Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

Insect personality: what can we learn from metamorphosis?

Isabelle Amat[1], Emmanuel Desouhant[1], Elisa Gomes[1], Jérôme Moreau[2] and Karine Monceau[3]

Ontogeny of animal personality is still an open question. Testing whether personality traits correlated with state variables (e.g. metabolic rate, hormones) and/or life history traits, and which ones are involved, requires more empirical studies. Insects with metamorphosis represent a good opportunity to tackle this question. Because of the various degrees of internal (physiological, nervous) and environmental changes linked to metamorphosis they allow testing whether these modifications drive consistency in personality traits between immature and adult stages. In this review, we establish general predictions for the effects of metamorphosis on personality in insects with complete or incomplete metamorphosis and suffering from a strong or weak niche shift after metamorphosis. We then reviewed the still rare empirical literature and discuss future research axes.

Addresses
[1] Univ Lyon, Université Claude Bernard Lyon 1, CNRS, Laboratoire de Biométrie et Biologie Evolutive, 69100 Villeurbanne, France
[2] UMR CNRS 6282 Biogéosciences, Equipe Ecologie Evolutive, Université de Bourgogne-Franche-Comté, 21000 Dijon, France
[3] Centre d'Etudes Biologiques de Chizé, UMR 7372 CNRS, Université de la Rochelle, 79360 Villiers en Bois, France

Corresponding author: Amat, Isabelle (isabelle.amat@univ-lyon1.fr)

Current Opinion in Insect Science 2018, **27**:46–51

This review comes from a themed issue on **Behavioural ecology**

Edited by **Eric Wajnberg** and **Emmanuel Desouhant**

For a complete overview see the Issue and the Editorial

Available online 14th February 2018

https://doi.org/10.1016/j.cois.2018.02.014

Introduction

Bold, aggressive, social, exploratory or active are now classically admitted terms to describe animal personality [1,2], defined as the consistency of inter-individual differences in behavioral traits across both time and contexts. For instance, repeated individual measures on great tits show that some individuals are consistently more explorer than others [3,4]. Nowadays, animal personality has been experimentally shown in a wide range of taxa including birds, fish, insects, etc. Personality is both described by these personality traits and their correlations, characterizing behavioral syndromes [1,5]. For instance, the exploration-aggressiveness behavioral syndrome has been well described in great tits: the more explorer are also the more aggressive [6].

Personality has ecological and evolutionary consequences (review in [7]). Within population, variation in personality traits may affect among others individual fitness, population growth rate, stability, and resource/forager dynamics with implication for invasion biology [8], conservation [9] or biological control. For instance, the composition of personality types in populations of the wolf spider *Pardosa milvina* (either active individuals, inactive individuals or a mix of both) generates contrasting pattern in its prey communities. A mixture of active and sedentary *P. milvina* performs best at diminishing abundance of different prey species [10].

Despite the last decade of animal behavior research has seen the rise of animal personality and an explosion of empirical studies, how personality traits arise (ontogeny), is maintained and evolved within a population is still debated. Two non-exclusive approaches are classically adopted: the intra-individual variability and the life history framework [11]. The former aims at identifying the ultimate causes of individual differences in behavioral consistency based on the classical optimization approach in behavioral ecology. The second integrates individual personality in an extended concept, the Pace Of Life Syndrome (POLS) hypothesis, derived from life-history theory. POLS hypothesis suggests that behavioral syndromes and their link with other traits (physiology and life-history) reflect different life strategies [12]. Indeed, within animal population, individuals are ranked along a slow to fast continuum, that is, reactive to proactive individuals. Contrary to reactive individuals, proactive individuals are bold, aggressive, active and explorers. These skills associated to fast lifestyle (rapid growth rate, early sexual maturity, high reproduction rate, high metabolism, low immune response and short lifespan) may facilitate the access to resource [12,13]. These reactive/proactive personalities may be maintained by means of temporal and/or spatial fluctuations of ecological factors like food availability or predation pressures which could favor one type to the detriment of another.

