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Evolution of behavioural consistency: environmental effects, fitness and genetics

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Background

Behaviour is one of the most variable phenotypic traits (West-Eberhard 2003), and still, consistent between-individual behavioural differences over time and ecological contexts are common in the animal kingdom (Smith and Blumstein 2008; Bell et al. 2009; Garamszegi et al. 2012). Further, such consistency is often genetically determined (Van Oers *et al*. 2005; Dochterman & Dingemanse 2013). The two main levels of behavioural consistency can be seen as (i) consistency within a single behaviour (called animal personality and tested with repeatability) and (ii) consistency seen across two or more functionally different behaviours (called behavioural syndrome and tested with between-individual correlation) (for reviews, see e.g.: Gosling 2001; Dall et al. 2004; Sih et al. 2004a,b). Behavioural consistency seems intuitively maladaptive, because it can severely constrain behavioural plasticity, i.e. the ability of an individual to change its behaviour upon environmental change (Wolf & Weissing 2010; Dingemanse & Wolf 2013). An animal's 'personality' is typically represented by its behavioural type, which is simply the average behaviour it expresses in a given or across a range of environments and can be estimated with various statistical approaches from means through intercepts to Best Linear Unbiased Predictors (BLUPs).

However, even though behavioural repeatability (which is used as the statistic to test for animal personality) is significantly higher than zero in a number of vertebrate and invertebrate taxa, its average value is rather low (0.37, Bell et al. 2009), leaving space for considerable within-individual variation. Therefore, behavioural consistency and behavioural plasticity can coexist, meaning that individuals can shift their behaviour following the environmental change, while their behavioural position relative to each other remains consistent (e.g. Dingemanse et al. 2010, Dingemanse and Wolf 2013; Mathot and Dingemanse 2015). Further, biological validity and importance of within-individual behavioural variation unrelated to environmental change, or with other words, the predictability of an individual's behaviour in a certain environment (behavioural predictability) was recognized lately (Stamps et al. 2012; Biro & Adriaenssens 2013; Briffa et al. 2013). Hence, there are three potentially independent components of individual behaviour: behavioural type, behavioural plasticity and behavioural predictability. However, despite a large number of theoretical studies (i.e. "data-free papers", DiRienzo & Montiglio 2015), we still lack an understanding how behavioural consistency develops and evolves and how consistent it is along different time periods. The main goal of the project was to gather information on the contribution of genetics, environment and individual state on the development and maintenance of behavioural consistency, using several model species and combining natural observations with laboratory experiments.

Conceptual work, meta-analyses

Right at the time of submitting the proposal, we published two papers. First, we proposed a method and philosophy to focus on individual deviations from the individual position predicted by a behavioural syndrome and suggested that this deviation can be an individual trait itself, potentially being under selection (Herczeg & Garamszegi 2012). Certain mathematical aspects of this proposal was criticised (the importance of this aspect seems to be less than thought at that time, Brommer & Class 2017), allowing us to prepare and publish a detailed response (during the project’s timeframe) based on simulations. We showed the challenge ‘personality” research faces when aiming for models that can separate between-individual correlations from within-individual correlations for detecting true behavioural syndromes (Garamszegi & Herczeg 2012).

Second, we started to prepare a large database about reported phenotypic behavioural correlations (indicative of behavioural syndromes, see a current study on this question: Brommer & Class 2017) and published the first result from a meta-analysis at the time of submitting the proposal, showing that behavioural correlations are rather common across vertebrates, however, the general correlation is weak (Garamszegi et al. 2012). Using the same database, we published a second metanalysis (during the project’s timeframe) showing that the strength of correlations varies among different behaviour pairs (Garamszegi et al. 2013). Partial correlation analyses also suggested that clustering different behavioural traits into the “Big Five” framework (activity, exploration, risk-taking, aggression, sociability, see e.g. Reale et al. 2007) might be misleading (Garamszegi et al. 2013). Building on this pattern, we have extended the database and based on a new analysis, we are currently preparing a manuscript questioning the use of the big behavioural domains in general (Markó et al. *in prep*.).

