



State and physiology behind personality in arthropods: a review

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Abstract

In the endeavour to understand the causes and consequences of the variation in animal personality, a wide range of studies were carried out, utilising various aspects to make sense of this biological phenomenon. One such aspect integrated the study of physiological traits, investigating hypothesised physiological correlates of personality. Although many of such studies were carried out on vertebrates (predominantly on birds and mammals), studies using arthropods (mainly insects) as model organisms were also at the forefront of this area of research. In order to review the current state of knowledge on the relationship between personality and the most frequently studied physiological parameters in arthropods, we searched for scientific articles that investigated this relationship. In our review, we only included papers utilising a repeated-measures methodology to be conceptually and formally concordant with the study of animal personality. Based on our literature survey, metabolic rate, thermal physiology, immunophysiology, and endocrine regulation, as well as exogenous agents (such as toxins) were often identified as significant affectors shaping animal personality in arthropods. We found only weak support for state-dependence of personality when the state is approximated by singular elements (or effectors) of condition. We conclude that a more comprehensive integration of physiological parameters with condition may be required for a better understanding of state's importance in animal personality. Also, a notable knowledge gap persists in arthropods regarding the association between metabolic rate and hormonal regulation, and their combined effects on personality. We discuss the findings published on the physiological correlates of animal personality in arthropods with the aim to summarise current knowledge, putting it into the context of current theory on the origin of animal personality.

Keywords Consistent behaviour · Repeatability · Physiology · State-dependent · Condition · Metabolic rate · Hormonal regulation

Introduction

Consistent behavioural differences among individuals in a population have been found in many species across a wide range of animal taxa (Gosling 2001; Sih et al. 2004). In the past few decades, among-individual variation in behavioural traits has been recognised as an important characteristic of animal populations with multiple evolutionary and ecological consequences (Dall et al. 2004). This variation is often consistent, i.e. is stable over time and/or across ecological contexts. In behavioural ecology, such repeatable individual variation in behaviour is termed as animal personality, which, in statistical terms, also means that when we partition within- and between-individual variance in behavioural measurements, we see substantial between-individual variation compared to the within-individual variation in the measured behaviour (for further details, see Réale et al. 2007;

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Carter et al. 2013; Sánchez-Tójar et al. 2022). Personality may refer to consistent behavioural traits such as aggression, activity, boldness, exploratory behaviour, or sociability (Réale et al. 2007). When repeatable individual differences are observed in suites of functionally separate behaviours, such traits form so-called behavioural syndromes (Sih et al. 2004; Jandt et al. 2014). Behavioural syndromes consist of suits of behaviours that show among-individual correlations (Niemelä and Dingemanse 2018a), for example between foraging activity and courtship behaviour (Johnson and Sih 2007).

One of the most stimulating areas of research in animal personality addresses the physiological background and correlates of personality, generally assessing the associations between certain personality traits (e.g. aggression or exploratory behaviour) and physiological variables (e.g. metabolic rate or circulating hormone levels), for which an underlying functional connection is hypothesised (for example: reviewed in Careau et al. 2008; Careau and Garland 2012; Sih et al. 2015). Following the ecological physiology paradigm (which has been substantially expanded in the last two–three decades), we refer to physiology as functions from molecular and cellular to organismal scale with profound influence on the maintenance of homeostasis (Ricklefs and Wikelski 2002). The relationship between physiology and personality has been investigated by a considerable number of studies in birds and mammals; yet, arthropods are also at the forefront in this area of research (e.g. Nakayama et al. 2012; Kralj-Fišer and Schuett 2014). Arthropods represent a valuable set of model organisms to study both animal personality and physiology. The immense diversity in their life histories may enable the identification of general patterns of how physiological traits shape personality. Also, this diversity grants us unique opportunities to identify mechanisms that are specific to the studied systems, the investigation of which is crucial to understand why there is variation in the mechanistic background of animal personality. Practical considerations may also favour arthropod models; for instance, many arthropod species are relatively easy to rear under laboratory conditions. They are generally smaller in size, therefore easier to house than most vertebrates to carry out tests on many individuals at a time. Therefore, reaching larger sample sizes is considerably easier than with vertebrates. Furthermore, arthropods are often characterised by relatively short life-cycles, allowing an easier investigation of ontogenetic and fitness-related (e.g. survival, reproductive effort) correlates of personality traits.

From a physiological point of view, arthropod species are arguably simpler than vertebrates. Therefore, investigating complex physiological mechanisms, for example the role of the endocrine system in shaping personality differences, can be more feasible in comparison to vertebrate model organisms (Mather and Logue 2013). Indeed, insects were often

used as models in studies of the physiological and genetic background of behaviour, and there is an ever-growing and convoluted literature using arthropod models in such studies (e.g. Adamo et al. 1995; Haller et al. 1997; Sokolowski 2001; Anholt and Mackay 2004; Armstrong and Robertson 2006; Meunier et al. 2007; Faßold et al. 2010; Nishi et al. 2010; Hebets et al. 2015). Unfortunately, however, relatively few studies focus explicitly on the mechanisms behind animal personality. Consequently, there is still limited knowledge on the proximate mechanisms that might shape animal personality per se (Niemelä and Dingemanse 2014) in arthropods.

Here, we review currently available empirical knowledge on the proximate mechanisms potentially driving personality variation in arthropods. We focus on personality traits rather than the average behaviour of the study populations: studies assessing individual-level behaviour but not accounting for within-individual variation not only make it difficult to draw robust conclusions on the proximate mechanisms shaping animal personality, but also lay the ground for biased conclusions (due to the “individual gambit”, see Niemelä and Dingemanse 2018a). Arguably, such caveats should be avoided if we are to clarify the causes of variation in personality and physiology, and the association between them (Rocheet al. 2016; Kaiser and Müller 2021). Although studies with designs not including repeated measures of animal behaviour may grant us valuable insights in this regard, we strictly focus on those papers that utilised a repeated-measures approach to be conceptually and formally concordant with the study of animal personality (Dingemanse and Wright 2020).

Methods

We searched for articles published up to 31 December 2020, using the Google Scholar, Science Direct, and Web of Science databases. In order to get good coverage of the published literature, we combined different search terms related to personality and physiology with names of the different taxa. Keywords used for the literature survey are summarised in the Appendix. Our literature survey resulted in 104 articles in total, out of which 41 (see Table 1 for their summary) adhered to our criteria on the repeated behavioural measures. We excluded studies in which (i) none of the assayed behavioural traits were consistent over time on the individual-level (i. e. none of the assessed behaviours were found to be repeatable at a statistically significant level), (ii) did not include any data about the repeatability of the tested behavioural trait(s), or (iii) there was no information about the repeatability of the trait(s) for the concerned species even in other published articles. (For example, in Nakayama et al. (2012) the authors did not test the repeatability of

Table 1 Summary of findings from the surveyed studies, including only those studies that specifically addressed the association between personality and physiological / state variables. In the “Behavioural variable” column we inserted the specification of behaviour used by the authors of the given study. The column “Association” summarizes main findings by showing the general relationship between the tested state (or environmental) variables and personality traits. In some cases we wrote “c” in the “Association”, indicating a complex relationship between the assessed traits (e.g. owing to interactions with sex or age, etc.)

