

Discussion on 'Comparative Personality Research: Methodological Approaches' by Jana Uher

OPEN PEER COMMENTARY

The Behavioural Repertoire Approach in Comparative Personality Research: Inconsistencies Between Theory and Practice

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Abstract

The use of the behavioural repertoire approach in comparative personality research involves the compilation of an ethogram. However, what behaviours should be included in the ethogram and whether they should be grouped into categories is unclear. To ensure that the behaviours belong to the natural repertoire of the species, certain assumptions regarding their underlying mechanisms are necessary. The selection of behaviours from which personality traits can be derived should take into account the notion that individuals with different personalities may seek out different stimuli and actively shape their own environment. Copyright © 2008 John Wiley & Sons, Ltd.

The target paper provides a useful review of different approaches used in comparative personality research and a discussion of the pros and cons of each approach. The author also presents a new 'bottom-up' approach to comparative personality research: the behavioural repertoire approach. This approach is intuitively simple and practically straightforward. There seem to be some inconsistencies, however, between the way this approach is described and conceptually justified and the way it is used in empirical research.

According to Uher, 'the behavioural repertoire approach starts with a biological classification of the species' universal behaviours'. What the author means by that is unclear. The use of this approach in a previous study of personality in captive great apes (Uher, Asendorpf, & Call, 2008) suggests that the first step in this approach is the

compilation of an ethogram. An ethogram is simply a list of behaviours that are of interest in a particular observational study, and which will be used for data collection and analysis. The individual behaviours in the ethogram can sometimes be grouped into categories, mostly for practical purposes (e.g. because this way they are easier to remember and to code). For example, the primate behaviours 'fear grimace' and 'hindquarter presentation' can be grouped into a 'submissive behaviour' category because both behaviours have a submissive function. If the emphasis of the study were on motor rather than on social behaviour, however, the fear grimace could be categorised as a facial expression whereas the presentation could be categorised as a body posture. Figure 2 in the target paper illustrates 'behavioural domains and subdomains described in the behavioural repertoire of the great apes'. In the figure, some 'domains' appear to correspond to functional behavioural categories: for example 'feeding behaviour' and 'sexual behaviour'. Other domains are ill-defined behavioural categories such as 'breeding behaviour', and others yet—such as social organisation—refer to the characteristics of a species rather than to the behaviour of an individual. The 'subdomains' include ill-defined behavioural categories such as 'general feeding behaviour' or 'general breeding behaviour', specific behaviours such as solitary play or food processing, generic non-behaviour items such as 'early development' and conceptual constructs such as 'leadership'.

The criteria for assembling such a heterogeneous ethogram are unclear. If by 'biological classification of the species' universal behaviour' the author meant something other than compiling an ethogram, this should have been clearer in the target paper. Uher should also have explained what she meant by 'species' universal behaviour'. An ethogram can be a comprehensive list of behaviours described in published studies of a particular species, but what is on the list can vary greatly depending on the number of studies being conducted, the relative proportion of captive versus field studies, whether the individuals in these studies had a normal or abnormal rearing history, and other variables. For example, if the majority of published studies on chimpanzee behaviour were conducted with zoo animals who were hand-reared by human caretakers, a chimpanzee ethogram compiled on the basis of these studies would be unlikely to include many 'universal behaviours'.

At the core of the theoretical rationale for the behavioural repertoire approach seems to be the notion that, with this method, personality traits are derived from observable behaviours, without making any assumptions about the underlying genetic, neurobiological or ontogenetic mechanisms or about any morphological or functional relationships between traits. One could argue, however, that if this approach requires the use of 'species' universal behaviours', then certain assumptions need to be made about the underlying mechanisms. For example, behaviours that are the product of an aberrant ontogenetic history such as self-biting shown by monkeys separated from their mothers in infancy and reared in isolation certainly do not qualify as 'species' universal behaviours'. Therefore, assumptions about ontogenetic mechanisms are necessary to avoid inclusion of aberrant behaviours. Similarly, assumptions about neuroendocrine mechanisms are necessary to exclude behaviours that may result from brain damage. Finally, why are the behavioural domains and subdomains presented in Figure 2 grouped in relation to their morphological and functional interrelations if such interrelations are not taken into consideration in the behavioural repertoire approach?

The theoretical rationale for the behavioural repertoire approach includes the assumption that 'all trait-relevant behaviour emerges only in response to trait-relevant stimuli' and that 'traits comprise specific behavioural tendencies that are related to specific situational stimuli'. The notion that all behaviour emerges in response to stimuli is popular

among Skinnerian psychologists, but not necessarily among other behavioural scientists. Many nonsocial and social activities are initiated by animals in the absence of 'specific situational stimuli'; for example looking for food or for a sex partner, or engaging in aggressive behaviour to improve one's social status. In fact, what is intrinsic to the concept of personality is not only the notion that individuals with different personalities may respond differently to the same stimuli, but also that these individuals seek out different stimuli in the first place. In other words, individuals with different personalities do not only respond to the environment differently; they also actively shape their own environment in ways that best fit their characteristics (Bateson, 1988). Regardless of its theoretical rationale, the use of the behavioural repertoire approach does not seem to require that behaviour occurs in response to specific situational stimuli and that these stimuli be identified. This is positive because identifying the specific situational stimuli eliciting behavioural subdomains such as 'early development' or 'leadership' may prove problematic.

Making inferences about personality traits from the observation of intra-individual consistencies and inter-individual differences in behaviour within and across contexts is an effective research approach that has already been successfully used in previous studies of animal personality (e.g. Gosling, Lilienfeld, & Marino, 2003). The behavioural repertoire approach was also nicely exemplified by the author's own study of great apes (Uher et al., 2008). Unfortunately, the description of this approach and the discussion of its conceptual underpinnings in the target paper are not as clear as the contributions this approach can potentially make to the field of comparative personality research.

Climbing Out of Our Minds to Understand Personality

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Abstract

Uher (this issue) proposed that we expand understanding of human personality and its biological, temperamental and evolutionary origins by cataloging behavioural repertoires of humans and nonhuman animals. The method is difficult to implement. It relies on the ability to distinguish behaviours showing interspecies or intercultural differences but not intraspecies or intracultural differences from those showing individual differences both within and across species or cultures. Nevertheless, it may be an important way to transcend anthropomorphism and cultural biases that may limit current understanding of social and temperamental transactions involved in personality development. Copyright © 2008 John Wiley & Sons, Ltd.

In her comprehensive review, Uher (this issue) has outlined five basic approaches that can be used to identify the major trait dimensions of personality in human and nonhuman

animals. As she has noted, the approach most commonly used within human cultures has been to compile collections of lexical personality descriptors, on the assumption that, taken together, such trait-related words are both ecologically valid indicators and comprehensive in their coverage of the personality 'space'. As she has also noted, studies of comparative personality, whether cross-cultural within humans or cross-species, have tended to rely on the presumption that what has been identified in the human personality lexicon of one human culture can be translated or transplanted onto another human culture or even other species.

Though these approaches have generated results that suggest both apparently stable personality dimensions within cultures and cross-cultural and even cross-species consistency, they do not test the underlying assumptions of concurrent validity and comprehensiveness on which they rely. Failure to test this assumption makes it particularly difficult to justify the common claims that results from these approaches reflect underlying temperament or biology. Uher suggested that studying and comparing the behavioural repertoires of human and nonhuman animals may expand our understanding of human personality and its biological, phylogenetic and evolutionary origins by making it possible to relax this assumption.

The method Uher suggested is difficult to implement, but its difficulties are precisely the reasons that successful implementation could be so valuable. We are always in danger of being completely unaware of our most blatant anthropomorphisms and their cultural analogues. Many of them may be intrinsic parts of our personality descriptor lexicons, which is what makes it so important to test the assumption underlying this approach. An example of our blindness to our culture may help to make this clear. Raven's Progressive Matrices was designed to measure intelligent reasoning ability independent of cultural upbringing and knowledge and is generally considered to be one of the best, most highly 'g-loaded' tests of this ability. Yet, within supposedly homogeneous cultures, it has shown some of the largest Flynn effects over time, requiring constant updating to avoid measurement ceilings. Unless we are prepared to believe that native human intellectual capacity has skyrocketed in the last 100 years or so, we have to consider that the test may tap culturally derived skills that we did not even realise we were teaching.

The success of Uher's approach relies on our ability to transcend our cultural and species-typical perspectives, both conscious and unconscious, to distinguish characteristics that differ across species or cultures but not within them from those that differ both across and within species or cultures. From within any group, it is always easy to see dimensions on which group members differ, but these dimensions are much more difficult to identify from outside the group. The real trick, however, is to understand to what degree and on what level any dimensions on which differences occur matter. Gorillas live in relatively stable family groups consisting of one silverback male, several females and their immature offspring. Though paternity is relatively secure (probably not substantially different from that in humans), gorilla fathers are generally much less involved with their offspring than are human fathers. Do we even notice whether, like human fathers, gorilla fathers show individual differences in involvement with offspring, with some indifferent to or avoiding their presence, others tolerating it well, and still others engaging even in active play with the babies? Would this be an expression of their personality development, as gorillas or as primates? Are the human individual differences expressions of human male (not to mention female) personality development as humans or as primates? Is the species-typical mean difference part of what distinguishes us as humans from gorillas, an important cross-species individual difference variable, or simply noise? I see my two children as very different individuals, with different sources of frustration and joy and

different ways of processing their trials and triumphs. But their schoolteachers see them as similarly bright, conscientious, sporty and engaged. Who is right? Does it matter?

Spend any time around animals, and one observes that what captures their attention is very different from what captures ours. A bug flies by, and a cat will wake seemingly from a sound sleep, something that would not make most of us blink even fully awake. A member of the herd strays too far, and the sheepdog runs it back before we even notice its departure. This is true among people as well: some miss that their bicycle tires need air but are very aware when someone else is upset, while others take care of the one right away and are oblivious to the other. These differences in what captures attention, and the inevitable differences in learning and especially socialisation that accompany them, considerably complicate the possible social, experiential, biological and genetic transactions underlying personality development, whether human or nonhuman animal. Not only may two different people or organisms process the same information differently, but also they may not glean the same information from any given situation.

At the same time, evolution is highly conservative, and there must be fundamental common biological processes underlying at least some personality traits in all human cultures and across a wide range of species. We may only see these biological processes and their transactions with social influences and individual experiences clearly if we can climb out of our own minds and look beyond them. This is a tall order, but Uher's approach at least gives us a way to try.

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Extending the Personality Triad to Nonhuman Samples

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Abstract

The present essay explores some implications of the target paper's taxonomy of approaches to identify trait dimensions in differing species for understanding behavioural and situational properties in humans. We agree with the behavioural repertoire approach advocated by the target paper, and observe that to understand how an individual organism will behave in a novel situation one must know something about the individual's personality and something about the psychological properties of the situation. Behaviour, personality and situations form the Personality Triad (Funder, 2006). Copyright © 2008 John Wiley & Sons, Ltd.

Personality researchers employ numerous methods to study trait dimensions in humans and nonhumans. The major contribution of the target paper is a proposed taxonomy of approaches to identify trait dimensions in differing species. While the target paper focuses primarily on comparative psychology and the assessment of nonhuman species, the aim of the present essay is to explore some of its implications for understanding behavioural and situational properties in humans. Personality psychology has been plagued by a paucity of research directed towards understanding the fundamental properties of behaviours and situations (Baumeister, Vohs, & Funder, 2007; Funder, 2001; Funder, in press; Wagerman & Funder, in press). To its credit, the target paper addresses this issue and offers several methodological suggestions for obtaining crucial information about situations and behaviour.

THE BEHAVIOURAL REPERTOIRE APPROACH

The target paper advocates a bottom-up approach for studying nonhuman species, in which patterns of observed behavioural covariance form the foundation of trait constructs. We wholeheartedly agree with this approach. For traits to be ecologically valid, they must stem from the behaviour of the organism. A bottom-up approach is therefore more likely to yield a valid understanding of personality in various species. Uher contends that applying traits developed in the study of humans in a top-down manner (e.g. using the Big Five in comparative psychology) is problematic on several fronts. One major problem is that the Big Five and other human trait taxonomies are based on human language, which inherently biases the researcher towards finding human-like components in other species. Uher contends that this is a misspecification of the reference population. We agree with Uher that convergence from independent directions is needed in order to argue that traits found in humans, such as the Big Five, have components that are universal across species.

But it is important to note that the behavioural repertoire approach discussed in the target paper is not *entirely* bottom-up. Instead, the approach relies on experts and prior research to identify particular species' behaviours and the situations they encounter. This approach is a step up from and an improvement upon truly bottom-up approaches that start from scratch, measuring many behaviours which may have little or no psychological meaning to the species (e.g. number of eye blinks). An advantage of Uher's modification of the bottom-up approach is that it taps the deep knowledge of experts on a particular species to identify situational and behavioural variables of psychological interest.

THE PERSONALITY TRIAD

To understand how an individual organism will *behave* in a novel situation, one must know something about the *personality* of the individual organism and something about the psychological properties of the novel *situation*. These three components, behaviour, personality and situations form the Personality Triad (Funder, 2006, in press). The trait approach has a long history of examining differences among individuals and relating the differences to meaningful outcomes, and indeed this activity is a fundamental aim of personality psychology. The same activity is beginning to occur in the study of nonhuman samples (Gosling, 2001; Vazire, Gosling, Dickey, & Schapiro, 2007).

