



Essay

Studying personality variation in invertebrates: why bother?

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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)

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