Taxon	State or environmental variable	Behavioural variable	Association	Reference
Araneae	Condition (linked with diet)	Tendency to attack prey	-	DiRienzo and Montiglio 2016
Araneae	Octopamine (OA) level	Activity, anti-predator response (length of thanatosis)	0, -	Jones et al. 2011
	Serotonin (5HT) level	Activity, anti-predator response (length of thanatosis)	0, +	
Araneae	Octopamine (OA) and serotonin (5HT) levels	Activity, aggression, boldness	c	DiRienzo et al. 2015a
Araneae	Serotonin (5HT) level	Activity, sociability	c	Price 2010
Araneae	Insecticide exposure	Activity, aggression, boldness, voracity	-, 0, 0, +	Royauté et al. 2014
Araneae	Insecticide exposure	Activity, voracity	0, 0	Royauté et al. 2015
Araneae	Predator chemical cues	Foraging time, web building behaviour	-, -	Ameri et al. 2019
Blattodea	Condition (linked with diet)	Risk acceptance	+	Mishra et al. 2011
Coleoptera	Condition (linked with diet)	Activity, boldness, exploration	+, -, 0	Tremmel and Müller 2013
Coleoptera	Immunity (multiple immune measures)	Activity, food neophobia, exploration, gregariousness	c	Monceau et al. 2017
Coleoptera	Metabolic rate	Anti-predator response (latency until immobilization, duration of immobilization)	+, -	Krams et al. 2013a
Coleoptera	Metabolic rate	Anti-predator response (latency until immobilization, duration of immobilization)	+, -	Krams et al. 2013b
Coleoptera	Metabolic rate	Anti-predator response (latency until immobilization, duration of immobilization)	+, -	Krams et al. 2014
Coleoptera	Caffeine exposure	Activity, duration of immobility	+, -	Nakayama et al. 2012
	Dopamine level	Activity, duration of immobility	+, -	
Decapoda	Haemolymph density	Exploration, immobility, risk propensity	0, 0, -	Fürtbauer 2015
Decapoda	Temperature	Startle response duration	c	Briffa et al. 2013
Decapoda	Temperature	Latency to emerge from shelter	-	Biro et al. 2013
Decapoda	Temperature	Activity, aggression, boldness	+, +, -	Zhao and Feng 2015
Decapoda	Metabolic rate	Activity	-	Toscano and Monaco 2015
Decapoda	Metabolic rate	Dominance	+	Brown et al. 2003
Decapoda	Metabolic rate	Startle response duration	0	Velasque and Briffa 2016
Decapoda	Copper exposure	Duration of startle response	+	White and Briffa 2017
Hemiptera	Melanotic encapsulation (immunity)	Activity, boldness, exploration	-, +, 0	Gyuris et al. 2016
	Parasite load	Activity, boldness, exploration	c, c, +	
Homoptera	Condition (linked with diet)	Anti-predator response (dropping from host plant)	0	Schuett et al. 2011
Hymenoptera	Juvenile hormone (JH) level	Aggression	+	Pearce et al. 2001
Hymenoptera	Fungal infection	Activity, aggression, sociability	0, 0, -	Turner and Hughes 2018
Isopoda	Metabolic rate	Activity	0	Wilson et al. 2017
Odonata	Condition (linked with diet)	Activity	0	Brodin and Drotz 2011
Odonata	Parasite infection	Activity, boldness	0	Filion et al. 2017
Odonata	Condition (linked with diet)	Activity	0	Brodin 2009
	Predator chemical cues	Activity	c	
Odonata	Insecticide exposure	Boldness, feeding activity	-, -	Debecker et al. 2016
Odonata	Zinc exposure	Activity, exploration, risk-taking	-, -, c	Debecker and Stoks 2019
Odonata	Insecticide exposure	Activity, exploration	c	Tüzün et al. 2015
Odonata	Insecticide exposure	Activity, boldness	+, c	Tüzün et al. 2017

Table 1 (continued)

Taxon	State or environmental variable	Behavioural variable	Association	Reference
Orthoptera	Condition (linked with diet)	Boldness	-	Stahlschmidt et al. 2014
Orthoptera	Octopamine (OA) level	Anti-predator responses (time of immobility, shelter seeking)	-, +	Adamo et al. 2013
Orthoptera	Pathogen exposure	Boldness	0	DiRienzo et al. 2016
Orthoptera	Phenoloxidase activity	Boldness	0	DiRienzo et al. 2015b
Orthoptera	Melanotic encapsulation (immunity)	Boldness	+	Niemelä et al. 2012
Orthoptera	Metabolic rate	Boldness, exploration	+, -	Krams et al. 2017
Orthoptera	Metabolic rate	Latency to leave shelter, duration of freezing time	+, 0	Careau et al. 2019

thanatos behaviour within their 2012 study, but referred to one of their previous study (Nakayama et al., 2010) in which they did test it.) Regarding the first point (i), consistency of studied behavioural traits was assessed from the surveyed study from their Results section, by checking whether or not there was evidence for consistent behaviour. Notably, in the large number of studies the methods of statistical test differed substantially between studies (e.g. in some cases within- and between-individual variation was explicitly quantified and tested, while in some other cases duplicate measurements were used to correlate measurements of the first trial with the second, etc.) We considered a study to be in agreement with our criteria when the authors of the study reported the tests' results and interpretation as supporting consistent behaviour (e.g. the used method showed a statistically significant correlation in behavioural measurements between separate trials).

Condition and organismal state

State of an individual mirrors a series of underlying physiological mechanisms, influenced by both intrinsic (e.g. body condition, immune functions, metabolic rate) and extrinsic factors (e.g. aspects of the social environment, parasite or predation pressure) that have the common potential to consume the resources of the organism. In the past, it was hypothesised that the organismal state is an important mechanistic contributor to animal personality, due to its feedback between state and behaviour that effectively shapes personality, ultimately driving the persistence of adaptive among-individual differences in behaviour (Wolf and Weissing 2010; Sih et al. 2015).

One of the most commonly used measures of individual state is body condition. Generally, condition correlates positively with individual survival, mating success, and effective reproductive success (i.e. number of reproducing offspring). Hereafter, we use body condition as a proxy for the general state of an individual (measured directly or indirectly; see references below), but we do not refer to mere measures of body size. Many of the studies associate

body condition with the energy reserves of the individual (being positively associated with resilience to starving), and consequently in most cases body condition is modified experimentally by manipulating food availability or quality (e.g. Tremmel and Müller 2013; DiRienzo and Montiglio 2016; Müller and Müller 2017; Reim et al. 2019; Segovia et al. 2019). Body condition can have both short-term and long-term effects on behavioural traits. Short-term effects can be defined as those changes in body condition for which the effects occur within the same life stage (e.g. larva, adult), whereas long-term effects are those changes in body condition which are experienced in one life stage (for instance, during an early developmental stage), but are translated into behavioural alteration at a later stage, e.g. during adulthood (Mishra et al. 2011; Tremmel and Müller 2013; Müller and Müller 2017). Based on the surveyed studies the relationship between state and personality is highly variable among species. For instance, low-nutrition diet during the instar stage decreased the level of boldness in adult Madagascar hissing cockroaches (*Gromphadorhina portentosa*) (Mishra et al. 2011). On the other hand, previous studies showed that mustard leaf beetles (*Phaedon cochleariae*) reared on low-quality diet and fasted Texas field crickets (*Gryllus texensis*) were bolder than their conspecifics on a control diet (Tremmel and Müller 2013; Stahlschmidt et al. 2014). However, no dietary effects on boldness were observed in pea aphids (*Acyrtosiphon pisum*) and mustard leaf beetle larvae (Schuett et al. 2011; Müller and Müller 2017). Similarly, in the case of activity, the state-dependence of the given personality trait appeared to depend on the species and the developmental stage as well. For instance, mustard leaf beetles reared on low-quality diet were less active, but in the case of the larvae, there is no relationship between activity and diet (Tremmel and Müller 2013; Müller and Müller 2017). Also, Brodin (2009) and Brodin and Drotz (2011) found no difference in activity between starved and well-fed spotted spreadwing (*Lestes congener*) larvae. These studies on activity may indicate that its state-dependence is a function of the developmental stage. In addition, diet did not

seem to have a general effect on exploration neither in the adult nor in the larvae of the mustard leaf beetle (Tremmel and Müller 2013; Müller and Müller 2017). Notably, however, western black widow spiders (*Latrodectus hesperus*) reared on a restricted diet were more aggressive towards prey than conspecifics reared on ad libitum food (DiRienzo and Montiglio 2016).