Psychology's understanding of the psychological properties of situations relevant to humans is unfortunately far less developed than its understanding of personality. Research investigating the power of situations, particularly in social psychology, is almost completely ad hoc (Wagerman & Funder, in press). Psychology has yet to specify the components of situations that influence behaviours, and the mechanisms by which situations do so. The behavioural signature approach mentioned in the target paper (see also Mischel, Shoda, & Mendoz-Denton, 2002; Uher, under review; Uher et al., 2008) seeks to identify consistent individual differences in response to various situations by plotting behaviour on the *y*-axis and situations along the *x*-axis. However, as implemented so far the behavioural signatures approach has neglected the specific aspects of situations that are important for determining behaviour. Yet such specification will be critical for any effort to understand the meaning a behavioural signature, its developmental origins or its implications for life outcomes.

In an attempt to begin to fill this empirical and conceptual gap, our lab has developed the Riverside Situational Q-Sort (RSQ; Wagerman & Funder, 2006), which includes items adapted from the California Adult Q-Sort (CAQ; Block, 1978, as modified by Bem & Funder, 1978) and the Riverside Behavioural Q-Sort (RBQ; Funder, Furr, & Colvin, 2000). The purpose of the RSQ is to characterise meaningful similarities and differences across situations that humans encounter, based (in its current version 2.0) on 81 characteristics. For example, RSQ items that characterise a party could include 'potentially enjoyable', 'social interaction possible' and 'has wide range of interpersonal cues', whereas items that characterise attending a funeral could include 'has behavioural limits', 'entails stress or trauma' and 'potentially anxiety inducing'. Early work using the RSQ has been largely successful in identifying the impact of psychological characteristics of situations on behaviour and illuminating how personality may influence both selection of situations and construal of the psychological properties of those situations.

We suggest that the development of parallel instruments within the behavioural repertoire approach might be used to not only understand particular behaviours and personality characteristics that are similar or unique within and across species, but also to understand properties of *situations* that are similar and different within and across species. Similar to the bottom-up approach, Uher advocates for developing trait constructs, a taxonomy of situations for a given species could be obtained by drawing on the knowledge of experts of particular species as well as through direct observation of the situations that a particular species encounters.

Like the understanding of situations, personality and social psychologists' understanding of behaviour in humans is also underdeveloped (Baumeister et al., 2007). The field of personality and social psychology has yet to establish a taxonomy of behaviours and to assess how individuals select particular behaviours, and the process by which behaviours come to fruition. The target paper reminds researchers that we need to consider properties of behaviours and situations when we are investigating personality, particularly when the goal is to establish aspects of personality that are universal or species specific.

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Putting Ethology (Back) into Human Personality Psychology

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Abstract

Uher's target paper shows clearly that the best approaches to personality in nonhuman species are grounded in the ethological tradition of careful observation of spontaneous behaviour. This commentary explores implications for human personality psychology, in which spontaneous behaviour has been neglected at the expense of self-report questionnaires. Copyright © 2008 John Wiley & Sons, Ltd.

Jana Uher's target paper recommends that personality researchers working on nonhuman animals take an approach that is grounded in the Tinbergian tradition of ethology. That is, it starts with careful and exhaustive direct observation of the spontaneous behaviour of the study species, quantifies its behavioural scores and considers behaviour in the context of adaptive problems that the animal has to solve. This proposal seems eminently reasonable, and obviously, is the only real solution for research on non-verbal species (asking nominated humans to provide ratings is a partial alternative, but even this is of course based on those humans' direct observations of behaviour). My purpose here is to briefly consider the value of the ethological approach for research on humans as well.

Human personality research has always contained twin traditions of observation of spontaneous behaviour on the one hand, and analysis of self-report and lexical data on the other. Indeed, both are present in the writings of the pioneer of personality psychology, Francis Galton. As well as seeing the value of lexical and rating information for measuring personality, Galton recommended that psychologists go out into London and look at people's actual reactions to shocks and confrontations, as an index of temperamental differences (see Nettle, 2007). As trait personality psychology has developed, however, the observational tradition has developed far less rapidly than the rating-based one. Indeed, direct observational studies of behaviour more or less had disappeared from personality and social psychology by the end of the 1980s (Baumeister et al., 2007).

The appeal of questionnaire-based approaches is obvious, and indeed, I confess all of my research has been based on them. They allow for a large amount of data to be gathered quickly, and as such, they have contributed enormously to the development of personality theory. However, reliance on rating data alone has a number of limitations. It leaves personality psychology open to the constant possibility of scepticism that the traits measured *only* reflect propensities to respond to questionnaires, and thus are uninformative about consequential outcomes 'in the wild'. It is noteworthy that Mischel's classic book that led to so much scepticism about broad personality traits was precisely based on an attempt to link up questionnaire reports with actual behaviour at a summer camp (Mischel, 1968).

The critique turns out to be unfair on questionnaire-based constructs, which do actually have a good track record of predicting consequential outcomes cumulatively over long periods (Ozer & Benet-Martinez, 2006; Soldz & Vaillant, 1999), and clearly relate to differences in spontaneous behaviour (e.g. Fast & Funder, 2008), but many researchers remain sceptical about constructs that are exclusively derived from questionnaires and whose main validation is that they predict scores on other questionnaires, particularly when, for example responses are compared across different cultures.

Moreover, the reliance on questionnaires (which assess traits at a rather abstract or domain-general level) has contributed to the persistence of the person-situation controversy. This problem seems to me to be solved, or possibly never to have existed (Funder, 2006), given that situations provide proximal triggers for behaviours but individuals varying in how easily those behaviours are evoked and also in what situations they put themselves in, but the controversy would probably never have arisen if personality studies were largely based on direct measurement of behaviour, in which the interplay of triggering situations and individual variability in thresholds is easier to assess (a classic ethological example is individual variability in distances from a predator at which fleeing occurs; no one questions that fleeing is caused by the predator, but individuals vary in the distance at which this response is evoked).

The ultimate aim of personality psychology in humans should be to answer all four of Tinbergen's (1963) key questions (phylogeny, function, proximate mechanism and ontogenetic development) with respect to personality functioning. Questionnaire-derived personality constructs such as the Big Five do seem to be valid, but the more we can understand what they mean in terms of behaviours performed 'in the wild', the more we will be able to assess their fitness costs and benefits, their developmental trajectories, and their phylogenetic continuity or lack of it. Thus, maybe Uher's sensible programme for research on our nonhuman cousins should be taken to heart by those of us who work on humans too.

A Quest for Universals in Comparative Personality Research: What Mad Pursuit

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Abstract

The proposed bottom-up approach for comparative personality assessment by Uher (this issue) is discussed, with particular attention to its roots in cross-cultural psychology. As it has proven very difficult to identify universal dimensions or invariable behavioural indicators that might apply to all members of our species, Homo sapiens, it is argued that one should be cautious concerning the ability of cross-cultural psychology to serve as a foundation on which the framework of comparative personality research will be built. Copyright © 2008 John Wiley & Sons, Ltd.

Jana Uher (this issue) has presented a timely and needed review of different methodological approaches to study personality differences both within and across species. She also proposes a bottom-up approach for comparative personality assessment—the behavioural repertoire approach—that, according to her words, is ‘tailored to the specific methodological requirements of comparative personality research’. This is an audacious attempt that success has yet to be decided upon by future research. What follows here is a discussion related to the proposed theoretical and methodological framework of comparative personality research and more specifically, to its claimed roots in cross-cultural psychology.

Uher (this issue) proposes a framework from a personality trait perspective that could be used to study personality variability of populations within and across different species. Following the approach by Leung and Bond (1989) for identifying dimensions of cultural variation in cross-cultural research, she proposes a typology of three dimensions—species-specific, weak and strong universal trait dimensions—for capturing the inter-individual personality variation either within or across species. According to Uher (this issue), ‘Species-specific trait dimensions are confined to particular species; only individuals of that species differ from one another along that dimension. There is thus no reason for comparisons of individuals of different species’. Universal trait dimensions, on the other hand, are applicable to all individuals of all (studied) species, thereby allowing comparison of individuals of different species.

For much of its existence, cross-cultural psychologists have been busy identifying ‘universal laws’ of human behaviour. In fact, it is one of the main assumptions of cross-cultural psychology that there are basic underlying psychological processes that are characteristic or common to all human beings, regardless of their ethnic or cultural background. The development and display of those universal processes, however, is substantially influenced by culture (Berry, Poortinga, Segall, & Dasen, 2002). Despite this guiding assumption, which basically reflects the third goal of cross-cultural psychology (Berry et al., 2002), the attempts of finding pancultural human universals in cross-cultural psychology have not been very successful. Over the years, a significant number of different universal dimensions of social behaviour have been proposed—none of which, however, has won an overarching support across different research schools and subfields of cross-cultural psychology. For instance, a universal model of social relations was proposed by Fiske (1991, p. 13) who argued that ‘just four elementary relational structures are sufficient to describe an enormous spectrum of forms of human social relations as well as social motive and emotions, intuitive social thought and moral judgment’. According to Fiske, these models are truly ‘universal’, being the basis for social relations among all people in all cultures (allowing for an enormous amount of culture-specific elaboration, embellishment and inhibition) and the essential foundation for cross-cultural understanding and intercultural agreement’ (p. 25). Seventeen years later, it is still not clear whether the universality of Fiske’s model of social relations can be established by empirical investigation or whether it is an abstract model with *a priori* true value.

Take another example of individualism-collectivism. This value dimension has been studied more thoroughly than any other construct in the history of cross-cultural psychology. It has been even argued that the concepts of individualism and collectivism are largely responsible for the growth of cross-cultural psychology over the past three decades (Schimmack, Oishi, & Diener, 2005). For years, it was widely believed that individualism-collectivism is perhaps the most important and useful dimension of cultural variation (Triandis, 1988, 1995; Vandello & Cohen, 1999) that can explain cross-cultural differences in

behaviour over a wide range of different situations (see Realo, 2003, for a review). Recently, however, several eminent cross-cultural researchers have argued that individualism and collectivism are questionable constructs that often fail to explain cross-cultural differences. It has even been said that the field will soon abandon these two over-freighted constructs altogether and move towards narrower theories of culture based on more specific constructs (Bond, 2002; Voronov & Singer, 2002). Despite the huge popularity of these constructs in psychology, cross-cultural researchers have not been able to agree upon the nature or number of attributes that are essential for defining and measuring individualism and collectivism. Besides the differences in definitions of individualism and collectivism, a conceptual leap exists between the theoretical descriptions of the concepts and the specific empirical indicators that are used to measure them. Different conceptualisations and research programmes often rely on non-identical sets of measures and indicators, whose congruence with each other has not always been established. To paraphrase what a well-known personality psychologist Oliver John once said about personality research, cross-cultural psychologists never reached a consensus on the best model of individualism-collectivism which would have transformed the present Babel of concepts and measurement scales into a community that speaks a common language (John, 1990).

The best example of finding 'true' universals in cross-cultural psychology comes actually from the field of personality psychology, which for years was not concerned with cultural differences at all. Indeed, in recent years, strong claims have been made about the universality of personality traits. Accumulating research evidence from more than 60 cultures suggests that the Big Five personality traits are basic features of the human species (Allik & McCrae, 2002; McCrae et al., 2005) that are equally applicable to all humans in all cultures (McCrae & Costa, 1997). The question is not so much about disagreement between nomenclature and labels of personality traits (see De Raad & Barends, 2008, for a recent review). The author of the target paper appears to be too optimistic about the ability of personality psychology to establish the number of basic personality dimensions. The best what debates between adherents of the five- and six-factor structures have demonstrated is that these solutions are not incompatible. Thus, a demonstration that chimpanzee's personality can be described by 'five factors plus dominance' (King & Figueredo, 1997) does neither contradict nor exclude another description in terms of 'only five factors'. This is understandable because in an hierarchical approach, the number of factors depends first of all on the level of magnification (Markon, Krueger, & Watson, 2005). In the light of this and previous examples, one should be cautious concerning the ability of cross-cultural psychology to serve as a foundation on which the framework of comparative personality research should be built.

Identification and comparability of universal dimensions is not the only problem. Another and perhaps the most substantial question is how to ensure that situations and behavioural indicators represent comparable properties for different species? Although bottom-up approaches look very promising, the comparability is not automatically achieved by making indicators more specific. Many very specific behavioural indicators have been devised on the basis of human analogues ('anxiety', 'depression' and 'panic', to name a few examples) and applied, more or less uncritically, to another species. For example, laughing is a good indicator of positive emotions and hence, extraversion. When it was discovered that juvenile rats emit short, high-frequency ultrasonic vocalisations in the range of 55 kHz (Knutson, Burgdorf, & Panksepp, 1998), it became attractive to treat these vocalisations as equivalents of human laughing (Panksepp & Burgdorf, 2003). But

even so, additional evidence is needed to demonstrate that there are individual differences in rats 'laughing' that can be used as indicators of rats personality (Mällo et al., 2007). This does not guarantee that it is generalisable to other species. As Uher (this issue) herself notes in her paper, specific behaviours are not free from the problem of the 'translation equivalence'. Thus, the problem of cross-species equivalence cannot be solved by bottom-up behavioural repertoire approaches alone.

As shown above, it has proven very difficult to identify universal dimensions or invariable behavioural indicators that might apply to all members of our species, *Homo sapiens*. A search for universal trait dimensions in a wide array of nonhuman species: what mad pursuit indeed, as Francis Crick would have said.

The Next Step: Towards Personality Development in Animals?

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Abstract

Uher's (this issue) paper on methodological approaches to comparative personality research provides an interesting starting point to think about other aspects of personality research for which comparative thinking could be useful. In this commentary, the focus for such other aspects is on personality development. Copyright © 2008 John Wiley & Sons, Ltd.

