Metamorphosis and animal personality: a neglected opportunity

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Developmental perspectives represent an underutilized area of animal personality research, in spite of their obvious importance in biology. Animals that undergo metamorphosis are particularly neglected and represent a unique *in situ* experimental opportunity to study how personality differences are associated with physiological, morphological, or ecological traits over development.

The study of animal personality traits and their underlying mechanistic bases is a subject of great current interest in the behavioural sciences [1]. This interest is driven by conceptual advances relating personality traits to underlying ecological and evolutionary processes and empirical studies on a wide range of taxa. Yet in many respects, important gaps remain in our understanding of how and why differences in personality arise, their adaptive significance, and the consistency of traits across ontogeny.

Developmental perspectives, although acknowledged [2–4], remain underappreciated and underutilized by animal personality researchers, in spite of their obvious importance in biology. Species that have complex life cycles or undergo abrupt ontogenetic niche shifts or morphological transformations (i.e., metamorphosis) are particularly neglected and represent an important research opportunity.

By definition, metamorphosis is a complex phenomenon, incorporating a series of abrupt changes in an individual's morphology, physiology, and behaviour during postembryonic development [5]. Frequently, these developmental processes are associated with discrete shifts in habitat or ecological niche (e.g., aquatic to terrestrial or aerial environments) and thus influence a range of important behaviours including predator avoidance, foraging, mating, and dispersal. Furthermore, many studies have shown that individuals are able to alter the timing and duration of developmental periods (i.e., larval, adult) based on ambient stimuli such as food availability or risk of predation. As such, there is great potential to study the adaptive nature of personality traits in light of potential tradeoffs between present mortality risk and future growth and reproductive investment. Similarly, such phenomena can provide a forum for characterizing which personality traits are correlated, for what duration or developmental period, and which, if any, persist across metamorphosis. Yet, it is remarkable that given this research potential, and the fact that more than 80% of all animal species are thought to have such complex multi-stage life cycles [5,6] (Figure 1), almost no research has been conducted on the consistency of personality across metamorphosis.

The absence of experimental research can likely be attributed to two key factors. Firstly, the relatively small number of theoretical and experimental studies by which to guide predictions on the consistency of behaviour across metamorphosis and secondly, by the logistical and experimental challenges associated with tracking individual differences in behaviour across ontogenetic niche shifts. Since many species that undergo metamorphosis inhabit dramatically different environments between pre- and post-metamorphic stages of development, one might predict that selection should act to uncouple behavioural syndromes (personality) and life-history characteristics across ontogeny [4]. Alternatively, some personality traits might have underlying mechanistic bases that are difficult to uncouple even across metamorphosis. For example, traits that are closely associated with underlying physiological state variables (i.e., metabolism) might remain robust to developmental changes because of consistency in energetic demands in both larval and adult stages of development.

Experiences in early development (e.g., rapid changes in environmental conditions) might also alter the trajectories of ontogenetic development and consequently, generate predictable patterns of consistency in behaviour irrespective of changes in morphology, physiology, and ecological niche. For example, individuals might become predisposed to adopt certain behavioural types because adverse conditions (e.g., pond drying out) early in ontogeny might result in changes to developmental trajectories (e.g., early metamorphosis). Such changes can have important consequences for organisms (e.g., decreased body size at maturation) that might limit or restrict future reproductive success when affecting fitness related traits (e.g., fecundity) [7]. That said, if behavioural types are generated primarily by random differences in experience between individuals, one might not expect any predictable associations between pre- and post-metamorphic behaviour as metamorphosis might in effect, reset the stochastic processes that result in phenotypic determination.

Studying behavioural consistency across metamorphosis also poses a unique set of experimental challenges. Firstly, if animals inhabit considerably different habitats in pre- and post-metamorphic environments, it might be asked which behaviours can be tested in a meaningful matter in both developmental stages? One way to deal with this challenge is to study species that inhabit similar

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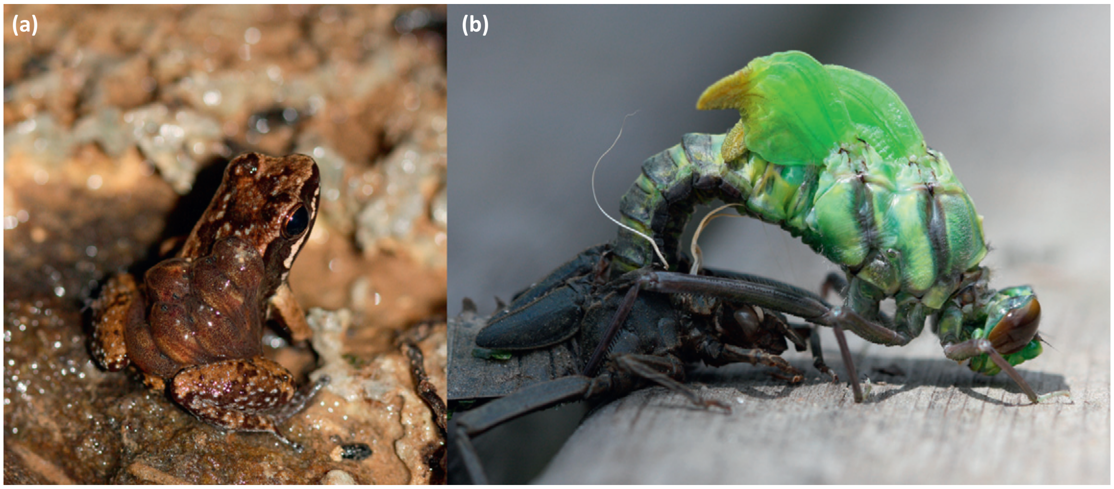

