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How Invertebrate Personalities Unfold

Как формируются личности беспозвоночных

Абстракт

Особи внутри видов воспринимают окружающую среду и реагируют на нее по-разному, при этом каждая из них обитает в собственном, уникальном и созданном ею умвельте. Поведенческие различия между особями одного вида, сохраняющиеся во времени или проявляющиеся в разных контекстах, в поведенческой экологии и сравнительной психологии принято определять как животные личности. Они формируются в результате случайных процессов, протекающих в ходе индивидуального развития, а также вследствие обработки и интеграции информации, унаследованной от предков и накопленной в течение жизни. С целью подчеркнуть роль взаимовлияния факторов, действующих на разных временных масштабах, в данной работе предлагается рассмотреть личность беспозвоночных с помощью четырех вопросов Николаса Тинбергена. Однако эволюция, онтогенез, причина и функция анализируются в диахронической перспективе с учетом информационного потока. Представленный обзор литературы направлен также на признание этого распространенного биологиче-

How Invertebrate Personalities Unfold

Abstract

Individuals within a species perceive and respond to their environment differently, and each inhabits and creates its own unique Umwelt. Consistent differences in behaviour between individuals of the same species that persist over time or through contexts are known in behavioural ecology and comparative psychology as animal personalities. They arise as a result of random processes occurring during individual development and as a result of processing and integrating information transmitted from ancestors and collected throughout one's life. To emphasize the role of the interaction of these factors operating on different time scales, it is proposed in this article to look at invertebrate personalities using Nikolaas Tinbergen's four questions, but tracing evolution, ontogeny, cause and function along the axis of time and information flow. The insight into the literature presented here is also intended to support the acceptance of this common biological phenomenon and the term describing it.

Keywords: animal personalities, invertebrates, ontogeny, boldness, behaviour

ского явления и терминологии, используемой при его описании.

Ключевые слова: личность животных, беспозвоночные, онтогенез, смелость, поведение

Introduction

Individuals within species perceive and respond to their environment differently, each dwelling in and creating its own unique Umwelt. Still, traditionally, we are rather used to assign averaged values that are supposed to encapsulate entire species. These include values of morphological traits, such as horn size or shape, life history traits, such as age at first reproduction, and also behavioural traits, such as movement speed or size of territory. But individuals in populations consistently differ from each other, both in the average value of these traits and – in the case of behaviour – also in their variability. Not all people feed as omnivores, not every magpie passes the mirror test, not every common octopus exhibits episodic-like memory, and not every pond snail extends its antennae within half a minute after retracting them in response to the same stimulus. The cognitive and behavioural differences between individuals arise jointly through random processes during development and as the result of the processing and integrating of the information passed from the ancestors and gathered throughout one's own lifetime. This is true for invertebrates, among others.

The aim of this article is to review the mechanisms of behavioural individuality emergence in invertebrates, with an emphasis on the processes at play during the individual's life. First, it is presented how individual invertebrates within a species consistently differ in their behaviour and how these differences are categorized and measured by human observers. Second, how personalities emerge is viewed in the lens of Tinbergen's four questions zooming in after Robert Sapolsky as well as Thore Bergman and Jacinta Beehner, with a light focus on the ontogeny – perhaps still the most neglected of the four. Finally, the consequences beyond individual fitness are briefly discussed.

How They Differ

While scientific literature has until recently presented invertebrates as robot-like or automata, literary fiction and non-fiction has anthropomorphized them vastly. On one end, when vertebrates have proved their sentience through vast neurobiological, cognitive, psychological and ethological research, invertebrates take it longer to escape the Descartes's "animal machines." Yet, what for long seemed obvious simple reflexes, upon closer look and under multiple-context approach reveals to be results of more complex decisions. Take escape response in crayfish or fruit flies, governed by the giant nerve action. Not solely by the giant fibre, though, as more subtle input comes from multiple outward and inward receptors and is processed to produce the most appropriate behavioural outcome.[1] And how this input is weighed may differ from individual to individual. Meanwhile, on the other end of the cultural representations, children's literature, for example, portrays invertebrate individualities. While valuing some better than others, like beetles over wasps, it apparently presents mostly flat, one-sided invertebrate characters without development.[2] Like in an animation series, the eponymous *Maya the Honey Bee*, cordial and inquisitive, and her gluttonous and lazy drone friend Willy.

Indeed, on leaving their nest on a nettle, when one *Aglais io* caterpillar climbs up the plant and her sibling slides down the stem, this may be repeatable, that is, given the choice again, each will do the same. These behaviours are thus neither a species specific programme nor a random result of pure chance. These consistent differences in behaviour, persistent over time or contexts between individuals of the same species, are known in behavioural ecology and comparative psychology as animal personalities. What is more, animal personality research takes the inter-individual differences and their developmental dynamics into serious consideration, while focusing on the behavioural outcome and not the mental representations or affects behind. Other languages may not give this link, yet the English term self-explains well by referring to the Greek *persona*, the mask of public identity. Thus the concept of invertebrate personalities makes no presumptions on the animal's cognitive processes or emotions, but refers to the expressed behaviours. No recalling of mental or affective states is needed to detect behavioural repeatability. And invertebrates are, as individuals, perhaps inevitably, repeatable – that is, different from each other within a species. When they are, this is called personalities.

[1] Björn Brembs, "Invertebrate Behavior – Actions or Responses?," *Frontiers in Neuroscience* 7 (2013): 221, https://doi.org/10.3389/fnins.2013.00221.

[2] Suzanne Agnes Reinoutje Claessen, "Life in the Underground: The Portrayal of Invertebrates in Children's Literature and Comics" (MSc thesis, University of Otago, 2015).

