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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).

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

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

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

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

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

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

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

### *Consistent individual differences in exploration*



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

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

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

#### *Consistent individual differences in activity*

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

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

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

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

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

#### *Offspring production rate*

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

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

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

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

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

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

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

#### *Ethical Note*

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

#### *Statistical Analyses*

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

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

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

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

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

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

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

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

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

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

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

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

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

## RESULTS

### *Consistent Individual Differences Exploration and Activity*

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

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

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

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

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

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

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

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



## DISCUSSION

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

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

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

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

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

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

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

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

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

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

## REFERENCES

- Adriaenssens, B., & Johnsson, J. I. (2011). Shy trout grow faster: exploring links between personality and fitness-related traits in the wild. *Behavioral Ecology*, 22(1), 135–143. <https://doi.org/10.1093/beheco/arq185>
- Amat, I., Desouhant, E., Gomes, E., Moreau, J., & Monceau, K. (2018). Insect personality: what can we learn from metamorphosis? *Current Opinion in Insect Science*, 27, 46–51. <https://doi.org/10.1016/j.cois.2018.02.014>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *ArXiv:1406.5823 [Stat]*. Retrieved from <http://arxiv.org/abs/1406.5823>
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77(4), 771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>
- Bielby, J., Mace, G. M., Bininda-Emonds, O. R. P., Cardillo, M., Gittleman, J. L., Jones, K. E., ... Purvis, A. (2007). The Fast-Slow Continuum in Mammalian Life History: An Empirical Reevaluation. *The American Naturalist*, 169(6), 748–757. <https://doi.org/10.1086/516847>
- Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23(7), 361–368. <https://doi.org/10.1016/j.tree.2008.04.003>
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3), 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>

- Castelo, M. K., Corley, J. C., & Desouhant, E. (2003). Conspecific Avoidance During Foraging in *Venturia canescens* (Hymenoptera: Ichneumonidae): The Roles of Host Presence and Conspecific Densities. *Journal of Insect Behavior*, 16(2), 307–318. <https://doi.org/10.1023/A:1023928204793>
- Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., & Réale, D. (2018). Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history. *Behavioral Ecology and Sociobiology*, 72(3), 62. <https://doi.org/10.1007/s00265-018-2473-y>
- Desouhant, E., Driessen, G., Amat, I., & Bernstein, C. (2005). Host and food searching in a parasitic wasp *Venturia canescens*: A trade-off between current and future reproduction? *Animal Behaviour*, 70(1), 145–152. <https://doi.org/10.1016/j.anbehav.2004.10.015>
- Desouhant, E., Lucchetta, P., Giron, D., & Bernstein, C. (2010). Feeding activity pattern in a parasitic wasp when foraging in the field. *Ecological Research*, 25(2), 419–428. <https://doi.org/10.1007/s11284-009-0671-9>
- Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, 64(6), 929–938. <https://doi.org/10.1006/anbe.2002.2006>
- Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences*, 270(1516), 741–747. <https://doi.org/10.1098/rspb.2002.2300>
- Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology*, 82(1), 39–54. <https://doi.org/10.1111/1365-2656.12013>

491 DiRienzo, N., & Montiglio, P.-O. (2016). The contribution of developmental experience vs.  
 492 condition to life history, trait variation and individual differences. *Journal of Animal*  
 493 *Ecology*, 85(4), 915–926. <https://doi.org/10.1111/1365-2656.12512>

494 Dray, S., & Dufour, A.-B. (2007). The ade4 package: implementing the duality diagram for  
 495 ecologists. *Journal of Statistical Software*, 22(4), 1–20.

496 Driessen, G., & Bernstein, C. (1999). Patch departure mechanisms and optimal host  
 497 exploitation in an insect parasitoid. *Journal of Animal Ecology*, 68(3), 445–459.  
 498 <https://doi.org/10.1046/j.1365-2656.1999.00296.x>

499 Faraway, J. J. (2006). *Extending the linear model with R: generalized linear, mixed effects*  
 500 *and nonparametric regression models* (Vol. 124). CRC press.

501 Gyuris, E., Feró, O., & Barta, Z. (2012). Personality traits across ontogeny in firebugs,  
 502 *Pyrhocoris apterus*. *Animal Behaviour*, 84(1), 103–109.  
 503 <https://doi.org/10.1016/j.anbehav.2012.04.014>

504 Hadfield, J. D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed  
 505 Models: The MCMCglmm R Package. *Journal of Statistical Software*, 33(2), 1–22.