In her target paper, Uher (this issue) presents an impressive account of theoretical and methodological aspects of the identification of valid and comparable personality dimensions across species. In this reaction, I would like to argue that we should not stop once comparative dimensions have been identified. In my opinion, this account, and the proposed taxonomies, can be impetuous for a stronger conceptualisation of the role of personality in various species, more specifically of the role of personality in individual development.

In recent work on personality development, a developmental task approach has been proposed (see Denissen, van Aken, & Roberts, 2008) A developmental task is defined a 'task which arises about a certain period in the life of the individual successful achievement of which leads to his happiness and to success with later tasks' (Havighurst, 1972, p. 2). In such an approach, it is suggested that development in personality is related to the fact that during the course of their development individuals are expected to master subsequent tasks, or issues. Adapting to these tasks is essential in the sense that the behaviours and emotions that are learned and regulated during a task have consequences for subsequent tasks, thus giving rise to a developmental continuity (Sroufe, 1979). It is also essential, in the sense that the mastering of these tasks can be linked to personality

maturation, and as such can be seen as one of the driving mechanisms behind personality development. In this respect, this approach resembles, for example Roberts, Wood, and Smith's (2005) Social Investment Theory.

It is interesting to see that the behavioural domains that Uher presents in Figure 2 of the target paper, show some resemblance to aspects of developmental tasks, as they are described by, for example Erikson or Havighurst. The difference, of course, is that there does not seem to be a temporal, or developmental, ordering of the domains. Such an ordering might give insight into the role that personality plays in animal functioning. For example, Bell (2007a) in a commentary on Wolf, van Doorn, Leimar, and Weissing (2007) notes that personality might mediate transitions in an individual's strategy for survival and reproduction, for example when bold and aggressive individuals switch from a 'reproduce early' towards a 'delay reproduction' strategy once their initial behaviour has led to enough resources. Depending on the species under study, it would therefore be insightful to look at central issues that occur within the development of an individual of that species, and think about whether the individual's personality plays a role in adapting to those issues, and perhaps even about personality stability and change, as a subsequent result of this adaptation.

A second element that has a prominent place in contemporary studies on personality development is the notion of person–environment interactions. It is assumed that individual differences in personality shape individual differences in environments. This can be an active interaction, in the sense that an individual actively shapes his environment, for example by changing things in the environment, or by making choices between environments. This can also be an evocative interaction, for example when an individual triggers certain reactions from the environment. It also can be an interpretative interaction, for example when an individual interprets environmental stimuli in a way that is consistent with his or her personality.

These person–environment interactions are important in personality development, because they are assumed to be the mechanism behind continuity in personality, and behind an increasing match between a certain personality and a certain environment. The connection with developmental tasks is that these tasks can be seen as a kind of transformation period, in which person–environment interactions can have effects on the life-course of an individual, and his environment. Again, it would be insightful to look at such transformation periods in the development of individuals of a certain species, to learn more about the role of personality, the role of the environment and the interaction between the two.

Thinking about the interactions between environment and personality this way might be related to the adaptive taxonomic approach to identify trait dimensions, as it is described in Uher's Figure 1. However, it should be noted that this refers more to a phylogenetic stance, where trait dimensions are identified based on their adaptive significance in the species' evolutionary past, whereas the person–environment interaction in developmental psychology more refers to the adaptation of the individual. In itself, the discussion on the adaptation of a species versus the adaptation of a single individual might be an interesting topic.

Why would these developmental ideas in animal research be interesting? First, the same possibilities offered by studying nonhuman species that are mentioned by Uher (such as easier observations, easier manipulations, shorter time-spans) apply here. But, second, empirical and theoretical results from the rapidly developing field of personality development (see, e.g. Mroczek & Little, 2006) could be translated into the nonhuman

domain. This concerns results regarding theoretical and methodological aspects of personality development, but also regarding conceptualisations of stability and change, or regarding the interaction between personality and environment. In this commentary, I have tried to give some examples.

It would at least be interesting to speculate about these ideas. Just as Uher's work on methodological approaches towards comparative research and recent work on the evolution of animal personalities (Wolf et al., 2007), thinking about comparative ontogenetic personality development might have interesting implications for the study of personality in humans and in animals.

Animal Personality, Behaviours or Traits: What Are We Measuring?

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Abstract

With the development of a new bottom-up methodology, the author aims at providing us with a tool for comparative personality research. This tool will indeed help us to identify differences between related species. However, to understand how differences within species are maintained and differences between species have evolved, we need to identify selection pressures on personality traits empirically. Copyright © 2008 John Wiley & Sons, Ltd.

In the target paper, the author discusses the current methodology for identifying traits and trait indicators in animal personality research and provides us with a methodology designed to study animal personality from a comparative perspective. The presented methodology is a great step forward in deriving trait dimensions in a more systematic and unbiased way. In this commentary, I will on one hand describe some limitations of the presented methodology for the study on the past and current evolutionary forces on animal personality. On the other hand, I want to show the opportunity the 'behavioural repertoire approach' might give to integrate empirical personality research from an (adaptive) evolutionary perspective with the vast existing theoretical knowledge in personality psychology going further than measuring single behaviours only.

But before doing that, I will start with a more general statement. When reading a review like the target paper, it seems that biology and psychology are still miles apart. Even though we work on similar species and have parallel interests, there is large scope for misunderstanding each others work. One reason for these misunderstandings lies in the use of certain jargon. The most important one in personality research thereby appears to be the word 'trait'. In ecology and evolutionary biology the word 'trait' is a common name for

any measurement on an individual, while the term has much more loading in psychology. Without knowledge of the existence of two distinct meanings of this simple word, a comparison between biological and psychological literature and theory on animal personality is at present almost impossible.

In contrast to what the target paper presents, there is no specific adaptive approach as a trait generation strategy *per se*. Biologists studying the adaptive significance of animal personality are interested in the mechanisms underlying and the forces that maintain within-species variation in personality traits (Dall, Houston, & McNamara, 2004). Their studies are based on the theory that in the presence of a selective advantage of any personality or behavioural type, directional selection should reduce variation in favour of this optimal personality type. However, processes like, for example balancing selection (Penke, Denissen, & Miller, 2007) could actively maintain this variation. Often several behavioural measurements are used as proxies or indicators for underlying personality traits. These measurements are mostly derived from simple tests having their origin mainly in mouse research, like for example open-field behaviour as proxy for explorative behaviour (Walsh & Cummins, 1976) or attack latency as proxy for aggressiveness (Van Oortmerssen & Bakker, 1981). They have been adapted for the specific study species like for example the great tit (Drent, Van Oers, & Van Noordwijk, 2003; Verbeek, Boon, & Drent, 1996), dumpling squid (Sinn & Moltschaniwskyj, 2005) or the North American red squirrel (Boon, Reale, & Boutin, 2007), to achieve ecological relevance. Only few studies have taken a more bottom-up approach or even constructed factors (e.g. Sinn, Apiolaza, & Moltschaniwskyj, 2006), and the choice of behaviours was far from exhaustive.

Evolutionary biologists are interested in how past and current selection pressures could translate into changes in personality gene frequencies over generations (Van Oers, De Jong, Van Noordwijk, Kempenaers, & Drent, 2005). This in contrast to the evolutionary approach described in Figure 1 of the target paper which refers to the evolutionary approach in evolutionary psychology. As was already pointed out by Bates (2007) in his commentary on an earlier issue, much of evolutionary psychology assumes evolution (especially in humans) has ended, while evolution is an ongoing process. Differences among species (like differences among populations) are therefore not caused by evolutionary divergence of these species alone, but also by selection pressures after divergence. This difference between the views of biologists and many psychologists has influence on the possibilities of using the species comparison proposed in the target paper for implications on the phylogenetic basis, the adaptive significance, the ecological relevance and the proposed role for personality differences in evolution.

From consistent individual differences between individuals to species-differences is a gradual scale and variation in personality can therefore be seen as the raw material for natural selection to act on. If selection pressures differ among distinct populations of a species, this can lead to behavioural isolation and speciation. In that case, personality can be seen as the catalyst, rather than a motor for speciation. Speciation is intimately associated with the evolution of sexually selected- and reproduction-related traits often located on the sex chromosomes (Saether et al., 2007) rather than personality *per se*. Sexually selected behaviours are therefore crucial but underrepresented parts of the personality concept (Van Oers, Drent, Dingemanse, & Kempenaers, in press).

Hence, populations of the same species might on one hand differ because of differences in the frequency of personality types among the populations, but on the other hand when different selection pressures act or have acted on the regulating mechanisms, traits or trait constructs themselves could also differ between the populations. When taking this one

level higher, species-typical behaviours may not only arise through differences in the regulation of different behaviours by internal regulating mechanisms such as personality traits (trait manifestations), but also because the mechanisms themselves may differ due to selection on these mechanisms. Whether the selection eventually acts on traits or on behavioural measurements, remains largely unknown. This gap in our knowledge is mainly caused by the lack of a systematic way of choosing behaviours and the absence of a systematic trait generation strategy. An important limiting factor hereby is that studies interested in the adaptive significance of variation in personality follow individuals in their natural environment. The intensive observations needed for approaches like the 'behavioural repertoire approach' are therefore nearly impossible without taking individuals into captivity for a longer time. 'Knowing thy species' is, however, an important aspect in animal personality research, and the 'behavioural repertoire approach' is a good tool to achieve that knowledge.

Species of Nonhuman Personality Assessment

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Abstract

The target paper sets out an ambitious approach to animal personality research. This approach uses bottom-up measures and behavioural repertoires. This method holds promise for understanding personality trait expression in a given species; however, it has limited applications for comparing personality between species because it does not specify a measurement of interspecific similarity or difference and does not consider phylogenetic relationships between organisms. Our research led us to develop a modified top-down trait approach which makes comparing species feasible, is sensitive to species-level differences and is consistent with evolutionary thinking. Copyright © 2008 John Wiley & Sons, Ltd.

You can't eat the orange and throw the peel away—a man is not a piece of fruit! (Miller, 1994/1949, p. 59)

We are pleased to see new empirical studies and methodological innovations in the study of animal personality. Methodological approaches from cross-cultural psychology are relevant for animal personality research, and showing how personality is reflected in responses to situations may clarify personality trait expression. However, we question the utility of Uher's method for *comparative* personality research because it neither provides a common metric for determining similarities or differences between species nor considers phylogenetic relationships between organisms.

Uher suggests that bottom-up approaches are superior because they involve 'study[ing] personality variation from inside the species, largely uninformed by findings from other species'. While interesting and informative, this approach would not lend itself to comparative personality research because it assumes little can be learned about the personality of one species from studying the personality of another. As species are not types (Mayr, 1985), disregarding other species ignores that species are related, structured hierarchically and thus not independent (Felsenstein, 1985). So, while it is reasonable to take an 'agnostic' view when investigating the personality of evolutionarily distant species, for example squid (Sinn et al., 2006), this would be ill-advised when comparing closely related species.

Incorporating situations is also problematic. By definition, personality traits are stable across situations (Allport, 1961). In fact, Mischel (1968) criticised early personality researchers for failing to demonstrate cross-situational stability. Also, no metric for categorising behaviour-trait signatures as being more or less similar in meaning exists and there is no way to measure the extent of differences. Finally, while subjective ratings involve assessing individuals' personality across a wide-range of situations over long periods of time, studying behavioural responses to particular situations restricts this natural variation. The result would therefore be a reduction in ecological validity.

A top-down approach to comparative personality research is not without limitations, including the possibility of implicit personality theory or its ill-behaved pet, anthropomorphism (see Gosling, 2001, for a discussion). While implicit personality theory was a concern in human personality research (Passini & Norman, 1966), cross-trait/cross-twin correlations have since shown that it is unlikely to explain human personality structure (McCrae, Jang, Livesley, Riemann, & Angleitner, 2001; Rowe, 1982). There are no animal twin registries, but, using Kenny's social relations model, Kwan, Gosling, and John (2008) found no evidence of anthropomorphic projection in ratings of dog personality.

Like those studying personality across cultures (Church, 2001), Uher is wary that, if a top-down approach is used, important traits may be missed. Before addressing this, we wish to correct a misperception of research conducted by ourselves and our colleagues (e.g. King, Weiss, & Farmer, 2005; Weiss, King, & Hopkins, 2007). We do not use a strict top-down approach, but a modified version of the top-down approach that developed (bottom-up) over time. This approach involves using as broad a set of indicators as possible to determine the personality structure of a particular species. Because the Big Five or Five-Factor Model (Goldberg, 1990; McCrae & Costa, 2003) have extensively catalogued human personality traits, they are a natural starting point. However, because trait expression differs among species, we include clarifying sentences to capture these differences. For example, *fearful* in zoo chimpanzees and zoo orangutans is defined as 'Subject reacts excessively to real or imagined threats by displaying behaviours such as screaming, grimacing, running away or other signs of anxiety or distress'. (King & Figueredo, 1997; Weiss, King, & Perkins, 2006). For horses, this same trait was defined as 'Subject reacts excessively to real or imagined threats by displaying behaviours such as side-stepping, shying, running away or other signs of anxiety or distress'. (Fairholm, in preparation). In addition, for horses, it was deemed desirable to split the trait *friendly* into *friendly to humans* and *friendly to horses*. (Fairholm, in preparation).

This approach is also reflected in our choice of analyses and how we interpret results. We do not impose the Five-Factor Model or any other structure via confirmatory factor analysis and instead use exploratory factor analyses such as principal components

analysis. The structure that emerges enables us to generate hypotheses based on similarities to domains found in other (preferably closely related) species (Harvey & Pagel, 1991). The next step is to determine whether similar domains in related species are homologues by testing for measurement invariance (Stark, Chernyshenko, & Drasgow, 2006) and whether they are similarly related to other factors, such as age (King, Weiss, & Sisco, under review), subjective well-being (King & Landau, 2003; Weiss et al., 2006), mortality (Weiss & Costa, 2005) and, ultimately genes.