The 'life history framework' requires more experimental works to identify the underlying mechanisms that could drive both life-history traits and personality ontogeny.

Consistent individual differences can result from intrinsic (genetic) differences among individuals and from differences in the value of state variables (such as metabolic rate, growth rate, energetic reserves). Studies on personality development may allow deciphering these underlying mechanisms by tracking when personality rises, how stable it is and how long it remains consistent [5,14–16]. Indeed, nowadays consistency in behavioral traits has often been quantified on a short time scale relative to the entire lifetime [17] (but see [18]). Relevant organisms for the study of the development of personality across ontogeny are those with complex life cycles involving metamorphosis [19]. Indeed, the metamorphosis implicates stop in the development and abrupt internal changes and sometimes leads to habitat changes [20,21]. These shifts influence the range of behaviors displayed by a given individual during its life, including predator avoidance, foraging, mating and dispersal. Hence, studying personality through metamorphosis allows appraising the relative effects of these changes on personality development and maintenance, independently from the effect of age. For instance, in the frog *Rana ridibunda*, inter-individual differences in activity, exploration and boldness are consistent within life stages. While no correlation between tadpole and frog boldness was detected, activity and exploration are maintained across metamorphosis [22]. This consistency is unexpected due to the strong internal changes and niche/dietary shift between tadpoles and adults, and suggest that these personality traits rest on a genetic (i.e. pleiotropic) or mechanistic (i.e. hormonal and metabolic) basis that is hardly uncoupled across metamorphosis. To go further in the study of the ontogeny of personality through metamorphosis, insects represent good candidates. Indeed, they display a wide variety of metamorphosis types hence encompassing various degrees of internal and environmental changes associated to modifications of the ecological constraints endured. Moreover, insects are highly amenable for experimental manipulations (notably easy to raise under experimental conditions and short lived).

In this paper, we aim at discussing how the metamorphosis represents an opportunity to understand the ontogeny of personality and its link with other traits affected during this process. We first propose general predictions for the effects of the different types of metamorphosis on personality. Then, we reviewed the existing literature to assess whether general patterns can be drawn. At last, we discuss what future direction researches on animal personality and metamorphosis could be.

Personalities coupling between juvenile and adult stages through insect metamorphosis

Predictions

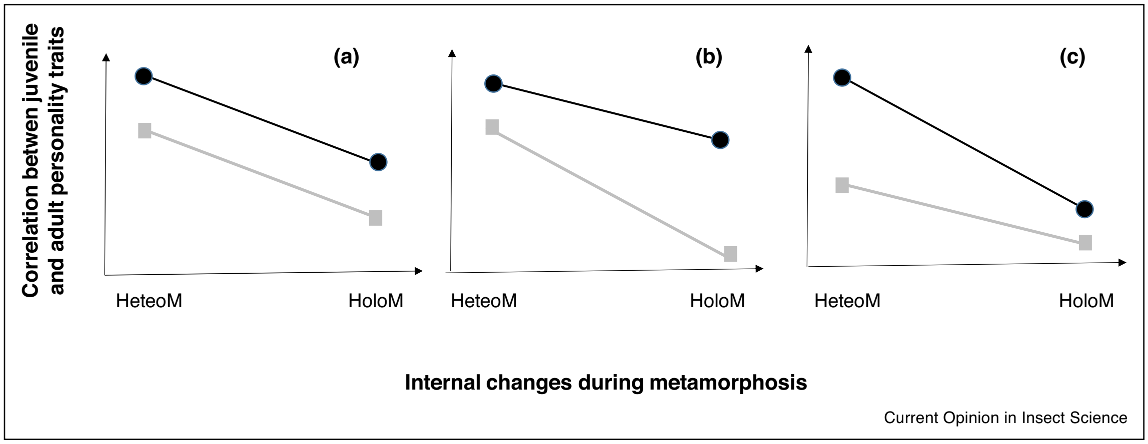
In insects, two major metamorphosis types can be distinguished, namely holo-metabolous versus hetero-metabolous, characterized by different intensities of changes in morphology, physiology and nervous systems [20]. Heterometabolous insects (characterized by an 'incomplete' metamorphosis) pass from larva to adult via successive molts, the last one (i.e. imaginal molt) leading to the adult. In holometabolous species ('complete' metamorphosis), the imaginal molt is represented by the pupation (motionless stage) involving a complete reorganization of the organism especially the neural organization [23–25]. Moreover, individuals can change their habitat and their diet between juvenile and adult stages Therefore, insects with metamorphosis can be classified into four categories: Firstly, strong internal changes and no habitat change (e.g. mealworm beetle *Tenebrio molitor*), secondly, strong internal changes with habitat shift (e.g. bees), thirdly, weak internal changes and no habitat change (paurometabolous species, e.g. crickets), and finally, weak internal changes with habitat shift (hemimetabolous species, e.g. damselflies). Predictions on personality changes through metamorphosis in each of these categories should depend on the proximate causes of the personality, the life-history trade-off implied and their environmental conditions. Here, we illustrate general predictions by figuring the correlation in behavioral traits between juveniles and adults according to internal changes and niche shift (Figure 1).