One of the first users and advocates of the term "animal personality," invertebrates included, has been psychologist Samuel D. Gosling.[3] In his comparative agenda, searching for how nonhuman animal models can inform human personality research, he also exposed what has been emphasized above: while human-personality psychologists may focus on a broad array of constructs, which include looking into patterns of feeling and thinking, most animal personality studies focus on just a subset of these constructs – on behavioral traits.[4] Gosling has defended using the term "animal personality," despite its "anthropomorphic associations," for not having a conceptual reason not to do so, for facilitating connections between disciplines, and for the term "temperament" that is also in use (see more below) having a narrower meaning and not encompassing the role of individual life experience.[5]

While Gosling has searched for cross-species commonalities and investigated whether animal personalities can be organized in terms of the human Five Factor Model, behavioural ecologists went another way. In their highly cited work[6] Denis Réale et al. provided ecologists with clearly defined terminology that does not make inferences on what dispositions or psychological processes underlie the repeatable behaviour. In an attempt to pool the multitudes of behaviours into few, potentially independent dimensions, five animal personality axes – independent of the Big Five in human personality research – have been proposed and are commonly used.[7] The first three refer to activity in relation to risk or novelty presence and without relation to conspecific presence. The latter two refer to how an individual interacts with conspecifics (Figure 1).

[3] Samuel D. Gosling, "From Mice to Men: What Can We Learn about Personality from Animal Research," *Psychological Bulletin* 127 (2001): 45–86, http://doi.org/10.1037/0033-2909.127.1.45; Samuel D. Gosling, "Personality in Non-human Animals," *Social and Personality Psychology Compass* 2 (2008): 985–1001, http://doi.org/10.1111/j.1751-9004.2008.00087.x.

[4] Gosling, "Personality in Non-human Animals."

[5] Gosling, "Personality in Non-human Animals."

[6] Denis Réale et al., "Integrating Animal Temperament within Ecology and Evolution," *Biological Reviews* 82 (2007): 291–318, https://doi.org/10.1111/j.1469-185X.2007.00010.x.

[7] Denis Réale et al., "Integrating Animal Temperament." It is interesting to note, that the authors use the term "temperament" in the title and abstract (perhaps to avoid "anthropomorphic associations" in a prominent biological journal), admitting in the text they use it as synonymous with "personality." And it is the latter term that got broadly accepted in the ecological literature, together with other trait definitions provided in the work cited here.

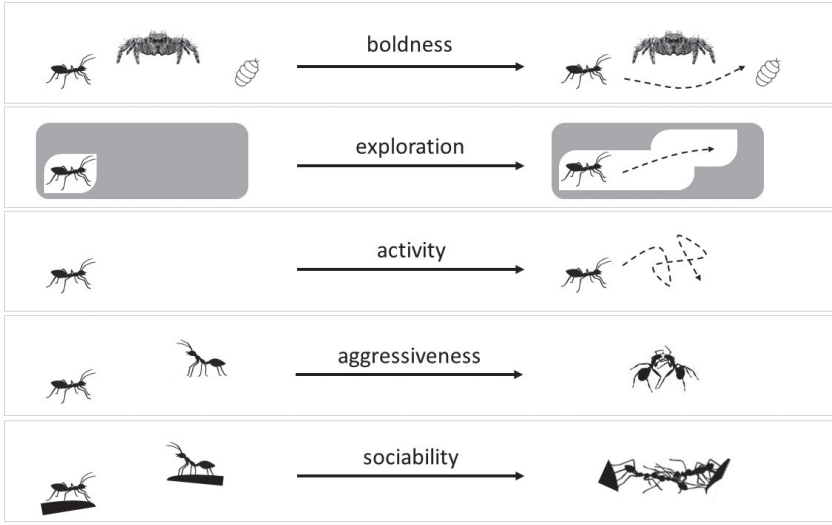

Figure 1. Five animal personality axes. Original graphics based on concepts and definitions presented by Denis Réale et al.[8]

1. Boldness[9] is defined as the tendency to take risks in the presence of a threat or the individual's reaction to a risky situation, but not to new situations. Boldness–shyness is often measured as the latency to leave the shelter or to approach food in the presence of a predator, or a response to predator in an open field test. In sea anemones or snails, for instance, it is often measured as time to re-extend tentacles after simulated threat.[10] In *Calopteryx splendens* damselflies, the distance that a territorial male flew and the time passed until he returned to his territory after the predatory attack simulation were recently proposed as reliable measures of this personality trait in the natural context in the field.[11]

2. Exploration is the individual's reaction to a new – but not threatening – situation. Exploration–avoidance is measured for instance by an individual's latency to explore novel objects or places, or the size of the explored territory. Theoretically clearly distinguishable, in practice, interpretation of the particular behaviour and

[8] Réale et al., "Integrating Animal Temperament."

[9] In Polish, I propose to use the direct translation term *śmiałość*, as opposed to *odwaga* (courage), also to encompass the fact that courage relates to internal processes behind bold actions.

[10] Daniel K. Maskrey et al., "The Impact of Personality, Morphotype and Shore Height on Temperature-Mediated Behavioural Responses in the Beadlet Anemone *Actinia equina*," *Journal of Animal Ecology* 89 (2020): 2311–2324, https://doi.org/10.1111/1365-2656.13301; Maxime Dahirel et al., "Boldness and Exploration Vary between Shell Morphs but Not Environmental Contexts in the Snail *Cepaea nemoralis*," *Ethology* 127 (2021): 321–333, https://doi.org/10.1111/eth.13129.

[11] Maria J. Golab et al., "Adult Insect Personality in the Wild – *Calopteryx splendens* as a Model for Field Studies," *Ecology and Evolution* 11 (2021): 18467–18476, https://doi.org/10.1002/ece3.8439.

its categorization into one of the axes may not be obvious. When some fruit flies *Drosophila melanogaster* repeatedly found a tiny opening in a test tube and moved to another, adjointed one, they were called dispersers,[12] but as well could be interpreted as explorers.[13] When some water louses *Asellus aquaticus* (isopod crustacean) repeatedly crossed more obstacles in a maze than others, they were called explorative.[14] One could argue, though, they were just more active.