Using this approach led to the identification of cross-species similarities and differences. Similarities include the presence of five human-like domains in chimpanzees (King & Figueredo, 1997) and the strikingly similar cross-sectional age differences of these domains and their human counterparts (King et al., under review). Differences arise in the domains that emerge and in factor loadings: chimpanzee personality includes a broad Dominance domain; chimpanzee Conscientiousness includes components of unpredictability and aggressiveness; and chimpanzee Agreeableness is unipolar, only incorporating positive markers (King & Figueredo, 1997). Orangutan personality is more different still, with a narrow Dominance domain consisting of low-Agreeableness markers; an Extraversion domain in which non-social components have higher loadings than social components; a unipolar Agreeableness domain and Intellect, a domain combining Conscientiousness and Openness markers. Studies of dogs (Mozolowski, White, & Weiss, in preparation) and horses (Fairholm, in preparation) using modified versions of the same questionnaire also reveal similarities and differences.

As with personality structure, we do not wish to impose a framework or methodology upon comparative personality research. Science is best served by multiple methods that address multiple competing hypotheses (Chamberlin, 1965/1890; Shadish, 1993). Researchers must decide on or develop the strategies that are best suited to address their particular questions. In our experience, the modified top-down approach is suitable for comparative personality research: it makes comparisons feasible, is sensitive to species-level differences and is consistent with evolutionary thinking.

Author's Response

Three Methodological Core Issues of Comparative Personality Research

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Abstract

Comparative personality research in human and nonhuman species advances many areas of empirical and theoretical research. The methodological foundations underlying these attempts to explain personality, however, remain an unpopular and often ignored topic. The target paper and this rejoinder explore three methodological core issues in the philosophy of science for comparative personality research: Conceptualising personality variation, identifying domains of variation and measuring variation. Clear distinctions among these issues may help to avoid misunderstandings among different disciplines concerned with personality. Copyright © 2008 John Wiley & Sons, Ltd.

I am delighted that colleagues from different disciplines commented on my target paper and I sincerely thank all commentators for their insightful contributions. Personality is studied from very different viewpoints; my attempt to consolidate some basic methodological issues across disciplines was therefore predestined to meet with some scepticism. The pattern of agreement and objection raised in the commentaries thus closely reflects the field's current fragmentation across different disciplines and demonstrates much better than any single author could do how largely unaware most disciplines are of developments in neighbouring fields. None of the methodological issues I proposed was criticised by all disciplines and the objections raised by some are countered by commentaries of others. What a potential for synergy! Concepts and findings of different disciplines are waiting to be systematically integrated to form a multidisciplinary and more complex knowledge base that has the potential to advance the field significantly.

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Removing the invisible barriers between disciplines is a major challenge. Not only is there a Babylonian gap that could be crossed by simple dictionary-like translation; but there are also difficulties understanding similarities and differences in the concepts underlying the disciplines' standard terms. Since each discipline has its own good reasons for its specific perspective on personality, attempts for conceptual integrations across disciplines are only possible with risk taking, openness to other perspectives and compromise. Unlike empirical findings, concepts and methodologies are designed to be modified and changed as empirical facts accumulate and alternative perspectives are proposed. It was my aim to encourage this kind of discussion by addressing a multidisciplinary audience.

In my rejoinder, I discuss the issues raised by the different commentators from animal personality psychology (**Weiss & Adams**), behavioural ecology (**van Oers**), behaviour genetics (**Johnson**), cross-cultural psychology (**Realo & Allik**), developmental psychology (**van Aken**), human personality psychology (**Nave, Sherman & Funder; Nettle**), neurobiology and psychobiology (**Carere & Maestripieri**) within a common methodological framework, and highlight perspectives for future research.

INTEGRATING THREE EPISTEMIC ISSUES WITHIN A COMMON METHODOLOGICAL FRAMEWORK

Personality in the broadest sense is the internal organisation of behaviour that is stable over considerable time periods in the individual yet varies among the individuals of a population on latent dimensions. To identify such dimensions, I offered several methodological suggestions based on pertinent approaches in cross-cultural research on the one hand and on philosophical traditions of science and well-established findings in trait psychology on the other hand.

The overall methodological framework I proposed integrates three different core issues that have to be distinguished from one another and that require different types of approaches. The first is a methodology to *conceptualise* the basic phenomenon of personality variation in different populations within and across species as structures recurring in the same qualitative form in different individuals but at different quantitative levels that constitute dimensions across the composite of a population. The second is a methodology to *identify* in which domains (e.g. in shyness–boldness, sociability or conscientiousness) such dimensions are exhibited by a particular population. The third covers methodological approaches to *measure* such dimensions in these domains in the given population empirically. It is obvious that all three issues are necessarily interdependent but refer to different epistemological stages that merge together in the concept of hierarchical trait taxonomies (Figure 1).

Dimensional conceptions of personality vary greatly in complexity across different disciplines. In biological disciplines, they range from variation in single behavioural measures (called proxies, **van Oers**) to more complex dimensions (called continua or axes), which also underlie the recent concept of behavioural syndromes as clusters (or suites) of correlated behaviours (also called traits or characters; Sih, Bell, Johnson, & Ziemba, 2004). This latter concept explicitly incorporates the pervasive empirical finding that single behavioural dimensions often covary empirically, thus forming a more complex higher order dimension. Psychological disciplines study dimensionality of high complexity and therefore obtain many different trait indicators. In *trait taxonomies*, narrow trait

Three methodological core issues of comparative personality research

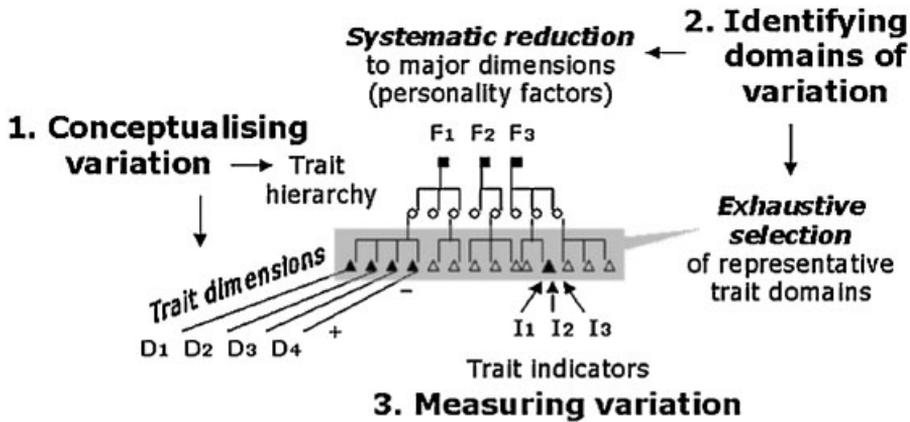


Figure 1. The three methodological core issues merging in the concept of hierarchical trait taxonomies.

dimensions are hierarchically subsumed within broader trait dimensions making the less complex dimensions sub-dimensions of the emergent more complex major dimensions (see Figure 1). With increasing complexity on higher order taxonomic levels, the shared variance of the summarised primary-level dimensions decreases and culminates in the statistical extraction of a few, statistically relatively independent, that is orthogonal, personality factors (such as the Big Five factors; Allport, 1937; Matthews, Deary, & Whiteman, 2003). Psychological disciplines therefore frequently use factor-analytic methods, whereas they are less common in biological disciplines (but see, e.g. Ibáñez, Ávila, Ruipérez, Moro, & Ortet, 2007; Sinn et al., 2006). Extending the complexity of the dimensions studied by biological disciplines, and thus the breadth and depth of correlational structures to analyse, will inevitably lead to the more frequent use of factor-analytic methods and the identification of different, independent behavioural syndromes in those disciplines as well.

Hierarchical trait taxonomies provide specific answers to the three methodological core issues. Trait taxonomies can vary across different populations according to their patterning effects. Understanding these patterning effects is necessary for a sound comparison of trait dimensions across populations (first core issue). It is obvious that the comprehensiveness of the empirical representation of a population's trait taxonomy depends on the selection of trait domains that determine its foundation and on the reduction processes that extract its major dimensions (second core issue). Trait taxonomies also help differentiate theoretical concepts from their empirical measurements, for which the terms construct and operationalisation are well established in psychological disciplines (third core issue). This distinction is the epistemic necessity for any scientific research on complex, not directly observable phenomena such as personality or cognition whose existence can only be inferred from repeated and systematic measurement of composite indicators (see Figure 1).

CONCEPTUALISING PERSONALITY VARIATION

I proposed to generalise the concept of dimensional personality variation within and across human cultures (Leung & Bond, 1989) to comparisons on other population levels including species by contrasting population-specific, weak and strong universal trait dimensions. This methodology requires distinguishing behaviours varying between populations but not within from those showing inter-individual differences both within and across populations; only the latter meet the criteria of personality variation (**Johnson**).

Universality of personality dimensions—a mad pursuit?

Realo and Allik objected to the idea that cross-cultural psychology could serve as a foundation for comparisons on other population levels, particularly across species, by illustrating the difficulties cross-cultural psychology has encountered in the attempt to identify pan-cultural human universals. Before I discuss this point, I want to warn against a misinterpretation of the distinctions among the three methodological core issues. The conceptualisation of personality variation that I borrowed from Leung and Bond (1989) has to be clearly distinguished from the behavioural repertoire approach I suggested as a methodology to identify trait domains in a species or population. Unlike Fiske's (1991) social relations model in the example given by **Realo and Allik**, the behavioural repertoire approach requires no assumptions about uniqueness or universality of the potential trait constructs it generates; instead, dimensionality and uniqueness versus universality are left entirely to empirical analysis. The approach is rooted in the emic–etic concept of cross-cultural psychology that can be generalised to bottom-up and top-down approaches in cross-species research (Gosling, 2008; **Weiss & Adams**; Weiss et al., 2006). Both in turn have to be clearly distinguished from any methodologies aimed at operationalising trait constructs. The behavioural repertoire approach neither specifies any particular assessment method nor any trait indicators to be used. Compared to lexical approaches, it facilitates the use of behavioural indicators that are needed to quantify the populations' positioning effects and that may be more appropriate for many species than single trait-descriptors like adjectives, but it does not exclude lexical indicators either. Similar to controversies between emic and etic traditions in cross-cultural research, achieving comparability and cross-population equivalence is a challenging issue that refers to both trait concepts and their operationalisations as I will discuss further below.

Realo and Allik illustrate nicely the difficulties encountered by cross-cultural research to identify universal psychological processes in view of their culturally influenced development and display; cross-species research encounters very similar difficulties given species-specific ontogenies and externalisations. The approach of Leung and Bond (1989) was successfully applied to identify different emic and etic dimensions in some cross-cultural studies (e.g. Triandis et al., 1993). As **Realo and Allik** emphasise, however, no universal dimension proposed by cross-cultural psychology 'has won an overarching support across different research schools and subfields of cross-cultural psychology'. Yet these difficulties may arise from the nature of culture, that is the studied constructs, rather than from the analytical methodology.

In its broadest sense, culture refers to 'symbolically mediated, shared systems of meaning' (Tuttle, 2001) that are arbitrary and therefore vary geographically. At their core are socially transmitted innovations spreading until they hit some barrier, thereby producing geographic differentiation (van Schaik, 2004). Compared to evolutionary

changes, cultural variations can evolve and change quite quickly (Chen, Cen, Li, & He, 2005; Lewin, 1947). Both arbitrariness in the meaning of behaviours and artifacts, and their rapid changeability suggest that pan-cultural findings on culturally derived traits may be much more unsteady than evolutionarily derived and thus neurobiologically influenced traits. Yet, the emergence of cultures itself is seen as an evolutionarily adaptive strategy used by human and nonhuman species (e.g. chimpanzees and orangutans), and may thus be a universal property of these species. Given that the cultures of different species (and maybe also of different same-species populations) can rely on different processes of social transmission, they can exhibit different global properties (Boesch & Tomasello, 1998). This may hinder identifying pan-cultural universals across the specific cultural systems that different populations produce.

Behavioural approaches may be more appropriate to identify human universals than language-based approaches such as lexical approaches given that people can communicate with hands and feet all over the world but not in their mother tongues. Behavioural approaches may also facilitate identifying cross-species universal trait dimensions (**Johnson**), for which there is already empirical evidence from animal personality psychology (Gosling, 2001; King & Figueredo, 1997; Weiss et al., 2006) and from biological disciplines that have established a substantial body of evidence for the existence of a shyness–boldness dimension in a number of species (Wilson, Clark, Coleman, & Dearstyne, 1994) including species of molluscs (Sinn et al., 2006), spiders (Riechert & Hedrick, 1990), crustaceans (Briffa, Rundle, & Fryer, 2008), fish (Bell & Sih, 2007; Sneddon, 2003), reptiles (Brodie III. & Russell, 1999), birds (Carere & van Oers, 2004) and mammals (Réale, Gallant, Leblanc, & Festa-Bianchet, 2000). Moreover, striking observable differences in shy–bold behaviour between species (*cf.* antelopes with lions) suggest that shyness–boldness may be even a strong universal trait dimension that differentiates individuals not only within but also across species depending on their degree of being prey or predator species. Given the present within-species data, it seems possible that such a strong universal shyness–boldness dimension spans even different animal *phyla* from *mollusca* and *arthropoda* to *chordata* covering both invertebrates and vertebrates. Studies testing this hypothesis empirically using universal and species-comparative analyses (see my target paper) to identify the species’ positioning effects seem promising but a little ‘mad’ indeed given the enormous effort required for this task.