First, if insects shift niche, and under the hypothesis that the ecological conditions determine individual personality, it has been assumed that natural selection could uncouple personality traits during ontogeny [5]. Thus weaker correlations between juvenile and adult personality traits are expected (in gray and filled squares in Figure 1). Second, because of the internal factor changes linked to metamorphosis, and under the hypothesis that personality traits are coupled with state variables, it is expected that the correlation is lower in holometabolous than in heterometabolous insects (Figure 1). The interaction between the effects of internal factors and niche shift might be expressed through synergetic (Figure 1b) or antagonistic (Figure 1c) effects. While in the first case, the uncoupling effect of habitat changes is intensified when animals experience changes in state variables, the opposite occurs in the second case. Figure 1a illustrates additive effect of internal and external factors on personality.

Empirical evidences

A review of the literature on personality through metamorphosis in insects highlights three main questions: Are there behavioral types in the larval stages? Are they conserved at the adult stage? Are behavioral syndromes conserved through metamorphosis? Eleven studies were found to appraise the correlation of personality traits between juvenile and adult insects (see Table 1): five in heterometabolous species (one hemimetabolous changing habitat and four paurometabolous species that

Figure 1



Expected variations of the correlations of personality traits between immature and adult stages in insects with metamorphosis. *X*-axis represents the gradient for intensity of internal changes (physiological, morphological and nervous) through metamorphosis. On the left hand of the gradient are insects with incomplete metamorphosis (i.e. heterometabolous insects, named HeteroM). At the other extremity of the gradient are insects with complete metamorphosis (i.e. holometabolous insects, HoloM). Black filled circles: insects with a weak (or no) niche shift (i.e. changes in habitat and/or diet); gray squares: insects with a strong niche shift. **(a)** Additional effects of internal and environmental changes on correlation, **(b)** interacting effect of internal changes and niche shift leading to a synergetic effect on correlation; **(c)** interacting effect of internal changes and niche shift leading to antagonistic effect on correlation of personality. Predictions are represented through linear relationships even if they could be non linear.

Table 1

Synthesis of the studies testing consistency across metamorphosis in insects.

Metamorphosis/Species (common name)	Environmental changes	Personality traits	Consistency across metamorphosis	Reference
Heterometabolous — Hemimetabolous				
Lestes congener (spotted spreadwing)	yes[a]	Activity, boldness	Yes	[34]
Heterometabolous — Paurometabolous				
Diploptera punctata (pacific beetle cockroach)	no	Boldness, exploration, sociality	Partly	[27•]
Gryllus integer (western Trilling Cricket)	no	Boldness	Yes	[26]
Gryllus integer (western Trilling Cricket)	no	Boldness	Only in females	[28]
Pyrrhocoris apterus (firebug)	no	Activity, boldness, exploration	Partly	[44]
Holometabolous				
Drosophila melanogaster (vinegar fly)	no	Activity, social behavior	No	[33]
Eriopis connexa (lady beetle)	no	Activity, aggressiveness, boldness, exploration	Yes	[29]
Phaedon cochleariae (mustard leaf beetle)	no	Activity, boldness	No	[31•]
Tenebrio molitor (yellow mealworm beetle)	no	Activity, boldness, exploration, gregariousness	No	[30•]
Tribolium castaneum (red flour beetle)	no	Activity, edge preference	No	[32]
Tribolium castaneum (red flour beetle)	no	Activity, boldness	No	[45]
Tribolium confusum (confused flour beetle)	no	Activity, boldness	No	[45]