3. Activity refers to physical movements in space or locomotion and is the general level of activity of an individual. It can be measured as speed, time in motion, distance travelled, importantly: in a both safe and familiar environment. As with other traits, the understanding of the biology of the species is crucial for proper assessment. Take the small planktonic crustacean water fleas *Daphnia* (branchiopod) with their hop-and-sink locomotion. Propelled by the overhead movements of extensive and branched antennae (compare to Daphne, a mythological nymph transformed into a laurel tree), they hop upon their stroke, and sink while motionless. The total distance that a *Daphnia* moves up and down in the water column appears to be an activity trait, yet, staying at one depth (say hop-sink-hop-sink) requires the same number of movements and energetic expense as changing depth and getting back (say hop-hop-sink-sink).[15]

4. Aggressiveness is an agonistic reaction towards a conspecific. It includes, among others, attacks, threats, and displays. Depending on the species, it may be expressed in different contexts via different behaviours and is often associated with competition for food, shelter, and mates. In territorial damselfly males this could be measured as time he moves toward the presented intruder male or how many times he bites or hits the intruder.[16]

Finally, 5. Sociability is defined as a reaction to the presence of conspecifics excluding aggressive behaviour. It can be measured simply as the number of conspecific interactions, time spent in proximity to others or the distance between, providing no agonism occurs. Still, more complex measures are also in use. For a darkling beetle *Bolitotherus cornutus*, social network position was shown to be

[12] Allan H. Edelsparre et al., "Alleles Underlying Larval Foraging Behaviour Influence Adult Dispersal in Nature," *Ecology Letters* 17 (2014): 333–339, https://doi.org/10.1111/ele.12234.

[13] Adam M. Koenig and Brittany H. Ousterhout, "Behavioral Syndrome Persists over Metamorphosis in a Pond-Breeding Amphibian," *Behavioral Ecology & Sociobiology* 72 (2018): 184, https://doi.org/10.1007/s00265-018-2595-2.

[14] Gergely Horváth et al., "Exploratory Behaviour Divergence between Surface Populations, Cave Colonists and a Cave Population in the Water Louse, *Asellus aquaticus*," *Behavioral Ecology & Sociobiology* 77 (2023): 15, https://doi.org/10.1007/s00265-022-03288-1.

[15] Piotr Dawidowicz and Carsten J. Loose, "Metabolic Costs During Predator-Induced Diel Vertical Migration of *Daphnia*," *Limnology and Oceanography* 37 (1992): 1589–1595, https://doi.org/10.4319/lo.1992.37.8.1589.

[16] Golab, "Adult Insect Personality in the Wild," 18471.

a consistent, and resilient to disturbance, property of individuals.[17] Also individual bees in a colony differ in their tendency to interact with other workers, for example, to be aggressive or to share food (tropholaxis), and these differences persist with age and with changing the role of the worker in the colony.[18] Noteworthily, in other insect species, individuals are even more repeatable in their sociability and aggression than bees.

Yet, in biological literature, there are several approaches to classifying animal personalities. The term "personality" adopted in behavioural ecology is sometimes used interchangeably with "behavioural type" or "behavioural individuality" and generally refers to the persistence of certain behavioural tendencies across various environmental contexts and at least at one stage of an individual's life. The terms "coping style" and "temperament," used more often for vertebrates and in biomedical and agricultural sciences, refer to selected aspects of personality. Coping styles – term maybe exaggeratedly applied for field crickets *Gryllus integer*[19] – refer to response strategies to aversive stimuli and stressful situations, and are generally categorized as either reactive or proactive. Temperament in its turn, in vertebrates, refers to early behavioural tendencies visible in juveniles,[20] and its rare uses for invertebrates appear as synonymous to personality (see above). Finally, even within the common five axes framework, often more insight can be gained not by dissecting a behavioural style into for instance boldness and activity but by describing it explicitly. Some sea cucumbers roll over to self-right after being put upside-down consistently faster than others.[21] Would it be right to categorize them simply as more or less active? For damselfly *Calopteryx splendens* males, beside boldness and aggressiveness, Maria Gołąb et al.[22] propose courtship style as an important personality trait, described and measured by their reaction to females, alighting display and engagement in other specific behaviours.

[17] Vincent Formica et al., "Consistency of Animal Social Networks after Disturbance," *Behavioral Ecology* 28 (2017): 85–93, https://doi.org/10.1093/beheco/arw128.

[18] Alexander Walton and Amy L. Toth, "Variation in Individual Worker Honey Bee Behavior Shows Hallmarks of Personality," *Behavioral Ecology and Sociobiology* 70 (2016): 999–1010, https://doi.org/10.1007/s00265-016-2084-4.

[19] Indrikis Krams et al. "Linking Organismal Growth, Coping Styles, Stress Reactivity, and Metabolism via Responses against a Selective Serotonin Reuptake Inhibitor in an Insect," *Scientific Reports* 8 (2018): 8599, https://doi.org/10.1038/s41598-018-26722-9.

[20] Marie-Antonine Finkemeier et al., "Personality Research in Mammalian Farm Animals: Concepts, Measures, and Relationship to Welfare," *Frontiers in Veterinary Science* 5 (2018): 131, https://doi.org/10.3389/fvets.2018.00131.

[21] Jeff C. Clements et al., "Roll, Right, Repeat: Short-Term Repeatability in the Self-Righting Behaviour of a Cold-Water Sea Cucumber," *Journal of the Marine Biological Association of the United Kingdom* 100 (2020): 115–120, https://doi.org/10.1017/S0025315419001218.

[22] Golab, "Adult Insect Personality in the Wild," 18471.