Universality and uniqueness in a population’s personality structure

Beyond the evidence for specific cross-species universal trait dimensions such as shyness–boldness, phylogenetic continuities implying homologous features inherited from common ancestors also suggest the existence of some universal trait dimensions (John & Srivastava, 1999), whereas niche-differentiated adaptations suggest the existence of species-specific trait dimensions (Tooby & Cosmides, 1989). Because all species have a phylogenetic history and show adaptations to a particular ecological niche, most species exhibit both universal *and* unique trait dimensions in their personality structure. For example, present results on the human personality structure suggest that fundamental common biological processes may underlie universal trait dimensions that are shared with other species (**Johnson**), whereas species-specific mechanisms such as cultural socialisation or higher cognitive information processing may underlie uniquely human dimensions (**Realo & Allik**). That is, both universal and unique dimensions co-occur in the human personality structure. Nevertheless, it is conceivable that some species share

exactly the same set of major dimensions without exhibiting any species-specific dimensions; given the diversity of species-specific adaptations and mechanisms such cases of universal personality structures may be rare.

IDENTIFYING DOMAINS OF VARIATION

Assumptions of phylogenetic continuities between species are also sometimes used as rationale to identify *domains* of trait dimensions (Weiss & Adams). I proposed a taxonomy differentiating basic types of approaches commonly used to identify trait domains at the population level in human and nonhuman species (ignoring theoretical approaches that start from intra-individual processes to derive personality traits, for example Smillie's target paper, this issue). These methodological approaches differ in starting points based on particular rationales.

A taxonomy of rationales to identify trait domains

Whereas some rationales refer to *strategies to overcome the selection bottleneck* (see my target paper), others focus primarily on the *content of the domains* to be studied for dimensionality. For example, the rationale behind lexical bottom-up approaches, that is the assumption that important human traits are socially perceived and lexically encoded (Allport & Odbert, 1936; Goldberg, 1990), formulates an exhaustive selection strategy; but it does not specify *which* domains this selection should cover. The assumption of phylogenetic continuity between different species, by contrast, suggests that the content of *specific* trait domains could be applied top-down to other species (John & Srivastava, 1999).

Weiss and Adams argue for the validity of a phylogenetic approach to animal personality at least for closely related species, which raises the question of where exactly on the phylogenetic continuum one should draw the line between 'closely' and 'distantly' related species. For example, one could argue that chimpanzees are more closely related to humans than are orangutans but compared to dogs orangutans are the more closely related species. Which criteria should we use to decide whether dogs or horses are related closely enough to humans to justify adapting the content of human trait domains top-down to these species?

Content-related rationales like that of the phylogenetic approach are problematic on two fronts. First, they may fail ecological validity (Gosling, 2001) and comprehensiveness (Uher & Asendorpf, 2008). That the primary-level trait dimensions covered by the human Big Five factors (even if complemented with elements of nomination approaches) cluster empirically into different higher order dimensions in different species (**Weiss & Adams**) does not show that these species-specific factor structures represent the species' true trait taxonomies appropriately. Instead, when applied top-down from humans some dimensions may suffer anthropomorphic or other biases while others may be even completely missing because they either are not exhibited by humans or were systematically excluded by non-empirical reduction in Big Five traditions (Saucier & Goldberg, 1998; Uher & Asendorpf, 2008). Failure to identify species-specific primary-level or even higher order dimensions results in biased or missing representations of the species' true major dimensions. Unless assumptions on the concurrent validity and comprehensiveness of the lexically derived Big Five domains for human and nonhuman animals are tested, which ultimately requires

convergence from different, independent approaches (**Nave, Sherman & Funder**), it is 'particularly difficult to justify the common claims that results from these approaches reflect underlying temperament or biology' (**Johnson**).

The second limitation of content-related rationales refers to the interpretation of empirical outcomes. A mere phylogenetic approach imposes an *a priori* theoretical explanation of any possible result ignoring alternative explanations. Rather than *homologues* indicating phylogenetic continuity (**Weiss & Adams**), similarity of personality traits among species could likewise indicate *analogues* that reflect shared adaptation to similar environments (Immerman & Mackey, 2003; Rychlak, 1968). For example, whereas orangutans share large parts of our phylogenetic tree but have adapted to swampy rain forests (van Schaik, 2004), dogs share much less of our phylogenetic tree but have adapted to our environments (Hare & Tomasello, 2005; Trut, 1999). Interpreting findings on factors resembling some of the human Big Five in orangutans (Weiss et al., 2006) and dogs (Gosling, Kwan, & John, 2003) alike as evidence of their phylogenetic origins (**Weiss & Adams**) ignores that this similarity could likewise result from evolutionary convergence (Gosling, 2001; Gosling & Graybeal, 2007). Evolutionary convergence may have happened not only in cognitive abilities (Hare & Tomasello, 2005) but also in personality traits given that initial domestication processes are based on artificial selection for personality traits (Belyaev, 1969) and that in dogs selective breeding for behavioural dispositions shows effects in only a few generations (Svartberg, 2006). It may therefore be not by chance that top-down approaches from the human Big Five factors concentrate either on closely related primate species or on domesticated species, whereas investigation of other species has largely evaded this tradition so far.

Given the complexity of the human brain and the diversity of habitats to which *Homo sapiens* has successfully adapted, there is little doubt that humans have developed the most complex personality structure of all species. But this does not mean that it covers *all kinds* of personality variability that possibly exist in the animal kingdom. An anthropocentric phylogenetic approach that is applying concepts just one-way from human to nonhuman species may therefore be misleading and may be prone to overlooking species-specific traits that humans do not exhibit but that even closely related species such as orangutans may have developed in adaptation to their particular ecological niches. It would be thus more consistent with evolutionary theory to complement phylogenetic approaches with adaptive approaches.

Strategy-based rationales such as those of systematic bottom-up approaches avoid restrictions to any particular theory in regard to the content of trait domains to be selected. Instead, they tackle the merely descriptive task of measuring and cataloguing observable personality variability in a population to provide this information for subsequent theoretical and further empirical analyses covering Tinbergen's (1963) four interrelated key questions (**Nettle**) of function (**van Oers**), evolution (**Johnson; Weiss & Adams**), causation (**Carere & Maestriperi; Nave, Sherman & Funder**) and development (**van Aken; Realo & Allik**). Strategy-based rationales thus distinguish descriptive methodology from any theoretical explanations and further empirical explorations of the yielded primary results. The most successful methodology applied to map trait taxonomy, the lexical bottom-up approach, was based on such a rationale. It established a reference model for theoretical and empirical developments in various fields including behaviour genetics (Jang et al., 2006; Yamagata et al., 2006), personality development (Roberts et al., 2005), evolutionary personality psychology (Buss, 1999; Nettle, 2006) and animal personality psychology (Gosling, 2001; King & Figueredo, 1997; Weiss et al., 2006). The

behavioural repertoire approach is also based on a systematic strategy-related rationale and thus constitutes an independent alternative to this approach.

The person–situation controversy 40 years after Mischel (1968)

Ultimate explanations of behaviour on the population level, that is phylogeny and adaptivity, require proximate explanations, that is proximate mechanisms and ontogenetic development, on the individual level (Tinbergen, 1963). Therefore, comparative personality research considers not only the environment of evolutionary adaptedness but also the individual's immediate and developmental environment (**Nave, Sherman & Funder; van Aken; van Oers**). **Van Aken** nicely illustrates the tight interrelations among individual–situation interactions, individual personality development and individual adaptation throughout different ontogenetic transformation periods affecting an individual's course of life. Pertinent empirical research is also beginning to emerge in the nonhuman domain (e.g. Bell, 2007a; Frost, Winfrow-Giffen, Ashley, & Sneddon, 2007). Ultimately, adaptation on the individual level underlies adaptation on the species level, of which successful adaptive variants are retained phylogenetically (**Johnson**).

All disciplines incorporate situations at least implicitly in their empirical research. For example, crabs and squids are exposed to threatening anti-predator situations (Briffa et al., 2008; Sinn, et al., 2006), birds and fish to novel objects (Carere & van Oers, 2004; Frost et al., 2007), mice and cattle to open field tests (Ibáñez et al., 2007; Müller & von Keyserlingk, 2006) and monkeys to social strangers (Fairbanks, 2001). Situations are also incorporated in animal personality ratings either explicitly in the items (Uher, under review), in clarifying sentences (**Weiss & Adams**) or implicitly in adjectival connotations (**Weiss & Adams**). Disciplines differ, however, in how explicitly they incorporate situations in their theoretical conceptions (see, e.g. **Carere & Maestriperi; Weiss & Adams**). They also differ in the standard terminology they use (**van Oers**), which requires first awareness that such differences exist at all, and second careful explanation and consideration of the concepts and terms used by different disciplines to facilitate mutual understanding. How easily communication across disciplines can go awry is shown by the commentary by **Carere and Maestriperi**.

Carere and Maestriperi wrote that to them as biologists it remained unclear what I meant by situations, universality and domains—terms that are commonly used in cross-cultural and mainstream psychology. Although these are just a very few terms, they proved to be so central that misunderstanding them let **Carere and Maestriperi** misunderstand the methodological approach that I proposed. The psychological notion of a situation is quite broad; for example 'absence of specific situational stimuli' as discussed by **Carere and Maestriperi** also characterises a situation, one of deprivation. An individual is always in some kind of immediate environmental situation with which it interacts and in which it thus behaves; situations provide the proximal triggers for behaviour (**Nettle**). That situations can be classified by their specific psychological properties for a particular individual or population (**Nave, Sherman & Funder; Ten Berge & De Raad, 1999**) has nothing to do with 'Skinnerian' views on behaviour (**Carere & Maestriperi**). Instead, situations are vital for personality research because individuals vary in how they perceive and respond to them, and which situations they seek out and shape (**Carere & Maestriperi; Fleeson, 2004; Funder, 2006; Nave, Sherman & Funder; Nettle; van Aken; Weiss & Adams**).

Whereas behavioural biology and general psychology study the general behaviour of the *average* individual, comparative personality research explores *inter-individual variability* in this general behaviour of a species or any other population. This differential perspective inevitably requires more fine-grained analyses of behaviour and the situations in which it occurs because not every behaviour is informative about inter-individual differences in personality and neither is every situation suited to the differential expression of behaviour. It is well established in psychology that the trait relevance of a situation and how much it restricts behaviour, that is situational strength, determine whether personality differences can be observed, and that individual situational responsiveness shows up in stable patterns of individual–situation interactions resulting in only moderate cross-situational consistency on the population level (Mischel, 1977; Mischel et al., 2002; Tett & Gutermann, 2000). These findings are also informative for animal personality research (Uher, under review; Uher et al., 2008).

In biological personality research, theoretical conceptions of context dependence and limited behavioural plasticity in regard to consistency across situations emerged only relatively recently (DeWitt, Sih, & Wilson, 1998; Sih et al., 2004). The growing number of pertinent empirical studies (e.g. Briffa et al., 2008; Spooler, Burbidge, Lawrence, Simmins, & Edwards, 1996; van Oers, Klunder, & Drent, 2005) indicates an increasing awareness of the role of environmental situations in basic concepts of personality. As the commentaries show, animal personality research seems to go through exactly the same controversies arising around individuals, situations and personality as human personality psychology did throughout the last four decades. This suggests that, in contrast to **Nettle's** assumption that 'the controversy would probably never have arisen if personality studies were largely based on direct measurement of behaviour, in which the interplay of triggering situations and individual variability in thresholds is easier to assess', the person–situation controversy seems in fact to be a profound conceptual issue, not one of measurement. While human personality psychology now regards the controversy as coming to an end (Fleeson, 2004) and being resolved (Funder, 2006; **Nettle**), it still needs much more attention in animal personality research. Animal researchers could profit greatly from the lessons learned by human personality psychologists, who in turn can use results gained in animal research to broaden and sharpen their concepts (**Nave, Sherman & Funder**).

The behavioural repertoire approach

The strategy-related rationale of the behavioural repertoire approach explicitly considers the triad of behaviour, situation and personality (Funder, 2006) and may be best expressed by Mischel's notion of personality traits as the 'conditional probability of a category of behaviours in a category of contexts' (Wright & Mischel, 1987). It thus reflects the basic nature of personality as inter-individual differences in the dynamic internal organisation of the individual's behavioural interactions with its environment *without* specifying any particular domains. Whereas animal researchers unanimously demand trait identification to be mandatorily linked with assumptions about underlying mechanisms (**Carere & Maestripieri**), processes of maintenance (**van Oers**) or phylogenetic origins (**Weiss & Adams**), the behavioural repertoire approach is stripped of any such beliefs as is the most widely used lexical bottom-up approach in human personality psychology. Instead, it explores the personality variability of a population descriptively as a first step *prior* to any

explanatory analyses aimed at answering Tinbergen's four key questions with respect to personality functioning (see also my target paper; Bell, 2007b; **Nettle**).

Unfortunately, terminological misunderstandings hindered **Carere and Maestripieri** from fully understanding the methodology of the bottom-up approach I suggested so that they relied instead on one of my empirical studies (Uher et al., 2008) in which I tested its viability. Because they picked the behavioural study and not the rating study (Uher, under review; Uher & Asendorpf, 2008), they erroneously concluded that the approach would be based on an ethogram, which is not the case. In contrast with most other behavioural or lexical bottom-up approaches, the behavioural repertoire approach starts at the *conceptual* level, not at the *operationalisational* level, which **Nave, Sherman and Funder** described as 'a step up from and an improvement upon truly bottom-up approaches that start from scratch, measuring many behaviours which may have little or no psychological meaning'. This again refers to the importance of distinguishing the three methodological core issues clearly. The behavioural repertoire approach itself only generates potential trait *constructs*. To analyse these theoretical concepts empirically for dimensionality and their hierarchical structure, they must then be operationalised for empirical tests, for example with rating items but also with behavioural measures that could be compiled in one or even several different ethograms (considering different situational properties).