There are still surprisingly few studies assessing condition and personality explicitly, hindering our understanding of the condition's role in shaping personality. Seemingly, developmental circumstances affecting body condition might have contrasting effects on multiple axes of personality, which, in the case of the studied arthropods, can also vary markedly during the different developmental stages. Indeed, a meta-analysis on the association between intrinsic state and personality shows weak support for state-dependent personality, based on the low proportion of behavioural variation explained by among-individual variation in state variables (Niemelä and Dingemanse 2018b). Methodological differences across studies and ecological differences between the studied species (e.g. predator *versus* herbivorous species) likely contribute considerably to the discrepant results, as personality traits labelled the same might have quite different functional roles in different species. For instance, increased exploration and risk-taking propensity may have substantially higher survival costs (e.g. due to predation risk) in aphids than in spiders, owing to differences in feeding behaviour and potential risks and pay-offs associated with foraging. Therefore, ecologically informed hypotheses and methods could clarify yet ambiguous associations between condition and personality traits. Notably, though, results might suggest that, besides life history and anatomical characteristics, the temporal extent of starvation (or of exposure to different quantities and qualities of food) may have varying effects, which might hint at intriguing study directions for the future, with the aim to refine the current theory on state-dependent personalities. For example, it could be questioned if short-term changes in condition as a result of temporary dietary restrictions, should be taken into account when investigating proximate mechanisms of personality. While such effects may reversibly change behaviour, they might not affect personality *per se*. For instance, starvation may result in increased foraging activity, aggression, and/or risk-taking propensity, which effect can quickly diminish upon satiation. In other words, short-term changes in condition may be more relevant to behavioural plasticity than to personality. Nevertheless, a closer focus on the mechanisms that mediate this association between reversible changes in behaviour and condition is important to understand the underlying mechanisms that effectively shape personality.

Metabolic rate and thermal physiology

Although ectotherm and endotherm metabolism can be both affected by ambient temperature, this environmental factor is more fundamental in the case of ectotherms, owing to their inability to directly regulate their body temperature (Gillooly et al. 2001). Because for ectotherms thermal physiology is strongly influenced by ambient temperatures, the relationship between thermal physiology and metabolic rate (MR) is more firm in them and can be successfully studied using thermal conditions and thermal traits as proxies for MR (Angilletta et al. 2002; Glazier 2005). Consequently, in ecophysiological studies on arthropods the experimental manipulation of ambient temperatures is often considered as manipulation of MR, and researchers frequently use “higher temperatures” and “higher metabolic rates” interchangeably (Gillooly et al. 2001; Briffa et al. 2013; Zhao and Feng 2015). In our review, we also considered the manipulation of ambient temperature as being a proxy for manipulating the animals' MR.

Metabolic rate is a key element in the theoretical framework called the “pace-of-life syndrome” (POLS) hypothesis, which states that the rate of living is a strong predictor of life history traits and behaviour (Réale et al. 2010). In the past years, a wealth of studies were carried out to investigate its predictions (Tieleman et al. 2005; Réale et al. 2010; Careau et al. 2011; Niemelä et al. 2012, 2013; Biro et al. 2014; Hall et al. 2015; Jacques-Hamilton et al. 2017; Rádai et al. 2017; Khelifa et al. 2019). Despite its shortcomings (see Monceau et al. 2017; Mathot and Frankenhuis, 2018; Polverino et al. 2018; Royauté et al. 2018), it is still one of the most widely used frameworks in studies of life history evolution (Dammhahn et al. 2018; Montiglio et al. 2018), and recent additions aimed to complement it to improve its robustness (Araya-Ajoy et al. 2018; Wright et al. 2020). One of these additions, relevant to this section, addresses thermal physiology, proposing the inclusion of a cold-hot axis into POLS, and hypothesising that an organism's thermal traits (i.e. its position on such a thermal continuum) would consistently covary with behavioural and physiological traits (Goulet et al. 2017a). Such a cold-hot axis refers to a continuum of thermal traits, including not only body temperature but also, for instance, the temperature of optimal physiological performance and critical thermal tolerances. As of now, some empirical observations provided intriguing support (Goulet et al. 2017a, b, 2018; Michelangeli et al. 2018), although mainly on vertebrate ectotherms (Bryant and Newton 1994; Chappell et al. 2004; Gębczyński and Konarzewski 2009; Mathot et al. 2009; Rezende et al. 2009; Sears et al. 2009; Bouwhuis et al. 2014). However, recent evidence suggests a considerably stronger presence of associations between traits classically included in POLS predicted by this hypothesis

among invertebrates (Royauté et al. 2018). Indeed, the assessment of thermal traits and their associations with other elements of POLS and behaviour may be more relevant in invertebrates such as arthropods, as the relationship between behaviours associated with considerable potential for energy acquisition or expenditure (e.g. boldness, or maximum sprint speed, respectively), and measures of metabolic rate (MR) were found to be stronger in ectotherms than in endotherms (Michelangeli et al. 2018; Mathot et al. 2019).

While POLS aims to describe the correlations between life history traits and behaviour based on the notion of traits co-evolving in response to environmental conditions, the so-called energy management models represent a different perspective, to describe how behaviour and metabolic rate might be associated with consideration of the energy expenditure and energy gain linked to the given behaviour (Mathot and Dingemanse 2015). These models are the allocation model, the independent allocation model, and the performance model, which differ in their predictions on how MR should be correlated with behaviours associated with energy expenditure and gain. The allocation model predicts that individuals characterized by higher maintenance MR have to trade-off between maintenance with energetically costly behaviours, leading to a negative correlation between basal MR and the expression of such behaviours, but behaviours of energy gain are uncorrelated with basal MR. The independent allocation model predicts no association between basal MR and behaviours linked with energy expenditure, while it predicts a positive correlation between the expression of behaviours linked to energy gain. Based on the performance model, the expression of behaviours associated with energy expenditure, as well as with acquisition, are expected to be positively correlated with basal MR, due to higher energetic demands of energetically costly behaviours.

Among the few studies in which personality traits and MR were studied in arthropods, there were mixed results reported regarding the relationship between measures of activity and MR. In a study on the western trilling cricket (*Gryllus integer*), exploratory behaviour showed a negative correlation with resting MR (calculated from flow-through CO₂ respirometry; Krams et al. 2017). In two large-bodied marine isopods (*Bathynomus giganteus* and *Booralana tricarinata*) there was no significant correlation between activity and routine MR (Wilson et al. 2017). In the red swamp crayfish (*Procambarus clarkii*), activity was found to be positively correlated with temperature (Zhao and Feng 2015), while in another decapod, the Atlantic mud crab (*Panopeus herbstii*), was shown that the correlation between measures of MR and activity differs when MR is measured in a respiration chamber (termed as routine MR), or in a so-called mesocosm (termed as standard MR; the mesocosm represented a close-to-natural habitat; (Toscano and Monaco 2015)). Specifically, routine MR was positively correlated with activity, but standard MR and activity showed a negative correlation.

Unlike in the case of activity, in arthropods the connection between MR and boldness appears to be a bit more (although not entirely) concordant, the two generally being positively associated. In *Tenebrio molitor*, time spent in tonic immobility in response to a physical stimulus (mimicking a predator attack) was negatively associated with resting MR; i.e., individuals with higher metabolic rate tended to be bolder (Krams et al. 2013a, b; 2014). Similarly, in *Gryllus integer*, crickets characterised by higher MR were bolder as they showed shorter time latency to resume activity after a disturbance event (Krams et al. 2017). In the black finger crab (*Ozius truncatus*), latency before emerging from shelter following a disturbance was negatively affected by temperature, i.e. on higher temperatures individuals emerged from the shelter sooner (Biro et al. 2013). Quite interestingly, though, in the study of Briffa et al. (2013) on the common hermit crab (*Pagurus bernhardus*) higher temperature had either a positive or negative effect on boldness, depending on whether an individual received low-then-high or high-then-low temperature treatments, respectively. Hence, the boldness of these animals seemed to depend on the order of temperature-change rather than temperature itself. Furthermore, in the case of *P. bernhardus*, no association between the mean duration of the startle responses and either routine MR or MR during startle response was apparent, indicating no correlation between MR and boldness (Velasque and Briffa 2016). In the giant freshwater prawn (*Macrobrachium rosenbergii*), individuals characterised by inherently higher resting MR were found to be more “dominant”, i.e. winning more frequently in aggressive interactions (Brown et al. 2003). Surprisingly, in the study of Careau et al. (2019) on fall field crickets (*Gryllus pennsylvanicus*), it was found that individuals with bolder personalities (leaving a shelter sooner) were characterised by consistently lower standard MR, interpreted by the authors as evidence for an allocation trade-off between activity *versus* maintenance (assessed as standard MR). In the same study, another measure of boldness (time spent immobile after a simulated predator attack) was uncorrelated with MR.