Whatever the approach, by definition, to assess any of the above five traits and call their estimates a personality, one needs to take repeated measurements for the same individuals. Behavioural consistency of individuals is thus often estimated over hours or days, but in fewer cases also over life stages or lifespan. Sometimes, the longer the considered period, the lower the individual repeatability, like activity in red flour beetles *Tribolium castaneum*[23] or in intertidal marine copepods *Tigriopus brevicornis* (crustacean).[24] Also, some are more predictable than others, like among hermit crabs *Pagurus bernhardus* in their time to reemerge.[25] In some cases, particularly in eusocial animals, personality is taken to the family level, like for boldness, exploration, and aggressiveness – and their consistency and correlations – assessed for colonies for different ant species.[26]

How They Come to Differ

Introductory Remarks

Like so many other phenotypes, animal personalities are the result of the interaction between the information selected in their evolutionary history – that is passed from their far ancestors in genes, the information passed from their recent ancestors epigenetically (*sensu lato*), and the moulding during one's own ontogeny – experiences accumulated throughout their lives. As they are expressed and observed at the timescales of individual lifespan, life stage or other part of it, the developmental context is of special importance.[27] Here, the look at invertebrate personalities

[23] Yonatan Wexler et al., "Behavioral Repeatability of Flour Beetles Before and After Metamorphosis and Throughout Aging," *Behavioral Ecology and Sociobiology* 70 (2016): 745–753, https://doi.org/10.1007/s00265-016-2098-y.

[24] Jan Heuschele et al., "The Hidden Dimension: Context-Dependent Expression of Repeatable Behavior in Copepods," *Environmental Toxicology and Chemistry* 39 (2020): 1017–1026. https://doi.org/10.1002/etc.4688.

[25] Judy A. Stamps et al., "Unpredictable Animals: Individual Differences in Intraindividual Variability (IIV)," *Animal Behaviour* 83 (2012): 1325–1334, https://doi.org/10.1016/j.anbehav.2012.02.017.

[26] Sarah Elizabeth Bengston and Anna Dornhaus, "Be Meek or Be Bold? A Colony-Level Behavioural Syndrome in Ants," *Proceedings of the Royal Society B* 281 (2014): 20140518, http://doi.org/10.1098/rspb.2014.0518; Olivier Blight et al., "A Proactive–Reactive Syndrome Affects Group Success in an Ant Species," *Behavioral Ecology* 27 (2016): 118–125, https://doi.org/10.1093/beheco/arv127.

[27] See also Fritz Trillmich and Robyn Hudson, "The Emergence of Personality in Animals: The Need for a Developmental Approach," *Developmental Psychobiology* 53 (2011): 505–509, https://doi.org/10.1002/dev.20573.

is guided by the four Nikolaas Tinbergen's questions,[28] yet, following the original evolution, ontogeny, causation and survival value as ordered along the time axis of their relevance. Thus, as also proposed by Thore Bergman and Jacinta Beehner,[29] personality emergence is viewed in a narrowing timescale (see also Robert Sapolsky[30]), from an evolutionary perspective, through the lifetime frame of an individual, through the instantaneous proximate mechanisms generating decision making and behavioural expression, to their function, that is, adaptive significance, upon their emergence (Figure 2).

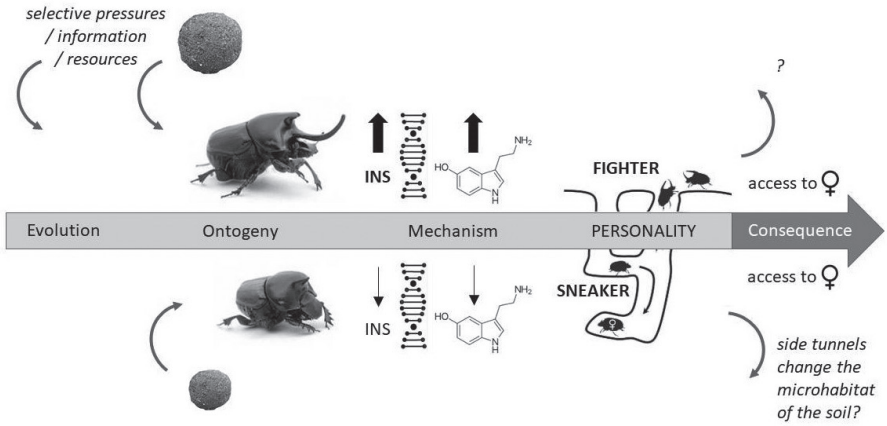

Figure 2. The unfolding of male *Onthophagus* beetles' personalities (see text for details). Combined after Westwick and Rittschof (2021) and Bergman and Beehner (2022, 2023)

Evolutionary History

Far from broadly acknowledged, personalities are omnipresent in the animal kingdom, throughout our phylogenetic tree (and beyond). Not an evolutionary novelty that emerged once, rather an immanent feature of those who behave. Of vertebrates, let us recall here just the least obvious, fish, even important for the advancement

[28] Nikolaas Tinbergen, "On Aims and Methods of Ethology," *Zeitschrift für Tierpsychologie* 20 (1963): 410–433, https://doi.org/10.1111/j.1439-0310.1963.tb01161.x.

[29] Thore J. Bergman and Jacinta C. Beehner, "Leveling with Tinbergen: Four Levels Simplified to Causes and Consequences," *Evolutionary Anthropology* 31 (2022): 12–19, https://doi.org/10.1002/evan.21931; but see also Thore J. Bergman and Jacinta C. Beehner, "Information Ecology: An Integrative Framework for Studying Animal Behavior," *Trends in Ecology & Evolution* 38 (2023): 1041–1050, https://doi.org/10.1016/j.tree.2023.05.017.

