



INVITED PERSPECTIVES AND REVIEWS

Unravelling the Philosophies Underlying 'Animal Personality' Studies: A Brief Re-Appraisal of the Field

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Abstract

The last decade has seen lots of studies on 'animal personality' (i.e. the study of consistent between-individual behavioural differences). As timely and promising as this field is, its development has come with a diversity of research questions. As an unfortunate consequence, it now suffers from substantial confusion about what 'animal personality' is, and how relevant related research frameworks are. Here, we stress the current inconsistencies and sources of confusion pertaining to the field, and their consequences on terminology used and miscommunication between researchers. In an attempt to unravel and clarify the concepts underlying the field, we identify two distinct, but complementary, theory-driven conceptual frameworks: the intra-individual variability (IIV) approach and the life-history (LH) approach, which we believe encompass the vast majority of existing 'personality studies'. Finally, we argue in favour of theory-driven studies of consistent behavioural differences and state that the integrative *statistical* properties of random regression models should not override the merit of alternative *conceptual* frameworks. We then provide brief guidelines and warnings for a parsimonious and sound use of terminology.

Fundamentally, behavioural ecology aims at determining how and why the environment in which a species lives shapes its behaviour. Traditionally, behavioural ecology seldom emphasized or anticipated evolutionarily meaningful continuous behavioural variation among individuals within populations or species (adaptive polymorphism and frequency-dependent evolutionary equilibria aside; see Fawcett et al. 2013 and Kight et al. 2013). Yet, evidence for consistent individual differences within populations has accumulated rapidly over the last 20 years (Wilson 1998; Careau & Garland 2012; Kight et al. 2013). This has resulted in the emergence of the so-called 'animal personality' field, which focuses on explaining behavioural variation at a scale not previously appreciated (Wilson 1998). 'Animal personality' studies aim to determine how and why consistent individual differences in behaviour evolve within

populations of a given species (Wolf & Weissing 2010; Kight et al. 2013; Monceau in press), and what their ecological relevance is (Wolf & Weissing 2012).

The field of 'animal personality' has received considerable attention. This burgeoning of interest inevitably went with a substantial diversity of research questions and inconsistent use of terminology, up to the point that the conceptual relevance and rigour of the whole field starts to be informally questioned by some. We believe that the lack of clarity between the different 'animal personality' research agendas, and in particular, the different evolutionarily adaptive approaches to 'animal personality' variation, is likely to raise confusion in several ways: about the terminology used, the relevance of the investigation methods employed, and the conceptual relevance of the whole field. The purpose of the present paper is first to

emphasize such potential pitfalls. So as to overcome these, we then unravel and draw up relevant conceptual frameworks for the study of consistent between-individual behavioural variation through identifying their very philosophies, and provide brief guidelines to the study of within-population variation.

Are 'Personality Researchers' Schizophrenic?

The 'animal personality' field has seen flourishing a rich, but potentially confusing, terminology, such as temperament, behavioural types, behavioural profiles, personality traits and so on. We do not intend to revisit the meaning of all the different terms that have been used since the first 'personality studies'. We acknowledge that, in principle, it should be acceptable to use any given term insofar as it has previously been properly defined by its users. However, we believe that the diverse terminology used so far brought very little from a conceptual viewpoint, and that substantial consistency and clarity in the meaning of terms used across studies is lacking although urgently needed (Careau & Garland 2012). In particular, the terms 'personality' or 'personality traits' are commonly used to define both the nature of an individual trait (often 'boldness-like behaviours', i.e. behaviours tightly linked to resource acquisition and mortality risks and that are influential in many contexts – boldness, exploration, aggressiveness, etc.) and a population-level property: when individuals of a given population differ consistently with respect to a specific behavioural trait (e.g. activity, brood provisioning, mating rate, boldness, scrounging, etc.). It becomes obvious that two such different definitions of the same terms can only lead to confusion. A single term cannot reasonably be used to define biological phenomena that differ in their conceptual and statistical properties.

