Larval personality does not predict adult personality in a holometabolous insect

KARINE MONCEAU*, JÉRÔME MOREAU, JULIENNE RICHET, SÉBASTIEN MOTREUIL, YANNICK MORET and FRANÇOIS-XAVIER DECHAUME-MONCHARMONT

UMR CNRS 6282 Biogéosciences, Equipe Ecologie Evolutive, Université de Bourgogne-Franche-Comté, 6 bd Gabriel, 21000 Dijon, France

Received 29 August 2016; revised 6 September 2016; accepted for publication 7 October 2016

Although personality (consistent inter-individual differences in behavioural traits across time and/or contexts) and behavioural syndromes (suites of correlated personality traits) have been widely studied in the last decades, the origin and development of these traits during ontogeny are still underexplored. In this context, species undergoing metamorphosis are of special interest. To date, however, the persistence of personality traits has been only little investigated in organisms undergoing complete metamorphosis such as in holometabolous insects, although this kind of studies may provide important insights from a functional point of view. Here, we tested whether the personality and the behavioural syndrome are maintained through metamorphosis in *Tenebrio molitor*, a holometabolous insect species. We found that personality and behavioural syndrome were present in both larval and adult stages. However, larval personality and behavioural syndrome did not predict adult behaviour. We suggest that the complete reorganization during metamorphosis may have profound effect on the behaviour of the beetles. These results challenge the established common thought that personality should persist along an individual lifespan.


INTRODUCTION

In the last decades, animal personality has received considerable interest due to its multiple implications in ecological and evolutionary processes (Chapple, Simmonds & Wong, 2012; Wolf & Weissing, 2012; Carere & Gherardi, 2013; David & Dall, 2016; Modlmeier et al., 2015). Many studies have shown the existence of personality traits (i.e. consistent inter-individual differences in behavioural traits across time and/or contexts, Réale et al., 2007) and behavioural syndromes (suites of personality traits correlated to each other, Réale et al. 2007), both in vertebrates and invertebrates (Bell, Hankison & Laskowski, 2009; Kralj-Fišer & Schuett, 2014). Although the major part of the literature aims at understanding how these consistent inter-individuals differences across contexts can be maintained and evolve in natural populations (see Carere & Maestripieri, 2013 for a review), the genesis of personality traits and how they progress during ontogeny are still underexplored (Stamps & Groothuis, 2010; Wilson & Krause, 2012a; Herde & Eccard, 2013; Sweeney et al., 2013).

Ontogeny is characterized by successive transitions from immature to mature stages until the death of the individual. In species undergoing metamorphosis, the individuals endure an extensive reorganization of neural tissues as well as major physiological, morphological, and/or behavioural modifications (Wigglesworth, 1954; Truman & Riddiford, 2002). These physical modifications are frequently linked to ecological niche shift and are thus associated with changes in the selective pressures exerted on individuals (Stoks & Córdoba-Aguilar, 2012). Despite these fundamental changes, memory acquired during immature stages can be maintained over lifetime and influence adult behaviour. For example, the chemical recognition acquired during larval stage is maintained in adults for nest mate recognition, host and/or host plant preference.

*Corresponding author. Current address: UMR CNRS 7372 Centre d’Etudes Biologiques de Chizé, Université de la Rochelle, 79360 Villiers-en-Bois, France. E-mail: karine.monceau@univ-lr.fr
as demonstrated in Hymenoptera (Hyssopus pallidus: Gandolfi, Mattiacci & Dorn, 2003 and Aphiognostes senilis: Signorotti, Jaisson & d’Étore, 2014) and in Lepidoptera (Manduca sexta: Blackiston, Silva Casey & Weiss, 2008; Spodoptera littoralis: Proffit et al., 2015). To date, different studies have evidenced that rank order for personality traits as well as behavioural syndrome could be maintained during ontogeny (Herde & Ecard, 2013; Petelle et al., 2013; Sweeney et al., 2013; McCowan & Griffith, 2014) and across metamorphosis in anurans (Wilson & Krause, 2012b) and heterometabolous insects (both in hemimetabolous metamorphosis: Brodin, 2009 and paurometabolous metamorphosis: Gyuris, Feró & Barta, 2012; Hedrick & Kortet, 2012; Niemelä et al., 2012). Some level of plasticity could be adaptive during ontogeny (Fischer et al., 2014; Nettle & Bateson, 2015). However, the range of expression of such a plasticity is genetically determined and should exhibit inter-individual differences, which should be conserved along ontogeny (Sih et al., 2004; Wilson & Krause, 2012b). These results are in line with the work by Sokolowski (2001) on the genetic determinism of the behavioural type rover and sitter in Drosophila melanogaster. However, unlike anurans and heterometabolous insects, holometabolous insects (e.g. Diptera, Coleoptera, Lepidoptera) undergo extreme transformations during metamorphosis, including a profound remodelling of the nervous system (Kalogianis, Consoulas & Theophilidis, 1989; Consoulas et al., 2000; Tissot & Stocker, 2000). To our knowledge, although it may represent a major constraint for the evolution of personality in these insect species, the persistence of personality and behavioural syndrome in insects with complete metamorphosis has only been tested twice so far, in Phaedon cockleariae (Müller & Müller, 2015) and in Tribolium castaneum (Wexler et al., 2016). In both cases, personality traits were present in larvae or adults but were not consistent across metamorphosis.