[30] Robert M. Sapolsky, *Behave: The Biology of Humans at Our Best and Worst* (New York: Penguin, 2018).

of this research field.[31] The existence of behavioural individualities in invertebrates recently deemed sentient in some legislations,[32] namely cephalopods[33] and decapods,[34] should thus come with little surprise. But personalities are also present in other mollusks and arthropods.[35] Furthermore, among annelids, some polychaete worms *Spirobranchus giganteus* reemerge consistently sooner after recession into their tube upon being disturbed than others.[36] Consistently bold and shy individuals are even recorded in the sedentary, radially symmetrical cnidarians, that is, animals of decentralized nervous system distributed throughout the body, such as sea anemones.[37] Inter-individual behavioural differences appear ubiquitous in both vertebrates and invertebrates,[38] in both natural and captive populations, and in wild and domesticated species.[39] Last common ancestors of all invertebrates exhibiting personalities might have been the first animals themselves, maybe similar to a modern sponge or a comb jelly. Moreover, it cannot be said that some personality traits are more predictable in some taxa than others. Apparently, these are continuously under system-specific constraints and selective pressures.[40]

And indeed, between species or within species but between population comparisons give insights into susceptibility of specific personality traits, and their correlations, to selective pressures, and thus to their macro- and microevolution. Between-species comparative agenda across phylogeny and ecologies can generate evolutionary hypotheses on whether a personality trait can be attributed to convergent evolution or to common ancestry.[41] Similar studies are frequently performed at a lower, within-species level. Water louses from cave-dwelling popula-

[31] Alicja Fudali and Barbara Pietrzak, "Freshwater Fish Personalities in the Anthropocene," *Ecohydrology & Hydrobiology* 24 (2024): 354–366, https://doi.org/10.1016/j.ecohyd.2024.01.002.

[32] Animal Welfare (Sentience) Bill, 3 March 2022, House of Commons Library, UK Parliament.

[33] Francesca Zoratto et al., "Variability in the 'Stereotyped' Prey Capture Sequence of Male Cuttlefish (*Sepia officinalis*) Could Relate to Personality Differences," *Animal Cognition* 21 (2018): 773–785, https://doi.org/10.1007/s10071-018-1209-8.

[34] Francesca Gherardi et al., "Behavioral Plasticity, Behavioral Syndromes and Animal Personality in Crustacean Decapods: An Imperfect Map is Better Than No Map," *Current Zoology* 58 (2012): 567–579, https://doi.org/10.1093/czoolo/58.4.567.

[35] Simona Kralj-Fišer and Wiebke Schuett, "Studying Personality Variation in Invertebrates: Why Bother?," *Animal Behaviour* 91 (2014): 41–52, https://doi.org/10.1016/j.anbehav.2014.02.016.

[36] Ariel K. Pezner et al., "Hiding Behavior in Christmas Tree Worms on Different Time Scales," *Behavioral Ecology* 28 (2017): 154–163, https://doi.org/10.1093/beheco/arw140.

[37] Maskrey, "The Impact of Personality, Morphotype and Shore Height."

[38] Kralj-Fišer and Schuett, "Studying Personality Variation in Invertebrates."

[39] Finkemeier et al., "Personality Research in Mammalian Farm Animals."

[40] Gergely Horváth et al., "Phylogenetic Meta-Analysis Reveals System-Specific Behavioural Type – Behavioural Predictability Correlations," *Royal Society Open Science* 10 (2023): 230303, http://doi.org/10.1098/rsos.230303.

[41] Gosling, "From Mice to Men."

tions are significantly less explorative and disperse more slowly than their conspecifics from surface populations, and it was suggested to be a result of adaptation to these habitats.[42] There is thus an important genetic component to personality. More to that, general heritability of personality appears higher than that of behaviour per se.[43] Like mother, like daughter. In invertebrates, low but significant heritability of activity and exploration was seen for instance in distinct genetic lines of the hymenopteran parasitoid wasp *Trichogramma evanescens*.[44] Further down to genes, in rare cases single natural gene variants can be responsible for big personality differences, like ones in general activity and locomotion while feeding seen in rovers and sitters among *Drosophila*, the behavioural types tightly linked to the *foraging* gene expression.[45]

Yet, persistent inter-individual differences in behaviour are also observed in populations consisting of genetically identical parthenogenetic individuals. Some of the freshwater crustacean *Daphnia* females are bolder than others – come back from the safety of the depths consistently earlier or closer to the water surface each dusk.[46] Some of the flightless insects, pea aphids *Acyrthosiphon pisum*, apply a drop-off-a-plant tactic to escape predation while some of their genetically identical siblings consistently do not.[47] These differences arise due to transgenerational transfers, in response to the environment and as a result of random processes.

Ontogeny

The first differences between individuals may appear at the very beginning of the existence of a new life, and even if they are not there yet, they will appear during

[42] Horváth et al., "Exploratory Behaviour Divergence."

[43] Ned A. Dochtermann et al., "The Contribution of Additive Genetic Variation to Personality Variation: Heritability of Personality," *Proceedings of Royal Society B* 282 (2015): 220142201, http://doi.org/10.1098/rspb.2014.2201.

[44] Silène Lartigue et al., "Consistent Variations in Personality Traits and Their Potential for Genetic Improvement in Biocontrol Agents: *Trichogramma evanescens* as a Case Study," *Evolutionary Applications* 15 (2022): 1565–1579, https://doi.org/10.1111/eva.13329.

[45] Marla B. Sokolowski, "Drosophila: Genetics Meets Behaviour," *Nature Reviews Genetics* 2 (2001): 879–890, https://doi.org/10.1038/35098592; see also hygenic behaviour in bees, originally thought to be determined by two genes, now seen as more complex: Brock A. Harpur et al., "Integrative Genomics Reveals the Genetics and Evolution of the Honey Bee's Social Immune System," *Genome Biology and Evolution* 11 (2019): 937–948, https://doi.org/10.1093/gbe/evz018.

[46] Piotr Dawidowicz et al., "Evidence of Personality in Migratory Behavior of Clonal *Daphnia magna*," *Fundamental and Applied Limnology* 196 (2023): 279–286, https://doi.org/10.1127/fal/2023/1465.