[a] Aquatic to terrestrial environment.

do not) and six studies in holometabolous species, all of which not experiencing strong niche/dietary shift between larval and adult stages. Boldness and activity were the most commonly traits studied (8/11 studies, see Table 1).

General trends can be drawn from this data corpus. As predicted, while consistency in personality traits has been shown, at least partially, in the five heterometabolous species, correlations between adults and juveniles are lower in holometabolous (consistency personality traits is observed in only one of the six species tested). In heterometabolous insects, larval personality (e.g. boldness) generally persists at the adult stage. However, either mean value of the trait decreases, with larvae being bolder that adults [26,27•], or the mean value is maintained only in females [28]. Modification in predation pressures through metamorphosis could explain these results. For instance, searching for mate in crickets may expose boldest individuals (in this case, mostly males) to additional predation risks, suggesting a reduction in boldness expression in males [28]. Contrary to our expectation, personality traits are maintained even in damselflies, despite the dramatic changes in habitat between larvae and adult (aquatic versus terrestrial). In all but one of the holometabolous species tested for correlations of personality traits through metamorphosis, these have been non-significant. In this species (lady beetle) while the morphological changes are dramatic (complete metamorphosis), there are no drastic changes between the environmental conditions experienced by larvae and adults [29]. However, in the mealworm beetle *Tenebrio molitor* which do not change habitat across metamorphosis, behavioral types are decoupled between stages [30•]. Such decoupling across metamorphosis seems characteristics of holometabolous species since it has also been shown in the fruit fly *Drosophila*, the flour beetle *Tribolium castaneum* and the leaf beetle *Phaedon cochleariae* [31•,32,33].

Discussion, conclusion and future research directions

Through the diversity in their metamorphosis, insects allow clarifying our understanding of the personality development and of the underlying mechanisms. Our review suggests that the strong internal reorganization experienced by holometabolous species at pupal stage is a key driver of personality uncoupling through metamorphosis. The apparent robustness of personality to niche shift is uncertain. Indeed, only one hemimetabolous species has been studied (for which no repeatability on adult measurements was performed [34]), and unfortunately there is no study on holometabolous species suffering strong dietary/niche shift limiting drastically our global understanding. Most of the holometabolous species studied in this stage are Coleopterans (5/6 and among these 5 species, 3 belong to the Tenebrionidae family). Therefore, more taxa are needed to appraise a general pattern in term of the impact of internal and environmental factors on personality ontogeny, and their potential synergetic/antagonistic effect through metamorphosis. Importantly, from a methodological point of view, how the maintenance of personality across stages is tested should be unified. In our review, we focused on whether or not a correlation was detected between larval and adult stage. Studying more different taxa with the same methodology would allow a meta-analysis approach where the effect size of correlations between juveniles and adults could be quantified and phylogenetic constraints could be taken into account. This would allow to compare more precisely differences in correlation for one factor (e.g. with versus without niche shift) between modalities of the other factor (holometabolous versus heterometabolous). Moreover, statistical tools to examine the effect of changes through metamorphosis on mean value of a personality trait and on its intra-individual variance or correlation among different personality traits are now available [35]. However, investigating consistency of personality through metamorphosis remains a difficult task since this poses the methodological problem of the quantification of a given trait (e.g. activity) in different forms of an individual (e.g. from a larval stage as caterpillar to adult stage as butterfly) and/or with distinct needs in their respective ecological niche. Finally, additional studies should also address the consistency of behavioral syndrome involving other, less studied, behavioral traits namely sociality or exploration (but see [29,30•,33]).