Based on the above-mentioned literature, it appears that higher metabolic rates are generally coupled with increased boldness (but see Careau et al. 2019) and aggression in the studied species, while results regarding activity are rather equivocal. These results, at least in part, are seemingly concordant with some of the predictions of the POLS hypothesis, which postulates that higher MR might be expected to be a part of a “syndrome” of trait characteristics, including the proactive behavioural type (Réale et al. 2010). It should be noted though that POLS does not predict whether MR should be a cause or a consequence of proactive behaviour—in fact, POLS merely predicts that a higher rate of living (i.e. fast pace of life) should be in concert with several physiological and behavioural properties. On the other hand, the

so-called performance model predicts a positive effect of MR on proactive behaviour, because higher activity, boldness, and aggressiveness (toward prey and conspecific alike) are necessary to meet the energetic demands of high metabolic activity (Careau et al. 2008; Biro and Stamps 2010). Indeed, the performance model was also found to be supported by a meta-analysis of a wide range of taxa, showing that behaviours associated with substantial net energy gain (or expenditure) pair with higher metabolic rates (Mathot et al. 2019). Notably, for the performance model to be an adequate frame to address the association between MR and personality, the studied behaviours should align with a biologically relevant role of metabolism, relating to the acquisition and expenditure of energy. Also, the utilised measure of MR should reflect relevant energetic mechanisms that can control the studied behaviour (e.g. total energy expenditure, or elements of self-maintenance; see Mathot and Dingemanse 2015). In contrast with the performance model, a negative association active between behaviour and MR could be expected in the frame of the allocation model. The reason behind this is that individual differences in resting MR may not be related to the differences in energy budget but to somatic maintenance, and individuals characterized by higher MR will have a decreased energy availability for costly behaviours.

Arguably, MR has the potential to affect and constrain animal personality, as the energetic expenditure on different behaviours and their expressions profoundly limit what an individual is capable of doing. This is in accordance with the positive feedback model of individual quality and personality, where individuals of inherently higher MR are more proactive, being more apt to gather resources and cope with some environmental hazards (Luttbeg and Sih 2010). Also, the flux of energy and speed of metabolic processes define the rate of higher level mechanisms in the body, such as post-embryonic growth, muscle contraction, digestion, building up somatic and reproductive tissues, and so on (Kushmerick and Conley 2002; Beard et al. 2002; Carlson and Srien 2004). Therefore increased metabolic activity requires increased input of resources, which in turn could be covered most efficiently by proactive behaviour. On the other hand, based on the surveyed publications, MR and locomotory activity shows an ambiguous relationship, sometimes contradicting the predictions from both the POLS hypothesis and the Performance Model. When considering that resting MR is an important element of self-maintenances (Burton et al. 2011) and that it is related to the acquisition and allocation of resources (Zera and Harshman 2001), the association between MR and personality traits might be expected to depend on the given traits' role in energy uptake and expenditure. Methodological limitations, however, may hinder robust conclusions, because different methods of measuring MR and behavioural activity across studies may

not always faithfully represent the metabolic trait researchers are actually interested about (Mathot and Dingemanse 2015). Consequently, measures of MR may show ambiguous associations with the assessed behavioural activity, even if it is ecologically relevant in the studied organism regarding its energy uptake and expenditure.

Aside from methodological factors, the ambiguity observed in the literature may also be resolved, when hypothesising that MR and behaviour are jointly regulated by some other mechanism (or multiple mechanisms), with some degree of variation in response to this regulator(s). Certain elements of the endocrine system could play such a regulatory role, and some invertebrate hormones were found to be associated with both metabolism and behaviour, in a quite conserved manner. For instance, it was reported from several studies that octopamine (OA), one of the invertebrate counterparts of the vertebrate adrenalin and noradrenalin, takes a crucial part in the regulation of metabolic processes, locomotion and behaviour (Roeder 1999, 2005; Roeder et al. 2003; see next section for more details).

Overall, the nature of the relationship between personality and MR in arthropods remains ambiguous. Although MR seems to be a biologically relevant regulator of personalities, other proximate mechanisms, such as hormonal regulation are likely to play considerable roles in affecting both (Lorenz and Gäde 2009; Trillmich et al. 2018). Clarifying the precise role of MR in shaping personality in arthropods is still ahead of us, and in future studies, the functional establishment of the assessed MR measures (i.e. their biological relevance) is imperative to unify the various results from previous studies (Mathot and Dingemanse 2015; Careau et al. 2019). Although the inclusion of a thermal axis in studies on these associations might provide valuable insights for the mechanistic understanding of them, such studies are still scarce. Future studies utilising the extended POLS perspective, assessing personality traits, functionally relevant and repeatedly measured MR, and the effect of both endo- and exogenous hormones on the first two would be invaluable if we are to reconcile their intertwined relationship and to shed light on the role of MR in contributing to the emergence of arthropod personalities.

Endocrine system

The endocrine system might be another key element underlying the evolution of personality. In general, endocrine phenotypes (often expressed through circulating hormone levels) can be highly plastic, being affected by both external (e.g. food availability, predation risk) and internal (e.g. nutritional status, reproductive state) stimuli that elicit adaptive responses (Harshman and Zera 2007; Bonier and Martin 2016). Among-individual differences in hormone production and/or sensitivity to the given hormones may act as important sources of variability in behaviour (Ball

and Balthazart 2008). Indeed, studies on vertebrates showed that hormones play a crucial role in shaping the behaviour and personality of individuals (Koolhaas et al. 1999; Kempenaers et al. 2008; Hau and Goymann 2015). While many studies investigated the endocrine modulation of behavioural traits in arthropods, these studies mostly assessed group-level changes in mean behaviour. This approach often lacks consideration for mechanisms behind the average individual behavioural expression and treats hormonal physiology as a short-term effect rather than a regulator of personality. Inducing a behavioural response by applying hormonal treatment may inform us about the behavioural traits that the given hormone might shape, and could also give us good starting points for identifying what elements of hormonal physiology might play a role in shaping animal personality.

The octopaminergic/tyraminergetic system has a similar role in invertebrates like the adrenergic system in vertebrates, as both systems mainly regulate fight or flight response and aggression. The octopaminergic/tyraminergetic system is present in all protostomes, and one of its endpoints is the non-peptide hormone octopamine (OA) (Roeder 2005). OA can modulate neuroendocrine processes, sensory functions, immune functions, and complex neuronal processes such as learning and memory or rhythmic behaviours (Roeder 1999; Unoki et al. 2006). In insects, OA was shown to stimulate muscle contraction and also the oxidation of glucose, trehalose, butyrate and diacylglycerol, i.e. to contribute to the regulation of energy homeostasis and motility (Candy 1978; Goosey and Candy 1980; Sombati and Hoyle 1984; Candy et al. 1997; Brembs et al. 2007). In crustaceans, it was also found to increase the frequency and amplitude of heart muscle contractions (Florey and Rathmayer 1978). OA may also indirectly shape personality by its effects on metabolism and thermal physiology. For example, Li et al. (2016) showed that *Drosophila melanogaster* flies lacking OA were characterised by low resting MR. Eriksson et al. (2017) had similar findings on *D. melanogaster*, although the calculated effect size representing the decrease in oxygen consumption in OA-deficient individuals was relatively small. However, food consumption of the OA-deficient flies showed a considerable decrease in the latter study. Therefore, OA seems to be a good candidate to play a key role in regulating metabolic processes and promoting proactive behaviours in arthropods. Although few studies were carried out incorporating temperature as a covariate when assessing OA levels, there is some evidence that a positive correlation exists between temperature and OA levels in invertebrates. For example, in the study of Hirashima et al. (1992), the effects of multiple thermal treatments on red flour beetle (*Tribolium castaneum*) larvae were compared to control larvae kept at 30 °C. The results showed that the level of OA in larvae kept at 20 °C and 25 °C was lower relative to the control, while a thermal treatment of 40 °C increased the OA

levels in the larvae. Similarly, Davenport and Evans (1984) found that in both locusts and cockroaches high-temperature treatments resulted in elevated OA concentration in the haemolymph. Additional studies hint at a role in thermal conditioning and heat-stress tolerance by OA as well (Armstrong and Robertson 2006; Armstrong et al. 2006). These findings suggest that higher ambient temperatures not only facilitate more active (and proactive) behaviours simply by providing more optimal kinetic conditions for biochemical processes but also increasing temperature elicits such physiological responses that result in upregulation of both metabolic and behavioural activity via endocrine signalling.