As exposed above, on the one hand, the term personality refers to whatever behaviour that exhibits some level of consistency within a population (broad-sense 'personality' *sensu* Careau & Garland 2012), whereas on the other, it refers to a type of behaviour (i.e. 'boldness-like behaviours'). We think that this generalized use of 'personality' bears several drawbacks. Proponents of the first definition would not use the term 'personality' to designate instances where 'boldness-like behaviours' are found to show non-significant repeatabilities within populations. Conversely, proponents of the second definition would not use the term 'personality' to refer to behaviours that are not commonly thought of as 'boldness-like behaviours' (Betini & Norris 2012), however consis-

tent they are found to be. This divergence may result in an awkward situation where researchers of the same field would attribute a totally different meaning to the term 'personality'. This can only be detrimental to a sound communication between 'personality researchers' and a healthy development of the field. Indeed, it turns out that 'boldness-like behaviours' have been found to be unrepeatable in some studies (van Dongen et al. 2010; Kekäläinen et al. 2014). Also, their relationships with life history has sometimes been assessed at the species or breed level (Møller et al. 2008, 2013; Careau et al. 2009, 2010; Møller & Garamszegi 2012; Cooper et al. 2014), clearly challenging the strict assumptions of the two aforementioned definitions. Making sense of these studies is likely to give headaches to 'personality researchers' lost among the profusion of terms and contradictory definitions employed so far. The reason why 'personality' has been associated with both behavioural consistency and so-called 'boldness-like behavioural traits' may be that the first papers highlighting consistent individual variation within populations focused on these type of behaviours (see Careau & Garland 2012 and Koski 2014 for short reviews). However, we believe that the artificial, implicit and automatic association between 'boldness-like behaviours' and behavioural consistency is likely to bring about misunderstandings between researchers and thus must be avoided. An unfortunate consequence of proposing alternative definitions for a concept thought of as being unique is potential miscommunication between researchers within the field. Depending on which definition they embrace, 'personality researchers' may potentially misjudge and fail to see the proper merit of studies that follow either of the two definitions. We see it as highly detrimental to the healthy development of the study of consistent behavioural differences within the community of behavioural ecologists.

The above-mentioned logical non-sense between alternative definitions of 'personality' and its consequences in terms of misunderstandings between researchers within the field makes obvious why clarifications are urgently needed. In this paper, we argue that a way to solve incoherencies and prevent miscommunication between researchers is to unravel and make sense of the different definitions and approaches undertaken so far from a *conceptual* viewpoint. This goes through identifying coherent and theoretically driven conceptual frameworks to which these approaches may belong (Dall & Griffith 2014), while stressing their differences, complementarities and proper merits.

Identifying and Detailing Two Conceptual Frameworks

The development of the 'animal personality' field must, as any major behavioural ecology topic, be theoretically driven (Dall & Griffith 2014), that is generating predictions that rely on strong conceptual models and experimental tests rather than on 'data-fishing'. We see it as crucial for the development of the field. This is all the more possible as more formal and verbal models become readily available (Dingemanse & Wolf 2010; Réale et al. 2010; Kight et al. 2013 and references therein). Here, we highlight two conceptual and explanatory frameworks that we believe encompass the majority of existing 'animal personality' studies, and that can provide a solid theoretical foundation for future studies on consistent between-individual differences: the intra-individual variability (IIV) framework and the life-history (LH) framework. Interestingly, these frameworks somewhat match the alternative definitions mentioned in the previous section. They are thus likely to cover the majority of research questions that have been addressed so far and be meaningful to all 'personality researchers'.