[47] Wiebke Schuett et al., "Personality Variation in a Clonal Insect: The Pea Aphid, *Acyrthosiphon pisum*," *Developmental Psychobiology* 53 (2011): 631–640, https://doi.org/10.1002/dev.20538.

the life of the animals. Even genetically identical eggs produced in the process of parthenogenesis may differ in the structure of chromosomes or the chemical state of the DNA molecule (epigenetic differences) or in non-genetic material transferred from the mother and contained outside the nucleus in the cell. These sometimes small initial differences are the starting point for the developmental trajectories of individuals to diverge. Then, even initially identical eggs will encounter at least slightly different environmental conditions – perhaps a different place in the brood chamber or the order of laying is enough for different genes to be expressed in response to the specific conditions encountered. Finally, the process of embryonic development itself is full of random events.

Recently, it has been shown that stochastic processes leading to asymmetry in the brain of isogenic *Drosophila* flies lead to the development of distinctly different types of visual orientation and associated behaviour ("asymmetric" flies walking straight versus "symmetric" flies walking in a zigzag manner[48]). This *Drosophila* case indicates the role of mechanisms related to the reception and processing of sensory stimuli – the role of basic interaction with the world. In the *Drosophila* case, the source of variability is random molecular events – developmental noise of one of the cell signalling pathways and the neuronal growth that depends on it (showing that individual insect brains are also unique). In this example, different brain microarchitecture translates into differences in visual orientation towards an object and, consequently, clear, lasting inter-individual differences in the way of moving towards it.

An important part of the puzzle of a developing organism is the fact that both prenatal and postnatal sensory experience influences the development of the brain and sense organs and has long-term behavioural consequences. The way in which individual tissues or the entire animal respond to the stream of incoming stimuli depends not only on the properties of the stimuli themselves, but also on the trajectory of previous stimulation and development and the current state of the sense organs. In invertebrates, sensory plasticity is observed not only at the level of neurons but also in behavioural adaptations that result from plastic changes in the nervous system during development, in response to both external and internal signals.[49] Like jumping spiders *Marpissa muscosa* developing in a physically and socially deprived environment develop to be less explorative that ones developing in an enriched one.[50]

[48] Suguru Takagi and Richard Benton, "Animal Behavior: A Neural Basis of Individuality," *Current Biology*, 30 (2020): R710–R712, https://doi.org/10.1016/j.cub.2020.04.05.

[49] Elzbieta M. Pyza, "Plasticity in invertebrate sensory systems," *Frontiers in Physiology* 4 (2013), https://doi.org/10.3389/fphys.2013.00226.

[50] Jannis Liedtke et al., "Early Environmental Conditions Shape Personality Types in a Jumping Spider," *Frontiers in Ecology and Evolution* 3 (2015): 134, https://doi.org/10.3389/fevo.2015.00134.

Experience thus shapes personality. For instance, in the honey bee, aggressive interaction with another individual leads to specific changes in gene transcription in the brain. Thus, hatching in an aggressive social environment leads to aggressive behaviour in adult life and even after the bee moves into a new environment.[51] Depending on nutrition level during early development, dung beetle *Onthophagus* males emerge either as small and hornless and adopt a sneaker reproductive tactic or as large individuals with a horn and become reproductive fighters.[52]

Regardless of the source of variation or the system involved, almost any initial differences may lead to divergence of behavioural types as a result of feedback. Behaviour is assumed to be a plastic element of the phenotype and is a response to both changes in the external environment and the internal state of the organism. It therefore depends on the physiological state of the animal, for example, the state of the neuroendocrine system, the morphotype of the individual, its current energy reserves and general condition, body size, reproductive status and skills. The behavioural response to the state of the body may lead to a change in this state – eliminating inter-individual differences in the case of negative feedbacks or leading to their differentiation in the case of positive feedbacks.

An example of negative feedback may be a situation in which an animal with low energy reserves displays risky behaviour, as a result of which reserves are restored, which in turn leads to a decrease in boldness and risk-taking tendency to protect the collected resources. Such a feedback loop may theoretically lead to the convergence of behavioural types.[53] Mustard leaf beetles *Phaedon cochleariae* feeding on low-quality food were indeed found bolder, despite their lower activity than well-fed beetles, thereby potentially increasing their success in foraging.[54] Potentially also, presenting a good model system to test personality convergence under negative feedback. A positive feedback loop in its turn may or may not be the result of a learning process. Bold individuals may acquire behavioural skills related to the implementation of a repertoire of bold behaviours, and shy ones – to timid ones, strengthening the differences between the types. Yet, theory predicts and still awaits empirical evidence for such mechanisms operating.[55]

[51] Clare C. Rittschof et al., "Early-Life Experience Affects Honey Bee Aggression and Resilience to Immune Challenge," *Scientific Reports* 5 (2015): 15572, https://doi.org/10.1038/srep15572.

[52] Rebecca R. Westwick and Clare C. Rittschof, "Insects Provide Unique Systems to Investigate How Early-Life Experience Alters the Brain and Behavior," *Frontiers in Behavioral Neuroscience* 15 (2021): 660464, https://doi.org/10.3389/fnbeh.2021.660464.

[53] Andrew Sih et al., "Animal Personality and State-Behaviour Feedbacks: A Review and Guide for Empiricists," *Trends in Ecology and Evolution* 30 (2015): 50–60, https://doi.org/10.1016/j.tree.2014.11.004.

[54] Martin Tremmel and Caroline Müller, "Insect Personality Depends on Environmental Conditions," *Behavioral Ecology* 24 (2013): 386–392, https://doi.org/10.1093/beheco/ars175.

[55] Sean M. Ehlman et al., "Developmental Feedbacks and the Emergence of Individuality," *Royal Society Open Science* 9 (2022): 221189, http://doi.org/10.1098/rsos.221189.