506 Hall, M. L., van Asten, T., Katsis, A. C., Dingemanse, N. J., Magrath, M. J. L., & Mulder, R.  
 507 A. (2015). Animal personality and pace-of-life syndromes: do fast-exploring fairy-  
 508 wrens die young? *Frontiers in Ecology and Evolution*, 3.  
 509 <https://doi.org/10.3389/fevo.2015.00028>

510 Harvey, J. A., & Thompson, D. J. (1995). Developmental interactions between the solitary  
 511 endoparasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae), and two of its  
 512 hosts, *Plodia interpunctella* and *Corcyra cephalonica* (Lepidoptera: Pyralidae).  
 513 *European Journal of Entomology*, 92(2), 427–435.

514 Harvey, J. A., & Vet, L. E. M. (1997). *Venturia canescens* parasitizing *Galleria mellonella*  
 515 and *Anagasta kuehniella*: differing suitability of two hosts with highly variable growth



potential. *Entomologia Experimentalis et Applicata*, 84(1), 93–100.

<https://doi.org/10.1046/j.1570-7458.1997.00202.x>

Keiser, C. N., Slyder, J. B., Carson, W. P., & Pruitt, J. N. (2015). Individual differences in predators but not producers mediate the magnitude of a trophic cascade. *Arthropod-Plant Interactions*, 9(3), 225–232. <https://doi.org/10.1007/s11829-015-9377-9>

Kralj-Fišer, S., & Schuett, W. (2014). Studying personality variation in invertebrates: why bother? *Animal Behaviour*, 91, 41–52. <https://doi.org/10.1016/j.anbehav.2014.02.016>

Leach, I. M., Ferber, S., Zande, L. van de, & Beukeboom, L. W. (2012). Genetic variability of arrhenotokous and thelytokous *Venturiacanesens* (Hymenoptera). *Genetica*, 140(1–3), 53–63. <https://doi.org/10.1007/s10709-012-9657-6>

Lucchetta, P., Bernstein, C., Théry, M., Lazzari, C., & Desouhant, E. (2008). Foraging and associative learning of visual signals in a parasitic wasp. *Animal Cognition*, 11(3), 525–533. <https://doi.org/10.1007/s10071-008-0144-5>

Lucchetta, P., Desouhant, E., Wajnberg, E., & Bernstein, C. (2007). Small but smart: the interaction between environmental cues and internal state modulates host-patch exploitation in a parasitic wasp. *Behavioral Ecology and Sociobiology*, 61(9), 1409–1418. <https://doi.org/10.1007/s00265-007-0372-8>

Michalko, R., Košulič, O., & Řežucha, R. (2017). Link between Aggressiveness and Shyness in the Spider *Philodromus albidus* (Araneae, Philodromidae): State Dependency over Stability. *Journal of Insect Behavior*, 30(1), 48–59. <https://doi.org/10.1007/s10905-017-9596-2>

Modlmeier, A. P., Keiser, C. N., Wright, C. M., Lichtenstein, J. L., & Pruitt, J. N. (2015). Integrating animal personality into insect population and community ecology. *Current Opinion in Insect Science*, 9(Supplement C), 77–85. <https://doi.org/10.1016/j.cois.2015.03.008>

541 Monceau, K., Dechaume-Moncharmont, F.-X., Moreau, J., Lucas, C., Capoduro, R., Motreuil,  
542 S., & Moret, Y. (2017). Personality, immune response and reproductive success: An  
543 appraisal of the pace-of-life syndrome hypothesis. *The Journal of Animal Ecology*.  
544 <https://doi.org/10.1111/1365-2656.12684>

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

549 Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a  
550 practical guide for biologists. *Biological Reviews*, 85(4), 935–956.  
551 <https://doi.org/10.1111/j.1469-185X.2010.00141.x>

552 Niemelä, P. T., & Dingemanse, N., J. (2018). On the usage of single measurements in  
553 behavioural ecology research on individual differences. *Animal behaviour*, 145, 99-  
554 105. <https://doi.org/10.1016/j.anbehav.2018.09.012>

555 Niemelä, P. T., Lattenkamp, E. Z., & Dingemanse, N. J. (2015). Personality-related survival  
556 and sampling bias in wild cricket nymphs. *Behavioral Ecology*, 26(3), 936–946.  
557 <https://doi.org/10.1093/beheco/arv036>

558 Pelosse, P., Bernstein, C., & Desouhant, E. (2007). Differential energy allocation as an  
559 adaptation to different habitats in the parasitic wasp *Venturia canescens*. *Evolutionary*  
560 *Ecology*, 21(5), 669–685. <https://doi.org/10.1007/s10682-006-9145-5>

561 R Core Team. (2016). R: A language and environment for statistical computing. *R*  
562 *Foundation for Statistical Computing, Vienna, Austria*. Retrieved from  
563 <https://www.R-project.org/>

564 Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male  
565 personality, life-history strategies and reproductive success in a promiscuous mammal.