In the present study, we tested whether personality and behavioural syndrome are maintained across the ontogeny of the holometabolous insect, Tenebrio molitor (Coleoptera: Tenebrionidae). This species represents a common pest that feeds on food resources stored for human purposes, and its use for laboratory studies presents two major advantages. First, it easily breeds under laboratory conditions closed to field conditions. Second, the neurophysiological reorganization occurring during metamorphosis has been widely studied in this species (see for example Breidbach, 1990a, b, c). Four behavioural traits, activity, exploration, food neophobia (that is a measure of boldness), and gregariousness, all commonly used to describe the different dimensions of personality (Réale et al., 2007) were tested here. Different trajectories (i.e. evolution of the traits) over the ontogeny have been found in holometabolous (Müller & Müller, 2015) and heterometabolous insect species (Brodin, 2009; Gyuris et al., 2012; Hedrick & Kortet, 2012; Niemelä et al., 2012). In T. molitor, there is neither a habitat nor dietary ontogenic shift: larvae and adults live in the same environment with overlapping generations and low dispersal, exploit the same resources, and are thus exposed to similar environmental constraints. We expected that, if existing at the larval stage, personality traits and behavioural syndrome should persist across metamorphosis in this insect species, unless the functional reorganization that occurs during metamorphosis influences the maintenance of these traits (Mather & Logue, 2013). The ontogenetic trajectories may also differ between males and females due to sexual selection. Indeed, conspicuous sex-specific behaviours such as male calling in Gryllus integer may select for lower boldness in males (Hedrick & Kortet, 2012). Since no such behaviours are known in T. molitor, we did not expect difference between females and males T. molitor for their ontogenetic trajectories.

MATERIAL AND METHODS

ETHICAL NOTE

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Tenebrio molitor larvae of different ages were obtained from a local producer (Insectes Production Vente, Dannemarie-sur-Crête, France) where they were fed on bran flour and supplemented with carrots and potatoes. They were obtained as larvae and then reared in the laboratory in large tanks (60 × 40 × 20 cm) containing a mix of bran and piglet flour (2:1 ratio), water ad libitum to limit cannibalism (Johnston & Lee, 1990), and large pieces of paper towel as refuge. No sign of parasitism or fungal/bacterial infection were observed. Insects were maintained at 28 ± 1 °C and 60 ± 5% relative humidity in the absence of light as they naturally avoid light (Cloudsley-Thompson, 1955). Experiments were performed under red light in order to create a darkness condition compatible with an observation by experimenters. Handling was restricted to the minimum required by the experiment to limit stress. The minimum number of individuals was used in this study to provide a sufficient sample size for the analyses.

GENERAL DESIGN

The experiment consisted of four behavioural tests realized sequentially in the same order for all individuals: (1) activity, (2) exploration, (3) food neophobia (i.e. reaction to a novel food source), and (4) gregariousness. All individuals were tested in the afternoon for standardization purpose. The exact lifetime of T. molitor is
highly variable according to the rearing conditions. In these experimental conditions, the adults typically live for 1–2 months. The larval developmental period is c. 160 days (see Kim et al., 2015), but the number of instars is also highly variable (from 14 to 20 instars; Park et al., 2014). Similar to the works by Wilson & Krause (2012b) and Wexler et al. (2016), we chose to repeat the sequences of the four tests on consecutive days (i.e. with a 24-h interval) for each larva or adult. Such an interval between two consecutive tests allowed assessing repeatability of the measurements within developmental stage and not across stages.