Environment- and state dependence of behavioural consistency

Developmental effects

Adaptive behavioural variation might emerge not only *via* genetic adaptations, but also *via* long-lasting direct environmental induction, i.e. phenotypic plasticity (the ability of a single genotype to produce different phenotypes induced by environmental variation, West-Eberhard 2003). There is evidence that (i) behavioural syndromes can be induced in predator-naive individuals originally lacking the syndrome by exposing them to predation risk and (ii) environmental complexity in general is a key factor in the formation of behavioural consistency (Bell & Sih 2007; Sweeney et al. 2013; Bengston et al. 2014; Härkönen et al. 2014; Johnson et al. 2015). However, studies investigating the role of the environment in the development of behavioural consistency within and across behaviours (animal personality and behavioural syndrome, respectively) in manipulative experiments were scarce at best.

We ran two laboratory-based manipulative common garden experiments with agile frog (*Rana dalmatina*) tadpoles to test the role of ontogenetic environment in the emergence of behavioural consistency and the Pace-of-Life Syndrome (POLS). POLS is a new framework integrating behaviour, life-history and physiology along a fast – slow lifestyle continuum (Realé et al. 2010). According to the POLS hypothesis, behavioural types may couple with life history characteristics, as certain combinations of life history and behaviour can be more adaptive in particular situations than others, but various combinations may eventually yield equal expected life-time fitness in a heterogeneous environment (Biro et al. 2006; Realé et al. 2010; Wolf and Weissing 2010).

In the first experiment (Urszán et al. 2015a), we found that predator- and conspecific-naïve *R. dalmatina* tadpoles have personalities but could not support the presence of behavioural syndromes unequivocally. A positive correlation between activity and the pace of development supported the POLS hypothesis. We have shown that even minor disturbance related to standard behavioural assays have considerable effects on later behaviour, potentially even uncoupling the POLS.

In the second experiment (Urszán et al. 2015b), we tested the effects of sociality and perceived predation risk during ontogeny on the strength of behavioural consistency in *R. dalmatina* tadpoles in a factorial common garden experiment. Tadpoles reared alone and without predatory cues showed zero repeatability within (i.e. lack of personality) and zero correlation between (i.e. lack of syndrome) activity and risk-taking. On the other hand, cues from predators alone induced both activity and risk-taking personalities, while cues from predators and conspecifics together resulted in an activity – risk-taking behavioural syndrome. It is worth noting that in the previous experiment, on the same population of the same species we found that 'naïve' tadpoles had moderate but significant levels of consistency in activity and exploration (Urszán et al. 2015a). However, that experiment was ran in another laboratory, individuals were housed in larger containers with a high contrast grid applied on their bottoms, compared to the smaller and plain containers of this study. It seems that even overly simple environmental variation has the potential to induce at least some forms of behavioural consistency.

In the third experiment (Urszán et al. submitted), we tested whether experience with predation during development affected predator-induced behavioural plasticity in *R. dalmatina* tadpoles. We found that (i) between-individual variation in predator-induced behavioural plasticity was present only in the group that developed in the presence of olfactory stimuli from predators and (ii) previous experience with predatory stimuli resulted in lower plastic response at the group-level. The latter pattern resulted from increased between-individual variation and not from universally lower individual responses.

Taken together, we have shown that ecologically relevant stimuli during development are important for the expression of behavioural consistency. We also draw attention in the fact that even the smallest, intuitively unimportant environmental effects stemming from standard laboratory manipulations have the potential to induce or inhibit behavioural consistency.

Environmental effects on adults

Even though we have demonstrated how the environment shapes behavioural consistency during ontogeny (Urszán et al. 2015a,b, submitted), yet another question regarding environment-dependence is whether short term environmental changes could affect behavioural consistency during adulthood (Sih et al. 2015). Here, we used adult male lacertid lizards (*Iberolacerta cyreni*, *Lacerta viridis*) during the short and synchronised reproductive season to test whether environmental shifts could decouple behavioural consistency.