Although OA is known to modulate behaviour in arthropods (Saraswati et al. 2004; Zhou et al. 2008; Li et al. 2016), relatively few studies investigated the possible link between OA and personality. Based on the limited amount of literature available we know that OA has a positive association with boldness in western black widows (*Latrodectus hesperus*), in orb-web spiders (*Larinioides cornutus*) and texas field crickets, but not in funnel-web spider (*Agelenopsis pennsylvanica*) (Jones et al. 2011; Adamo et al. 2013; DiRienzo et al. 2015a, b). In contrast, some other studies found no evidence for OA influencing either activity or aggressiveness in the same spider species (Jones et al. 2011; DiRienzo et al. 2015a, b).

Another important hormone with considerable potential in shaping personality is serotonin (also known as 5-hydroxytryptamine: 5HT), a monoamine neurotransmitter in the nervous system, present in most animal taxa, from invertebrates to humans (Berger et al. 2009). It is usually associated with submissive behaviour affecting aggression and escape behaviours (Dayan and Huys 2009). Although 5HT has been shown to influence various behavioural traits in both invertebrates and vertebrates (Falibene et al. 2012; Kiser et al. 2012; Olivier 2015; Winberg and Thörnqvist 2016), it is yet far from being clear how it can shape personality in arthropods (Erber et al. 1993; Huber 2005; Falibene et al. 2012). 5HT has a negative influence on boldness but does not affect activity in orb-web spiders (Jones et al. 2011). Tangle-web spiders (*Anelosimus studiosus*) showed higher sociability by increased 5HT levels (Price 2010). The fact that the 5HT level showed a positive relationship with sociability in tangle-web spiders may be attributed to that tangle-web spiders are the only social spiders from the studied species above. This finding hints at intriguing questions regarding the role of 5HT in the evolution of sociality in spiders.

The juvenile hormone (JH) plays a crucial role primarily in the development of insects. In larvae and pupae JH levels drop before the final moult (Jindra et al. 2013). In adults, JH production is again restarted and controls various reproductive and feeding behaviours (Wyatt and Davey 1996; Pearce et al. 2001). In honeybees (*Apis mellifera*), they found that individuals with lower JH levels were less

aggressive than individuals characterised by high JH levels (Pearce et al. 2001). Also, both JH levels and aggressiveness of individuals were lower during winter than during summer. Furthermore, differences between casts were observed: nurse bees were less aggressive, and they concomitantly had lower JH levels in comparison with guard bees. Moreover, colonies with higher mean JH levels were more aggressive than colonies with lower JH levels (Pearce et al. 2001).

Even though there is a wealth of studies on the effects of different hormones on behaviour in arthropods, the number of studies that explicitly investigate the hormonal background of personality are still surprisingly scarce. Throughout our literature review, we found studies assessing hormonal effects on personality only for three hormones, while it is likely that several other hormonal pathways could affect personality in arthropods (Scheiner et al. 2002). Based on the reviewed studies, it seems that OA, 5HT, and JH all have the potential to play key roles in shaping personality. For example, OA may be part of the state-dependent maintenance or modulation of consistent individual behaviour through its influence on energy metabolism, by which feeding behaviour and activity may be controlled. Also, 5HT appears to exert influence on boldness, activity, and/or sociability. It is also worth noting that, while JH analogues were found to be present in non-insect arthropods as well (e.g. in arachnids and crustaceans: Laufer et al. 1993; Homola and Chang 1997), studies on JH and JH-like compounds are predominantly carried out in insects (Li et al. 2019), hindering our capacity to infer on the role of JH in shaping personalities in other arthropods. Notably, the number and density of the different receptor types may be highly variable across taxa, contributing to variations in behavioural responses across species (Kroeze et al. 2002). To better understand the relationship between hormones and personality and the role of hormonal regulation in the evolution of personalities, additional studies will be necessary, preferably even taking the types and densities of specific receptors into account.

Immunity and parasite infection

Immune responses have high costs, and animals have to allocate limited resources from other maintenance processes to protect themselves from both microscopic and macroscopic threats (Moreno-García et al. 2013). Consequently, if an organism invests too much in immunity, it will limit other mechanisms, e.g. reproduction, growth, or tolerance, for other stress factors to balance this trade-off (Schmid-Hempel 2005). Considering the relationship between immunity and personality, two hypotheses have been proposed (Jacques-Hamilton et al. 2017). The risk-of-parasitism hypothesis suggests that individuals, which are characterised by being bolder, more active and risk-taking (also called “proactive”; Koolhaas et al. 1999), have

a greater chance of encountering pathogens and parasites throughout their lives, than individuals that are shy, less active and risk-taking (called “reactive”; Koolhaas et al. 1999). Hence, proactive individuals should benefit from having a stronger immune system (in terms of increased resistance or tolerance) against these agents than reactive individuals (Kortet et al. 2010). The POLS hypothesis, on the other hand, predicts negative correlation between proactive personality and immune function. An efficient immune system entails considerable costs associated with the maintenance and deployment of its elements (McKean et al. 2008), and proactive individuals may invest their energy in fast reproduction rather than long-term survival. By contrast, reactive animals invest more in survival, prioritising somatic maintenance (and with that immunocompetence) over reproduction (Réale et al. 2010; Monceau et al. 2017).

Studies investigating this relationship in invertebrates almost exclusively used arthropod species as model organisms. Arthropods, and especially insects, are ideal models for studying the relationship between personality and immunity since a number of relatively simple but reliable methods were developed to study their immune systems (Schmid-Hempel 2005). In contrast with vertebrates, insects do not have adaptive, only innate immune system (although see Contreras-Garduño et al. 2016; Cooper and Eleftherianos 2017), which is based on the distinction of self and non-self, and non-specific immune response to pathogens. Insect immune defence and methods developed to measure its capacity are reviewed by Moreno-García et al. (2013); however, we would like to highlight some frequently examined markers to aid the interpretation of the studies discussed below. One of the most commonly used methods is to insert a nylon monofilament into the haemocoel to mimic natural infection. This will initiate a nodulation/encapsulation response during which a melanin layer is formed. The filament is then removed and the encapsulation rate is calculated from the volume of melanised and non-melanised cells (Siva-Jothy 2000). Another approach is to expose individuals directly to pathogens. In this way, immune capacity can be assessed by measuring e.g. the haemocyte density or phenol- and prophenoloxidase activity in the haemolymph. Haemocytes are the first line of defence against bacteria, thus estimating the total number of them is a direct way to infer the cellular immune ability of an organism (Rantala et al. 2000). Phenoloxidase enzyme is essential in wound healing, clotting, encapsulation, and production of cytotoxic molecules, and haemocytes are involved in recognition, phagocytosis, and encapsulation; therefore, these molecules should be produced in increased levels when any kind of infection appears (Moreno-García et al. 2013).

Although several studies have been published that were designed to examine the relationship of immune capacity with behaviour in arthropod species, merely a few of them

included measurements on the repeatability of the tested personality traits. In a study by Niemelä et al. (2012), association between boldness and encapsulation response of the field cricket *Gryllus integer* was examined. The authors tested the boldness of individuals during their development, and then performed the encapsulation experiment in their adulthood. They detected a negative correlation between boldness in early age and immune response; i.e., cautious juvenile individuals had better immunity as adults.

In another study on the same species, juvenile crickets were injected with a bacterial pathogen (*Serratia marcescens*), following which their boldness and encapsulation response were assessed as adults (DiRienzo et al. 2015a). Results showed no influence of pathogen exposure on either analysed trait, but in individuals infected early in their life repeatability of their latency to emerge from shelter diminished, whereas in control individuals, it remained repeatable. Notably, the repeatability of latency to become active remained significant in all treatment groups. In another experiment, field cricket adults were exposed to *S. marcescens*, and then their boldness was assessed (DiRienzo et al. 2016). Pathogen exposure did not affect the mean boldness of individuals; however, it increased among-individual variation of emergence measures.

The relationship between ectoparasite mite infection and personality was investigated by (Gyuris et al. 2016) in wild-caught firebugs (*Pyrhocoris apterus*), and the association between encapsulation response and personality was tested in laboratory-reared specimens. Three personality traits were measured: boldness, exploratory behaviour, and activity. Results on wild animals were in line with the risk-of-parasitism hypothesis, as more explorative bugs had more mites. Moreover, activity and boldness positively correlated with the degree of mite infection, although only in females. Among laboratory-reared firebugs, no relationship between immunity and exploration was detected. However, a strong immune response was associated with higher boldness, but lower activity, even though both trends were only marginally significant.

In a study on wild red damselfly (*Xanthocnemis zealandica*) nymphs, the association between trematode infection and personality (activity and boldness) was investigated (Filion et al. 2017), in which no relationship was found between personality traits and parasite infection. Turner and Hughes (2018) challenged wood ants (*Formica rufa*) with virulent fungal parasites (*Metarhizium pingshaense*) and examined whether it had an effect on boldness, sociability (proportion of time spent in close contact with a nestmate) and aggressiveness, also finding no significant difference between control and parasite-challenged groups in either behavioural trait.

Monceau et al. (2017) correlated activity, exploration, food neophobia and gregariousness, then studied its

relationship with innate immunity of the mealworm beetle (*Tenebrio molitor*). Specifically, they measured haemocyte concentration, phenoloxidase activity and total phenoloxidase activity (phenoloxidase and prophenoloxidase together) in the haemolymph. Their results showed that in males more proactive individuals tended to be characterised by lower phenoloxidase activity and higher haemocyte concentrations than reactive males, whereas the contrary was observed in females (although both correlations had 95% confidence intervals overlapping zero). Additionally, in individuals that were exposed to an entomopathogenic bacterium, *Bacillus thuringiensis*, no significant association was found between personality and resistance to the infection.

Not only insects, but crustaceans are also an interesting group of model organisms for investigating personality. Fürtbauer (2015) examined the crab species *Carcinus maenas* to assess the relationship between immunity and personality. In this study, haemolymph density (which is proportional to the protein concentration of the haemolymph, used to infer on the physiological state in crustaceans) was measured repeatedly during an experiment about exploration, immobility, and risk-taking propensity of individuals. Individuals with higher haemolymph density spent more time near the shelter, i.e. they took less risk compared to individuals with lower haemolymph density which result is in line with the POLS hypothesis.

Overall, the results of these studies support both risk-of-parasitism and POLS hypotheses. However, many experiments resulted in no significant association between personality and immunity. It is also noteworthy that many studies are rather correlative in nature (e.g. correlating parasitisation with personality traits), which makes it more difficult to identify those factors that effectively shape personality. Yet, these studies highlighted some thought-provoking points. For example, based on the experiment of DiRienzo et al. (2015a, b), pathogen infection of juveniles can affect the repeatability of behaviour. Considering the results of Gyuris et al. (2016) and Monceau et al. (2017), it is necessary to control for sex differences, as males and females can highly differ in resource allocation for immune responses (Zuk et al. 2004; Rádai et al. 2018). Such sex-dependent characteristics of immunity, and sex-dependent associations between immunity and personality likely reflect life history differences between the sexes. For example, differences in foraging activity, or mating strategies could also contribute to sex differences in the above-mentioned associations. Furthermore, as suggested by Fürtbauer (2015), it is worth considering to measure not only personality traits but also immune system characteristics several times, even through ontogeny, in order to get a whole and more reliable picture on the link between personality and immunity. Experiments and studies taking into account these suggestions are needed to further clarify how immunity contributes to animal personalities.

Exogenous molecules

Both the abiotic and biotic components of the environment may have a substantial effect on arthropods via the effect of different exogenous molecules on physiology and behaviour. For example, pollutants from anthropogenic contaminants, such as heavy metals or chemicals, can influence both physiological and behavioural traits (reviewed by Wong and Candolin 2015). In many cases, sublethal doses of pollutants have been shown to cause changes in activity, boldness, orientation and navigation behaviour, and even in anti-predator behaviour or foraging activity (Relyea and Mills 2001; Cheung et al. 2004; Colin et al. 2004). Although the existence of consistent behavioural differences between individuals is widely accepted, the number of studies on the relationship between the physiological changes induced by potentially toxic agents and changes in personality in arthropods is still scarce. Behavioural studies involving insects and chemical agents or insecticides focus on populations rather than on individuals.

A large number of arthropod species show a high affinity for crop systems (Samu and Szinetár 2002), and they are frequently exposed to contamination and insecticides used in agriculture, which can adversely affect their physiology and behaviour, even at sublethal doses (Desneux et al. 2007). Royauté and colleagues investigated the changes in personality traits and behavioural syndrome structure of jumping spiders (*Eris militaris*) in response to pesticide treatments, both in the field and in the laboratory (Royauté et al. 2014, 2015). In the field, spiders from the treated orchard were exposed to several commonly used pesticides, while in the laboratory experiment, sublethal doses of the insecticide organophosphate phosmet were used for the treatment. They found that jumping spiders collected from a pesticide-treated orchard showed a significant decrease in activity but tended to be more voracious (Royauté et al. 2014). Interestingly, behavioural syndrome structure differed significantly between treated and non-treated orchards. In the case of the pesticide-treated population, the syndrome structure was broken, while in the non-treated one, all assessed personality traits (activity, voracity, aggressiveness and boldness) were retained without any significant change. By contrast, during their laboratory experiment, sublethal doses of the insecticide organophosphate phosmet did not lead to changes in the behavioural syndrome structure of jumping spiders (Royauté et al. 2015). However, a decrease in the consistency of the behavioural traits was observed among treated individuals. Additionally, females exposed to insecticide showed a collapse of the correlation between activity and voracity. It is important to note that the two studies differed in the experimental setup, in insecticide exposure source, and in the measured behavioural variables. In the case of the field study (Royauté et al. 2014), orchards served as study sites,

and in the treated one, several pesticides were used, such as insecticides, fungicides and arachnicides. In the laboratory study (Royauté et al. 2015), however, the experiments were carried out under controlled conditions, the organophosphate phosmet treatment was directly and acutely administered, and only activity and voracity were defined as personality traits. The results of these two studies suggest that pesticide effects are more complex than was thought before and hint at a considerable degree of variation in how individuals cope with insecticide exposure.

Copper is both a common toxic marine pollutant and essential metal in all living organisms. White and Briffa (2017) tested the effect of seawater-borne copper exposure on the behaviour of hermit crabs (*Pagurus bernhardus*), measuring the length of the crabs' startle response (time being receded in their protective shells) as a proxy for individual boldness. They found that copper exposure increased startle response duration; i.e., hermit crabs subjected to copper treatment were less bold. A likely explanation proposed by the authors was that copper exposure might have depressed specimens' performance, rendering them to be more cautious. Alternatively, as the authors argued, impaired decision-making might have also contributed to their observations.

Besides toxic agents, secondary metabolites may also influence the behaviour of arthropods, such as those produced by plants, like caffeine, which is supposed to act through several mechanisms in the dopamine signalling pathway. Nakayama et al. (2012) investigated the relationship between the tonic immobility/activity and the dopaminergic system in artificially selected two strains ("L-strain" and "S-strain") of confused flour beetles (*Tribolium confusum*) by using caffeine treatment. Individuals originating from the "L-strain" are basically less active and show longer duration and higher frequency of tonic immobility, while individuals from the "S-strain" are more active and display shorter duration with lower frequency of tonic immobility. Furthermore, the brain dopamine level is lower in "L-strain" individuals than in "S-strains." Caffeine administration significantly decreased the duration of tonic immobility and increased the activity level in "L" strain specimens but not in "S" strain specimens. However, despite caffeine administration, "L-strains" were still less active and showed longer durations of tonic immobility compared to "S-strains." These results suggest that "S-strain" individuals, as a result of artificial selection, might have reached the limits for both examined traits. With these experiments, it has been demonstrated that (i) the dopaminergic system plays an important role in controlling a putative genetic correlation between tonic immobility and activity, hence contributing to the emergence of personality elements, and (ii) caffeine modulates repeatable behaviour via its effect on the dopaminergic pathway.