Figure 1. More than 80% of all animal species undergo metamorphosis or possess complex life cycles incorporating ontogentic niche shifts, including both vertebrate [e.g., *Mannophryne trinitatis* **(a)**, a terrestrial adult male transporting aquatic larvae to water] and invertebrate [e.g., *Aeshna sp*. **(b)**, aquatic larval stage metamophosing into aerial adult form] species.

environments between developmental stages (terrestrial–terrestrial versus aquatic–aerial habitats). Alternatively, another method for dealing with this challenge is to choose behavioural tests that reflect similar individual properties irrespective of ecological niche. For example, measures of risking-taking (boldness) or activity might have a higher likelihood of remaining consistent across metamorphosis because these characteristics might be tightly associated with underlying metabolic properties that are robust to changes during ontogeny.

Marine invertebrates and holometabolous insects represent the bulk of taxa that undergo metamorphosis. Easy rearing, short generation times, and breadth of taxonomic diversity make insects ideal for studying developmental tradeoffs and trait transitions across ontogenetic niche shifts. Indeed, what little is known about personality across metamorphosis is largely restricted to two examples from the insect literature [8,9]. One study investigated the relation between different predator treatments (familiar versus unfamiliar predator cues) and physiological states (food deprived versus satiated) on personality in the damselfly (*Lestes congener*) and found that individual differences in activity were consistent across metamorphosis [8]. Another study on field crickets (*Gryllus integer*) found that females that were tested for their latency to emerge from refuge (boldness) once as juveniles and once as adults were consistent across metamorphosis; although this was not the case for males [9].

Vertebrate examples are almost entirely lacking when it comes to personality and metamorphosis. Amphibians, unique among tetrapods in that they undergo metamorphosis, represent a rarely studied, yet potentially valuable taxonomic group in the personality debate. Anurans in particular exhibit some of the most extreme ecological transitions during ontogeny, with herbivorous aquatic larval stages and carnivorous terrestrial (or semi-aquatic) adult life history stages. Larval and adult stages also tend to inhabit different habitats, possess different developmental goals (growth versus reproduction and dispersal), and are subject to different selection pressures. Anurans therefore provide a unique and valuable opportunity to study behavioural traits across ontogeny and for comparison with other more commonly studied vertebrate groups (i.e., fishes, birds, mammals, reptiles). We recently tested whether individual-level differences in behaviour (activity, exploration, boldness) were consistent within given life history stages (i.e., larval, frog) as well as across metamorphosis in the lake frog (*Rana ridibunda*). We found that most behaviours were highly consistent within life history stages and at least some traits were consistent across metamorphosis (e.g., activity, exploration) [10]. Interestingly, our study and those previously mentioned invertebrate studies all find consistency across metamorphosis in some measure of activity in conjunction with exploration and/or risk-taking (boldness) behaviour. As such, this trend highlights an important area for future studies.

Characterizing individual-level differences in personality traits across metamorphosis can revolutionize how we study important ecological traits. Understanding how and why certain characteristics are consistent across metamorphosis in spite of profound changes in hormones, morphology, and environmental selection pressures represent critical gaps in our knowledge base. The use of developmental perspectives in studying animals across ontogeny is paramount if a better more holistic understanding of individual-level differences in behaviour is to be achieved.

Personality traits have been argued to be flexible and adaptive as well as fixed and maladaptive, but a general consensus cannot be reached as behavioural properties vary by study, species, and focal trait [1,4]. Studies of metamorphosis can be of significant value in this regard, providing an explanatory framework on how and why certain behaviours can appear maladaptive within a given life history stage by tracking behavioural changes across different stages of development. Species that undergo ontogenetic niche shifts provide a unique type of *in situ* experimental opportunity to study how personality differences might couple or uncouple with physiological, morphological, or ecological traits over development. Since these studies focus on the same behaviours in the same animals but at different life history stages and selection regimes; what we propose is a unique and valuable approach that is worth further thought and research attention by behavioural biologists.

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