First (Horváth et al. 2017), we manipulated available energy (low *vs*. high food) and the amount of vitamin D_3 (supplemented *vs*. placebo) in the food in reproductive male *I. cyreni*. Femoral glands of *I. cyreni* males, among many other compounds, secrete provitamin D_3 (cholesta–5,7–dien–3–ol), which is the precursor of vitamin D_3, a chemical essential for calcium metabolism and a potent immune system (Laing and Fraser, 1999; Griffin et al. 2003;

Hayes et al. 2003). Females prefer males with high levels of provitamin D_3 in their femoral secretion, making this pheromone an honest signal (Martín and López 2006, 2008, 2012), and thus a male lizard's vitamin D_3 level is a informative state-variable within the given reproductive season. Animal personality in activity was present in all treatments, however, it was present only in the high food × vitamin D_3 supplementation treatment in shelter use and was present in all but the low food × placebo treatment in risk-taking. Therefore, our ecologically relevant short-term treatments affected the level of behavioural of adult *I. cyreni* males during the reproductive season.

Second (Horváth et al submitted), we manipulated available energy (low *vs*. high food) and time available for efficient physiological performance (short *vs*. long basking time) in reproductive adult male *L. viridis*. We have shown earlier that similar treatments could affect the development of the ultraviolet-blue nuptial colour patch of males (Bajer et al. 2012), a signal that is both under intra- and intersexual selection (Bajer et al. 2010, 2011). Again, we found that experimentally induced short-term environmental variation affected the expression of behavioural consistency in adult animals both in presence/absence patterns of animal personality and behavioural syndromes, and in the variation of individual behavioural predictability.

By showing that differences in environmental conditions can not only shift the mean behaviour in animal groups during a short timeframe, but it might affect the level of between-individual variation too, we demonstrated the lability of behavioural consistency. This is not only relevant from a methodological aspect for researchers studying animal personality in the wild or under laboratory settings, but also demonstrates how a certain behavioural trait can be or be not under selection (note that selection operates on between-individual phenotypic variation) depending on some simple environmental factors.

State-dependence in the wild

One step towards understanding the mechanisms behind behavioural variation in the wild is to link behaviour to individual quality. However, linking behaviour to individual quality is not straightforward in most cases. One reason for this is the controversy around the definition and measurement of 'individual quality' (Wilson & Nussey 2010). Since individual quality can only be approached through fitness, a viable and relatively easy solution to this problem could be focussing on individual traits that are linked to fitness (Wilson & Nussey 2010). These traits can also be seen as state-variables. Classically, internal state reflects various inherently stable (e.g. size, sex differences) and labile features (e.g. energy reserves, health state) of an individual affecting the costs and benefits of its behavioural actions. A growing body of theory-based studies suggests that links between behaviour and state variables can be responsible for the observed behavioural consistency (Dingemanse and Wolf 2010; Wolf and Weissing 2010). During the project, we ran several studies where we tried to find links between fitness-related state traits and different components of behavioural consistency.

In the collared flycatcher (*Ficedula albicollis*), we could not detect any links between malaria infection and risk-taking or health state and risk-taking, however, we found a negative correlation between the allele numbers of the MHC complex and risk-taking (Garamszegi et al. 2015a). We also found a positive correlation between escape ability and risk-taking in young males (Jablonszky et al. 2017).

We found that large or ectoparasite-free male *L. viridis* were more explorative than small or ectoparasitised males (Bajer et al. 2015). *I. cyreni* males highly parasitized with blood parasites took more risk than their less parasitized conspecifics (Horváth et al. 2016). The escape strategy of *Lacerta schreiberi* depended entirely on environmental settings (Kopena et al. 2015).

In a laboratory experiment with wild-caught pillbugs (*Armadillidium vulgare*), we found that body size, sex and *Wolbachia* infection affected risk-taking and its plasticity (Horváth et al. submitted). We ran this experiment primarily to look for a new model species where mass phenotyping is possible. Since we could get 30 repeated behavioural measurements from pillbugs easily, this species is a promising model for future personality research.

Genetic background

While all common garden studies on *R. temporaria* tadpoles (see in "***Developmental effects***" above) was available to draw evolutionary conclusions, mainly about how environmental triggers are needed for the expression of genetically based between-individual variation in behaviour or behavioural plasticity, we also ran some targeted genetic studies.

It has been shown that the dopamine receptor D4 (*DRD4*) gene affects boldness in some birds and mammals (e.g. Fidler et al. 2004; Momozawa et al. 2005). We also found that *DRD4* polymorphisms affected risk-taking and novelty-avoidance of collared flycatchers (Garamszegi et al. 2014).