The IIV framework refers to identifying the sources of direct and indirect selection on individual differences in behavioural consistency, or flexibility (Stamps et al. 2012). In other words, it aims at identifying when and why it is optimal for animals to behave in a consistent way rather than to be flexible, and why the optimal solution may differ between individuals (Kight et al. 2013). Determining how and why between-individual variation in behavioural consistency emerges within populations is crucial towards understanding how consistent between-individual behavioural variation evolves. These research questions are investigated using mathematical models (McNamara et al. 2009; Dubois et al. 2010; Wolf et al. 2011; Wolf & McNamara 2012), which to a large extent use a game-theory approach, and experimental inquiries (Briffa 2013; Laskowski & Bell 2013; David et al. 2014; Highcock & Carter 2014), and mostly rely on an adaptationist perspective (i.e. consider phenotypes as the optimal outcome of natural selection). For instance, experimental evidence supports the hypothesis that behavioural consistency or flexibility is non-neutral with regard to natural selection (Jennings et al. 2013) and is expected to vary within populations (David et al. 2012, 2014; Laskowski & Bell 2013; Highcock & Carter 2014). Also, several models predict that populations should be composed of a stable mixture of consistent and flexible individuals when the pay-offs associated with the use of these

two strategies are frequency-dependent (Wolf et al. 2008; Dubois et al. 2010, 2012). Being consistent can pay off because the flexible strategy incurs diverse costs associated with, among others, information sampling (Morand-Ferron et al. 2011). The varying pay-offs obtained by consistent and flexible strategies in formal models do not genuinely imply that these strategies evolve through frequency-dependent selection *stricto sensu* (but see Wolf & McNamara 2012; Stamps et al. 2013). Rather, individuals may possess evolved decision rules as to when and when not to behave in a consistent way, that follow the predictions of game-theoretic models (see Fawcett et al. 2013).

The LH framework refers to studies investigating the between-individual relationships between variation in life-history strategies (Biro & Stamps 2008) and variation in so-called 'boldness-like behavioural traits' (i.e. behaviours tightly related to resource acquisition and mortality risks and that are influential in many contexts) (Dall & Griffith 2014), such as aggressiveness, neophobia, exploration, risk-taking, activity (also called narrow-sense 'personality traits' *sensu* Careau & Garland 2012). The rationale behind this approach is that individuals of the same population vary in their life-history strategies and that 'boldness-like behaviours' represent the co-adapted behavioural dimension of a wider adaptive 'pace-of-life' including physiology and life-history traits (Réale et al. 2010). This approach has originally been derived from the study of 'pace-of-life' syndromes at the inter-specific level (Ricklefs & Wikelski 2002), where, for instance, individuals of long-lived bird species have lower metabolic rates than short-lived ones (Wiersma et al. 2007). The LH framework involves theoretical and experimental considerations on, among others, the relationships between behavioural traits and life-history strategies (Stamps 2007; Wolf et al. 2007a; Biro & Stamps 2008), fitness-maximizing traits (Wilson et al. 2010; Adriaenssens & Johnsson 2011; Auclair et al. 2013; David et al. 2015) or metabolism (Careau et al. 2008, 2011; Biro & Stamps 2010). The LH framework offers very simple predictions from which to draw experimental tests. Individuals showing more productive and fast life-history trajectories are expected to display 'boldness-like behavioural traits' allowing them to sustain such a fast 'pace-of-life' and high productivity. More explicitly, individuals that prioritize current over future reproduction (Wolf et al. 2007a) or that grow at higher rate than other conspecifics (Stamps 2007) are expected to access more energetic resources (Careau et al. 2008), be more dominant, less neophobic, risk-prone, more