Finally, experience may be of little use, if during ontogeny the animal changes its environment or itself completely. Most invertebrates go through distinct life stages over their development, through some form of metamorphosis with radical morphological and physiological transformations. Holometabolous insects, with their larva transforming through the pupa stage into a very unlike imago, are the end example. These transformations often go together with the shift of the habitat or ecological niche, like aquatic to terrestrial, or herbivore to carnivore. In consequence, behaviours change or new ones arise according to new challenges, with a common prediction of personality breakage upon metamorphosis.[56] Yet, empirical studies on holometabolous insects bring mixed results. In three species of beetles, larval personality did not predict adult behaviour, despite the lack of habitat or dietary ontogenetic shift.[57] Meanwhile, in the also all-life terrestrial lady beetle, correlations between larval and adult behaviours were found,[58] like in the habitat-shifting damselflies, where both adult activity and boldness were correlated with larval behavioural type.[59] There thus appears to be no single pattern, but instead, personality retention could be influenced by factors other than the juvenile to adult niche shift only.[60]

Direct Causation (Proximate Causal Mechanism)

Intuitively, boldness, exploration and activity, are expected to be correlated with physiological traits, metabolism among others, forming so-called pace-of-life syndromes (live fast, die young, or the reverse). These associations are not simple or obvious, though.[61] These three personality traits do form behavioural syndromes sometimes, more often than not, yet, they are not correlated themselves. Boldness,

[56] Barbara Płaskonka et al., "Predation Risk Experienced by Tadpoles Shapes Personalities Before but Not After Metamorphosis," *Ecology and Evolution* 14 (2024): e70532, https://doi.org/10.1002/ece3.70532.

[57] Koenig and Ousterhout, "Behavioral Syndrome Persists over Metamorphosis," 3; Karine Monceau et al., "Larval Personality Does Not Predict Adult Personality in a Holometabolous Insect," *Biological Journal of the Linnean Society* 120 (2017): 869–878, https://doi.org/10.1093/biolinnean/blw015.

[58] Alice S. Rodrigues et al., "Ontogenic Behavioral Consistency, Individual Variation and Fitness Consequences among Lady Beetles," *Behavioural Processes* 131 (2016): 32–39, https://doi.org/10.1016/j.beproc.2016.08.003.

[59] Tomas Brodin, "Behavioral Syndrome over the Boundaries of Life – Carryovers from Larvae to Adult Damselfly," *Behavioral Ecology* 20 (2009): 30–37, https://doi.org/10.1093/beheco/arn111.

[60] Aurélien Kaiser et al., "Urbanisation and Sex Affect the Consistency of Butterfly Personality across Metamorphosis," *Behavioral Ecology and Sociobiology* 72 (2018): 188, https://doi.org/10.1007/s00265-018-2616-1.

[61] Zoltán Rádai et al., "State and Physiology behind Personality in Arthropods: A Review," *Behavioral Ecology and Sociobiology* 76 (2022): 150, https://doi.org/10.1007/s00265-022-03259-6.

for instance, is often coupled with higher metabolic rates, yet, it was not found so in crickets[62] and it correlated to different metabolic traits and states in two unrelated gastropods.[63] There, freshwater snails *Helisoma* which grew their shell faster were the ones to use this shelter of the shell more, making them shy. Counterintuitively, also activity is not consistently associated with higher metabolic rates in arthropods.[64] *Drosophila* rovers and sitters, indeed, differ in their metabolism, yet in a more complex way than just being slower or faster. Rovers store energy predominantly as lipids, whereas sitters store it as carbohydrates.[65]

Maybe more pronounced are the links of personality traits related to interactions with conspecifics to individual hormonal and neuroendocrine internal environment. The above-mentioned fighter *Onthophagus* beetle males have increased expression of insulin-responsive genes in the brain and upregulation of serotonin, while the sneakers have downregulated brain insulin and serotonin signaling. Serotonin is also linked to sociability in social species, like in tangle-web spiders, *Anelosimus studiosus*.[66]

In honey bee colonies, scouts, namely, individuals showing a strong tendency to look for new food sources and places for a new nest, have a significantly different gene expression profile in the brain than other foragers. This includes differences related to signalling dependent on various neurotransmitters: dopamine, glutamate and gamma-aminobutyric acid. Scouts are naturally high on octopamine, a hormone chemically closely related and with functions similar to that of noradrenaline in mammals, mobilizing the body and the nervous system for action. At the same time, administering octopamine or glutamate to the bee increases the likelihood of exploratory behaviour, while administering the antagonist, dopamine, reduces it. These findings show intriguing similarities in the tendency to seek novel sensations in humans and insects and suggest that this trait, which most likely evolved independently in these two lineages, may be based on highly conserved molecular mechanisms.[67]

Immunity and infections, as well as the external chemical environment, such as the presence of toxins or secondary metabolites of other organisms, may also shape

[62] Vincent Careau et al., "Energy Metabolism and Personality in Wild-Caught Fall Field Crickets," *Physiology & Behavior* 199 (2019): 173–181, https://doi.org/10.1016/j.physbeh.2018.11.023.

[63] Benjamin J. Toscano et al., "Among-Individual Behavioral Responses to Predation Risk Are Invariant within Two Species of Freshwater Snails," *Ethology* 129 (2023): 269–279, https://doi.org/10.1111/eth.13363.

[64] Rádai et al., "State and Physiology behind Personality in Arthropods."

[65] Aaron M. Allen et al., "Feeding-Related Traits Are Affected by Dosage of the Foraging Gene in *Drosophila melanogaster*," *Genetics* 205 (2017): 761–773, https://doi.org/10.1534/genetics.116.197939.

[66] Rádai et al., "State and Physiology behind Personality in Arthropods."

[67] Zhengzheng S. Liang et al., "Molecular Determinants of Scouting Behavior in Honey Bees," *Science* 335 (2012): 1225–1228, https://doi.org/10.1126/science.1213962.

invertebrate personalities. For instance, virus-infected house crickets *Acheta domesticus* were found shyer than not infected.[68] Water fleas *Daphnia magna* exposed to fish kairomones – here chemical cues of predator presence – exhibited either bold or shy personality, differentiation that was absent in the absence of the chemicals.[69] Again though, studies are still few and consistent patterns or mechanisms have not been elucidated yet. That the individuals in question are in fact consortia of the animals and their microbiomes is also yet to be acknowledged.