Twenty-four hours before the first test, larvae were individually isolated in Petri dishes (Ø 9 cm) containing ad libitum bran and piglet flour (2:1 ratio), water, and a piece of paper towel as refuge. Larvae significantly reduced their activity and feeding behaviour 24 h before metamorphosis as previously observed by Howard (1955), and there was no unambiguous a priori cue for assessing the time to metamorphosis. We therefore had to rely on a conservative a posteriori criterion to select our experimental individuals. Additionally, the manipulation of the larvae seemed to shorten the delay until the beginning of metamorphosis (Karine Monceau, personal observation). We thus limited our manipulation to two replicates for each behavioural test per individual at the larval and the adult stages. Only larvae for which the metamorphosis began at least 3 days after the second session of behavioural tests were considered in the analysis (n = 96, 44 females, 52 males). We also verified that no variation in activity was observed below this limit. The mean delay between the second session of larval tests and the onset of metamorphosis was 13 ± 5 days (mean ± SD, median = 12 days). After the behavioural assessments at the larval stage, larvae were kept individually in their Petri dish until adulthood in the same conditions as previously described. Therefore, they could be followed individually from the larval to the adult stages. Behavioural assessments of the adults were performed at 11 ± 1 days after emergence. All individuals were sexed after the last behavioural experiment to limit handling stress. All tests were video monitored (Sony HDR-CX405 HD Handycam), and video records were subsequently analyzed by the same person (JR) to avoid inter-observer bias in scoring (Burghardt et al., 2012).

**Behavioural tests**

The four tests were designed to quantify inter-individual variance in behaviour (see Supporting Information 1). Each behavioural test was performed for 5 min as preliminary tests proved that such a duration was sufficient to assess between-individual variability. A 1-min acclimatization period occurred prior to each test: the focal individual was kept in a small plastic cup (Ø 3 cm × 3 cm height) in the middle of the arena for exploration and gregariousness tests and at the opposite of the food source for the neophobia test. During the acclimatization period prior to the activity test, the focal individual was free to move in the arena without being isolated under a plastic cup. The recording of the behaviour began when the acclimatization period ended. Except for the food neophobia test, no resource (water or food) was provided within the apparatus.

**Activity test**

The activity arena was made of a 9-cm-diameter Petri dish fixed upside down in the centre of a 14-cm Petri dish, forming a 2.5-cm-wide circular pathway. The bottom of the arena was lined with a paper sheet on which eight radial sectors were drawn. The paper sheet was changed after each test to prevent bias caused by odour released by the insect. The number of transitions between sectors was recorded as the individual score of activity: the higher the score, the more the individual was active.

**Exploration test**

The exploration arena was made of a 9-cm-diameter Petri dish regularly divided in three radial sectors, each containing substrates of different grain size: sand (0.1 mm), small (c. 2–3 mm), and large gravels (c. 5–6 mm). These three different substrates differed in term of sensitive environment and burrowing potential, which is an important behaviour in T. molitor (Cloudsley-Thompson, 1953). The substrates were changed after each individual test to remove potential pheromonal marking. A circular area (Ø 3 cm) in the centre of the Petri dish where the individual was acclimatized was free of substrate. The number of transitions between sectors was recorded as the exploration score: the higher the score, the more the individual was explorative.

**Food neophobia**

Food neophobia was measured as the feeding response to new food items that our focal individuals never encountered either at the larval or adult stage. A new piece of novel food item (c. 125 mm³) known to be accepted by both larvae and adults of T. molitor was used for each test. Larvae were transferred in a new 14-cm-diameter Petri dish and were tested first with cucumber and second with orange. Similarly, adults were tested first with apple and second with banana. These food sources were used for two reasons. First, they are known to be used by some raisers to feed their beetles. Second, these fruits and vegetables contain more than 70% moisture that is susceptible to attract...
activity and exploration followed a negative binomial distribution. Following Nakagawa & Schielzeth (2010), repeatability for these measurements was assessed using concordance correlation coefficients (Lin, 1989, 2000; Carrasco, 2010; Schweitzer, Motreuil & Dechaume-Moncharmont, 2015) using the package epiR (Stevenson et al., 2016). The scores of food neophobia and gregariousness (or their transformation) did not follow any classical distribution. For these measurements, we therefore assessed the repeatability based on ranks using Spearman’s correlation coefficients. In each case, repeatability coefficients were reported with their bootstrapped 95% confidence interval (95% CI). To assess the potential impact of the distance to the metamorphosis, we divided our sample of larvae based on the delay to metamorphosis (below and above the median of our sample, i.e. 12 days) and then computed de novo the repeatability coefficients that allow direct comparisons of the 95% CI for the two groups. Differences between sexes for each replicate were tested using the Cliff’s $d$ assorted with its 95% CI using effsize package (Torchiano, 2014). This effect size estimator was preferred to the classical Cohen’s $d$ because the data did not fit with classical probability distribution (Cliff, 1996; Nakagawa & Cuthill, 2007; Macbeth, Razumiejczyk & Ledesma, 2011; Ivarsson et al., 2013). The Cliff’s $d$ was also used to compare the score at the larval and adult stages. The interpretation of the magnitude of the differences between sexes or between larval and adult stages was based on thresholds provided by Romano et al. (2006): $d < 0.147$: negligible differences, $d < 0.33$: small differences, $d < 0.474$: medium differences, and $d \geq 0.474$: large differences.