566 *Journal of Evolutionary Biology*, 22(8), 1599–1607. <https://doi.org/10.1111/j.1420->  
567 9101.2009.01781.x

568 Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O.  
569 (2010). Personality and the emergence of the pace-of-life syndrome concept at the  
570 population level. *Philosophical Transactions of the Royal Society B: Biological*  
571 *Sciences*, 365(1560), 4051–4063. <https://doi.org/10.1098/rstb.2010.0208>

572 Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating  
573 animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–  
574 318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>

575 Rogers, D. (1972). The Ichneumon Wasp *Venturia Canescens*: Oviposition and Avoidance of  
576 Superparasitism. *Entomologia Experimentalis et Applicata*, 15(2), 190–194.  
577 <https://doi.org/10.1111/j.1570-7458.1972.tb00195.x>

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

581 Royauté, R., Greenlee, K., Baldwin, M., & Dochtermann, N. A. (2015). Behaviour,  
582 metabolism and size: phenotypic modularity or integration in *Acheta domesticus*?  
583 *Animal Behaviour*, 110, 163–169. <https://doi.org/10.1016/j.anbehav.2015.09.027>

584 Royauté, R., & Pruitt, J. N. (2015). Varying predator personalities generates contrasting prey  
585 communities in an agroecosystem. *Ecology*, 96(11), 2902–2911.  
586 <https://doi.org/10.1890/14-2424.1>

587 Salt, G. (1975). The fate of an internal parasitoid, *Nemeritis canescens*, in a variety of insects.  
588 *Transactions of the Royal Entomological Society of London*, 127(2), 141–161.  
589 <https://doi.org/10.1111/j.1365-2311.1975.tb00562.x>

590 Santostefano, F., Wilson, A. J., Niemelä, P. T., & Dingemanse, N. J. (2017). Behavioural  
591 mediators of genetic life-history trade-offs: a test of the pace-of-life syndrome  
592 hypothesis in field crickets. *Proc. R. Soc. B*, 284(1864), 20171567.  
593 <https://doi.org/10.1098/rspb.2017.1567>

594 Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and  
595 evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378.  
596 <https://doi.org/10.1016/j.tree.2004.04.009>

597 Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of  
598 behavioural syndromes. *Ecology Letters*, 15(3), 278–289.  
599 <https://doi.org/10.1111/j.1461-0248.2011.01731.x>

600 Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-  
601 analysis. *Behavioral Ecology*, 19(2), 448–455. <https://doi.org/10.1093/beheco/arm144>

602 Stamps, J. A. (2007). Growth-mortality tradeoffs and ‘personality traits’ in animals. *Ecology*  
603 *Letters*, 10(5), 355–363. <https://doi.org/10.1111/j.1461-0248.2007.01034.x>

604 Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and  
605 variance decomposition by generalized linear mixed-effects models. *Methods in*  
606 *Ecology and Evolution*. <https://doi.org/10.1111/2041-210X.12797>

607 Therneau, T. (2015). A Package for Survival Analysis in S. R package version 2.37-7. 2014.  
608 *URL Http://CRAN.R-Project.Org/Package= Survival.*

609 van Alphen, J. J. M., Bernstein, C., & Driessen, G. (2003). Information acquisition and time  
610 allocation in insect parasitoids. *Trends in Ecology & Evolution*, 18(2), 81–87.  
611 [https://doi.org/10.1016/S0169-5347\(02\)00035-6](https://doi.org/10.1016/S0169-5347(02)00035-6)

612 Van Santen, M. C. P., & Schneider, M. V. (2002). Courtship description in the solitary  
613 parasitoid wasp *Venturia canescens* (Hymenoptera). In *Proceedings of Experimental*  
614 *and Applied Entomology, NEV Amsterdam* (Vol. 13, pp. 87–92).

615 Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and  
616 evolution. *Trends in Ecology & Evolution*, 27(8), 452–461.  
617 <https://doi.org/10.1016/j.tree.2012.05.001>  
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Table 1. Repeatability  $R$  of the three behavioural traits tested (exploration, movement activity, patch exploitation activity) with its standard error (SE), 95% confidence interval ( $CI$ ) and P-value ( $P$ ).

Trait	N	Random effect			Fixed effects		
		$R$ (SE)	$CI$ (95%)	$P$	$\chi^2_3$		$P$
<b>Exploration</b>	55	0.103 (0.069)	[0 , 0.259]	0.049			
Day					11.502		0.009
<b>Movement activity</b>	57	0.342 (0.075)	[0.197 , 0.486]	<0.001	$F$	$NUMdf, DENdf$	$P$
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 (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

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

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> , <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.

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641



APPENDIX

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

	PC1	PC2
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

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

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

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

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

## APPENDIX

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

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

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

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