How This Makes the Difference

At the level of the individuals, when personalities arise, they may be adaptive, that is function as means towards higher fitness. Both being a daredevil among shybies and the other way round may bring opportunities not accessible to others. And as these are individuals that shape biological reality, their personalities exert their effects around. The daredevils and the shybies may both eat different diets and fall prey to different species, thus making part of distinct food webs. Similar can be expected of the zigzag and straight walkers among *Drosophila* flies.

During organismal development, various buffering mechanisms can operate to maintain the "one right" target structure and function – to canalise the phenotype to the optimal one – but still, maintaining phenotypic diversity within a population may also prove beneficial.[70] And as animals within a species differ in their behaviour, this means an individual does not do all that the species as a whole is capable of. This narrowing of the behavioural repertoire and of the plastic response to unexpected environmental challenges is sometimes perceived as maladaptive, yet natural selection maintains inter-individual variation in populations. Theoretical considerations indicate that differences between individuals are favoured by selection when individual benefits of having a specific personality (e.g. bold) depend both on the frequency of occurrence of other personalities (e.g. shy) and on the history of the individual's own experiences.[71]

[68] Matthew Low et al., "Viral Infection Changes the Expression of Personality Traits in an Insect Species Reared for Consumption," *Scientific Reports* 12 (2022): 9503, https://doi.org/10.1038/s41598-022-13735-8.

[69] Dawidowicz et al., "Evidence of Personality in Migratory Behavior."

[70] Takagi and Benton, "Animal Behavior."

[71] Sasha R. X. Dall et al., "The Behavioural Ecology of Personality: Consistent Individual Differences from an Adaptive Perspective," *Ecology Letters* 7 (2004): 734–739, https://doi.org/10.1111/j.1461-0248.2004.00618.x.

In social animals, like in bees, differences in personality could potentially contribute to the division of labour in colonies, creating variation in individual tendencies to perform different tasks. At the same time, entire families often permanently differ from each other. This includes differences in the intensity of the defence reaction, collecting food, tidying up the hive or repairing combs. And these differences clearly translate into the fitness of the family measured by its biomass or patch area.[72] Personality affects colony productivity in social insects, learning in crickets, or dispersal and invasion in crayfish and shrimps.[73]

From an evolutionary perspective, differences among individuals are important as they are the raw material for the evolution of behaviour. From an ecological perspective, personalities matter for ecosystem processes. Individual variation in paper wasp *Polistes metricus* queen morphology and behaviour predicts colony performance in the wild.[74] Populations of crayfish of different behavioural types are predicted to exert different impacts on leaf litter breakdown in streams.[75] From an applied perspective, behavioural differences between individuals are relevant in many fields: invasion biology, biological control, ecotoxicology, and welfare, among others, increasingly important in the face of the development of invertebrate farming for food for people.[76]

Individual processes scale up: these are the unique phenotypes that undergo selection, constitute populations, interact with other species, and thus shape biological reality. Understanding how behavioural personalities emerge leads us to a better understanding of how higher level systems, such as food webs, communities, or ecosystems, function. As such, explaining individuality has far-reaching practical and applied implications for management and conservation issues. Naturally, the efficiency of the conservation management tools will differ between individuals of different behavioural types. So will their vulnerability to habitat deterioration and loss, in the first place. On the other hand, application of specific conservation measures, like captive-breeding programmes, may lead to shifts in personality traits, affecting other aspects of species biology. In fact, personalities can mediate responses

[72] Margaret K. Wray et al., "Collective Personalities in Honeybee Colonies Are Linked to Colony Fitness," *Animal Behaviour* 81 (2011): 559–568, https://doi.org/10.1016/j.anbehav.2010.11.027.

[73] Rosie Ann Rickward et al., "Among-Individual Behavioural Variation in the Ornamental Red Cherry Shrimp, *Neocaridina heteropoda*," *Ecology and Evolution* 14 (2024): e11049, https://doi.org/10.1002/ece3.11049.

[74] Colin M. Wright et al., "Individual Variation in Queen Morphology and Behavior Predicts Colony Performance in the Wild," *Behavioral Ecology and Sociobiology* 73 (2019): 122, https://doi.org/10.1007/s00265-019-2739-z.

[75] Bana A. Kabalan et al., "Intraspecific Variation in Crayfish Behavioral Traits Affects Leaf Litter Breakdown in Streams," *Oecologia* 205 (2024): 515–531, https://doi.org/10.1007/s00442-024-05593-0.

[76] Rickward et al., "Among-Individual Behavioural Variation."

to all anthropogenic impacts, including human contact, exploitation, habitat fragmentation and disease transmission.

Finally, amassing evidence that individual history matters also in non-human animals, in non-primates, non-mammals, even in invertebrates, might have deep consequences for fields such as human health and medicine. It brings a strong message to all, the public, the policy-makers, and the practitioners, from educators to medicine doctors, that there are no general solutions to individual problems, no directions, such as dietary recommendations, that are fit-for-all. Individuality in non-human animals brings also hidden implications for humanities and philosophy, as changes in approaches to animals may follow the growing understanding of how such individualities arise within the animal kingdom.

Summary

By no means this is a comprehensive review of all the research done on invertebrate behavioural individualities. It is rather a glimpse into the literature to sketch the picture of the state of the art with a zooming-in-time perspective on how invertebrate personalities emerge. As a "bycatch" of the review of the interindividual differences in invertebrate behaviour and on how they are moulded in individual experiences, it is advocated for the biologically ubiquitous phenomenon of invertebrate personalities to be accepted without surprise or resentment, as still it is not. It is here just reminded, each animal has its unique history, and hence, thus shaped its unique phenotype.

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