exploratory and/or more active (Réale et al. 2010). Evidence for these links have been largely documented (Biro & Stamps 2008 and references therein; Betini & Norris 2012). However, it is noticeable that numerous studies also found unexpected opposite patterns (Smith & Blumstein 2010; Wilson et al. 2010; Timonin et al. 2011; Le Galliard et al. 2013; Bridger et al. 2015; Careau et al. 2015; David et al. 2015). For instance, more exploratory zebra finches (*Taeniopygia guttata*) have a lower feeding success than less exploratory ones in a scramble competition context (David et al. 2011), and shy brown trout (*Salmo trutta*) were found to grow faster in the wild than bold individuals (Adriaenssens & Johnsson 2011). These latter studies highlight the potential importance of the context or situation in which the links between life-history and 'boldness-like behavioural traits' are investigated (Dall & Griffith 2014; David et al. 2015). Also, it fosters the investigation of when and why behaviour/life-history associations are selected for and shaped by natural selection (Adriaenssens & Johnsson 2009). To sum up, the LH framework consists of explaining the evolution of variation in 'boldness-like behavioural traits' through their relationships with other phenotypic dimensions within an extended 'pace-of-life' syndrome hypothesis (Réale et al. 2010). The LH framework mostly relies on a selectionist perspective (i.e. considers the genetic architecture of phenotypes as both the means and outcome of natural selection).

On the Rationale and Goals of the IIV and LH Frameworks

The IIV and LH frameworks differ in several important respects (Table 1). First, the IIV framework seeks to

explain the emergence of between-individual differences in the consistency of *any* behaviour (Koski 2014), whereas the LH framework commonly focuses on 'boldness-like behaviours'. Let us illustrate this difference with studies from the literature: following the IIV framework, Dubois et al. (2012) investigated whether a sequential access to resources can promote individual differences in the consistency of producer and scrounger foraging tactic use (David et al. 2014). Wolf et al. (2008) examined the influence of state on the tendency to consistently play hawk or dove tactics during contests. These studies obviously focus on the consistency and flexibility of behavioural expression. Alternatively, following the LH framework, Nicolaus et al. (2012) experimentally demonstrated that reduced survival likelihood increases exploration tendencies in great tits (*Parus major*). In the same species, Mutzel et al. (2013) found that parental brood provisioning is linked to individual aggressiveness. Here, the focus is on individual average behaviour and between-individual relationships between life-history and behaviour. Second, and more importantly, the IIV and LH frameworks differ in their *rationale* and *goals* (Table 1). More specifically, understanding how and why individual consistency can emerge is the IIV framework's rationale, whereas the LH framework does not explicitly question consistency and rather focuses on individual average behaviour and on the covariation between life history and behaviour. Under the IIV framework, individual consistency is the variable to be explained whereas in the LH framework it is taken for granted, or at least rarely explicitly questioned (see Biro & Stamps 2008). Third, from a methodological viewpoint, IIV-based studies obviously imply the repeated assessment of an individual's behaviour, as individual behavioural expression is the

Table 1: Summary table of the main distinctions between the two identified frameworks

	Intra-individual variability (IIV) framework	Life-history (LH) framework
Theoretical foundations	Mostly rely on an adaptationist perspective and on game theory	Mostly rely on a selectionist perspective and on life-history theory
Variable to be explained	Individual behavioural variance	Individual behavioural average
Behaviours under scrutiny	Any	Mostly boldness-like behaviours (i.e. tightly linked to resource acquisition and mortality)
Framework's main goal	Explaining how and why individual behavioural consistency can emerge	Explaining the coevolution of behaviour, physiology and life-history
Examples	Intra-individual variance in foraging tactic use found related to a sequential access to resources (Dubois et al. 2012; David et al. 2014) Intra-individual behavioural variance increasing under predation threat (Briffa 2013)	Boldness found related to fecundity (Bridger et al. 2015) Parents with similar exploration behaviour providing more effort into brood provisioning (David et al. 2015)

Please note that the comparisons emphasized here are simplified for clarity and conciseness purposes. We argue that both frameworks are complementary and that any sort of combinations between their distinct features is conceivable.

variable under scrutiny. In the LH framework, repeated measures are not a prerequisite, although researchers are obviously encouraged not to limit themselves to a single measure per individual (Smith et al. 2011; Dall & Griffith 2014; Sih et al. 2015).