For repeatable measurements, we computed the average of individual scores measured during the first and the second behavioural tests and used it as data point thereafter. In order to characterize behavioural syndromes, the correlations between repeatable personality traits were tested using Spearman’s rank correlation with Benjamini–Hochberg correction for multiple tests in order to minimize inflation of Type 1 error (Benjamini & Hochberg, 1995). The first axis of the principal component analysis (PCA) taking into account all the repeatable personality traits correlated in syndrome was then used as an asynthetic personality score for the larvae and the adults separately. The link between the synthetic score and each personality trait of the individuals at the larval and adult stages was assessed using Spearman’s correlation coefficient.

**RESULTS**

The scores for all tests are presented in Figure 1. For all replicates, no differences between sexes were detected either in larvae or in adults (Table 1). Adults were always more active and explorative.
[activity: Cliff’s δ = 0.73 with 95% CI = (0.61; 0.82) and exploration: δ = 0.65 with 95% CI = (0.50; 0.76)], less food neophobic and gregarious than larvae [food neophobia: δ = −0.56 with 95% CI = (−0.68; −0.42) and gregariousness: δ = −0.17 with 95% CI = (−0.33; −0.01)]. For all traits, the two groups of larvae (less than 12 days and more than 12 days to metamorphosis) did not differ. Therefore, we pooled these two stages and considered the overall sample of larvae in the subsequent analysis (Supporting Information 2). We found short-term repeatability for the activity and exploration scores both at the larval and adult stages with similar level of repeatability (Table 2). Measurements of food neophobia were also found repeatable but at the adult stage only, while gregariousness was repeatable neither at the larval nor at the adult stage. Activity and exploration were positively correlated in both larvae and adults (Table 1).

Table 1. Sexual dimorphism in the four behavioural traits for each replicate (R1 and R2) at the larval and the adult stages measured with Cliff’s δ and its 95% confidence interval on 44 females and 52 males

<table>
<thead>
<tr>
<th>Behavioural trait</th>
<th>Replicate</th>
<th>Larvae</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R1</td>
<td>0.09 (−0.14; 0.32)</td>
<td>0.12 (−0.11; 0.35)</td>
</tr>
<tr>
<td></td>
<td>R2</td>
<td>0.13 (−0.10; 0.35)</td>
<td>0.12 (−0.12; 0.34)</td>
</tr>
<tr>
<td>Activity</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exploration</td>
<td>R1</td>
<td>0.01 (−0.21; 0.24)</td>
<td>0.22 (−0.008; 0.43)</td>
</tr>
<tr>
<td></td>
<td>R2</td>
<td>0.11 (−0.12; 0.32)</td>
<td>0.07 (−0.17; 0.29)</td>
</tr>
<tr>
<td>Food neophobia</td>
<td>R1</td>
<td>0.01 (−0.18; 0.20)</td>
<td>0.03 (−0.21; 0.26)</td>
</tr>
<tr>
<td></td>
<td>R2</td>
<td>−0.12 (−0.30; 0.07)</td>
<td>0.14 (−0.09; 0.36)</td>
</tr>
<tr>
<td>Gregariousness</td>
<td>R1</td>
<td>0.07 (−0.16; 0.30)</td>
<td>−0.01 (−0.24; 0.22)</td>
</tr>
<tr>
<td></td>
<td>R2</td>
<td>−0.004 (−0.24; 0.23)</td>
<td>0.11 (−0.13; 0.34)</td>
</tr>
</tbody>
</table>