Even rare, results obtained since first works by Stamps and Groothuis and Wilson and Krause [14,16,19] sounds promising for clarifying proximate causes of personality via a careful examination of physiological and genetic correlations during development. For instance, in blue tits, a quantitative genetic approach reveals that personality change through development is linked to a breakdown of a strong genetic correlation between personality traits as nestlings mature due to genotype/age interaction [36]. A general result from our literature survey is that behavioral traits are expressed quite early in the development. Differences in state associated with positive feedbacks loops between state and behavior are usually mentioned to account for consistent inter-individual differences in behavior [37]. However, at early life, these differences are generally too small, suggesting that genetically or maternally effects could be involved in consistency set up.

Concerning POLS hypothesis, experimental works showed contrasting results [38•,39,40,41,42•]. By inducing potentially strong changes in physiological and life history traits, insect metamorphosis offers a rare opportunity to test their correlation with personality and the existence of paces of life within and across stages. In its simplest form, POLS hypothesis assumes that behavioral syndrome should be constant throughout lifespan since it characterizes the individual ‘life style’. For species in which it has been tested, the comparison of behavioral syndromes between larval versus adult stages showed that these correlations could change strongly suggesting plasticity in the correlation among personality traits [27•,30•]. Whether these results challenge the POLS hypothesis requires evaluating if these changes in syndromes remain however correlated with life history traits and lead to comparable fitness outcome of the various adult life styles in their habitat.

Finally, the studies in Table 1 reported correlation between personality traits before versus after metamorphosis, but there is variability in the timing and the duration of the nymphal stage. This variability may impact survival of adults and thus fitness outcome of the adult life styles along the continuum proactive/reactive. Clarifying whether and how timing and duration of metamorphosis correlate to larval personality should help appraising whether and how early life conditions impact the expression of adult behavioral trait and eventually affect behavioral strategies [43].

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Acknowledgements

We thank Eric Wajnberg, as editor of the special issue in Behavioral Ecology, for its invitation to write this review. We thank reviewers for their helpful comments on the manuscript.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest

1. Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ: **Integrating animal temperament within ecology and evolution**. *Biol Rev* 2007, **82**:291-318.
2. Sih A, Bell A, Johnson JC: **Behavioral syndromes: an ecological and evolutionary overview**. *Trends Ecol Evol* 2004, **19**:372-378.
3. Verbeek MEM, Drent PJ, Wiepkema PR: **Consistent individual differences in early exploratory behaviour of male great tits**. *Anim Behav* 1994, **48**:1113-1121.
4. Dingemanse NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ: **Natal dispersal and personalities in great tits (*Parus major*)**. *Proc R Soc B Biol Sci* 2003, **270**:741-747.
5. Sih A, Bell AM, Johnson JC, Ziemba RE: **Behavioral syndromes: an integrated overview**. *Q Rev Biol* 2004, **79**:241-277.
6. Verbeek MEM, Boon A, Drent PJ: **Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits**. *Behaviour* 1996, **133**:945-963.
7. Wolf M, Weissing FJ: **Animal personalities: consequences for ecology and evolution**. *Trends Ecol Evol* 2012, **27**:452-461.
8. Rehage JS, Cote J, Sih A: **The role of dispersal behaviour and personality in post-establishment spread**. In *Biological Invasions and Animal Behaviour.* Edited by Weis JS, Sol D. Cambridge University Press; 2016:96-116.
9. Smith BR, Blumstein DT: **Animal personality and conservation biology the importance of behavioral diversity**. In *Personalities: Behavior, Physiology, and Evolution.* Edited by Carere C, Maestripieri D. University of Chicago Press; 2013:380-413.
10. Royauté R, Pruitt JN: **Varying predator personalities generates contrasting prey communities in an agroecosystem**. *Ecology* 2015, **96**:2902-2911.
11. David M, Dall SRX: **Unravelling the philosophies underlying “animal personality” studies: a brief re-appraisal of the field**. *Ethology* 2016, **122**:1-9.
12. Reale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O: **Personality and the emergence of the pace-of-life syndrome concept at the population level**. *Philos Trans R Soc B Biol Sci* 2010, **365**:4051-4063.
13. Biro PA, Stamps JA: **Are animal personality traits linked to life-history productivity?** *Trends Ecol Evol* 2008, **23**:361-368.
14. Stamps J, Groothuis TGG: **The development of animal personality: relevance, concepts and perspectives**. *Biol Rev* 2010, **85**:301-325.
15. Hedrick AV: **Editorial: the development of animal personality**. *Front Ecol Evol* 2017:5.
16. Stamps JA, Groothuis TGG: **Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences**. *Philos Trans R Soc B Biol Sci* 2010, **365**:4029-4041.
17. Bell AM, Hankison SJ, Laskowski KL, Manuscript A: **The repeatability of behaviour: a meta-analysis**. *Anim Behav* 2009, **77**:771-783.
18. Herde A, Eccard JA: **Consistency in boldness, activity and exploration at different stages of life**. *BMC Ecol* 2013, **13**:49.
19. Wilson ADM, Krause J: **Metamorphosis and animal personality: a neglected opportunity**. *Trends Ecol Evol* 2012, **27**:529-531.
20. Wilbur HM: **Complex life cycles**. *Annu Rev Ecol Syst* 1980, **11**:67-93.
21. Kralj-Fiser S, Schuett W: **Studying personality variation in invertebrates: why bother?** *Anim Behav* 2014, **91**:41-52.
22. Wilson ADM, Krause J: **Personality and metamorphosis: is behavioral variation consistent across ontogenetic niche shifts?** *Behav Ecol* 2012, **23**:1316-1323.
23. Kalogianni E, Consoulas C, Theophilidis G: **Anatomy and innervation of the abdominal segmental muscles in larval and adult *Tenebrio molitor* (Coleoptera)**. *J Morphol* 1989 http://dx.doi.org/10.1002/jmor.1052020212.
24. Consoulas C, Duch C, Bayline RJ, Levine RB: **Behavioral transformations during metamorphosis: remodeling of neural and motor systems**. *Brain Res Bull* 2000, **53**:571-583.
25. Tissot M, Stocker RF: **Metamorphosis in *Drosophila* and other insects: the fate of neurons throughout the stages**. *Prog Neurobiol* 2000, **62**:89-111.
26. Niemelä PT, Vainikka A, Hedrick AV, Kortet R: **Integrating behaviour with life history: boldness of the field cricket, *Gryllus* integer, during ontogeny**. *Funct Ecol* 2012, **26**:450-456.
27. • Stanley CR, Mettke-Hofmann C, Preziosi RF: **Personality in the cockroach *Diploptera punctata*: evidence for stability across developmental stages despite age effects on boldness**. *PLOS ONE* 2017, **12**:1-23.
This study shows on heterometabolous-hemimetabolous species both consistency for boldness and exploration through metamorphosis despite differences in mean scores of boldness between juveniles and adults.
28. Hedrick AV, Kortet R: **Sex differences in the repeatability of boldness over metamorphosis**. *Behav Ecol Sociobiol* 2012, **66**:407-412.
29. Rodrigues AS, Botina L, Nascimento CP, Gontijo LM, Torres JB, Guedes RNC: **Ontogenic behavioral consistency, individual variation and fitness consequences among lady beetles**. *Behav Process* 2016, **131**:32-39.

30. • Monceau K, Moreau J, Richet J, Motreuil S, Moret Y, Dechaume-Moncharmont F-X: **Larval personality does not predict adult personality in a holometabolous insect**. *Biol J Linn Soc* 2017, **120**:869-878.
This study investigates personality and behavioral syndromes in a holometabolous species (red flour beetle) including four different traits (activity, boldness through food neophobia, exploration and gregariousness); personality and behavioral syndrome are present in both larvae and adults but completely uncorrelated across metamorphosis.