Possible Sources of Confusion that Justify the Two Frameworks

We believe that the IIV and LH frameworks are worth distinguishing because their philosophies, rationale, associated methods and goals, differ (Table 1). Yet, testing hypotheses requires identifying a unique response variable, which is what the definitions of 'personality' mentioned earlier fail at, and the potential causal agents, the whole generating clear predictions to be tested. The distinction between both frameworks thus appears critical to build a sound and coherent research agenda based on readily identifiable response variables. Between-individual differences in consistency is the focus of the IIV framework whereas in the LH framework it is on between-individual differences in average behavioural expression. Behavioural variance usually is the variable to be explained under the IIV framework, whereas it is behavioural average under the LH framework. The distinction between the two frameworks is justified with regard to these possible sources of confusion: first, individual variation in behavioural consistency may hamper the characterization of average behavioural expression aimed to be related to life-history variation in the LH framework. Indeed, more flexible individuals may, by definition, show a larger range of behavioural values in a given situation, which makes their behavioural profile trickier to assess reliably. The LH approach requires individuals to be characterized by their exact and reliable average behaviour, whereas the IIV approach genuinely investigates intra-individual variation. This can lead to an obvious conceptual and methodological conflict, should the underlying research questions be thought of as belonging to the same explanatory framework. Second, life-history/behaviour associations rarely provide any prediction or adaptive rationale about why individuals are consistent in their behaviour (but see Wolf et al. 2007a and Biro & Stamps 2008). The LH framework alone is not sufficient to make sense of all aspects of interindividual variation and behavioural stability. The same obviously holds for the IIV framework. Overall, we believe that the true *conceptual* contribution of both approaches cannot be appropriately appraised if they are thought of as belonging to the same explanatory framework. They indeed do not

attempt to explain the same variable nor do they involve the same underlying explanatory logic. Mixing both under a single label (i.e. 'personality') is likely to prevent 'personality researchers' from seeing their respective proper merit, generate miscommunication and misunderstanding between them, and generally add confusion to the whole field.

A Brief Warning

Our identification of the two conceptual frameworks for the study of consistent behavioural differences may misleadingly appear as if both were 1/mutually incompatible and 2/the only valid frameworks. We strongly argue against these claims. First, we see both frameworks as complementary given that IIV mainly focuses on within-individual variation while LH rather investigates between-individual variation. The study of consistent behavioural variation within populations precisely relies on these two frameworks and we believe that both are relevant if we are to provide a complete understanding of how and why within- and between-individual variations (co-) evolve within populations. Our plea is that the two frameworks do not rely on the same rationale and as a consequence their explanatory properties are worth distinguishing. This does not mean that, technically speaking, both cannot be investigated simultaneously. A few studies have provided theoretical evidence for mechanisms generating both within-individual stability and between-individual variation (Dall et al. 2004; McElreath et al. 2007; Wolf et al. 2007a,b; McNamara et al. 2009; Betini & Norris 2012; Kight et al. 2013), and promoted the simultaneous investigation of both within- and between-individual variation (Van de Pol & Wright 2009; Dingemanse et al. 2010). Also, univariate and multivariate random regression models are commonly used in the 'personality' field (Dingemanse et al. 2010; Dingemanse & Doctermann 2013; Boulton et al. 2014). These models can take both intra- and interindividual variation simultaneously into account (Cleasby et al. 2015). However, that does not make our distinction between the two frameworks less relevant. Because a single type of statistical models can handle both intra- and interindividual variation does not mean that the conceptual logic of the questions it answers to is unique. We do not see it as sufficient to quantify or model variation at different levels (e.g. between and within individuals) to provide assertions about how variation has evolved through natural selection. In brief, concepts cannot be reduced to technique. Second, we do not argue that the two approaches we propose are the

only valid frameworks within which to study consistent between-individual behavioural differences (Bergmüller & Taborsky 2010; Sih et al. 2015). Our purpose only is to focus on existing theoretically driven approaches that encompass the majority of existing 'animal personality' studies because we think that they are the best foundations for an evolutionary-based study of consistent between-individual behavioural differences.