Traits in which intervals cross 0 are not dimorphic. R1, replicate 1; R2, replicate 2.
3). In adults, exploration was also negatively correlated to food neophobia, but there was no correlation between activity and food neophobia (Table 3). In order to allow comparisons between larval and adult personality scores, the PCA for both stages were computed using the same behaviours, exploration and activity scores. For larvae, the first axis of the PCA explained 73.41% of the total variance (factor loadings: activity and exploration, −0.71 both, Fig. 2a). Low synthetic behavioural scores (i.e. low PC1 score) corresponded to highly active and explorative larvae and high scores to the less active and exploratory larvae (negative factor loadings). For adults, the first axis of the PCA explained 66.75% of the total variance (factor loadings: activity and exploration, 0.71 both, Fig. 2b). Low synthetic behavioural scores corresponded to the less active and exploratory adults and, high scores to highly active and explorative adults. Finally, the behaviour of the individuals at the larval and the adult stages was not correlated (Spearman’s rank correlation: activity: \( r_s = 0.02, N = 96, P = 0.84, 95\% \text{ CI} = (-0.18; 0.22) \); exploration: \( r_s = -0.01, N = 96, P = 0.89, 95\% \text{ CI} = (-0.22; 0.19) \); synthetic behavioural score: \( r_s = -0.02, N = 96, P = 0.82, 95\% \text{ CI} = (-0.19; 0.23) \), Fig. 3). This result was consistent in males and females (synthetic behavioural score, males: \( r_s = 0.10, N = 52, P = 0.44, 95\% \text{ CI} = (-0.17; 0.36) \) and females: \( r_s = -0.07, N = 44, P = 0.68, 95\% \text{ CI} = (-0.38; 0.22) \)).

### Table 2. Repeatability assorted with their 95% confidence interval for each behavioural trait for individuals at the larval and adult stages (\( n = 96 \))

<table>
<thead>
<tr>
<th>Behavioural trait</th>
<th>Larvae</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>Activity*</td>
<td>0.41 (0.23; 0.55)</td>
<td>0.50 (0.34; 0.63)</td>
</tr>
<tr>
<td>Exploration*</td>
<td>0.26 (0.06; 0.43)</td>
<td>0.29 (0.09; 0.46)</td>
</tr>
<tr>
<td>Food neophobia†</td>
<td>0.05 (−0.17; 0.26)</td>
<td>0.33 (0.15; 0.51)</td>
</tr>
<tr>
<td>Gregariousness†</td>
<td>0.18 (−0.08; 0.36)</td>
<td>0.12 (−0.08; 0.32)</td>
</tr>
</tbody>
</table>

Traits in which intervals do not cross 0 are significantly repeatable (bold).
*Repeatability tested with Lin’s concordance correlation coefficient.
†Repeatability tested with Spearman’s rank correlation.

### DISCUSSION

This study supports the existence of personality both in larvae and adults of *T. molitor*. Overall, individuals at the adult stage were more active and explorative but less neophobic and gregarious than at the larval stage. Activity and exploration were found to be repeatable and correlated, thus forming a so-called behavioural syndrome. The existence of such a syndrome is consistent with previous studies on animal (vertebrates and invertebrates) personality because these behaviours are closely related to general locomotion abilities, although they were tested differently (Réale et al., 2007). However, in our study, the personality traits and the behavioural syndrome of the larvae did not predict those of the adult. This result contrasts with previous studies (Sokolowski, 2001; Brodin, 2009; Gyrus et al., 2012; Niemelä et al., 2012; Wilson & Krause, 2012b) but is in agreement with the results obtained in holometabolous species (Müller & Müller, 2015; Wexler et al., 2016).

Personality and behavioural syndrome are assumed to be maintained within population due to their association with life-history and physiological traits, thus resulting in different fitness payoff strategies that form a continuum of slow to fast living individuals. This theoretical framework is an extension of the life-history theory, the so-called pace-of-life syndrome (POLS) hypothesis (Réale et al., 2010). Several studies suggested for instance a functional relationship between personality and energy metabolism (see Careau et al., 2008, 2015). In *T. molitor*, Krams et al. (2013) reported a link between metabolic rate and boldness that is also linked to higher mortality risk under predation. However, the POLS hypothesis implicitly assumes that an individual born as slow or fast living type belongs to this category for its entire life, except when the individuals experienced contrasting pressures during ontogeny (Fischer et al., 2014; Nettle & Bateson, 2015). Yet, in *T. molitor*, larvae and adults share the same resources and live in high promiscuity (Howard, 1955). To our knowledge, sexual behaviour has been poorly investigated in this species, and no obvious sex differences are reported to date. Anyway, we might have found sex differences similar to *T. castaneum* (Wexler et al., 2016).