31. • Müller T, Müller C: **Behavioural phenotypes over the lifetime of a holometabolous insect**. *Front Zool* 2015, **12**:S8.
The authors test whether the personality traits are maintained across metamorphosis in a holometabolous species (mustard leaf beetle) and the relationship with the individual developmental time. Personality is not maintained through metamorphosis and results show a negative correlation between larval activity and developmental time that is in line with POLS hypothesis.

32. Wexler Y, Subach A, Pruitt JN, Scharf I: **Behavioral repeatability of flour beetles before and after metamorphosis and throughout aging**. *Behav Ecol Sociobiol* 2016, **70**:745-753.

33. Anderson BB, Scott A, Dukas R: **Social behavior and activity are decoupled in larval and adult fruit flies**. *Behav Ecol* 2016, **27**:820-828.

34. Brodin T: **Behavioral syndrome over the boundaries of life – carryovers from larvae to adult damselfly**. *Behav Ecol* 2009, **20**:30-37.

35. Dingemanse NJ, Dochtermann NA: **Quantifying individual variation in behaviour: mixed-effect modelling approaches**. *J Anim Ecol* 2013, **82**:39-54.

36. Class B, Brommer JE: **A strong genetic correlation underlying a behavioural syndrome disappears during development because of genotype–age interactions**. *Proc R Soc B* 2015, **282**:20142777.

37. Sih A, Mathot KJ, Moiron M, Montiglio P-O, Wolf M, Dingemanse NJ: **Animal personality and state – behaviour feedbacks: a review and guide for empiricists**. *Trends Ecol Evol* 2015, **30**:50-60.

38. • Debecker S, Sanmartín-Villar I, de Guinea-Luengo M, Cordero-Rivera A, Stoks R: **Integrating the pace-of-life syndrome across species, sexes and individuals: covariation of life history and personality under pesticide exposure**. *J Anim Ecol* 2016, **85**:726-738.
This study tests the POLS hypothesis within and between species (damseflies) and the effect of pesticides on the magnitude of the correlations life history and personality. Little evidence is found for POLS hypothesis: covariation between life history and personality traits is detected only in the most fast-lived species and this covariation is altered by the exposition to pesticides.

39. Monceau K, Dechaume-Moncharmont F-X, Moreau J, Lucas C, Capoduro R, Sébastien M, Moret Y: **Personality, immune response and reproductive success: an appraisal of the pace-of-life syndrome hypothesis**. *J Anim Ecol* 2017, **86**:932-942.

40. Niemelä PT, Dingemanse NJ, Alioravainen N, Vainikka A, Kortet R: **Personality pace-of-life hypothesis: testing genetic associations among personality and life history**. *Behav Ecol* 2013, **24**:935-941.

41. Royauté R, Greenlee K, Baldwin M, Dochtermann NA: **Behaviour, metabolism and size: phenotypic modularity or integration in *Acheta domesticus*?** *Anim Behav* 2015, **110**:163-169.

42. • Santostefano F, Wilson AJ, Niemelä PT, Dingemanse NJ: **Behavioural mediators of genetic life-history trade-offs: a test of the pace-of-life syndrome hypothesis in field crickets**. *Proc R Soc B Biol Sci* 2017, **284**:20171567.
This study challenges the POLS hypothesis by testing the genetic correlations between personality traits and life history traits; the authors show that in a population of Mediterranean field crickets (*Gryllus bimaculatus*) risky traits do not mediate the genetic correlations between the life history traits involved in trade-offs.

43. Krause ET, Krüger O, Schielzeth H: **Long-term effects of early nutrition and environmental matching on developmental and personality traits in zebra finches**. *Anim Behav* 2017, **128**:103-115.

44. Gyuris E, Feró O, Barta Z: **Personality traits across ontogeny in firebugs, *Pyrrhocoris apterus***. *Anim Behav* 2012, **84**:103-109.

45. Matsumura K, Fuchikawa T, Miyatake T: **Decoupling of behavioral trait correlation across life stages in two holometabolous insects**. *Behav Genet* 2017, **47**:459-467.