity + | 50       | 2.286               | 1, 49                         | 0.137    |
| Patch Exploitation activity                            |          | 0.057               | 1, 49                         | 0.813    |
|  |          | <i>Hazard ratio</i> | <i>z</i>                      |          |
| <b>Longevity</b> ~ Exploration                         | 27       | 1.51                | 0.567                         | 0.571    |
| <b>Longevity</b> ~ Movement activity +                 | 28       | 1.471               | 1.382                         | 0.167    |
| Patch exploitation activity                            |          | 1.008               | 0.023                         | 0.982    |

636 The results for the response variables “Egg load” and “Offspring production rate” were obtained from Poisson  
637 GLMs (with log link), and the results for the response variable “Longevity” were obtained from Cox  
638 proportional hazards models. *NUMdf* and *DENdf* stand for numerator degrees of freedom and denominator  
639 degrees of freedom respectively.

640

641



642 APPENDIX

643 Table A1. Contributions (in percentage) on the two principal components of the PCA (PCA1 & PCA2) for the  
644 five activity variables.

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|   | <b>PC1</b> | <b>PC2</b> |
|---|------------|------------|
| Total distance moved                                    | 46.55      | 1.00       |
| Mean speed  | 28.37      | 6.79       |
| Mean angular velocity                                   | 0.004      | 38.97      |
| Total movement duration                                 | 14.83      | 12.72      |
| Total duration of <i>probing</i> and <i>antennating</i> | 10.24      | 40.51      |

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645

646

647 Figure 1. Organisation of a five-day session of data collection. From day 1 (D1) to day 5  
648 (D5), the figure shows the tasks and experiments performed each day (AM: morning, PM:  
649 afternoon). After the quantification of offspring production rate, the insects were split in two  
650 groups (see arrows) to measure egg load and longevity.

651 Figure 2. Exploration score (“0” black circles or “1” grey triangles) obtained by each  
652 individual ( $N = 55$ ) on the four days of measure (excepting for individuals 21, 53 and 83 that  
653 have only been tested three times). We ordered the individuals according to the number of  
654 scores of “1” they obtained.

655 Figure 3. Individual variation in movement activity (a) and patch exploitation activity (b) ( $N =$   
656  $57$  each). The individual boxplots are classified by ascending order, based on their median  
657 score (boxplot black lines).

658 Figure 4. Representation of the interaction between the day of measure and the kairomone  
659 solution used to mimic a host patch, for the movement activity. Vertical bars represent  
660 standard errors.

661

662

663 APPENDIX

664 Figure A1. Schema of the experimental setup used to assess the consistency of individual  
665 differences in exploration in *Venturia canescens* females. Two obstacles are placed in the  
666 tube: (a) a plasticised disc with six 1-cm square holes, represented by the white squares on the  
667 figure; (b) a plasticised funnel with an exit diameter of 1.5 cm. The obstacles define three  
668 zones in the tube: Zone 1 (between the entrance and the obstacle 1), Zone 2 (between the  
669 obstacles) and Zone 3 (between the obstacle 2 and the end of the tube). The three zones and  
670 the two obstacles define five steps to cross for the insects.

671 Figure A2. Schemas of the experimental setup used to assess the egg-laying rate of *V.*  
672 *canescens* females. **Left panel:** image of the labyrinth seen from the top containing three host  
673 patches (H) and a food patch (F). A fan, located outside the labyrinth (top), blows air in the  
674 setup (symbolised by the little dark arrows). The labyrinth entrance is located in the bottom  
675 left-hand corner; the crosses associated with the letter a represent the five gaps in the labyrinth  
676 walls and the crosses associated with the letter b represent the gaps allowing the air blown by  
677 the fan to circulate throughout the setup. **Right panel:** detailed drawings of (a) a gap located  
678 on an inside wall of the labyrinth and (b) a ventilation gap located on the edges of the  
679 labyrinth

680 Figure A3. Distribution of the variable corresponding to the total number of steps passed in  
681 the tube by the insects, in the experiment testing for the presence of consistent individual  
682 differences in exploration behaviour.

683 Figure A4: Circle representing the correlation between the five variables and the two principal  
684 components (PC1 & PC2) of the PCA on activity data. These variables are the mean speed  
685 “Mean.Speed”, the total distance moved “Dist.Moved”, the total movement duration  
686 “Mov.Duration”, the mean angular velocity “Ang.Velocity” and the duration of *probing* and  
687 *antennating* weighted by the patch residence time “ProbAnt”.

688

689

**D1****D2****D3****D4****D5****AM**Emergence  
Mating

Exploration test (1)

Exploration test (2)

Exploration test (3)

Exploration test (4)

**PM**

Activity test (1)

Activity test (2)

Activity test (3)

Activity test (4)

Quantification of  
offspring production  
rate