We also applied Quantitative Trait Locus (QTL) mapping to identify potential genomic regions associated with the reported behavioural population variation in ninespined stickleback (*Pungitius pungitius*; Herczeg et al. 2009, 2013). Our QTL mapping revealed two genome-wild candidate locations and six chromosome-wild candidate locations for genes affecting boldness (Laine et al. 2014). These patterns can serve as springboards for finer-scale mapping to identify the genes in the future.

We also successfully ran a large-scale quantitative genetic experiment with common toad (*Bufo bufo*) tadpoles using a modified North Carolina II breeding scheme, with half of the tadpoles reared under perceived predation risk, while the other half reared predation-naïve. Unfortunately, the time needed for analysing the behavioural videos was underestimated. We also decided to include brain traits in the analyses and for this, brains had to be dissected and measured, which also took time. At the moment, the behavioural database is ready and soon the brain database will be ready too. Estimating the genetic background and linkage (heritability, genetic correlations) of the different behavioural and brain traits, together with general antipredator morphology in individuals developing in different environments will give extremely valuable information about the predation-risk-linked evolvability of behaviour and brain. In our opinion, this subproject is the most promising/valuable one that we made during the funding period.

Miscellaneous

During the funding period, we purposefully aimed to broaden the scope of the project as much as possible and incorporate any new ideas that would help us in reaching our research goals.

Using an 8-year database of direct field observation of *F. albicollis*, we could assess the strength and variation of animal personality and behavioural syndromes in a wild population. We found that the correlation between aggression and novelty avoidance could vary in sign between years, the variation being explained by population demographic variables like density or age composition (Garamszegi et al. 2015b). Strength of animal personality also showed considerable between-year variation. The results draw attention to the challenge of finding general patterns in the wild without applying a longitudinal approach.

We also applied the hierarchical statistical approach used in personality research on birdsong, based on a 17 year *F. albicollis* song database recorded in the wild (Zsebők et al. in press). We were interested to see that at which hierarchical level (song, song sequence, individual) and which timeframe (within day, within year, between years) can the song convey reliable information about the individual. Only repertoire size was repeatable within and between years, suggesting that this trait can signal individual attributes shaped by genetic background, permanent environmental effects or long-term experience. Song traits (rate, length, bandwidth, etc.) were repeatable only within day, suggesting that these traits can signal labile states of the signaller or quality of its immediate environment.

Finally, we published results regarding predation-induced plasticity in the aggression of threespined sticklebacks (*Gasterosteus aculeatus*), dissecting the effects of past experience with predation and immediate predation threat in a factorial design (Herczeg et al. 2016). We found complex interactions, experience with predation had opposite effects on hesitation before attack and attack intensity under perceived predation risk.

Summary and future prospects

Overall, the funded project was a success. We could reach all planned goals, further, we could incorporate several studies that were not planned at the time of submitting the application. We published 14 papers in high ranked journals like *Oecologia*, *Behavioural Ecology and Sociobiology, Behavioural Ecology*. We have another paper in press, two under ‘major revision’, two submitted and several more in preparation. We also published another nine papers that were only loosely connected to the proposed project, but where the funding still helped, including journals like *Proceedings of the Royal Society B*, *Molecular Ecology* or *Journal of Evolutionary Biology*. We also presented our results in numerous national and international conferences.

Besides publishing the scientific results, the educational string of the project was also strong. Tamás János Urszán had already defended his PhD thesis, and Gergely Horváth will also defend this year. Stephanie Orf works as a PhD student on the *B. bufo* quantitative genetic experiment and expected to defend in two years.

During the project, we collaborated with Profs José Martín and Pilar López Prof. José Martín (National Museum of Natural Sciences, CSIC, Spain), Prof. László Garamszegi (Doñana Biological Station, CSIC, Spain), Prof. Juha Merilä (Ecological Genetics Research Unit, University of Helsinki, Finland) and Prof Niclas Kolm (Department of Ethology, Stockholm University, Sweden). In Hungary, we collaborated with Prof. Attila Hettyey (Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences (MTA ATK NÖVI), Budapest, Hungary). We also started a promising collaboration with Prof. Gábor M. Kovács (Department of Plant Anatomy, Eötvös Loránd University, Hungary).

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