### Table 3. Matrix of correlations between repeatable personality traits in larvae (above diagonal) and adults (below diagonal)

<table>
<thead>
<tr>
<th></th>
<th>Activity</th>
<th>Exploration</th>
<th>Food neophobia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Activity</td>
<td>−</td>
<td>0.52 (0.35; 0.66)</td>
<td>NT</td>
</tr>
<tr>
<td>Exploration</td>
<td>0.35 (0.17; 0.53)</td>
<td>−</td>
<td>NT</td>
</tr>
<tr>
<td>Food neophobia</td>
<td>−0.10 (−0.31; 0.11)</td>
<td>−0.37 (−0.55; −0.16)</td>
<td>−</td>
</tr>
</tbody>
</table>

Spearman’s rank coefficients are provided with their 95% confidence interval. Correlations in which intervals do not cross 0 are significant (bold). NT, not tested.
due to the phylogenetical proximity between these two species (Zhang et al., 2016). However, no such difference was detected in T. molitor either in larvae or in adults. Therefore, no fundamental shift in behaviour was expected here, except those that would arise from the metamorphosis process itself.

Previous works that investigated the effects of metamorphosis on the behaviour of T. molitor were however in accordance with the prediction of behavioural type persistence of the POLS hypothesis. These experiments aimed at testing the retention of learning across metamorphosis; interestingly, they found that memory was preserved in this species suggesting that at least some parts of the brain remain stable over this radical process (Borsellino, Pierantoni & Schieti-Cavazza, 1970; Alloway, 1972). Here, we show that larval personality does not predict the adult personality although the behavioural measurements were repeatable within each stage. These results suggest that the existence of such a within-stage consistency is constitutive, that is genetically determined while the intensity of the behaviour (i.e. the score per se) would be functionally determined, that is related to the metabolism, physiological, and/or neurological processes or under genetic regulation that could be modified during metamorphosis (Krams et al., 2013). In Schistocerca americana (Orthoptera), changes in the metabolism of locomotory behaviour were observed between young and adult individuals although this species is heterometabolous (Kirkton & Harrison, 2006; Kirkton, Nyberg & Fox, 2011). Some proteins such as heat shock proteins (Hsp) whose expression is related to the resistance to stress are known to be weakly related between life stages (Sørensen, Kristensen & Loeschcke, 2003). In a recent study on T. molitor, Lardies et al. (2014) suggested that heat-inducible genes might differ between larvae and adults. This kind of regulation (i.e. age-dependent genetic regulation) may thus provide a potential mechanism that could explain why some behaviours may differ between the larval and the adult stages. We would like to emphasize here that testing behavioural traits closer to the metamorphosis was almost impossible due to the major change in activity level.
we observed in the late instar larvae and in the newly emerged non-melanized adults.

CONCLUSION AND PERSPECTIVES

Although our results challenge the POLS hypothesis as a way to explain the consistency of personality traits and behavioural syndrome, they also question the adaptive value of this shift in behaviour observed across metamorphosis. This study also opens new perspectives in a similar way of those highlighted by Class & Brommer (2015), who stressed the importance of considering behavioural syndromes at different stages of the development of the individuals. Indeed, although the emphasis has been already put on the need of understanding the evolution of personality during development, the effects of ontogeny on personality and behavioural syndrome are still rarely considered (Stamps & Groothuis, 2010; Groothuis & Trillmich, 2011; Wilson & Krause, 2012a; Biro & Stamps, 2015; Class & Brommer, 2015). To date, we still lack evidence for a functional basis of personality, but T. molitor might represent an ideal model species to understand the role of metamorphosis.

ACKNOWLEDGEMENTS

We thank Jenny Sauvage and Camille Lucas for their technical help during the experiments. We are also grateful to Simon Ducatez and two anonymous reviewers for their contributions.

REFERENCES


at less than 12 days (21 females and 28 males) prior to metamorphosis.

divided into two groups: the larvae tested at more than 12 days (23 females and 24 males) and the larvae tested
cient for activity and exploration, Spearman’s coefficient for food neophobia and gregariousness). The sample was
Supporting Information 2.

Supporting Information 1.

Additional Supporting Information may be found in the online version of this article at the publisher’s website: