



Essay

Studying personality variation in invertebrates: why bother?

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ARTICLE INFO

Article history:

Received 12 October 2013

Initial acceptance 18 November 2013

Final acceptance 3 February 2014

Published online

MS. number: 13-00849R

Keywords:

behavioural syndrome

comparative analysis

eusociality

evolution

invertebrate

life history

metamorphosis

parasite

personality

sexual selection

Research on animal personality variation has been burgeoning in the last 20 years but surprisingly few studies have investigated personalities in invertebrate species although they make up 98% of all animal species. Such lack of invertebrate studies might be due to a traditional belief that invertebrates are just 'minirobots'. Lately, studies highlighting personality differences in a range of invertebrate species have challenged this idea. However, the number of invertebrate species investigated still contrasts markedly with the effort that has been made studying vertebrates, which represent only a single subphylum. We describe how investigating proximate, evolutionary and ecological correlates of personality variation in invertebrates may broaden our understanding of personality variation in general. In our opinion, personality studies on invertebrates are much needed, because invertebrates exhibit a range of aspects in their life histories, social and sexual behaviours that are extremely rare or absent in most studied vertebrates, but that offer new avenues for personality research. Examples are complete metamorphosis, male emasculation during copulation, asexual reproduction, eusociality and parasitism. Further invertebrate personality studies could enable a comparative approach to unravel how past selective forces have driven the evolution of personality differences. Finally, we point out the advantages of studying personality variation in many invertebrate species, such as easier access to relevant data on proximate and ultimate factors, arising from easy maintenance, fast life cycles and short generation times.

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The phenomenon of animal personality variation, that is, between-individual differences in behaviour that persist through time and/or across situations or contexts (e.g. Dall, Houston, & McNamara, 2004; the latter is often referred to as 'behavioural syndromes', sensu Sih, Bell, Johnson, & Ziemba, 2004), has been widely studied in the last 20 years. Most personality studies have been conducted within a single subphylum, the Vertebrata (phylum: Chordata) (e.g. Gosling, 2001). Surprisingly few studies have investigated personality variation in any other animal (sub-)phylum (i.e. all invertebrate species) although the species diversity of those phyla is much broader than in vertebrates (invertebrates make up 98% of all species; Pechenik, 2000). The lack of data on invertebrate personality might be due to a traditional belief that invertebrates are just 'minirobots', which stereotypically respond to stimuli and thus should exhibit few or no individual differences in behaviour (e.g. Brembs, 2013). Lately, however, studies highlighting personality

differences in an increasing range of invertebrate species have challenged this idea. Mather and Logue (2013) reviewed studies assessing personality variation in invertebrates: they reported consistent behavioural differences between individuals in 19 invertebrate genera with the majority of these (15 genera) within the Arthropoda. The remaining studies were conducted in the Mollusca (three genera) and Nematoda (one genus). In addition, we conducted a systematic ISI Web of Knowledge search in December 2013 using the search terms 'personality' in combination with 'invertebra*'. This initial search led to 243 publications (a comparable search on 'personality' and 'vertebra*' led to 3809 publications). A more detailed investigation of these studies revealed 47 empirical studies that assessed personality variation in invertebrates (summarized in Table 1). The majority of these studies found support for the existence of personality differences in invertebrates (see Table 1). Most personality studies on invertebrates have been conducted in the Arthropoda (mainly Insecta, but also Crustacea and Chelicerata); the remaining studies investigated Cnidaria and Mollusca (see Table 1). Taken together, even such an increased number of invertebrate studies in a personality context is almost negligible given the size of the taxa (four invertebrate phyla investigated out of 34; following systematics

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Table 1
Invertebrate studies assessing consistent behavioural differences between individuals over time, situations and/or contexts

Systematic group	Species	Species/Group common name	Behavioural trait(s) tested	Time consistency tested	Situation consistency tested	Evidence time/situation consistency	Context consistency/BS tested	Study
Arthropoda								
Chelicerata:	<i>Anelosimus studiosus</i>	Comb-footed spider	Aggression (towards prey); boldness; exploration (NE); social tendency (inter-individual distance)	No	No	Not tested	Yes (among tests)	Pruitt et al. (2010)
Arachnida	<i>Argiope aurantia</i>	Corn spider	Aggression (towards prey; as juvenile and adult)	Yes†	Yes†	Yes	Yes (with sexual cannibalism)	Foellmer and Khadka (2013)
	<i>Larinioides scolopetarius</i>	Bridge spider	Aggression (different contexts); boldness (different contexts); exploration (NE); mating behaviour	Yes	No	Yes	Yes (among tests)	Kralj-Fišer and Schneider (2012)
	<i>Larinioides scolopetarius</i>	Bridge spider	Aggression (towards same-sex conspecific)	No	No	Not tested	Yes (with aggression during mating)	Kralj-Fišer et al. (2013)
	<i>Nephilingys livida</i>	Madagascar hermit spider	Activity; aggression (different contexts); boldness (simulated predator encounter)	Yes	No	Yes	Yes (among tests)	Kralj-Fišer et al. (2012)
	<i>Phidippus clarus</i>	Old field jumping spider	Activity (ascension from vial)	Yes	No	Yes	No	Sweeney et al. (2013)
	<i>Stegodyphus sarasinorum</i>	Velvet spider	Aggression/boldness (2 different tests)	Yes	No	Yes	Yes (among tests)	Pruitt, Grinsted, and Settepani (2013)
Crustacea:	<i>Astacus astacus</i>	Noble crayfish	Boldness (under low, intermediate, high risk)	Yes	Yes	Yes	No	Vainikka, Rantala, Niemela, Hirvonen, and Kortet (2011)
Malacostraca	<i>Coenobita clypeatus</i>	Terrestrial hermit crab	Boldness (emergence from shell; 4 different tests); exploration (NE)	Yes	No	Yes	Yes (among tests)	Watanabe et al. (2012)
	<i>Ozius truncatus</i>	Reef crab	Boldness (startle response; under 2 temperature regimes)	Yes	Yes	Yes	No	Biro, O'Connor, Pedini, and Gribben (2013)
	<i>Panopeus herbstii</i>	Mud crab	Foraging versus hiding (under low and high risk)	No	Yes	Yes	No	Griffen, Toscano, and Gatto (2012)
	<i>Pagurus bernhardus</i>	Hermit crab	Boldness (startle response; under low and high risk)	Yes	Yes	Yes	No	Briffa and Bibost (2009)
	<i>Pagurus bernhardus</i>	Hermit crab	Boldness (startle response; under low and high risk; field and lab)	Indirectly*	Yes	Yes	No	Briffa, Rundle, and Fryer (2008)
	<i>Pagurus bernhardus</i>	Hermit crab	Boldness (startle response; different shell coloration and background coloration)	No	Yes	Yes	No	Briffa and Twyman (2011)
	<i>Pagurus bernhardus</i>	Hermit crab	Aggression (towards conspecific with shell); boldness (startle response); exploration (NO); (all under low and high risk)	No	Yes	Yes	Yes (among tests)	Mowles, Cotton, and Briffa (2012)
	<i>Palaemon elegans</i>	Rock pool prawn	Activity; boldness (startle response); exploration; shoaling tendency	Yes	No	Yes	Yes (among tests)	Chapman, Hegg, and Ljungberg (2013)
Crustacea:	<i>Calanus</i> sp. (3 species)	(Marine copepod)	Consumption rates	Yes	No	Yes	No	Morozov, Pasternak, and Arashkevich (2013)

Arthropoda Hexapoda: Insecta	<i>Acheta domesticus</i>	House cricket	Activity/exploration (NE)	Yes	No	Yes	No	Sweeney et al. (2013)
	<i>Acyrtosiphon pisum</i>	Pea aphid	Boldness (escape response upon predator encounter)	Yes	No	Yes	No	Schuett et al. (2011)
	<i>Apis mellifera</i>	Honey bee	Activity (across comb); boldness (defensive response); foraging; comb repair; removal of dead bees	On colony level	No	Yes	Yes (among tests)	Wray, Mattila, and Seeley (2011)
	<i>Apis mellifera</i>	Honey bee	Decision-making behaviour (decision speed; waggle dance rate; shaking/piping signals; scouting activity)	On colony level	No	Yes	Only within test	Wray and Seeley (2011)
	<i>Bombus terrestris</i>	Bumblebee	Feeding duration; flight time (in foraging context under no risk and post predation attempt)	(Yes, within trial)	No	(Yes, within trial)	Only within test	Muller (2012)
	<i>Bombus terrestris</i>	Bumblebee	Neophilia (feeding latency novel flower colours)	Yes	No	Weak**	No	Muller, Grossmann, and Chittka (2010)
	<i>Drosophila</i> sp. (3 species)	Fruit fly	Startled phototaxis behaviour (light-choice probability)	Yes	No	Yes	No	Kain et al. (2012)
	<i>Enallagma ebrium</i>	Marsh Bluet	Response to mite parasites and/or fish predators	No	Yes	Weak††	No	Rutherford, Baker, and Forbes (2007)
	<i>Gromphadorhina portentosa</i>	Hissing cockroach	Aggression (intruder); boldness (emergence after disturbance); exploration (NE); latency to forage; sexual behaviour	No	No	Not tested	Yes (among tests)	Mishra, Logue, Abiola, and Cade (2011)
	<i>Gryllus integer</i>	Field cricket	Aggression (male-male); boldness (emergence from shelter)	Yes§§	No	Yes	Yes (among tests)	Niemela, DiRienzo, and Hedrick (2012)
	<i>Gryllus integer</i>	Field cricket	Boldness (emergence from shelter; during ontogeny)	Yes	Yes†	Yes	No	Niemela, Vainikka, Hedrick, and Kortet (2012)
	<i>Gryllus integer</i>	Field cricket	Aggression (male-male); boldness (emergence from shelter)	No	No	Not tested	Yes (among tests)	Niemela, Vainikka, Lahdenpera, and Kortet (2012)
	<i>Messor andrei</i>	Black harvester ant	Responsiveness (to food bait, disturbance); speed (retrieval of food, removal of debris) (all at different dew points)	On colony level	(Yes, on colony level)	Yes	Yes (among tests)	Pinter-Wollman, Gordon, and Holmes (2012)
	<i>Phaedon cochleariae</i>	Mustard leaf beetle	Boldness (emergence from refuge; death feigning); exploration (three different tests)	Yes	No	Yes	Yes (CA, among all variables)	Tremmel and Müller (2013)
	<i>Pieris brassicae</i>	Large white butterfly	Boldness (willingness to fly into a tunnel); exploration (flight distance)	Yes	No	Yes	Yes (among tests)	Ducatez et al. (2012)
	<i>Platythyrea punctata</i>	(Ant species)	Aggression (attacks against reproductives after fusion and against heterospecific intruders)	No	No	Not tested	Yes (among tests)	Barth, Kellner, and Heinze (2010)
<i>Pyrrhocoris apterus</i>	Firebug	Boldness (emergence from refuge); exploration (NE; all at juvenile and adult stage)	Yes	Yes†	Yes	Yes (among tests)	Gyuris, Fero, and Barta (2012)	
<i>Pyrrhocoris apterus</i>	Firebug	Boldness (emergence from refuge); exploration (NE)	Yes	No	Yes	Yes (among tests)	Gyuris, Fero, Tartally, and Barta (2011)	
<i>Sitophilus zeamais</i>	Maize weevil	Activity (four different tests); boldness (death-feigning); inter-/intraspecific interactions	Yes	No	Yes	Yes (CVA, among tests)	Morales et al. (2013)	
<i>Temnothorax longispinosus</i>	Acorn ant	Aggression (towards dead non-nestmate); brood care (pupa grooming); exploration (NO, NE)	On colony level‡	No	Yes	Yes, on colony level (among tests)	Modlmeier, Liebmann, and Foitzik (2012)	

(continued on next page)

Table 1 (continued)

Systematic group	Species	Species/Group common name	Behavioural trait(s) tested	Time consistency tested	Situation consistency tested	Evidence time/situation consistency	Context consistency/BS tested	Study
	<i>Temnothorax nylanderii</i>	(Ant species)	Aggression (intruders); nest relocation; removal of infected corpses; nest reconstruction	On colony level	No	Yes	Yes (FA, among tests)	Scharf, Modlmeier, Fries, Tirard, and Foitzik (2012)
	<i>Tenebrio molitor</i>	Mealworm beetle	Boldness (tonic immobility)	Yes	No	Yes	Only within test	Krams et al. (2013)
Cnidaria	<i>Actinia equina</i>	Beadlet anemone	Boldness (startle response)	Yes	No	Yes	No	Briffa and Greenaway (2011)
Anthozoa:	<i>Actinia equina</i>	Beadlet anemone	Boldness (startle response; prior and post stage fight)	Yes	Yes	Yes	No	Rudin and Briffa (2012)
Anthozoa	<i>Condylactis gigantea</i>	Giant sea anemone	Boldness (startle response)	Yes	No	Yes	No	Hensley, Cook, Lang, Petelle, and Blumstein (2012)
Mollusca	<i>Euprymna tasmanica</i>	Dumpling squid	Boldness (threat); feeding test (all over lifetime)	Yes	Yes†	Yes	Yes (among tests)	Sinn et al. (2008)
Conchifera:	<i>Euprymna tasmanica</i>	Dumpling squid	Boldness (threat); feeding test	Yes	No	Yes	Yes (among tests)	Sinn and Moltzschaniwskyj (2005)
Cephalopoda	<i>Octopus rubescens</i>	Red octopus	Boldness (2 different tests); feeding	Partly‡	No	Partly	Yes (FA; among tests)	Mather and Anderson (1993)
	<i>Octopus tetricus</i>	Gloomy octopus	Behaviour towards videos of conspecific, food item, NO	Yes	No	Weak‡‡	Yes (among tests)	Pronk, Wilson, and Harcourt (2010)

Studies were obtained from a systematic ISI Web of Knowledge search (search terms: 'personality' in combination with 'invertebra*'). From all obtained studies those were selected that had tested for consistent behavioural differences between individuals over time, situations and/or contexts within an invertebrate species. Among tests: correlations conducted between variables measured in different tests; BS tested: correlations between behaviours tested, behavioural syndromes; only within test: correlations conducted only among variables measured in the same test; CA: cluster analysis; CVA: canonical variate analysis; FA: factor analysis; NE: novel environment; NO: novel object.

* Consistency over five trials, one in field, four in lab: two with, two without predator cues.

† Juvenile versus adult stage; or over lifetime.

‡ Not tested for brood care.

§ Behaviour over first four test series tested against behaviour over last three test series.

** Consistency only within a day not between days.

†† Four out of 24 correlations.

‡‡ Consistency only within a day among different stimuli, not between days.

§§ Not for aggression.

in Brusca & Brusca, 2003), which essentially confines us in applying comparative analyses. A comparative personality approach that includes numerous and highly diverse invertebrate taxa (alongside vertebrate taxa) might facilitate an understanding of how the past selective forces have driven the evolution of personality differences. Besides the clear paucity of data and consequent lack of broader comparative analyses, we outline below several reasons for studying personality variation in invertebrate species. We aim to show that investigating proximate, evolutionary and ecological correlates of invertebrate personalities could shed light on questions on the existence and maintenance of personality variation currently not satisfactorily addressed with vertebrate studies. Importantly, invertebrates exhibit a range of aspects in their life histories, social and sexual behaviours that are extremely rare or absent in vertebrates, but that offer new avenues for personality research. Examples are complete metamorphosis from larval to adult stage, asexual reproduction and peculiar sexual behaviours (e.g. sexual cannibalism, male emasculation during copulation), eusociality and parasitism. Furthermore, numerous invertebrates offer several methodological advantages (see also Mather & Logue, 2013), such as relative straightforward access to relevant data testing proximate and ultimate factors underlying personality variation. Many invertebrates are easy to rear, maintain and manipulate, including various species that can be obtained in large numbers from local pet shops (e.g. *Anemone* sp., *Sabellastarte* sp., *Dendrobaena* sp., *Astraea* sp., *Daphnia* sp., *Acanthogonathus* sp., *Acheta* sp., *Tenebrio* sp., *Blaptica* sp., *Drosophila* sp., *Gryllus* sp., *Artemia* sp.). Besides, many invertebrates (including those above) have fast life cycles (i.e. generation turnovers) with normally high reproductive output (for studies that made use of these advantages see e.g. Andrewartha & Burggren, 2012; Kafel, Zawisza-Raszka, & Szulińska, 2012; Kralj-Fišer & Schneider, 2012; Schuett et al., 2011) compared to many vertebrates; especially those vertebrate species that are often used as model systems in personality studies, such as chimpanzees, *Pan troglodytes*, various other primate species, pigs, *Sus* sp., dogs, *Canis lupus familiaris* (reviewed in Gosling, 2001), great tits, *Parus major* (reviewed in Groothuis & Carere, 2005) or zebra finches, *Taeniopygia guttata* (e.g. David, Auclair, & Cézilly, 2011; Schuett & Dall, 2009). Fast life cycles and high reproductive output allow for systematic monitoring of numerous individuals over their lifetime and for studying several generations within relatively short time periods. Such multigenerational studies in which individuals are monitored over their lifetime are often required when studying the evolution of personality variation but are frequently not feasible with the classical models of animal personality research owing to long generational times, logistic limitations (e.g. Schuett et al., 2011) or ethical standards (see Mather & Logue, 2013 for further discussion).

First, we present a set of ideas that, if addressed in invertebrates, are likely to enhance our general comprehension of the evolution of proximate mechanisms underlying animal personality variation: that is, how genes, genomes, physiology and environmental factors interact to shape personalities across species. We point out probable differences in links between energy metabolism and personality variation in endothermic versus ectothermic animals (i.e. all invertebrates). Furthermore, we describe the advantages of studying personality development in invertebrates, including unique opportunities of investigating personality over metamorphosis. We detail how eusociality and a parasitic lifestyle, which are commonly found in invertebrates (but are rare in vertebrates), may relate to lower between-individual behavioural variation than observed in other species. We continue by pointing out advantages

invertebrates might offer to the study of ultimate causes of personality variation, with special focus on sexual selection and life history trade-offs. Here, we propose a new avenue of research linking sexual selection, life history trade-offs and behavioural plasticity over an animal's lifetime.

GENOMES, GENES AND ENVIRONMENTS

To understand the selective forces acting on personality differences it is important to know the genetic architecture underpinning such behavioural variation (e.g. van Oers & Sinn, 2011). There is good evidence that personality traits, such as aggression and boldness, are moderately heritable in vertebrates (reviewed in e.g. van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005; van Oers & Sinn, 2011). Data on heritability of personality traits in invertebrates are still scarce (see e.g. van Oers & Sinn, 2011). The few existing studies on invertebrates have shown, for instance, that aggression in spiders (*Anelosimus studiosus*: Pruitt & Riechert, 2009a; *Larinioides sclopetarius*: Kralj-Fišer & Schneider, 2012) and antipredator behaviour in dumpling squid, *Euprymna tasmanica*, are heritable (Sinn, Apiolaza, & Moltschanivskyj, 2006), while genetically identical individuals of the same clone vary consistently in their risk-taking behaviour in pea aphids, *Acyrtosiphon pisum* (Schuett et al., 2011). These results may suggest that individual differences in aggression and boldness levels are heritable across various animal taxa. To understand the evolution of these and other personality traits better, we need to explore the genetic variability of behavioural traits and their genetic (and nongenetic) transmission in more species further. Many invertebrate species are highly suitable for this (see e.g. Zwarts, Versteven, & Callaerts, 2012).

Knowing the heritability of a personality trait is only a starting point towards pinpointing its genetic architecture. The genes contributing to personality differences in animals are largely unknown (e.g. Korsten et al., 2010; Mueller et al., 2013). Invertebrates allow powerful approaches to shed light on the genetics of personality variation by investigating the behaviour of genetically altered strains or selection lines (but also see Groothuis & Trillmich, 2011 for disadvantages of the general use of such lines), or by employing direct genetic analyses of natural heterogeneity or other molecular approaches, such as linkage and association gene mapping (QTL; see e.g. van Oers & Mueller, 2010 for general techniques), which usually require studies over several generations. The often short generation times of invertebrates (e.g. red flour beetle, *Tribolium castaneum*: Roth, Sadd, Schmid-Hempel, & Kurtz, 2009; pea aphid, *A. pisum*: Schuett et al., 2011; water flea, *Daphnia magna*: Andrewartha & Burggren, 2012) allow researchers to obtain several generations quickly, even compared to those species with relatively short generation times within the vertebrates that have been used in genetic studies to date (e.g. house mouse, *Mus musculus*: Benus, Bohus, Koolhaas, & Van Oortmerssen, 1991; great tits: Drent, van Oers, & van Noordwijk, 2003). Genetically accessible invertebrate model organisms, such as *Drosophila* sp., have already been used to study the molecular basis of a common personality trait: aggression (Edwards & Mackay, 2009; Edwards, Rollmann, Morgan, & Mackay, 2006; reviewed in Zwarts et al., 2012; although whether aggression is indeed a personality trait in *Drosophila* has not yet been tested). However, much more data are required for fine-scale analyses and cross-species comparisons. For instance, analyses of the genetic differences, for example comparing genome expression data between closely related species, could help identify the evolutionary forces conserving traits and/or leading to divergent (species-specific) behaviours (Bell & Aubin-Horth, 2010).

Besides genes, environmental factors also influence personality development, particularly in early life (Carere, Drent, Koolhaas, & Groothuis, 2005; Groothuis & Trillmich, 2011; Stamps &

Groothuis, 2010a, 2010b; Trillmich & Hudson, 2011). Despite a growing interest in (early) environmental effects on animal personality (see e.g. special issue in *Developmental Psychobiology* 2011, 53 (6)), this field is still in its infancy. To date, the impact of environmental conditions such as temperature, food availability or predation risk on personality development in invertebrates has rarely been studied (but see Schuett et al., 2011; Tremmel & Müller, 2013); Schuett et al. (2011) raised (clonal) pea aphids on high- and low-quality food, respectively; but such environmental manipulation had no influence on consistent behavioural differences in risk-taking behaviour. Food quality experienced during development did, however, affect later boldness and activity in a beetle, *Phaedon cochleariae* (Tremmel & Müller, 2013). More data on further species differing in biology are needed to unravel when and how the environment significantly influences personality development.

The interplay between genes and environmental factors in shaping personality variation remains largely unknown and might be even more complicated, for instance because of epigenetic effects or developmental noise (e.g. Kain, Stokes, & de Bivort, 2012; Lewejohann, Zipser, & Sachser, 2011; Stamps, Saltz, & Krishnan, 2013; see Wong, Gottesman, & Petronis, 2005 for general review on (non-)environmentally induced epigenetic effects). Progress in genomics and transcriptomics as well as gene manipulation technologies, however, offer the opportunity to study how genes/genomic regions, environmental factors and their interactions (GxG, GxE) contribute to the expression of personality traits (e.g. Kain et al., 2012; van Oers & Mueller, 2010). Many invertebrates are ideal for testing the causal relationships between genes, epigenetic processes, environmental influences and behaviour owing to the above mentioned characteristics. It is likely to be even more convenient to investigate how GxE shapes personality variation in those invertebrates with (at least temporal) asexual reproduction (e.g. several species in: rotifers; crustaceans, e.g. *Daphnia*, *Artemia*, *Triops*; insects, e.g. *Acyrtosiphon*, *Ceratina*, *Trichogramma*; Brusca & Brusca, 2003) or that can be experimentally reproduced owing to a high regeneration capacity (e.g. cnidaria, sea stars, turbellariae; Brusca & Brusca, 2003) than in exclusively sexually reproducing animals (most vertebrates). Research on GxE in sexually reproducing animals, which generally produce genetically diverse offspring, normally requires sophisticated analytical tools and extensive knowledge of the genetic similarity of the individuals studied (see also discussion in Schuett et al., 2011). Asexual reproduction, on the other hand, leads to (often many) genetically identical individuals (clones) that can be utilized for direct assessment of genetic mechanisms underlying personality variation. For instance, experiments in which genetically identical clones are raised under changing environmental parameters allow researchers to estimate how much variation in personality traits can be attributed to genetic and to environmental factors. Despite such advantages of using asexually reproducing species, we are only aware of a single study making use of invertebrate clones in personality research (Schuett et al., 2011). A more frequent utilization of clonal invertebrates (as well as clonal vertebrates) in studies on GxE could help to increase significantly our understanding of mechanisms underlying personality variation.

Although we are increasingly aware of the fact that environmental effects during early stages of development can have a strong impact on personality development (see above; e.g. Carere et al., 2005; Groothuis & Trillmich, 2011), we still know relatively little about the mechanisms underlying these effects. Most studies to date have investigated the role of early maternal effects (e.g. Ruuskanen & Laaksonen, 2010; Tobler & Sandell, 2007) or sometimes of more general parental effects (e.g. Schuett, Dall, Wilson, & Royle, 2013) on later offspring behaviour, including personality, in vertebrates (reviewed in e.g. Maestripieri & Groothuis, 2013). Such

maternal effects, or parental effects in general, enable parents to optimize their fitness in quick response to changing environmental conditions by varying their investment in offspring quality and/or quantity (Mousseau & Fox, 1998) or by controlling offspring phenotypic traits (Price, 1998). In invertebrates there is also some evidence for environmental maternal effects, such as females choosing favourable oviposition sites (e.g. Pike, Webb, & Shine, 2012), which influence the pre- and posthatching environment the offspring encounter with profound effects on offspring phenotypes (reviewed in Mousseau & Dingle, 1991). It is likely that these or similar maternal effects also influence offspring behavioural traits in invertebrates (e.g. Storm & Lima, 2010) and potentially offspring personality, but this proposition remains to be tested. Parasitoid wasps, for instance, may be good systems to test the influence of maternal effects on offspring personality in invertebrates. Female parasitoid wasps have been shown to adjust their brood's sex ratio to current environmental conditions (e.g. *Nasonia vitripennis*, Shuker & West, 2004) and the brood's sex ratio influences offspring dispersal behaviour (e.g. *Goniozus nephantidis*, Hardy, Pedersen, Sejr, & Linderoth, 1999). Natal dispersal behaviour, in turn, correlates with personality traits in several vertebrate species (e.g. Debeffe et al., 2013; Dingemans, Both, van Noordwijk, Rutten, & Drent, 2003).

NEUROBIOLOGY AND ENDOCRINOLOGY

A logical further step is investigating the neurobiology, physiology and endocrinology underlying personality variation. There is evidence that even invertebrates with very simple nervous systems, such as nematodes (de Bono & Bargmann, 1998) and cnidarians (Briffa & Greenaway, 2011; Rudin & Briffa, 2012) show personality differences in activity, aggression and boldness. These and similar organisms with relatively few nerve cells and simple neural circuits might simplify studying basic pathways underpinning personality differences. To date, the neurobiology of behaviour in invertebrates has mainly been investigated on aggression in *Drosophila* sp. (reviewed in Alekseyenko, Chan, Li, & Kravitz, 2013; Zwartz et al., 2012; for a review on other invertebrates see e.g. Kravitz & Huber, 2003). Studies on other insect species corroborate findings in *Drosophila*, indicating that neurotransmitters, receptors and certain brain structures mediate insect aggression (Zwartz et al., 2012 and references therein). An understanding of how widespread these mechanisms are across invertebrate taxa and across other behaviours, and how they relate to consistent behavioural differences, requires further studies. Such knowledge, however, could help to identify whether neurobiological networks underpinning personality variation are conserved across species (e.g. across species with various degrees of complexity in their nervous system, such as from cnidarians with a simple nervous system to insects with a more complex one) and, if not, how they have changed over evolutionary time. The emerging field of neurogenetics, which combines approaches from neurobiology and genetics to study the genetic and neural basis of behaviour, could further reveal whether any conservation occurs mainly at the gene level or at the systems level (i.e. functional systems and (neural) networks; Zwartz et al., 2012).

METABOLIC RATE

Increasing evidence suggests a link between individual energy metabolism and personality traits (e.g. Biro & Stamps, 2010; Careau & Garland, 2012). It has been proposed that these links might occur at both the proximate and ultimate level (see Careau, Thomas, Humphries, & Réale, 2008 for more details). In short, life history trade-offs, coupled with individual differences in states,

are thought to favour the evolution of personality variation (see [Social and Sexual Behaviour and Evolutionary Origins of Personality](#)). Energy metabolism might play a key underlying mechanistic role in this [link between personality and life history strategy](#) (Biro & Stamps, 2010; Réale et al., 2010). As a consequence individuals with a fast pace of life are expected to have, for instance, high metabolism, high growth rate, high early reproduction and short life span and to show high activity and risk-taking (vice versa for individuals with a slow pace of life; for more details see Réale et al., 2010). To date, there is little empirical research testing the theory (e.g. Biro & Stamps, 2008; Dingemanse & Wolf, 2010). In particular we lack field data (but see e.g. Nicolaus et al., 2012), where, in contrast to most laboratory conditions, animals do not have ad libitum access to food (Biro & Stamps, 2010). Short-lived invertebrates would again offer good model systems to test how metabolism, personality and life history strategies correlate and contribute to fitness over time. Especially suitable systems for such research could be more or less sedentary organisms, which can be easily followed in the field over long periods of their lives, such as *Actinia* (see e.g. Briffa & Greenaway, 2011), *Cirripedia* or orb-web spiders. The latter, for instance, do not change their web position much, mature and reproduce quickly and have highly plastic life history traits (e.g. *Zygiella x-notata*: Mayntz, Toft, & Vollrath, 2003; *Larinioides*: Kleinteich & Schneider, 2011).

Most studies correlating energetics with personality traits have been conducted in vertebrates (e.g. reviewed in Biro & Stamps, 2010; Careau & Garland, 2012). Data for other taxa are widely lacking. However, individual behavioural differences in invertebrates might be interesting from an energetics' point of view, because invertebrates are, in contrast to relatively well-studied mammals (in this context), ectothermic and thus crucially dependent on environmental temperature. Of the few available studies on ectothermic vertebrates some have found a correlation between individual energetics and personality (e.g. Cutts, Adams, & Campbell, 2001); others have not (e.g. D'Silva, 2013; Farwell & McLaughlin, 2009), or the relationship between behaviour and energetics was context dependent (e.g. Killen, Marras, & McKenzie, 2011). There are several possible reasons for failing to find a correlation between energetics and personality (see e.g. Killen et al., 2011). However, we wonder whether we should even expect comparable results between energetics and personality across ectothermic and endothermic animals. Ectotherms' metabolic rate, and presumably behaviour, varies with temperature in a different manner from that in endothermic animals: metabolic rate in ectotherms increases exponentially with a rise in temperature (e.g. Clarke & Johnston, 1999). For instance, a change in temperature by 3 °C resulted in an average 2.5- to 6-fold increase in activity, boldness and aggression in two damselfish species, *Pomacentrus* sp. (Biro, Beckmann, & Stamps, 2010). Consistent individual differences in behaviour (e.g. ranks of activity behaviour) and energetics could theoretically still remain in this process. In the damselfish, however, even these small alterations in temperature changed rank orders among individuals in activity, aggression and boldness (Biro et al., 2010). Similarly, the degree of behavioural consistency changed in individual hermit crabs, *Pagurus bernhardus*, in response to changes in temperature (Briffa, Bridger, & Biro, 2013). In addition, ectothermic animals in general seem to exhibit lower behavioural repeatability than endothermic animals (at least when tested in the field; Bell, Hankison, & Laskowski, 2009). It is still unknown why rank orders in behaviour might be affected in ectothermic individuals in response to changed environmental temperature (see also Biro et al., 2010). Yet, we perhaps should not simply assume a general linkage between energetics and personality across endothermic and

ectothermic animals. More studies on ectothermic animals are required to solve this issue.

LIFE HISTORY: DEVELOPMENTAL STRATEGIES

Above we mentioned that genes, environmental conditions and interactions between them shape personality differences. It has been proposed that a profound understanding of such personality development is important to unravel the evolution of personality variation (e.g. Groothuis & Trillmich, 2011; Stamps & Groothuis, 2010a, 2010b). Thus far, it is still largely unknown when stable individual differences occur during ontogeny, whether personality traits are stable over a lifetime and, if not, at which life stage they are stable. Studies addressing such questions require monitoring of behaviour over long periods of an individual's life, which might prove challenging in long-lived vertebrates. As for the approaches outlined above, the ontogenetic approach towards understanding personalities should be generally easier to conduct in those invertebrates with relatively short life spans. Indeed, a few invertebrate studies have assessed behavioural consistency of individuals over most or all of their lifetime yielding mixed results (e.g. squid, *E. tasmanica*: Sinn, Gosling, & Moltschaniewskyj, 2008; damselfly, *Lestes congener*: Brodin, 2009; cricket, *Gryllus integer*: Hedrick & Kortet, 2012). These mixed results might be a consequence of the low number of studies available or of the different biology of the species assessed. Invertebrates show a wide range of different life histories, which has both advantages and disadvantages for personality research: some invertebrates have a complex life cycle and might therefore be challenging targets of research (e.g. Mather & Logue, 2013); other aspects of invertebrate life histories offer new avenues for research on personality development that cannot be investigated in most vertebrates, as exemplified in the following.

Particularly salient for personality development may be a shift from a juvenile to an adult stage that often involves significant changes in hormonal profiles and morphology (Truman & Riddiford, 2002; Wilbur, 1980). These changes are specifically dramatic in animals that undergo a metamorphosis (e.g. invertebrates: insects, molluscs, crustaceans, cnidarians, echinoderms, tunicates; vertebrates: amphibians) and change their lifestyle and environment (Wilbur, 1980). For example, numerous insect species shift from crawling and swimming in aquatic environments to flying in terrestrial environments. During this transition the neural and motor systems need to be changed and/or replaced (Consoulas, Duch, Bayline, & Levine, 2000). Consequently, it has been assumed that selection could uncouple personality differences during ontogeny if early environmental conditions experienced differ considerably from those experienced at adulthood (Sih et al., 2004). Nevertheless, in damselflies, *L. congener*, with incomplete metamorphosis, activity and boldness exhibited during the larval stage predicted adult behaviour (Brodin, 2009), whereas in crickets, *G. integer*, behavioural consistency before and after sexual maturity appeared to be sex specific (Hedrick & Kortet, 2012). Within vertebrates a recent study in *Rana ridibunda* found that some behavioural traits were stable across different life stages, whereas others were not (Wilson & Krause, 2012a). Taken together, animals with metamorphosis 'represent a unique in situ experimental opportunity to study how personality differences are associated with physiological, morphological, or ecological traits over development' (Wilson & Krause, 2012b, p. 529). The complexity of life cycles and the related life histories in a range of invertebrates may provide fruitful insights into within-individual behavioural plasticity and proximate mechanisms underlying personality change/stability.

PARASITISM

A number of species exhibit a parasitic lifestyle, either constantly or over parts of their lives. Parasites are mainly invertebrates, for instance various Platyhelminthes, Nematoda and Arthropoda (e.g. Bush, Fernandez, Esch, & Seed, 2001; or micro-parasites such as protists, bacteria/viruses which are beyond the scope of this essay). Only a few species within the vertebrates are parasites, for instance lampreys and vampire bats (e.g. Bush et al., 2001). A few studies have shown that parasites can co-shape the personality of the host (reviewed in Barber & Dingemans, 2010; Poulin, 2013). On the other hand, we have little insight into between- and within-individual behavioural variability in species exhibiting a parasitic lifestyle. There is some evidence for the existence of personality differences in parasitic arthropods, i.e. pea aphids, *A. pisum* (Schuett et al., 2011) and maize weevils, *Sitophilus zeamais* (Morales, Cardoso, Della Lucia, & Guedes, 2013), but we are not aware of any personality study, for instance, on parasitic helminths. Helminths are generally highly specialized on the host species and on the life stage at which they are parasitic (Price, 1980). They exhibit a range of morphological and physiological adaptations for a parasitic lifestyle and can show high plasticity in their life histories within a host such as adaptation of their development to host immunity (e.g. Babayan, Read, Lawrence, Bain, & Allen, 2010). Consequently, we predict that parasitic helminths may show little variability between individuals and high within-individual plasticity in behaviour; hence they may not exhibit personality differences. At this stage the evidence of parasites' personality (non-)existence may only add to our basic knowledge of how widespread personality variation is across taxa, although it could have important further applications. For example, in maize weevils, a grain pest that shows high insecticide resistance, individuals consistently varied in their activity from one another (Morales et al., 2013). Active individuals survived longer after insecticide exposure than less active individuals (Morales et al., 2013). Further personality research on pest species in the context of drug resistance, for instance, could provide important implications for the control of pest species.

SOCIALITY, SEXUAL BEHAVIOUR AND EVOLUTIONARY ORIGINS OF PERSONALITY

Eusociality

Personality is a form of behavioural specialization; another form of behavioural specialization, division of labour, can be observed in eusocial species (e.g. Dall, Bell, Bolnick, & Ratnieks, 2012). Eusociality is characterized by cooperative brood care, overlapping adult generations and division of labour by reproductive and (partially) nonreproductive groups (Wilson, 1971). In vertebrates, eusociality can be found in only some species of mole-rats and potentially some social voles; but even this classification is controversial (Burda, Honeycutt, Begall, Locker-Grutjen, & Scharff, 2000). Within invertebrates, the eusocial insects such as ants, bees, wasps and termites represent highly diverse taxa and most of the world's insect biomass (Wilson & Hölldobler, 2005). Nevertheless, relatively few eusocial species have been studied in a personality context and personality research to date has rarely considered existing research on variation in behaviour in eusocial insects (Dall et al., 2012; Jandt et al., 2014; see Table 1). This is surprising since social insect research has long identified differences between social insect castes in certain behaviours related to their tasks (e.g. Jandt et al., 2014). The lack of personality data in eusocial species (and partly the lack of merging knowledge from two fields) might have resulted from an assumption that selection forces might act more at the

colony than at the individual level (Dall et al., 2012). If so, processes generating between-individual differences could differ between eusocial insects and less socially organized species (Dall et al., 2012), which deserves the attention of future studies.

Eusocial Hymenoptera offer unique models to study personality differences owing to high genetic relatedness within colonies. In many species queens mate with several males resulting in different patriline (i.e. full- and half-sibs within a colony); in other species, several unrelated queens can produce offspring of different matriline (e.g. Jeanson & Weidenmüller, 2013). Both cases lead to different degrees of genetic similarity within a colony, enabling investigations of genetic and environmental effects on task specialization and personality differences, respectively. For instance, honeybee, *Apis mellifera*, queens mate with several males (e.g. Page & Robinson, 1991) and the resulting half-sibs differ in their sensitivity to stimuli related to their tasks and may also differ in their caste differentiation (Jeanson & Weidenmüller, 2013 and references therein), which may result in consistent behavioural differences. Further research could also explore how mating strategies in eusocial insects (in which all offspring share the same mother) promote and maintain personality variability. Specifically, we wonder whether haploid drones vary in their personality types and whether the queen considers the drones' personality during mate choice. The drones' personality may determine the personality types/behavioural specialization in the brood. Consequently, the queen may mate with drones of diverse personality types to enhance the performance of the colony. Previous research has shown that at least high genetic diversity is advantageous: colonies of queens that had been inseminated with genetically highly diverse sperm had lower parasite load and higher reproductive success than colonies resulting from genetically similar sperm in bumblebees, *Bombus terrestris* (Baer & Schmid-Hempel, 1999). Two recent reviews (Dall et al., 2012; Jandt et al., 2014) discuss further insights that could be gained from studying the division of labour in social insects from a personality point of view and from combining existing knowledge in the separate research fields on personality variation, and social insects, respectively.

Social and Sexual Behaviour and Evolutionary Origins of Personality

We still have little insight into the origin and maintenance of personality variation. Several potential functional explanations as to why personality differences might exist have been proposed (reviewed in Biro & Stamps, 2008; Dall et al., 2004; Dingemans & Wolf, 2010; Sih & Bell, 2008; Wolf, van Doorn, Leimar, & Weissing, 2013; Wolf & McNamara, 2012) but these have rarely been tested empirically. Such empirical tests often require multigenerational studies, which are often not feasible in long-lived vertebrates but which might be easier to target in invertebrates (for reasons see above). Most of the proposed hypotheses assume that differences in states (e.g. variation in morphology, physiology, experience or neurobiology; sensu Houston & McNamara, 1999) coupled with state-dependent behaviour mediate adaptive personality differences (reviewed in Dingemans & Wolf, 2010). Other (not mutually exclusive) hypotheses are based, for instance, on fluctuating or negative frequency-dependent selection (Wolf et al., 2013). Within invertebrates, there is some support for negative frequency-dependent selection maintaining consistent variation in aggression in *L. sclopetarius* (Kralj-Fišer & Schneider, 2012) and cooperativeness in *A. studiosus* (Pruitt & Riechert, 2009b, 2011).

Relatively recently, sexual selection was proposed as a further potential mechanism to generate and maintain personality variation through nonrandom mate choice and male–male competition (Schuett, Tregenza, & Dall, 2010). Studies testing the link between personality variation and sexual selection are still rare and have

mostly been conducted in such vertebrate systems in which males offer direct benefits to the female or offspring, often via paternal care (reviewed in Schuett et al., 2010). In such systems nonrandom mate choice for personality might result from improved offspring care coordination of certain personality combinations within (biparental) pairs (e.g. Royle, Schuett, & Dall, 2010; Schuett et al., 2010), leading to an increased reproductive success of these combinations (e.g. Schuett, Dall, & Royle, 2011). Much less is known about the influence of sexual selection on personality variation in species without parental care, such as most invertebrate species. In such systems males provide only sperm. This means benefits of female choice should be restricted to good and/or compatible genes that improve offspring fitness (Andersson, 1994; Bateson, 1983; Kokko, Brooks, Jennions, & Morley, 2003; Neff & Pitcher, 2005). The few existing studies on invertebrates suggest that personality also plays a role during mate choice in these taxa: In dumpling squid, *E. tasmanica*, bold females were more likely to reproduce when paired with a bold male than if paired with a shy male (Sinn et al., 2006). Similarly, positive assortative mating for aggression was found in the bridge spider, *L. sclopetarius* (Kralj-Fišer, Mostajo, Preik, Pekár, & Schneider, 2013). These results corroborate findings in vertebrates, suggesting that assortative mating by personality (potentially coupled with negative frequency-dependent selection) might maintain consistent behavioural differences (see also Schuett et al., 2010). However, in the social spider *A. studiosus*, both male phenotypes, aggressive and social, preferentially courted social females (Pruitt & Riechert, 2009c); yet aggressive males had competitive advantages over social males when courting females of the preferred phenotype (Pruitt & Riechert, 2009a). In *A. studiosus*, females are larger and often cannibalize males; thus selection might operate differently on males and females (Pruitt & Riechert, 2009a, 2009c). A follow-up study showed that large aggressive males experienced increased risk of cannibalism and reduced reproductive success in mating trials involving at least one aggressive female, whereas males' reproductive success in trials with social females did not differ between an aggressive and social male phenotype (Pruitt, Riechert, & Harris, 2011). This example shows the importance of personality variation in intrasexual competition and intersexual mate choice resulting in nonrandom mating patterns for personality. Whether personality plays a role during mate choice in other taxa and which mechanisms underlie this potential role, depending on the biology of the group, is largely unknown and requires further study.

We propose a new avenue of research linking sexual selection, life history trade-offs and behavioural plasticity. According to theory, an individual should adjust its behaviour to its future reproductive expectations: it should take low risks when its future residual reproductive potential is high, but should take higher risks when its future residual reproductive potential is low ('asset protection principle'; Clark, 1994). This theoretical work was aimed at determining optimal antipredator behaviour but the reasoning may be extendible to a context of male–male competition over access to females. Accordingly, one could expect males to avoid fighting (related to aggressive behaviour) and therefore injury when their future residual reproductive potential is high (and vice versa for low residual reproductive potential). Such adaptive adjustment of behaviour may seem to conflict with the personality concept of limited plasticity of aggressiveness and boldness. Yet, theoretical models also suggest that individuals that take high risks will have relatively low future residual reproductive value (owing to an increased mortality risk) which reinforces consistent high risk taking (vice versa for low risk-takers; see e.g. Wolf, van Doorn, Leimar, & Weissing, 2007). Again, this theory could potentially be extended to aggressive behaviour (fighting) and boldness (risk taking during a fight) in a reproductive context (male–male

competition over access to females). In some invertebrates, we find life history aspects that are very different to those in other systems but that offer a test of an extreme application of Wolf et al.'s (2007) theory: there are examples where individuals instantly shift from full to zero reproductive potential. Males in several spider and some insect species obligatorily break their genital organs within female genitals during copulation in order to produce mate plugs which avoid/reduce sperm competition with subsequent mates (Uhl, Nessler, & Schneider, 2010). Males with broken or missing genitals are functionally sterile after one or two copulations (spiders have paired genitals; Kuntner, Kralj-Fišer, Schneider, & Li, 2009), and have no further reproductive options. It has been shown that such emasculated males change their aggression and boldness according to the 'extended' asset protection principle (see above), that is, they fight more and take more risk (Kralj-Fišer, Gregorič, Zhang, Li, & Kuntner, 2011). By vigorously guarding the female they mated with prior to their emasculation (i.e. fighting forcefully against any potential male (sperm) competitor) they may decrease the risk of losing paternity. However, to test the applicability of Wolf et al.'s (2007) model in this or similar contexts, we would also need to study whether individuals still differ consistently in their aggression and boldness after this extreme shift in their reproductive potential (from full to zero).

CONCLUSIONS

We have outlined several reasons and examples for using invertebrates more frequently in personality research, a research field that has mainly concentrated on one single (sub-)phylum: the Vertebrata. Invertebrates, belonging to all 34 phyla, have rarely been studied in the personality field. Despite increasing effort made to understand how past selective forces have driven the evolution of personality differences it is still impossible to employ a comparative approach, which would require data from a diversity of invertebrates (alongside vertebrates). Such an approach would enable us to understand whether and to what extent behavioural traits and related proximate mechanisms have been conserved across species and/or how they have been modified over evolutionary time and why. Invertebrates have diverse features and biology, including life history strategies, social and sexual behaviours which could help shed further light on the function and development of personality, including causal relationships between genes, environmental factors and personality. We have provided several examples and potential invertebrate model systems that may help to tackle these issues.

Acknowledgments

We thank Jutta M. Schneider, Cene Fišer and two anonymous referees for constructive comments on the manuscript and Claudio Carere for discussion on the topic.

References

- Alekseyenko, O. V., Chan, Y. B., Li, R., & Kravitz, E. A. (2013). Single dopaminergic neurons that modulate aggression in *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 6151–6156.
- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Andrewartha, S. J., & Burggren, W. W. (2012). Transgenerational variation in metabolism and life-history traits induced by maternal hypoxia in *Daphnia magna*. *Physiological and Biochemical Zoology*, 85(6), 625.
- Babayan, S. A., Read, A. F., Lawrence, R. A., Bain, O., & Allen, J. E. (2010). Filial parasites develop faster and reproduce earlier in response to host immune effectors which determine filarial life expectancy. *PLoS Biology*, 8, e1000525.
- Baer, B., & Schmid-Hempel, P. (1999). Experimental variation in polyandry affects parasite loads and fitness in a bumble-bee. *Nature*, 397(6715), 151–154.

- Barber, I., & Dingemans, N. J. (2010). Parasitism and the evolutionary ecology of animal personality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 4077–4088.
- Barth, M. B., Kellner, K., & Heinze, J. (2010). The police are not the army: context-dependent aggressiveness in a clonal ant. *Biology Letters*, 6, 329–332.
- Bateson, P. P. G. (1983). *Mate choice*. Cambridge, U.K.: Cambridge University Press.
- Bell, A. M., & Aubin-Horth, N. (2010). What can whole genome expression data tell us about the ecology and evolution of personality? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4001–4012.
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77, 771–783.
- Benus, R. F., Bohus, B., Koolhaas, J. M., & Van Oortmerssen, G. A. (1991). Heritable variation for aggression as a reflection of individual coping strategies. *Experimentia*, 47(10), 1008–1019.
- Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23(7), 361–368.
- Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology & Evolution*, 25(11), 653–659.
- Biro, P. A., Beckmann, C., & Stamps, J. A. (2010). Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences*, 277(1678), 71–77.
- Biro, P. A., O'Connor, J., Pedini, L., & Gribben, P. E. (2013). Personality and plasticity: consistent responses within-, but not across-temperature situations in crabs. *Behaviour*, 150, 799–811.
- de Bono, M., & Bargmann, C. I. (1998). Natural variation in a neuropeptide Y receptor homolog modifies social behavior and food response in *C. elegans*. *Cell*, 94, 679–689.
- Brembs, B. (2013). Invertebrate behaviour – actions or responses? *Frontiers in Neuroscience*, 7, 221. <http://dx.doi.org/10.3389/fnins.2013.00221>.
- Briffa, M., & Bibost, A.-L. (2009). Effects of shell size on behavioural consistency and flexibility in hermit crabs. *Canadian Journal of Zoology*, 87, 597–603.
- Briffa, M., Bridger, D., & Biro, P. A. (2013). How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. *Animal Behaviour*, 86, 47–54.
- Briffa, M., & Greenaway, J. (2011). High in situ repeatability of behaviour indicates animal personality in the beadlet anemone *Actinia equina* (Cnidaria). *PLoS One*, 6(7), e21963.
- Briffa, M., Rundle, S. D., & Fryer, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1305–1311.
- Briffa, M., & Twyman, C. (2011). Do I stand out or blend in? Conspicuousness awareness and consistent behavioural differences in hermit crabs. *Biology Letters*, 7, 330–332.
- Brodin, T. (2009). Behavioral syndrome over the boundaries of life-carryovers from larvae to adult damselfly. *Behavioral Ecology*, 20, 30–37.
- Brusca, R. C., & Brusca, G. J. (2003). *Invertebrates* (2nd ed.). Sunderland, MA: Sinauer Associates.
- Burda, H., Honeycutt, R. L., Begall, S., Locker-Grutjen, O., & Scharff, A. (2000). Are naked and common mole-rats eusocial and if so, why? *Behavioral Ecology and Sociobiology*, 47, 293–303.
- Bush, A. O., Fernandez, J. C., Esch, G. W., & Seed, J. R. (2001). *Parasitism: the diversity and ecology of animal parasites*. Cambridge, U.K.: Cambridge University Press.
- Careau, V., & Garland, T. (2012). Performance, personality, and energetics: correlation, causation, and mechanism. *Physiological and Biochemical Zoology*, 85, 543–571.
- Careau, V., Thomas, D., Humphries, M. M., & Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, 117(5), 641–653.
- Carere, C., Drent, P. J., Koolhaas, J. M., & Groothuis, T. G. (2005). Epigenetic effects on personality traits: early food provisioning and sibling competition. *Behaviour*, 142, 1329–1355.
- Chapman, B. B., Hegg, A., & Ljungberg, P. (2013). Sex and the syndrome: individual and population consistency in behaviour in rock pool prawn, *Palaemon elegans*. *PLoS One*, 8(3), e59437.
- Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, 5, 159–170.
- Clarke, A., & Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68(5), 893–905.
- Consoulas, C., Duch, C., Bayliss, R. J., & Levine, R. B. (2000). Behavioral transformations during metamorphosis: remodeling of neural and motor systems. *Brain Research Bulletin*, 53, 571–583.
- Cutts, C. J., Adams, C. E., & Campbell, A. (2001). Stability of physiological and behavioural determinants of performance in Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 58(5), 961–968.
- D'Silva, J. (2013). *Causes of intra-specific variation in metabolic rate in zebrafish*, Danio rerio (Unpublished doctoral dissertation). University of Ottawa.
- Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecology Letters*, 15, 1189–1198.
- Dall, S. R., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734–739.
- David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, 81, 219–224.
- Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Coulon, A., Gaillard, J. M., et al. (2013). Exploration as a key component of natal dispersal: dispersers explore more than philopatric individuals in roe deer. *Animal Behaviour*, 86(1), 143–151.
- Dingemans, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences*, 270, 741–747.
- Dingemans, N. J., & Wolf, M. (2010). Recent models for adaptive personality differences: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3947–3958.
- Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2003). Realized heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences*, 270(1510), 45–51.
- Ducatez, S., Legrand, D., Chaput-Bardy, A., Stevens, V. M., Freville, H., & Baguette, M. (2012). Inter-individual variation in movement: is there a mobility syndrome in the large white butterfly *Pieris brassicae*? *Ecological Entomology*, 37, 377–385.
- Edwards, A. C., & Mackay, T. F. C. (2009). Quantitative trait loci for aggressive behavior in *Drosophila melanogaster*. *Genetics*, 182, 889–897.
- Edwards, A. C., Rollmann, S. M., Morgan, T. J., & Mackay, T. F. C. (2006). Quantitative genomics of aggressive behavior in *Drosophila melanogaster*. *PLoS Genetics*, 2(9), e154.
- Farwell, M., & McLaughlin, R. L. (2009). Alternative foraging tactics and risk taking in brook charr (*Salvelinus fontinalis*). *Behavioral Ecology*, 20(5), 913–921.
- Foellmer, M. W., & Khadka, K. K. (2013). Does personality explain variation in the probability of sexual cannibalism in the orb-web spider *Argiope aurantia*? *Behaviour*, 150, 1731–1746.
- Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, 127, 45–86.
- Griffen, B. D., Toscano, B. J., & Gatto, J. (2012). The role of individual behavior type in mediating indirect interactions. *Ecology*, 93, 1935–1943.
- Groothuis, T. G. G., & Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, 29, 137–150.
- Groothuis, T. G. G., & Trillmich, F. (2011). Unfolding personalities: the importance of studying ontogeny. *Developmental Psychobiology*, 53, 641–655.
- Gyuris, E., Fero, O., & Barta, Z. (2012). Personality traits across ontogeny in firebugs, *Pyrrhocoris apterus*. *Animal Behaviour*, 84, 103–109.
- Gyuris, E., Fero, O., Tartally, A., & Barta, Z. (2011). Individual behaviour in firebugs (*Pyrrhocoris apterus*). *Proceedings of the Royal Society B: Biological Sciences*, 278, 628–633.
- Hardy, I. C., Pedersen, J. B., Sejr, M. K., & Linderoth, U. H. (1999). Local mating, dispersal and sex ratio in a gregarious parasitoid wasp. *Ethology*, 105(1), 57–72.
- Hedrick, A. V., & Kortet, R. (2012). Sex differences in the repeatability of boldness over metamorphosis. *Behavioral Ecology and Sociobiology*, 66, 407–412.
- Hensley, N. M., Cook, T. C., Lang, M., Petelle, M. B., & Blumstein, D. T. (2012). Personality and habitat segregation in giant sea anemones (*Condylactis gigantea*). *Journal of Experimental Marine Biology and Ecology*, 426, 1–4.
- Houston, A. I., & McNamara, J. M. (1999). *Models of adaptive behaviour: An approach based on state*. Cambridge, U.K.: Cambridge University Press.
- Jandt, J. M., Bengston, S., Pinter-Wollman, N., Pruitt, J. N., Raine, N. E., Dornhaus, A., et al. (2014). Behavioural syndromes and social insects: personality at multiple levels. *Biological Reviews*, 89, 48–67. <http://dx.doi.org/10.1111/brv.12042>.
- Jeanson, R., & Weidenmüller, A. (2013). Interindividual variability in social insects: proximate causes and ultimate consequences. *Biological Reviews*. <http://dx.doi.org/10.1111/brv.12074>.
- Kafel, A., Zawisza-Raszka, A., & Szulinska, E. (2012). Effects of multigenerational cadmium exposure of insects *Spodoptera exigua* larvae on anti-oxidant response in haemolymph and developmental parameters. *Environmental Pollution*, 162, 8–14.
- Kain, J. S., Stokes, C., & de Bivort, B. L. (2012). Phototactic personality in fruit flies and its suppression by serotonin and white. *Proceedings of the National Academy of Sciences*, 109(48), 19834–19839.
- Killen, S. S., Marras, S., & McKenzie, D. J. (2011). Fuel, fasting, fear: routine metabolic rate and food deprivation exert synergistic effects on risk-taking in individual juvenile European sea bass. *Journal of Animal Ecology*, 80(5), 1024–1033.
- Kleinteich, A., & Schneider, J. M. (2011). Developmental strategies in an invasive spider: constraints and plasticity. *Ecological Entomology*, 36(1), 82–93.
- Kokko, H., Brooks, R., Jennions, M. D., & Morley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society B: Biological Sciences*, 270, 653–664.
- Korsten, P., Mueller, J. C., Hermannstadter, C., Bouwman, K. M., Dingemans, N. J., Drent, P. J., et al. (2010). Association between DRD4 gene polymorphism and personality variation in great tits: a test across four wild populations. *Molecular Ecology*, 19, 832–843.
- Kralj-Fišer, S., Gregorić, M., Zhang, S. C., Li, D. Q., & Kuntner, M. (2011). Eunuchs are better fighters. *Animal Behaviour*, 81, 933–939.
- Kralj-Fišer, S., Mostajo, G. A. S., Preik, O., Pekár, S., & Schneider, J. M. (2013). Assortative mating by aggressiveness type in orb weaving spiders. *Behavioral Ecology*, 24(4), 824–831.
- Kralj-Fišer, S., & Schneider, J. M. (2012). Individual behavioural consistency and plasticity in an urban spider. *Animal Behaviour*, 84(1), 197–204.
- Kralj-Fišer, S., Schneider, J. M., Justinek, Z., Kalin, S., Gregorić, M., Pekár, S., et al. (2012). Mate quality, not aggressive spillover, explains sexual cannibalism in a size-dimorphic spider. *Behavioral Ecology and Sociobiology*, 66, 145–151.
- Krams, I., Kivleniece, I., Kuusik, A., Krama, T., Freeberg, T. M., Maend, R., et al. (2013). Predation selects for low resting metabolic rate and consistent individual differences in anti-predator behavior in a beetle. *Acta Ethologica*, 16, 163–172.

- Kravitz, E. A., & Huber, R. (2003). Aggression in invertebrates. *Current Opinion in Neurobiology*, 13, 736–743.
- Kuntner, M., Kralj-Fišer, S., Schneider, J. M., & Li, D. (2009). Mate plugging via genital mutilation in nephilid spiders: an evolutionary hypothesis. *Journal of Zoology*, 277, 257–266.
- Lewejohann, L., Zipser, B., & Sachser, N. (2011). 'Personality' in laboratory mice used for biomedical research: a way of understanding variability? *Developmental Psychobiology*, 53(6), 624–630.
- Maestriperi, D., & Groothuis, T. G. (2013). Parental influences on offspring personality traits in oviparous and placental vertebrates. In C. Carere, & D. Maestriperi (Eds.), *Animal personalities: Behavior, physiology, and evolution* (pp. 317–352). Chicago, IL: University of Chicago Press.
- Mather, J. A., & Anderson, R. C. (1993). Personalities of octopuses (*Octopus rubescens*). *Journal of Comparative Psychology*, 107, 336–340.
- Mather, J. A., & Logue, D. M. (2013). The bold and the spineless: invertebrate personalities. In C. Carere, & D. Maestriperi (Eds.), *Animal personalities: Behavior, physiology, and evolution* (pp. 13–35). Chicago, IL: University of Chicago Press.
- Mayntz, D., Toft, S., & Vollrath, F. (2003). Effects of prey quality and availability on the life history of a trap-building predator. *Oikos*, 101(3), 631–638.
- Mishra, S., Logue, D. M., Abiola, I. O., & Cade, W. H. (2011). Developmental environment affects risk-acceptance in the hissing cockroach, *Gromphadorhina portentosa*. *Journal of Comparative Psychology*, 125(1), 40–47.
- Modlmeier, A. P., Liebmann, J. E., & Foitzik, S. (2012). Diverse societies are more productive: a lesson from ants. *Proceedings of the Royal Society B: Biological Sciences*, 279, 2142–2150.
- Morales, J. A., Cardoso, D. G., Della Lucia, T. M. C., & Guedes, R. N. C. (2013). Weevil x insecticide: does 'personality' matter? *PLoS One*, 8(6), e67283.
- Morozov, A., Pasternak, A. F., & Arashkevich, E. G. (2013). Revisiting the role of individual variability in population persistence and stability. *PLoS One*, 8(8), e70576.
- Mousseau, T. A., & Dingle, H. (1991). Maternal effects in insect life histories. *Annual Review of Entomology*, 36(1), 511–534.
- Mousseau, T. A., & Fox, C. W. (1998). The adaptive significance of maternal effects. *Trends in Ecology & Evolution*, 13(10), 403–407.
- Mowles, S. L., Cotton, P. A., & Briffa, M. (2012). Consistent crustaceans: the identification of stable behavioural syndromes in hermit crabs. *Behavioral Ecology and Sociobiology*, 66, 1087–1094.
- Mueller, J. C., Korsten, P., Hermannstaedter, C., Feulner, T., Dingemans, N. J., Matthysen, E., et al. (2013). Haplotype structure, adaptive history and associations with exploratory behaviour of the DRD4 gene region in four great tit (*Parus major*) populations. *Molecular Ecology*, 22, 2797–2809.
- Muller, H. (2012). Individual consistency in foraging behaviour and response to predator threat in the bumblebee *Bombus terrestris* (Hymenoptera: Apidae). *Entomologia Generalis*, 34, 9–22.
- Muller, H., Grossmann, H., & Chittka, L. (2010). 'Personality' in bumblebees: individual consistency in responses to novel colours? *Animal Behaviour*, 80, 1065–1074.
- Neff, B. D., & Pitcher, T. E. (2005). Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. *Molecular Ecology*, 14, 19–38.
- Nicolaus, M., Tinbergen, J. M., Bouwman, K. M., Michler, S. P. M., Ubels, R., Both, C., et al. (2012). Experimental evidence for adaptive personalities in a wild passerine bird. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4885–4892.
- Niemela, P. T., DiRienzo, N., & Hedrick, A. V. (2012). Predator-induced changes in the boldness of naive field crickets, *Gryllus integer*, depends on behavioural type. *Animal Behaviour*, 84, 129–135.
- Niemela, P. T., Vainikka, A., Hedrick, A. V., & Kortet, R. (2012). Integrating behaviour with life history: boldness of the field cricket, *Gryllus integer*, during ontogeny. *Functional Ecology*, 26, 450–456.
- Niemela, P. T., Vainikka, A., Lahdenpera, S., & Kortet, R. (2012). Nymphal density, behavioral development, and life history in a field cricket. *Behavioral Ecology and Sociobiology*, 66, 645–652.
- van Oers, K., de Jong, G., van Noordwijk, A. J., Kempenaers, B., & Drent, P. J. (2005). Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour*, 142(9–10), 1185–1206.
- van Oers, K., & Mueller, J. C. (2010). Evolutionary genomics of animal personality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3991–4000.
- van Oers, K., & Sinn, D. L. (2011). Toward a basis for the phenotypic gambit: advances in the evolutionary genetics of animal personality. In M. Inoue-Murayama, S. Kawamura, & A. Weiss (Eds.), *From genes to animal behavior* (pp. 165–183). Tokyo, Japan: Springer.
- Page, R. E., & Robinson, G. E. (1991). The genetics of division of labour in honey bee colonies. *Advances in Insect Physiology*, 23, 117–169.
- Pechenik, J. A. (2000). *Biology of the invertebrates* (2nd ed.). New York: McGraw-Hill.
- Pike, D. A., Webb, J. K., & Shine, R. (2012). Hot mothers, cool eggs: nest-site selection by egg-guarding spiders accommodates conflicting thermal optima. *Functional Ecology*, 26(2), 469–475.
- Pinter-Wollman, N., Gordon, D. M., & Holmes, S. (2012). Nest site and weather affect the personality of harvester ant colonies. *Behavioral Ecology*, 23, 1022–1029.
- Poulin, R. (2013). Parasite manipulation of host personality and behavioural syndromes. *Journal of Experimental Biology*, 216(1), 18–26.
- Price, P. W. (1980). *Evolutionary biology of parasites*. Princeton, NJ: Princeton University Press.
- Price, T. (1998). Maternal and paternal effects in birds: effects on offspring fitness. In T. A. Mousseau, & C. W. Fox (Eds.), *Maternal effects as adaptations* (pp. 202–226). Oxford, UK: Oxford University Press.
- Pronk, R., Wilson, D. R., & Harcourt, R. (2010). Video playback demonstrates episodic personality in the gloomy octopus. *Journal of Experimental Biology*, 213, 1035–1041.
- Pruitt, J. N., Grinstead, L., & Settepani, V. (2013). Linking levels of personality: personalities of the 'average' and 'most extreme' group members predict colony-level personality. *Animal Behaviour*, 86(2), 391–399.
- Pruitt, J. N., & Riechert, S. E. (2009a). Sex matters: sexually dimorphic fitness consequences of a behavioural syndrome. *Animal Behaviour*, 78(1), 175–181.
- Pruitt, J. N., & Riechert, S. E. (2009b). Frequency-dependent success of cheaters during foraging bouts might limit their spread within colonies of a socially polymorphic spider. *Evolution*, 63(11), 2966–2973.
- Pruitt, J. N., & Riechert, S. E. (2009c). Male mating preference is associated with risk of pre-copulatory cannibalism in a socially polymorphic spider. *Behavioral Ecology and Sociobiology*, 63(11), 1573–1580.
- Pruitt, J. N., & Riechert, S. E. (2011). How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proceedings of the Royal Society B: Biological Sciences*, 278(1709), 1209–1215.
- Pruitt, J. N., Riechert, S. E., & Harris, D. J. (2011). Reproductive consequences of male body mass and aggressiveness depend on females' behavioral types. *Behavioral Ecology and Sociobiology*, 65(10), 1957–1966.
- Pruitt, J. N., Riechert, S. E., Iturralde, G., Vega, M., Fitzpatrick, B. M., & Aviles, L. (2010). Population differences in behaviour are explained by shared within-population trait correlations. *Journal of Evolutionary Biology*, 23(4), 748–756.
- Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4051–4063.
- Roth, O., Sadd, B. M., Schmid-Hempel, P., & Kurtz, J. (2009). Strain-specific priming of resistance in the red flour beetle, *Tribolium castaneum*. *Proceedings of the Royal Society B: Biological Sciences*, 276(1654), 145–151.
- Royle, N. J., Schuett, W., & Dall, S. R. X. (2010). Behavioural consistency and the resolution of sexual conflict. *Behavioral Ecology*, 21, 1125–1130.
- Rudin, F. S., & Briffa, M. (2012). Is boldness a resource-holding potential trait? Fighting prowess and changes in startle response in the sea anemone, *Actinia equina*. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1904–1910.
- Rutherford, P. L., Baker, R. L., & Forbes, M. R. (2007). Do larval damselflies make adaptive choices when exposed to both parasites and predators? *Ethology*, 113, 1073–1080.
- Ruuskanen, S., & Laaksonen, T. (2010). Yolk hormones have sex-specific long-term effects on behavior in the pied flycatcher (*Ficedula hypoleuca*). *Hormones and Behavior*, 57, 119–127.
- Scharf, I., Modlmeier, A. P., Fries, S., Tirard, C., & Foitzik, S. (2012). Characterizing the collective personality of ant societies: aggressive colonies do not abandon their home. *PLoS ONE*, 7(3), e33314. <http://dx.doi.org/10.1371/journal.pone.0033314>.
- Schuett, W., & Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, 77, 1041–1050.
- Schuett, W., Dall, S. R. X., Baeumer, J., Kloesener, M. H., Nakagawa, S., Beinlich, F., et al. (2011). 'Personality' variation in a clonal insect: the pea aphid, *Acyrtosiphon pisum*. *Developmental Psychobiology*, 53, 631–640.
- Schuett, W., Dall, S. R. X., & Royle, N. J. (2011). Pairs of zebra finches with similar 'personalities' make better parents. *Animal Behaviour*, 81, 609–618.
- Schuett, W., Dall, S. R., Wilson, A. J., & Royle, N. J. (2013). Environmental transmission of a personality trait: foster parent exploration behaviour predicts offspring exploration behaviour in zebra finches. *Biology Letters*, 9(4), 20130120. <http://dx.doi.org/10.1098/rsbl.2013.0120>.
- Schuett, W., Tregenza, T., & Dall, S. R. X. (2010). Sexual selection and animal personality. *Biological Reviews*, 85, 217–246.
- Shuker, D. M., & West, S. A. (2004). Information constraints and the precision of adaptation: sex ratio manipulation in wasps. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 10363–10367.
- Sih, A., & Bell, A. M. (2008). Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior*, 38, 227–281.
- Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: an integrative overview. *Quarterly Review of Biology*, 79, 241–277.
- Sinn, D. L., Apiolaza, L. A., & Moltschanivskiy, N. A. (2006). Heritability and fitness-related consequences of squid personality traits. *Journal of Evolutionary Biology*, 19, 1437–1447.
- Sinn, D. L., Gosling, S. D., & Moltschanivskiy, N. A. (2008). Development of shy/bold behaviour in squid: context-specific phenotypes associated with developmental plasticity. *Animal Behaviour*, 75, 433–442.
- Sinn, D. L., & Moltschanivskiy, N. A. (2005). Personality traits in dumpling squid (*Euprymna tasmanica*): context-specific traits and their correlation with biological characteristics. *Journal of Comparative Psychology*, 119, 99–110.
- Stamps, J. A., & Groothuis, T. G. G. (2010a). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, 85, 301–325.
- Stamps, J. A., & Groothuis, T. G. G. (2010b). Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4029–4041.
- Stamps, J. A., Saltz, J. B., & Krishnan, V. V. (2013). Genotypic differences in behavioural entropy: unpredictable genotypes are composed of unpredictable individuals. *Animal Behaviour*, 86(3), 641–649.

- Storm, J. J., & Lima, S. L. (2010). Mothers forewarn offspring about predators: a transgenerational maternal effect on behavior. *American Naturalist*, *175*(3), 382–390.
- Sweeney, K., Cusack, B., Armagost, F., O'Brien, T., Keiser, C. N., & Pruitt, J. N. (2013). Predator and prey activity levels jointly influence the outcome of long-term foraging bouts. *Behavioral Ecology*, *24*, 1205–1210.
- Tobler, M., & Sandell, M. I. (2007). Yolk testosterone modulates persistence of neophobic responses in adult zebra finches, *Taeniopygia guttata*. *Hormones and Behavior*, *52*, 640–645.
- Tremmel, M., & Müller, C. (2013). Insect personality depends on environmental conditions. *Behavioral Ecology*, *24*(2), 386–392.
- Trillmich, F., & Hudson, R. (2011). The emergence of personality in animals: the need for a developmental approach. *Developmental Psychology*, *53*, 505–509.
- Truman, J. W., & Riddiford, L. M. (2002). Endocrine insights into the evolution of metamorphosis in insects. *Annual Review of Entomology*, *47*(1), 467–500.
- Uhl, G., Nessler, S. H., & Schneider, J. M. (2010). Securing paternity in spiders? A review on occurrence and effects of mating plugs and male genital mutilation. *Genetica*, *138*(1), 75–104.
- Vainikka, A., Rantala, M. J., Niemela, P., Hirvonen, H., & Kortet, R. (2011). Boldness as a consistent personality trait in the noble crayfish, *Astacus astacus*. *Acta Ethologica*, *14*, 17–25.
- Watanabe, N. M., Stahlman, W. D., Blaisdell, A. P., Garlick, D., Fast, C. D., & Blumstein, D. T. (2012). Quantifying personality in the terrestrial hermit crab: different measures, different inferences. *Behavioural Processes*, *91*, 133–140.
- Wilbur, H. M. (1980). Complex life cycles. *Annual Review of Ecology and Systematics*, *11*, 67–93.
- Wilson, A. D. M., & Krause, J. (2012a). Personality and metamorphosis: is behavioral variation consistent across ontogenetic niche shifts? *Behavioral Ecology*, *23*, 1316–1323.
- Wilson, A. D. M., & Krause, J. (2012b). Metamorphosis and animal personality: a neglected opportunity. *Trends in Ecology and Evolution*, *27*(10), 529–531.
- Wilson, E. O. (1971). *The insect societies*. Cambridge, MA: Belknap Press of Harvard University Press.
- Wilson, E. O., & Hölldobler, B. (2005). Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 13367–13371.
- Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *447*(7144), 581–584.
- Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2013). The evolution of animal personalities. In C. Carere, & D. Maestripieri (Eds.), *Animal personalities: Behavior, physiology, and evolution* (pp. 250–273). Chicago, IL: University of Chicago Press.
- Wolf, M., & McNamara, J. M. (2012). On the evolution of personalities via frequency-dependent selection. *American Naturalist*, *179*(6), 679–692.
- Wong, A. H. C., Gottesman, I. I., & Petronis, A. (2005). Phenotypic differences in genetically identical organisms: the epigenetic perspective. *Human Molecular Genetics*, *14*(1), R11–R18.
- Wray, M. K., Mattila, H. R., & Seeley, T. D. (2011). Collective personalities in honeybee colonies are linked to colony fitness. *Animal Behaviour*, *81*, 559–568.
- Wray, M. K., & Seeley, T. D. (2011). Consistent personality differences in house-hunting behavior but not decision speed in swarms of honey bees (*Apis mellifera*). *Behavioral Ecology and Sociobiology*, *65*(11), 2061–2070.
- Zwarts, L., Versteven, M., & Callaerts, P. (2012). Genetics and neurobiology of aggression in *Drosophila*. *Fly*, *6*, 35–48.