Conclusion and Guidelines

To conclude, in the present paper, we have emphasized the current confusion pertaining to the field of 'animal personality', mainly based on terminological incoherencies. We stress that these may have unfortunate consequences on the communication between researchers and the further development of the field (Table 2). For instance, 'personality researchers' may inadvertently restrict themselves to a single approach depending on which definition of 'personality' they embrace. As a solution to this issue, we propose to identify two relevant theoretically driven conceptual frameworks for the evolutionary study of consistent behavioural differences within populations. These frameworks are thought of as overcoming terminological inconsistencies and make sense of existing studies. The IIV framework typically involves the repeated measurement of an individual's behaviour and attempts to explain between-individual variation in behavioural consistency (but does not directly address between-individual variation in average behavioural expression). The LH framework does not explicitly questions behavioural consistency but explores the co-adaptations between behavioural traits and life-histories within an extended 'pace-of-life' syndrome hypothesis. We have argued that both approaches differ in their rationale, their goals, their perspectives and their philosophies (summarized in Table 1), but remain complementary in explaining the evolution of consistent behavioural differences within populations.

As concluding guidelines (summarized in Table 2), we strongly encourage researchers to base their research hypotheses on existing theory-based predictions. This goes with adjusting the existing terminology to the question under investigation so as to avoid confusion, and clearly identifying the variable under investigation (intra-individual variation, i.e. behavioural variance, under the IIV approach, and individual behavioural profile, i.e. behavioural average, under the LH approach). From a terminological viewpoint, we encourage behavioural ecologists to explicitly refer to the population or individual property they investigate. Repeatability and stability are sufficient and useful to describe and investigate how individuals of the same population consistently differ in their behaviour (David et al. 2012). Also, we cannot see why so-called 'boldness-like behaviours' should be termed 'personality traits' imprecisely and not directly like the very behaviour under scrutiny (boldness, exploration, activity, aggressiveness and potentially lots more; see Koski 2014). By way of example, one does not use the general and vague term 'reproduction behaviour' to address all the reproductive activities in which an individual may be engaged (displaying, mating, lactating, provisioning and so on). The consistency of behavioural traits should not be taken for granted but rather considered as a property or a trait in itself that is shaped by natural selection (Jennings et al. 2013) and fluctuate at the population level depending on context (Laskowski & Bell 2013; David et al. 2014). There is no reason to expect that 'boldness-like behaviours' should always be consistent (van Dongen et al. 2010; Kekäläinen et al. 2014), and how consistency evolves is a question that falls within the IIV framework. Finally, we encourage 'personality researchers' to think outside of the statistical toolbox: because random regression models are great tools that integrate different levels of variation (Dingemanse et al. 2010; Dingemanse & Dochtermann 2013) does not mean that they are self-explanatory nor allow conceptual assertions. They

Table 2: Summary table of the main conclusions and guidelines

Summary of the main conclusions and guidelines

- Two distinct frameworks for 'personality studies' have been identified: the intra-individual variability (IIV) and the life-history (LH) framework
 - These frameworks show differences in their rationale and goals but remain complementary
 - 'Personality studies' should heavily rely on existing theory-based predictions
 - The variable under investigation (e.g. behavioural variance or behavioural average) should always be clearly identified
 - The terms 'repeatability' or 'stability', or the name of the exact behaviour under scrutiny should be used instead of the rather imprecise term 'personality'
 - Behavioural consistency is shaped by natural selection, and boldness-like behaviours should not always be expected to be consistent
 - Random regression models are useful tools but lack explanatory and conceptual power. Think outside models!
-

can answer different questions pertaining to different conceptual frameworks. We believe that greater rigorous reliance on theory should considerably reduce the confusion existing in the field, stimulate the testing of relevant predictions across multiple levels of variation, and then significantly improve our understanding of how and why consistent between-individual behavioural differences evolve.

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