While secondary metabolites such as caffeine are generally produced by plants (e.g. for pest deterrence; Kim et al. 2010), agents of animal origin may also affect average behaviour in arthropods. For example, in *Argiope keyserlingi* spiders, it was found that females modulate their foraging and web-building behaviour in response to chemical cues from predators (Ameri et al. 2019). Specifically, they exhibited shortened latency to catch prey (i.e. tended to be more voracious), shortened prey handling time, and rebuilt their web less frequently.

Cumulative effects of metal or chemical pollutants and climate change were also found to drive changes in behavioural types in aquatic arthropods from water communities, for instance in damselfly larvae (Dinh Van et al. 2014). Populations generally show distinct variations in behavioural types (Debecker et al. 2016; Debecker and Stoks 2019), as habitats, and thus, individuals living there are differently exposed to urbanisation (Tüzün et al. 2015, 2017). Because of increasing urbanisation, intraindividual and between-population behaviour changes are expected in species due to changes in physiological traits induced by an impression of different contaminants. In the blue-tailed damselfly (*Ischnura elegans*) it has been found that the exposure to both zinc and the insecticide chlorpyrifos caused decreased activity, exploration, and risk-taking behaviour in damselfly larvae (Debecker et al. 2016; Debecker and Stoks 2019). Similarly to *Ischnura elegans*, in azure damselfly (*Coenagrion puella*) larvae, behavioural types can be affected by insecticides, such as chlorpyrifos or esfenvalerate, depending on the degree of urbanisation (rural versus urban) and increasing temperature of aquatic habitats. Both chlorpyrifos and esfenvalerate exposure caused depressed levels of activity in *Coenagrion puella* larvae from rural habitats (Tüzün et al. 2015, 2017) depending on temperature. But in the case of urban habitats, insecticides had different effects on larval activity: while chlorpyrifos increased the level of activity (Tüzün et al. 2015), esfenvalerate exposure depressed it (Tüzün et al. 2017). Esfenvalerate was found to depress the level of boldness in *Coenagrion puella* larvae from rural but not from urban habitats, while chlorpyrifos showed no significant effect on the boldness of larvae. Interestingly, chlorpyrifos was found to influence the level of exploration depending on habitat type and depressed the level of food intake in larvae of the damselfly *Coenagrion puella*, but only when the temperature was higher (Tüzün et al. 2015). This suggests that the changing effect of chlorpyrifos on predatory behaviour types depends more on temperature than sensitivity to insecticides if we assume that larvae from urban areas are less sensitive to chlorpyrifos due to involved higher tolerance against insecticides (Tüzün et al. 2015).

Personality traits are influenced by the physiological response to internal and external stimuli and their associations, and exogenous chemical agents can induce significant changes in the mean level and repeatability of behavioural traits in arthropods. We still do not have much information

about the proximate mechanisms underlying personality among arthropod taxa, and we need a broader understanding of the effects of contaminants and biogenic compounds on animal personality. However, based on our current understanding of their mechanisms of action, they seem to exert their effects mainly by disrupting hormonal and/or metabolic processes (Mu et al. 2005; Du et al. 2019; Arambourou et al. 2020). Furthermore, the reviewed literature suggests that anthropogenic contaminants and chemicals jointly affect individuals' behaviour. However, in most cases, the effects of each compound on behavioural traits are unclear. Arthropods are still understudied concerning induced changes in personality traits by often used heavy metals (for example, lead, cadmium, manganese, uranium, iron), fertilisers, plant-produced secondary metabolites, drugs or heterospecific chemical cues (Montiglio and Royauté 2014), even though in several environments they are exposed to those regularly. By investigating the physiological background of behavioural types and the effects of exogenous chemical agents on personality, we can get a more comprehensive picture of the evolutionary and ecological functions of consistent behavioural differences among individuals.

Current state of knowledge and future directions

Consistent individual differences in behaviour (i.e. personality) have been observed in a large number of animal species, invertebrates and vertebrates alike. Despite the efforts invested in personality research in the last two decades, questions about the adaptive value of the substantial variability in personalities within- and among populations are still largely unanswered. Arguably, however, if we are to understand the evolutionary background of how considerable variation in personality traits is maintained within populations, we will need a better understanding of the underlying mechanisms. In the endeavour to untangle the associations between certain physiological variables and personality, arthropods proved to be a valuable resource. Studies carried out in the past decades on arthropod model organisms helped us gain considerable insights into what mechanisms influence personality. However, during our literature survey, we found that the number of studies on arthropods that explicitly investigate personality and its physiological correlates is still rather small in comparison to studies not utilising a repeated-measure design. Also, the results and their interpretations from these studies vary substantially, sometimes even contradicting one another. Owing to the small number of studies and their often ambiguous results, it is difficult to identify a general pattern of which proximate mechanisms might play a role in shaping personality in arthropods and how. Methodological differences between studies, no doubt, play a significant role in yielding discrepant results and interpretations, as well as the frequent

lack of ecological context and functional interpretation for measured behaviours (Dall and Griffith 2014). Nevertheless, some of the published observations hint at intriguing directions and questions for future studies. For example, comparative analyses of the correlation of ecological and life history characteristics with the association between proximate mechanisms and personality will help us to better understand the various results from the different studied organisms.

We found little support for individual condition (used as a proxy for organismal state) to contribute to individual-level differences in personality. Still, it was apparent that factors influencing condition and/or organismal state may affect personality traits, depending on how persistent these factors are. For example, an acute decrease in food availability or quality may promote an increase in boldness and activity, with the adaptive role of mitigating the temporary shortage of resources (Biro and Stamps 2008). Note, however, that this phenomenon could be interpreted as an instance of behavioural plasticity. Similarly, in some of the reviewed studies on toxin and pathogen exposures, it was the level of consistency of the different behaviours that changed, rather than the average behaviour of individuals. Changes in behaviour in response to nutrition regimes or exogenous molecules, in principle, are concordant with state-behaviour feedbacks (Sih et al. 2015). But such modulation of behaviour tells us more about an individual's capacity to change its behaviour (i.e. about its plasticity) than about its mean level expression of the behaviour in question.

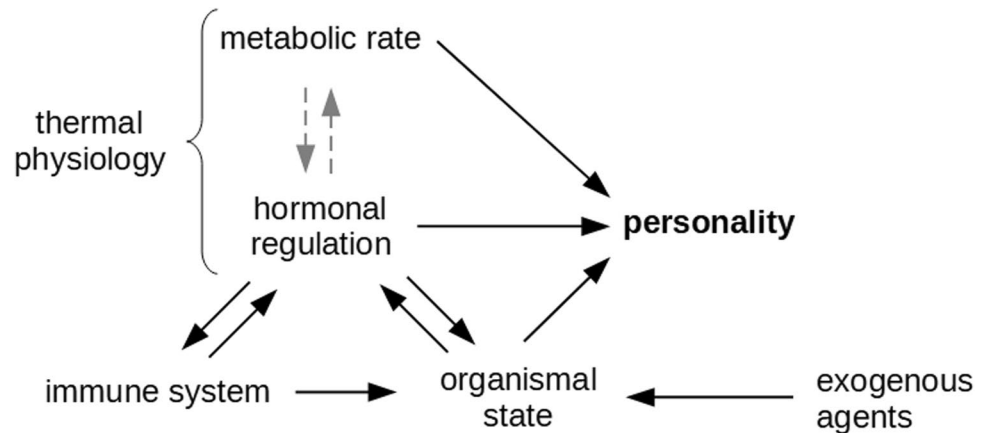
Based on the surveyed studies (and on Niemelä and Dingemanse 2018b), the organismal state appears to have a small contribution to personality in arthropods. Notably, though, this conclusion might be biased by methodological and conceptual inconsistencies in the surveyed studies. Quantification of organismal state widely varies between studies. Yet it is still not clear what types of measurements would qualify as reliable in an empirical setup. Arbitrary interpretation of different phenotypic traits representing the state can thus hinder true insights into its significance. Of course, the organismal state is difficult to quantify as it is composed of a myriad of state variables that also can be correlated via causal links, feedback loops, and/or correlations arising from indirect associations. Arguably, such an intricate network of dynamically changing traits is hard to be represented by a select few macroscopic phenotypes, which further complicates the problem of their identification and the interpretation of observations. Especially so when we also consider that multiple feedback loops may affect a given behaviour (Luttbeg and Sih 2010; Sih et al. 2015), and the directions of feedback loops that link a specific state variable with a specific behaviour may vary across individuals (Sih et al. 2015; Zucchini et al. 2008). Accordingly, it is imperative to test behavioural and state variables multiple times within individuals, and, where appropriate, with the inclusion of explicit experimental treatments that can highlight the nature of feedback mechanisms at play.