Several steps are needed to generate potential trait constructs systematically. First, all important behavioural domains and related situational properties known in a species must be identified. I have already highlighted the broad psychological notion of situations and their role in personality research. The notion of domains is similarly very broad in psychology (e.g. cognitive, emotional or motivational domains of personality in Chen & West, 2008) and is more abstract than that of homogeneous and disjunctive categories. Behavioural domains broadly refer to groups of different behavioural categories that are meaningfully related but do not necessarily share the same type of category and interrelatedness. This notion of domains is very similar to that incorporated in the widely discussed concept of domain-specific versus domain-general expression of personality traits in both biological and psychological disciplines (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005; Chen et al., 2005; Sih et al., 2004; Sinn & Moltschaniwskyj, 2005; van Oers et al., 2005).

Carere and Maestripieri are completely correct in saying that one and the same behaviour can be studied from various perspectives (e.g. as social or motor behaviour) for which different ethograms are needed. This is exactly the reason that single ethograms are insufficient for comprehensive attempts to map a species' personality structure. I therefore argued for relying on the existing expert knowledge gathered on the particular species' behavioural repertoire instead of studying behaviour from scratch (**Nave, Sherman & Funder**). Figure 2 of the target paper relies on four decades of behavioural research in great apes predominantly done in their natural environments to ensure capturing all known important parts of their natural behavioural repertoires (for references see my target paper). Under natural conditions, aberrant behaviours occur only infrequently and are considered by many as having little relevance for personality research that focuses on normal variation, not on pathological deviation. Figure 2 in the target paper thus summarises the domains of expert knowledge gained from countless different ethograms and research agendas studying very different aspects of these species' behaviours covering diverse functional and conceptual behavioural categories, societal structures and different periods of life. I referred to these domains as the 'biological classification of the species'

universal behaviours' because these are the topics primatologists typically identify as important. I also used all labels from this literature.

The rigid thinking in terms of homogeneous and disjunct categories inherent to ethograms is helpful for collecting behavioural data for a particular research question, but hinders a comprehensive selection of domains of potential behavioural variability in a population on the *conceptual* level. **Carere and Maestripieri** asked why the grouping of the behavioural domains and subdomains in Figure 2 of the target paper is not considered in the behavioural repertoire approach. The reason is that morphological and functional interrelations of observable behaviour need not be related to underlying personality variation (see also Bell, 2007b). This is consistent with the notion that personality pervasively influences behaviour in all areas of life and is thus not limited to particular types of behavioural categories to which ethograms are confined.

Each of the domains and sub-domains in Figure 2 of the target paper comprises several broader behaviour categories that are not necessarily of the same type and that might not necessarily fit into one single ethogram. I referred to them as universal behaviours because these behaviours are generally shown by most if not all members of a species, rather than only by certain individuals (e.g. approach, investigation, play, attack). This is consistent with the usage of this term in cross-cultural and human personality psychology, which is also reflected in the proposed conceptualisation of universal trait dimensions within and across populations (see my target paper).

In the last step of trait generation, these universal, psychologically meaningful behaviours and related situational properties are then plotted against each other to derive potential trait *constructs*. Merging both behavioural *and* situational categories is central to the strategy-based rationale of the behavioural repertoire approach; this point seems partly misinterpreted by some commentaries. Instead, it explicitly considers individual–situation interactionism, which has arisen as the resolution of the person–situation controversy in trait psychology (Fleeson, 2004; Funder, 2006; **Nettle; Nave, Sherman & Funder**; Ten Berge & De Raad, 1999; see above and my target paper).

MEASURING VARIATION

After conceptualising personality variation (first core issue) and identifying *potential* trait domains (second core issue), the next epistemological step concerns measuring *empirical* variability in the selected domains in the given population with suitable trait indicators (third core issue). Hierarchical trait taxonomies are again useful to highlight basic principles (see Figure 1). The more primary-level dimensions located near to the bottom of the hierarchy such as specific habitual acts and trait facets can be measured with homogeneous and less diverse trait indicators, whereas the broad personality factors near to the top of the hierarchy can only be inferred from diverse, more heterogeneous trait indicators (Costa & McCrae, 1995; Eysenck, 1990).

Ratings and behaviour observations

Extracting personality traits as stable individual *tendencies* from the fluctuations of spontaneous behaviour requires (unlike transient states) extensive direct observation. Behaviour measures must therefore rely on sufficient aggregation at least across multiple occasions if not even across different situations and behaviours (Epstein, 1979, 1980).

Personality ratings capitalise on the human ability to aggregate such observations mentally to form overall judgements (Funder, 1995, 1999), which facilitates the large-scale data collection needed to establish trait taxonomies but renders ratings prone to bias and leaves their validity open to some extent. Therefore, ratings should be validated through convergence with observable behaviour measures of personality (Baumeister et al., 2007; **Johnson; Nave, Sherman & Funder; Nettle**). For nonhuman research, this step is indispensable (Uher & Asendorpf, 2008). Researchers favouring ratings often seem to forget that this method's economy largely derives from the division of labour with those colleagues who make the extensive and long-lasting empirical effort to validate them in the first place. In animal personality psychology, such efforts are still missing (Uher, under review).

Behaviour measures have high ecological validity and can be obtained as reliably as ratings (Uher & Asendorpf, 2008; Uher et al., 2008) provided they have sufficient levels of aggregation, for example regarding the number of occasions or the diversity of situations they reflect (the so-called principle of symmetry, Wittmann, 1987). Behaviour measures are neither inferior nor poor measures of personality (Gosling, 2008; Vazire et al., 2007); instead, they are essential to quantify positioning effects of populations, which are biased by reference group effects on the part of the raters (see my target paper; Heine, Lehman, Peng, & Greenholtz, 2002). Moreover, behavioural personality measures can be obtained in all species, whereas ratings may overextend human ability to differentiate larger numbers of individuals reliably and to aggregate their behavioural differences mentally, for example in morphologically small or distantly related species such as of molluscs, insects, spiders or fish. Such species are typically not among those studied with ratings; the majority of species studied with this method (developed in human personality psychology) constitute again primate and domesticated species (see for an overview Gosling, 2001, pp. 48–57).

Levels of comparability

To be meaningful at all, trait measures must consider differences in trait expression among populations, particularly among species. **Weiss and Adams** and to some extent also **Realo and Allik** objected that the lack of a common metric would render such measures incomparable. However, populations are compared on the *conceptual* level, not on the operationalisational level; this again refers to the distinctions among the three methodological core issues (see Figure 1). Neither making trait indicators more specific (**Realo & Allik**) nor relying on identical indicators (**Weiss & Adams**) will automatically achieve comparability of trait constructs; instead, congruence must be established *empirically* for each set of indicators in each population anew. The same argument applies to the comparability of situations across different populations (**Nave, Sherman & Funder**).

The issue of trait operationalisation across populations, especially species, involves one of the most fundamental issues in the philosophy of sciences: How can we pursue objectivity? What does it mean to peer into the world scientifically (Daston & Galison, 2007)? Identical trait expressions never occur among species (and in fact often not even among same-species individuals). Attempts to generate trait indicators as 'common metrics' that are comparable across species by filtering out these obvious incongruities *implicitly* are therefore prone to bias (Uher & Asendorpf, 2008). Such trait indicators are the results of 'fallible human' researchers 'who impose regularity and comparability that

shuns incongruence' in trait expressions and may never be accurate for all species (Daston & Galison, 2007, p. 15). Instead, operationalisations of the same trait constructs have to be (and often can be) adjusted to the specifics of each population.

For example, the situational settings and the behavioural measures used to study shyness–boldness differ between species. Whereas squids (*Euprymna tasmanica*) are touched on their arms with eyedroppers (Sinn et al., 2006), birds (*Parus major*) are confronted with plates springing up in front of them (van Oers et al., 2005), and crabs (*Pagurus bernhardus*) are lifted out of the water and held shortly upside-down before they are replaced with their shell aperture facing upwards (Briffa et al., 2008). These different procedures simulate species-specific threat situations that are ecologically valid for each species but not identical across them. The behavioural responses elicited in these studies are likewise species specific; squids move away by jet propulsion or grab the stimuli with their arms, birds fly away and crabs withdraw into their shells; latencies to return or re-emerge respectively are measured as indicators of shyness–boldness. Despite their obvious incongruence, all these trait indicators reflect a degree of risk taking and recovery from a startle within each species' behavioural ecology. The common metric thus arises from the shared biological functions of the situations and behaviours, and from the structure of empirical convergence of the multiple indicators within each species that are used to infer the underlying trait construct.

A methodology for establishing structural equivalence of trait constructs for comparisons at different population levels *empirically* was developed in cross-cultural psychology (van de Vijver & Poortinga, 2002). These authors point out four fallacies in multi-level research due to crossing two fallacy dimensions. The first dimension refers to the kind of characteristic that is incorrectly applied to another level, which can be either a score value, that is data obtained from the individuals might not apply to the population and vice versa (*level fallacies*), or a concept (*structural fallacies*). The second dimension specifies the direction of this incorrect inference, that is to a population level of higher order (*generalisation fallacies*) or lower order (*specification fallacies*). Whether level fallacies are committed is analysed with hierarchical linear models (e.g. Bryk & Raudenbush, 1992); to analyse structural fallacies, van de Vijver and Poortinga (2002) proposed a methodology based on exploratory multi-level factor analysis.

Structural or functional equivalence of constructs across different population levels forms important evidence that these constructs have the same psychological meaning across these levels. Van de Vijver and Poortinga (2002) emphasise that even when structural equivalence was shown at the individual level, aggregation on the population level may cause shifts in the meaning of trait constructs (van de Vijver & Leung, 1997a, 1997b). This means that equivalence at the individual level is a necessary but insufficient condition for cross-level equivalence. Demonstrating factorial congruence at different levels of aggregation is both a necessary and sufficient condition for the structural equivalence of a set of indicators reflecting same meaning of the constructs across different population levels and thus an *empirical* common metric. If constructs are not structurally equivalent, scores at one level involve partially or entirely different constructs so that interpretations become vulnerable to generalisation or specification fallacies (van de Vijver & Poortinga, 2002). If a construct is not adequately measured, correlations with important external variables (e.g. environmental parameters) are also compromised (Chen & West, 2008).

Generalising the technique of Muthén (1991, 1994), van de Vijver and Poortinga (2002) proposed to examine congruence of constructs by comparing the data structure of the

studied trait indicators using three types of covariance matrices. Similar to the Leung and Bond (1989) methodology, the first is a (*universal*) common-covariance matrix of the total sample performed on all individuals ignoring their population membership; the second is a (pooled *population-specific*) pooled-within covariance matrix based on the separate populations' factor loadings (weighted by their sample size); the third is a (*population-comparative*) between-covariance matrix computed on the basis of the population means of the various indicators. After target rotation has been carried out, the degree to which the factor loadings of comparable trait indicators are equal at different population levels is then analysed statistically as agreement between the different matrices using factor congruence coefficients (for detailed descriptions on the specific procedures see van de Vijver & Leung, 1997a, 1997b; van de Vijver & Poortinga, 2002).

First steps towards full application of this methodology have already been taken in animal personality research. For example, the structures of anxiety-related behaviours in the widely used elevated plus-maze test were compared in mice (*Mus musculus*) and pigs (*Sus scrofa*), two mammalian species with different evolutionary origins, morphological sizes and behavioural repertoires (Janczak, Andersen, Frevik, Bøe, & Bakken, 2002). The similarities of the correlation matrices of these two species' behaviours were compared only descriptively in this study (due to lack of pertinent statistical methods, p. 159), but a more recent study could demonstrate a statistical analysis of the cross-setting equivalence of some Big Five factors rated in two different populations of captive chimpanzees (Weiss et al., 2007). The methodology of van de Vijver and Poortinga (2002) can be used to analyse the cross-level equivalence of trait constructs in multiple populations or species.

In principle, analyses of the equivalence of trait operationalisations across language- and culture-specific trait indicators are structurally identical to those of the equivalence of operationalisations across species-specific behavioural trait indicators. Lexical personality research can take advantage of the tremendous efforts taken in linguistic research to compile dictionaries that translate different languages into one another. To analyse the structural equivalence of species-specific behavioural trait indicators and related situational properties across species, behavioural personality research has to rely on the efforts taken in the behavioural sciences to uncover the biological functions of specific behaviours and situations in each species.

Given the enormous diversity of species, this task can only advance stepwise and requires separate consideration of behaviours and situational properties that are nevertheless interdependent. The Janczak et al. (2002) study used a suitable design to compare species-typical factor structures of behavioural trait indicators in a more or less identical situation. Designs that allow comparing different situational properties across species are also needed. An often neglected but crucial aspect is situational strength. It is obvious that the proportion of individuals classified as shy or bold in a sample varies with the strength of the studied situation; too strong stimuli restrict behavioural variation too much so that most individuals will appear shy. Therefore, the strength of each studied situation has to be chosen such that similar distributions of behavioural types across species result (e.g. norm distribution). This will lay the foundations for empirical studies of universal trait dimensions (see my target paper). For example, because antelopes as a species are observably shyer than lions, the absolute situational strength needed to obtain a norm distribution of shyness–boldness behaviour in antelopes will be much weaker than that needed to obtain a norm distribution in lions. This difference in absolute situational strength is thus informative for comparisons of the species' mean scores that identify their

positioning effects on the shared dimension. These positioning effects are needed to distinguish weak from strong universal trait dimensions.