The considerable (although not unequivocal) support for the performance model is in accordance with the state-behaviour feedback. For instance, metabolic rate shows considerable potential for participating in a feedback loop between state and behaviour, as higher MR promotes more active and/or bold behaviour, which, in turn, can maintain high MR, leading a positive feedback between MR and active behaviour, and contributing to the emergence and persistence of among-individual variation in personality. Similarly, the results from studies on the association between immunity and personality also provide some support for state dependence. The capacity to resist or tolerate parasites entails various costs (Sheldon and Verhulst 1996), which might pose a relatively smaller burden on individuals of good condition (Kortet et al. 2010); hence, “good quality” individuals can maintain higher activity even in the face of increased probability of encountering parasites. Also, in the case of parasite infection, an increased resource demand in the host might drive more active behaviour to improve resource acquisition that can meet this demand (DiRienzo et al. 2015b; Kortet et al. 2010).

On a different note, when total energy expenditure does not vary within individuals, MR and behaviours associated with energy expenditure may show a negative correlation due to the trade-off between metabolic investment into self-maintenance and costly behaviours (Mathot and Dingemanse 2015). The different taxa studied may utilize different strategies of energy management, which could explain some of the seemingly contradictory results in the association between behavioural activity and metabolic rate. An important future direction should be the identification of the employed energy management strategy in the model organisms, for example in relation to life history attributes (Brown et al. 2004). Also, comparative studies could help us understand how different energy management strategies arise in different organisms.

Based on the results of the surveyed studies a likely candidate for a mechanistic link by which we can connect MR and immunity with the organismal state is arguably endocrine regulation (Fig. 1). Metabolic and hormonal processes are likely key components in shaping personality and plasticity in behaviour as well, as they can be sources of both within- and between individual phenotypic variation (Jandt et al. 2014; Hau and Goymann 2015; Taff and Vitousek 2016). Also, they were shown to exert a strong and consistent influence on organismal state and behaviour, often in a quite conserved manner across a wider range of taxa (see for example Roeder 1999, 2005; Stay and Tobe 2007; Jindra et al. 2013). Octopamine (OA), serotonin (5HT) and juvenile hormones (JHs) were found to play key roles in a wide range of metabolic processes that affect the organismal state. Also, some hormones play key roles in immunological processes (e.g. Flatt et al. 2008; Roved et al. 2017), which implies a common ground with the hormonal regulation of

Fig. 1 Hypothesized associations of organismal state with key physiological effectors based on the surveyed studies. Arrows represent direction of causality; arrows oriented in both directions represent feedback between the linked elements. The grey dashed arrows between metabolic rate and hormonal regulation indicate the apparent knowledge gap on this hypothesized association in arthropods



consistent individual behaviour (Flatt et al. 2005, 2008). Furthermore, hormonal regulation of metabolic processes may also indirectly affect personality via their effects on resource acquisition and allocation (Careau et al. 2008; Bourg et al. 2019). Behaviours associated with the substantial net change in resource acquisition and/or allocation are fundamentally constrained by physiological and metabolic processes. An inherently higher metabolic activity is predicted—and in a significant number of studies found—to be associated with more active and bold behaviours, although mainly in contexts associated with substantial net changes in resource management (Mathot et al. 2019). It is worth noting that metabolism and hormonal regulation are also of relevance when considering the effects of exogenous agents, which generally act on metabolic processes, or on certain hormonal pathways. Consequently, their potential as effectors on organismal state and personality should always be discussed concerning the pathways they influence (e.g. Nakayama et al. 2012).

In many arthropod species, the aforementioned hormones also act as neurohormones, i.e. can have a direct impact on personality. These assertions, of course, are not new, but a better understanding of animal personality will require a deeper understanding of both the direct and indirect effects by which endocrine systems shape personality (e.g. via neurohormones *versus* modulators of energy metabolism, respectively). It is also worth noting that hormonal pleiotropy and potential interactions between hormones complicate the picture of regulatory mechanisms that might act on personality. Although in terms of feasibility it is anything but trivial, future studies will undoubtedly benefit from more composite approaches in which the levels of multiple hormones are assessed investigating their roles in shaping personality.

A substantial gap in our current knowledge persists regarding the association between MR and hormonal regulation (Fig. 1), and its effect on the organismal state in arthropods. Although some studies in insects help us to peek into the regulation of metabolism (Arrese and Soulages 2010), the importance of

metabolic rate and hormonal regulation relative to one another is still largely unknown, therefore hindering our understanding of how exactly they might collectively shape state and personality in arthropods. This area of research, therefore, seems to be quite promising in providing novel and complex insights into the proximate background of arthropod personalities.

Conclusions

In this review, we aimed to summarise and put into context the current state of knowledge of the most frequently assessed physiological factors shaping personality in arthropods. The surveyed studies draw a still ambiguous picture. However, in the state-dependent personality framework, we can still make reasonable attempts to interpret the various empirical observations, by considering the dynamical nature of organismal state and the complex associations between physiological processes behind it. Overall, we found only weak support for state-dependence of personality when the state is approximated by singular elements (or effectors) of condition. However, the interpretation of empirical observations from past studies becomes more nuanced when considering organismal state as an integration of multiple, often interrelated physiological processes. Interpreting the surveyed studies is still not without difficulties; to resolve some of the outstanding questions, future studies should (i) explicitly address personality in a conceptually and methodologically adequate manner, (ii) assess multiple, functionally separate physiological traits in relation to personality, and (iii) use multiple measurements on the addressed physiological parameters whenever feasible. One of the most interesting questions focuses on the hormonal regulation of metabolic rate, and its role in shaping state, and ultimately personality, in arthropods. Filling this knowledge gap will provide invaluable insights into the dynamics of regulated changes in consistent individual behaviour, granting us a deeper understanding of animal personality.

Appendix

Table 2

Table 2 Table containing taxa names and searching terms we used for literature sweep

Name of the taxon	Search names for the taxon	Search terms
Anellida	Anellida, Christmas tree worm, Earthworm	Animal Personalit*, Behavio* Syndrome*, Condition, Courtship song, Development, Gen*, Haemolymph density, Hormon*, Immun*, Metabol*, Morpholog*, Oxidative stress, Oxygen consumption, Pesticide, Physiolog*, Repeatable Behavio*, Stress
Arachnida	Spider	
Archaeognatha	Archaeognatha, Bristletail	
Coleoptera	Beetle, Coleoptera	
Crustacea	Barnacle, Crayfish, Crab, Crustace*, Isopod*, Krill, Shrimp, Lobster, Woodl*	
Diptera	Diptera, Fly	
Ephemeroptera	Ephemeroptera, Mayfly	
Hymenoptera	Ant, Bee, Bumblebee, Honeybee, Hymenoptera, Sawfl*, Wasp	
Lepidoptera	Butterfly, Lepidoptera, Moth	
Mecoptera	Hangingfly, Mecoptera, Scorpionfly	
Mollusca	Bivalvia, Cephalopod*, Cuttlefish, Gastropod*, Mollusc*, Octopus, Slug, Snail, Squid	
Nematoda	Nematod*	
Odonata	Anisoptera, Damselfly, Dragonfly, Zygoptera	
Polyneoptera	Blattodea, Cockroach, Cricket, Dermaptera, Earwig, Embioptera, Grasshopper, Gryllidae, Grylloblattid*, Gryllus, Heelwalker, Locust, Locusta Migratoria, Mantid, Mantodea, Mantophasmatodea, Phasmatodea, Plecoptera, Rock crawler, Stonefly, Tettigoniidae, Walking stick, Web-spinner, Weta, Zoraptera	
Paraneoptera	Aphid, Bug, Cicada, Hemiptera, Heteroptera, Lice, Psocodea, Thrips, Thysanoptera	
Platyhelminthes	Platyhelminthes	
Siphonaptera	Flea, Siphonaptera	
Trichoptera	Caddisfly, Trichoptera	
Zygentoma	Zygentoma, Silverfish	

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Data availability Data sharing is not applicable to this article as no datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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