PERSPECTIVES FOR FUTURE RESEARCH

A substantial body of methodology has been developed over the last century that permits tackling central issues in comparative personality research. But this expertise is scattered over various disciplines that are unfortunately lacking systematic exchange and collaboration. Biological disciplines that have started to study inter-individual differences only relatively recently (Sih et al., 2004) could profit greatly from the methodological and statistical advances made in psychological disciplines. Many fascinating studies are published on an ever growing number of species that often fail to unfold their full potential because suitable analytical methods are only insufficiently known. This applies in particular to factor analytic methods that are central to extract complex trait dimensions such as behavioural syndromes from a wide range of behaviours and to analyse their structural equivalence across populations.

In its relatively short history, biological personality research could nonetheless establish impressive evidence for the existence of personality differences even in distantly related species that—if someone had merely hypothesised the possibility of their existence—would have been regarded as audacious by most psychologists. Yet, human personality psychology continues to ignore this growing evidence beyond the species borders (Gosling, 2008), and only a small group of psychologists is concerned with animal personality. However, incorporating evolutionary theory into human personality research has already paved the way for broader, less anthropocentric psychological views on personality. Instead of restricting their interests to the most recent evolutionary past of one single species, *Homo sapiens*, psychologists would profit from considering the full scope of Darwinian theory to learn more about the evolutionary origins of our species and about basic mechanisms of phylogeny and adaptivity that can only be unravelled by exploring the evolved diversity of species.

It will be of foremost interest to identify comprehensive representations of the species' major dimensions of personality variation (i.e. their *hierarchical trait taxonomies*) as systematic reference models for any research aimed at their evolution, function, causation and development. Ideally, the *domains* of personality variation covered by each species' trait taxonomy should be identified through convergent evidence from different comprehensive methodologies (e.g. systematic bottom-up approaches and adaptive approaches, see my target paper). Suitable *measures* of these domains that match their specific manifestation should be identified for each studied population. Their ability to operationalise a trait construct comparably across different populations and population levels (i.e. their structural equivalence) should be analysed empirically using the methodology proposed by van de Vijver and Poortinga (2002).

A key component in such endeavours is the development of *basic principles to establish functional equivalence* and thus comparability of non-identical behavioural trait indicators and situational properties across different populations, particularly species. These principles will have to be based on the ecological properties of behaviours and situations for each population that provide the basis of cross-level comparisons of covariance

matrices. For example, functional equivalence of shyness–boldness indicators could be established by the degree of risk taking inherent to different situations for each species and by the probability to which different behaviours allow perceiving, reducing, escaping from or even repelling acute threats. More fine-grained analyses could follow that analyse the proportion of different types of risk-taking behaviours typically shown in a species as further indicators of species-level differences in shyness–boldness. For example, prey species such as antelopes will show more flight than fight behaviours, whereas predator species such as lions will show an opposite pattern, and species that are both prey and predator may show a more balanced proportion of both. Species may also be differentiated by their proportions of different types of risk-taking behaviours when seeking out situations in the first place.

Merging the evolutionary notion of personality traits as evolved strategies based on trade-offs with different costs and benefits (Bell, 2007b; Buss, 1991; Sih et al., 2004) with Mischel's notion of personality traits as the 'conditional probability of a category of behaviours in a category of contexts' (Wright & Mischel, 1987) could thus permit defining personality traits by their bio-socio-ecological functions. These functions probably become more apparent in behavioural trait indicators than in lexical indicators that are based on perceptions of lay people filtered and modified by cognitive, social and cultural appraisal processes. Concepts of folk psychology often fail to reflect underlying biological and evolutionary processes and mechanisms adequately. Defining trait constructs by their bio-socio-ecological functions may therefore help to reduce the 'present Babel' (Realo & Allik) of the predominantly lexically derived concepts and measurement scales in psychology. For more strongly biologically determined universal trait constructs, bio-socio-ecological functions are probably more obvious and more general than for predominantly culturally or cognitively determined uniquely human trait constructs, for which bio-socio-ecological functions may be much more fine-grained and therefore more difficult to unravel.

Comprehensive trait taxonomies and structurally equivalent trait constructs form the basis of systematic species comparisons to identify species-specific, weak and strong universal trait *dimensions* (see my target paper) that will be particularly illuminative in understanding evolutionary principles underlying personality variation.

I have explored three methodological core issues framing a voluminous but promising research agenda for comparative personality research that capitalises on the complementarity of the different expertises of the disciplines involved. We should start to diminish the hindering barriers and establish systematic exchange and cross-disciplinary collaborations to exploit this synergy. My suggestions of a common methodological framework within which I began to consolidate established conceptions across disciplines and to expand them to species comprehensive approaches can only be a starting point for future research.

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REFERENCES TO DISCUSSION SECTION

- Allik, J., & McCrae, R. R. (2002). A five-factor theory perspective. In R. R. McCrae, & J. Allik (Eds.), *The five-factor model of personality across cultures* (pp. 303–321). New York, NY: Kluwer Academic/Plenum Publishers.
- Allport, G. W. (1937). *Personality: A psychological interpretation*. New York, NY: Macmillan.
- Allport, G. W. (1961). *Pattern and growth in personality*. New York: Holt, Rinehart, and Winston.
- Allport, G. W., & Odbert, H. G. (1936). Trait names: A psycholexical study. *Psychological Monographs*, 47, 1.
- Bates, T. C. (2007). Discussion on 'The evolutionary genetics of personality' by Penke, Denissen and Miller. *European Journal of Personality*, 21, 589–591.
- Bateson, P. (1988). The active role of behaviour in evolution. In M.-W. Ho, & S. Fox (Eds.), *Process and metaphors in evolution* (pp. 191–207). Chichester, UK: Wiley.
- Baumeister, R. F., Vohs, K. D., & Funder, D. C. (2007). Psychology as the science of self-reports and finger movements: Whatever happened to actual behavior? *Perspectives in Psychological Science*, 2, 396–408.
- Bell, A. M. (2007a). Animal personalities. *Nature*, 447, 539–640.
- Bell, A. M. (2007b). Future directions in behavioral syndromes research. *Proceedings of the Royal Society Biological Sciences Series B*, 274, 755–761.
- Bell, A. M., & Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, 10, 828–834.
- Belyaev, D. K. (1969). Domestication of animals. *Science Journal (U.K.)*, 5, 47–52.
- Bem, D. J., & Funder, D. C. (1978). Predicting more of the people more of the time: Assessing the personality of 477 situations. *Psychological Review*, 85, 485–501.
- Berry, J. W., Poortinga, Y. H., Segall, M. H., & Dasen, P. R. (2002). *Cross-cultural psychology: Research and applications* (2nd ed.). Cambridge, UK: Cambridge University Press.
- Block, J. (1978). *The Q-sort method in personality assessment and psychiatric research*. Palo Alto, CA: Consulting Psychologists Press. (Original work published in 1961.)
- Boesch, C., & Tomasello, M. (1998). Chimpanzee and human cultures. *Current Anthropology*, 39, 591–634.
- Bond, M. H. (2002). Reclaiming the individual from Hofstede's ecological analysis—A 20-year Odyssey: Comment on Oyserman et al. (2002). *Psychological Bulletin*, 128, 73–77.
- Boon, A. K., Reale, D., & Boutin, S. (2007). The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters*, 10, 1094–1104.
- Briffa, M., Rundle, S. D., & Fryer, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: Animal personalities in the hermit crab (*Pagurus bernhardus*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, 275, 1335–1311.
- Brodie, III, E. D., & Russell, N. H. (1999). The consistency of individual differences in behaviour: Temperature effects on antipredator behaviour in garter snakes. *Animal Behaviour*, 57, 445–451.
- Bryk, A. S., & Raudenbush, S. W. (1992). *Hierarchical linear models: Applications and data analysis*. Newbury Park, CA: Sage.
- Buss, D. M. (1999). *Evolutionary psychology: The new science of the mind*. Boston, MA: Allyn & Bacon.
- Carere, C., Drent, P. J., Privitera, L., Koolhaas, J. M., & Groothuis, T. G. G. (2005). Personalities in great tits (*Parus major*): Stability and consistency. *Animal Behaviour*, 70, 795–805.
- Carere, C., & van Oers, K. (2004). Shy and bold great tits (*Parus major*): Body temperature and breath rate in response to handling stress. *Physiology and Behavior*, 82, 905–912.
- Chamberlin, T. C. (1965). The method of multiple working hypotheses. *Science*, 148, 754–759. (Original work published, 1890.)
- Chen, F. F., & West, S. G. (2008). Measuring individualism and collectivism: The importance of considering different components, reference groups, and measurement invariance. *Journal of Research in Personality*, 42, 259–294.
- Chen, X., Cen, G., Li, D., & He, Y. (2005). Social functioning and adjustment in Chinese children: The imprint of historical time. *Child Development*, 76, 182–195.
- Church, A. T. (2001). Personality measurement in cross-cultural perspective. *Journal of Personality*, 69, 979–1006.

- Costa, P. T., & McCrae, R. R. (1995). Domains and facets: Hierarchical personality assessment using the revised NEO Personality Inventory. *Journal of Personality Assessment*, *64*, 21–50.
- Cronbach, L. J., & Meehl, P. E. (1955). Construct validity in psychological tests. *Psychological Bulletin*, *52*, 281–302.
- Dall, S. R. X., Houstain, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, *7*, 734–739.
- Daston, L., & Galison, P. (2007). *Objectivity*. Boston, MA: Zone Books.
- De Raad, B., & Barelds, D. P. H. (2008). A new taxonomy of Dutch personality traits based on a comprehensive and unrestricted list of descriptors. *Journal of Personality and Social Psychology*, *94*, 347–364.
- Denissen, J. J. A., van Aken, M. A. G., & Roberts, B. W. (2008). *Personality development across the life span* (submitted for publication).
- DeWitt, T. J., Sih, A., & Wilson, D. S. (1998). Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution*, *13*, 77–81.
- Drent, P. J., Van Oers, K., & Van Noordwijk, A. J. (2003). Realized heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, *270*, 45–51.
- Epstein, S. (1979). The stability of behavior: I. On predicting most of the people much of the time. *Journal of Personality and Social Psychology*, *37*, 1097–1126.
- Epstein, S. (1980). The stability of behavior: II. Implications for psychological research. *American Psychologist*, *35*, 790–806.
- Eysenck, H. J. (1990). Biological dimensions of personality. In L. Pervin (Ed.), *Handbook of personality theory and research* (pp. 244–276). New York, NY: Guilford.
- Fairbanks, A. (2001). Individual differences in response to a stranger: Social impulsivity as a dimension of temperament in vervet monkeys (*Cercopithecus aethiops sabaeus*). *Journal of Comparative Psychology*, *115*, 22–28.
- Fairholm, E. E. (in preparation). *Horses and ponies: More than just a size difference?*
- Fast, L. A., & Funder, D. C. (2008). Personality as manifest in word use: Correlations with self-report, acquaintance report, and behaviour. *Journal of Personality and Social Psychology*, *94*, 334–346.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, *125*, 1–15.
- Fiske, A. P. (1991). *Structures of social life: The four elementary forms of human relations*. New York, NY: The Free Press.
- Fleeson, W. (2004). Moving personality beyond the person-situation debate: The challenge and the opportunity of within-person variability. *Current Directions in Psychological Science*, *13*, 83–87.
- Frost, A. J., Winfrow-Giffen, A., Ashley, P. J., & Sneddon, L. U. (2007). Plasticity in animal personality traits: Does prior experience alter the degree of boldness? *Proceedings of The Royal Society B*, *274*, 333–339.
- Funder, D. C. (1995). On the accuracy of personality judgment: A realistic approach. *Psychological Review*, *102*, 652–670.
- Funder, D. C. (1999). *Personality judgment: A realistic approach to person perception*. San Diego, CA: Academic Press.
- Funder, D. C. (2001). Personality. *Annual Review of Psychology*, *52*, 197–221.
- Funder, D. C. (2006). Towards a resolution of the personality triad: Persons, situations and behaviors. *Journal of Research in Personality*, *40*, 21–34.
- Funder, D. C. (in press). Persons, situations and person-situation interactions. In O. P. John, R. Robins, & L. Pervin (Eds.), *Handbook of personality research* (3rd ed.). New York, NY: Guilford.
- Funder, D. C., Furr, R. M., & Colvin, C. R. (2000). The Riverside behavioral Q-sort: A tool for the description of social behavior. *Journal of Personality*, *68*, 451–489.
- Goldberg, L. R. (1990). An alternative “description of personality”: The Big-Five factor structure. *Journal of Personality and Social Psychology*, *59*, 1216–1229.
- Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, *127*, 45–86.
- Gosling, S. D. (2008). Personality in nonhuman animals. *Social and Personality Psychology Compass*, *2*, 985–1001.

- Gosling, S. D., & Graybeal, A. (2007). Tree thinking: A new paradigm for integrating comparative data in psychology. *Journal of General Psychology, 134*, 259–277.
- Gosling, S. D., Kwan, V. S. Y., & John, O. P. (2003). A dog's got personality: A cross-species comparative approach to evaluating personality judgments. *Journal of Personality and Social Psychology, 85*, 1161–1169.
- Gosling, S. D., Lilienfeld, S. O., & Marino, L. (2003). Personality. In D. Maestriepieri (Ed.), *Primate psychology* (pp. 254–288). Cambridge, MA: Harvard University Press.
- Guilford, J. P. (1959). *Personality*. New York, NY: McGraw-Hill.
- Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Science, 9*, 439–444.
- Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford, UK: Oxford University Press.
- Havighurst, R. J. (1972). *Developmental tasks and education*. New York, NY: Mac Kay Company.
- Heine, S. J., Lehman, D. R., Peng, K., & Greenholtz, J. (2002). What's wrong with cross-cultural comparisons of subjective Likert scales: The reference-group problem. *Journal of Personality and Social Psychology, 82*, 903–918.
- Ibáñez, M. I., Ávila, C., Ruipérez, M. A., Moro, M., & Ortet, G. (2007). Temperamental traits in mice (I): Factor structure. *Personality and Individual Differences, 43*, 255–265.
- Immerman, R. S., & W. C. Mackey (2003). Perspectives on human attachment (pair bonding): Eve's unique legacy of a canine analogue. *Evolutionary Psychology, 1*, 138–154.
- Janczak, A. M., Andersen, I. L., Frevik, G., Bøe, K. E., & Bakken, M. (2002). Factor analysis of behaviour in the porcine and murine elevated plus-maze models of anxiety. *Applied Animal Behavior Science, 77*, 155–165.
- Jang, K. L., Livesley, W. J., Ando, J., Yamagata, S., Suzuki, A., Angleitner, A., et al. (2006). Behavioral genetics of the higher-order factors of the Big Five. *Personality and Individual Differences, 41*, 261–272.
- John, O. P. (1990). The “Big Five” factor taxonomy: Dimensions of personality in the natural language and questionnaires. In L. A. Pervin (Ed.), *Handbook of personality: Theory and research* (pp. 66–100). New York, NY: The Guilford Press.
- John, O. P., & Srivastava, S. (1999). The Big Five trait taxonomy: History, measurement, and theoretical perspectives. In L. A. Pervin, & O. P. John (Eds.), *Handbook of personality: Theory and research* (2nd ed., pp. 102–138). New York, NY: Guilford.
- King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality, 31*, 257–271.
- King, J. E., & Landau, V. I. (2003). Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? *Journal of Research in Personality, 37*, 1–15.
- King, J. E., Weiss, A., & Farmer, K. H. (2005). A chimpanzee (*Pan troglodytes*) analogue of cross-national generalization of personality structure: Zoological parks and an African sanctuary. *Journal of Personality, 73*, 389–410.
- King, J. E., Weiss, A., & Sisco, M. M. (submitted). Aping humans: Stability and change in chimpanzee and human personality.
- Knutson, B., Burgdorf, J., & Panksepp, J. (1998). Anticipation of play elicits high-frequency ultrasonic vocalizations in young rats. *Journal of Comparative Psychology, 112*, 65–73.
- Kwan, V. S. Y., Gosling, S. D., & John, O. P. (2008). Anthropomorphism as a special case of social perception: A cross-species comparative approach and a new empirical paradigm. *Social Cognition, 26*, 129–146.
- Leung, K., & Bond, M. H. (1989). On the empirical identification of dimensions for cross-cultural comparisons. *Journal of Cross Cultural Psychology, 20*, 133–151.
- Lewin, K. (1947). Frontiers in group dynamics: I. Concept, method and reality in social science; social equilibria and social change. *Human Relations, 1*, 5–41.
- Mällo, T., Matrov, D., Herm, L., Kiv, K., Eller, M., Rincken, A., et al. (2007). Tickling-induced 50-kHz ultrasonic vocalization is individually stable and predicts behaviour in tests of anxiety and depression in rats. *Behavioural Brain Research, 184*, 57–71.
- Markon, K. E., Krueger, R. F., & Watson, D. (2005). Delineating the structure of normal and abnormal personality: an integrative hierarchical approach. *Journal of Personality and Social Psychology, 88*, 139–157.

- Matthews, G., Deary, I. J., & Whiteman, M. C. (2003). *Personality traits* (2nd ed.). Cambridge, UK: Cambridge University Press.
- Mayr, E. (1985). *The growth of biological thought: Diversity, evolution, and inheritance*. Cambridge, MA: Belknap Press.
- McCrae, R. R., & Costa, P. T., Jr. (1997). Personality trait structure as a human universal. *American Psychologist*, *52*, 509–516.
- McCrae, R. R., & Costa, P. T., Jr. (2003). *Personality in adulthood: A five-factor theory perspective*. New York, NY: Guilford Press.
- McCrae, R. R., Jang, K. L., Livesley, W. J., Riemann, R., & Angleitner, A. (2001). Sources of structure: Genetic, environmental, and artifactual influences on the covariance of personality traits. *Journal of Personality*, *69*, 511–535.
- McCrae, R. R., Terracciano, A., & 78 Members of the Personality Profiles of Cultures Project. (2005). Universal features of personality traits from the observer's perspective: Data from 50 cultures. *Journal of Personality and Social Psychology*, *88*, 547–561.
- Miller, A. (1994). *Death of a salesman*. Oxford, England: Heinemann Educational Publishers. (Original work published, 1949.)
- Mischel, W. (1968). *Personality and assessment*. New York, NY: Wiley.
- Mischel, W. (1977). The interaction of person and situation. In D. Magnusson, & N. S. Endler (Eds.), *Personality at the crossroads: Current issues in interactional psychology* (pp. 333–352). Hillsdale, NJ: Erlbaum.
- Mischel, W., Shoda, Y., & Mendoza-Denton, R. (2002). Situation-behavior profiles as a locus of consistency in personality. *Current Directions in Psychological Science*, *11*, 50–54.
- Mroczek, D. K., & Little, T. D. (Eds.) (2006). *Handbook of personality development*. Mahwah, NJ: Erlbaum.
- Müller, R., & von Keyserlingk, M. (2006). Consistency of flight speed and its correlation to productivity and to personality in *Bos Taurus* beef cattle. *Applied Animal Behaviour Science*, *99*, 193–204.
- Muthén, B. O. (1991). Multilevel factor analysis of class and student achievement components. *Journal of Educational Measurement*, *28*, 338–354.
- Muthén, B. O. (1994). Multilevel covariance structure analysis. *Sociological Methods and Research*, *22*, 376–398.
- Nettle, D. (2006). The evolution of personality variation in humans and other animals. *American Psychologist*, *61*, 622–631.
- Nettle, D. (2007). *Personality: What makes you the way you are*. Oxford, UK: Oxford University Press.
- Ozer, D.J., & Benet-Martinez, V. (2006). Personality and the prediction of consequential outcomes. *Annual Review of Psychology*, *57*, 401–421.
- Panksepp, J., & Burgdorf, J. (2003). “Laughing” rats and the evolutionary antecedents of human joy? *Physiology and Behaviour*, *79*, 533–547.
- Passini, F. T., & Norman, W. T. (1966). A universal conception of personality structure. *Journal of Personality and Social Psychology*, *4*, 44–49.
- Pavlov, I. P. (1906). The scientific investigation of the psychological faculties or processes in the higher animals. *Science*, *24*, 613–619.
- Penke, L., Denissen, J. J. A., & Miller, G. F. (2007). The evolutionary genetics of personality. *European Journal of Personality*, *21*, 549–587.
- Mozolowski, B. P., White, E. V., & Weiss, A. (in preparation). Personality and relationship factors may predict problem behaviours in dogs. Paper presented at the *Annual Meeting of the Society for Personality and Social Psychology*, Palm Springs, CA.
- Réale, D., Gallant, B. Y., Leblanc M., & Festa-Bianchet, M. (2000). Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, *60*, 589–597.
- Realo, A. (2003). Comparison of public and academic discourses: Estonian individualism and collectivism revisited. *Culture and Psychology*, *9*, 47–77.
- Riechert, S. E., & Hedrick, A. V. (1990). Levels of predation and genetically based anti-predator behavior in the spider (*Agelenopsis aperta*). *Animal Behaviour*, *40*, 679–687.
- Roberts, B. W., Wood, D., & Smith, J. L. (2005). Evaluating five factor theory and social investment perspectives on personality trait development. *Journal of Research in Personality*, *39*, 166–184.

- Rowe, D. C. (1982). Monozygotic twin cross-correlations as a validation of personality structure: A test of the semantic bias hypothesis. *Journal of Personality and Social Psychology*, *43*, 1072–1079.
- Rychlak, J. F. (1968). *A philosophy of science for personality theory*. Boston, MA: Houghton Mifflin.
- Saether, S. A., Saetre, G. P., Borge, T., Wiley, C., Svedin, N., Andersson, G., et al. (2007). Sex chromosome-linked species recognition and evolution of reproductive isolation in flycatchers. *Science*, *318*, 95–97.
- Saucier, G., & Goldberg, L. R. (1998). What is beyond the Big Five? *Journal of Personality*, *66*, 495–524.
- Schimmack, U., Oishi, S., & Diener, E. (2005). Individualism: A valid and important dimension of cultural differences between nations. *Personality and Social Psychology Review*, *9*, 17–31.
- Shadish, W. R. (1993). Critical multiplism: A research strategy and its attendant tactics. *New Directions for program evaluation*, *60*, 13–57.
- Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioural syndromes: An integrative overview. *The Quarterly Review of Biology*, *79*, 241–277.
- Sinn, D. L., Apiolaza, L. A., & Moltschaniwskyj, N. A. (2006). Heritability and fitness-related consequences of squid personality traits. *Journal of Evolutionary Biology*, *19*, 1437–1447.
- Sinn, D. L., & Moltschaniwskyj, N. A. (2005). Personality traits in dumpling squid (*Euprymna tasmanica*): Context-specific traits and their correlation with biological characteristics. *Journal of Comparative Psychology*, *119*, 99–110.
- Sneddon, L. U. (2003). The bold and the shy: Individual differences in rainbow trout. *Journal of Fish Biology*, *62*, 971–975.
- Soldz, S., & Vaillant, G.E. (1999). The big five personality traits and the life course: A 45-year longitudinal study. *Journal of Research in Personality*, *33*, 208–232.
- Spoolder, H. A. M., Burbidge, J. A., Lawrence, A. B., Simmins, P. H., & Edwards, S. A. (1996). Individual behavioural differences in pigs: Intra-and inter-test consistency. *Applied Animal Behaviour Science*, *49*, 185–198.
- Sroufe, L.A. (1979). The coherence of individual development: Early care, attachment, and subsequent developmental issues. *American Psychologist*, *34*, 834–841.
- Stark, S., Chernyshenko, O. S., & Drasgow, F. (2006). Detecting differential item functioning with confirmatory factor analysis and item response theory: Toward a unified strategy. *Journal of Applied Psychology*, *91*, 1292–1306.
- Stern, W. (1911). *Die differentielle Psychologie in ihren methodischen Grundlagen* (2. Auflage). [Differential Psychology in its methodological foundations (2nd ed.)]. Leipzig, Germany: Barth.
- Svartberg, K. (2006). Breed-typical behaviour in dogs—Historical remnants or recent constructs? *Applied Animal Behaviour Science*, *96*, 293–313.
- Ten Berge, M. A., & De Raad, B. (1999). Taxonomies of situations from a trait psychological perspective. A review. *European Journal of Personality*, *13*, 337–360.
- Tett, R. P., & Guterman, H. A. (2000). Situation trait relevance, trait expression, and cross-situational consistency: Testing a principle of trait activation. *Journal of Research in Personality*, *34*, 397–423.
- Tinbergen, N. (1963). On aims and methods in ethology. *Zeitschrift für Tierpsychologie*, *20*, 410–433.
- Tooby, J., & Cosmides, L. (1989). Adaptation versus phylogeny: The role of animal psychology in the study of human behavior. *International Journal of Comparative Psychology*, *2*, 175–188.
- Triandis, H. C. (1988). Collectivism and individualism: A reconceptualization of a basic concept in cross-cultural psychology. In G. K. Verma, & C. Bagley (Eds.), *Personality, attitudes, and cognitions* (pp. 60–95). London, UK: MacMillan.
- Triandis, H. C. (1995). *Individualism and collectivism*. Boulder, CO: Westview.
- Triandis, H. C., McCusker, C., Betancourt, H., Iwao, S., Leung, K., Salazar, J. M., et al. (1993). An emic-etic analysis of individualism-collectivism. *Journal for Cross-Cultural Psychology*, *24*, 366–383.
- Trut, L. N. (1999). Early canid domestication: The farm-fox experiment. *American Scientist*, *87*, 160–169.
- Tuttle, R. (2001). Culture and traditional chimpanzees. *Current Anthropology*, *42*, 407–409.
- Uher, J. (under review). Personality in nonhuman primates: What can we learn from human personality psychology? In A. Weiss, J. E. King, & L. Murray (Eds.), *Personality and behavioral syndromes in nonhuman primates*. New York, NY: Springer.

- Uher, J., & Asendorpf, J. B. (2008). Personality assessment in the Great Apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality, 42*, 821–838.
- Uher, J., Asendorpf, J. B., & Call, J. (2008). Personality in the behaviour of Great Apes: Temporal stability, cross-situational consistency and coherence in response. *Animal Behaviour, 75*, 99–112.
- van de Vijver, F. J. R., & Leung, K. (1997a). Methods and data analysis of comparative research. In J. W. Berry, Y. H. Poortinga, & J. Pandey (Eds.), *Handbook of cross-cultural psychology* (2nd ed., Vol. 1, pp. 257–300). Boston, MA: Allyn & Bacon.
- van de Vijver, F. J. R., & Leung, K. (1997b). *Methods and data analysis for cross-cultural research*. Newbury Park, CA: Sage.
- van de Vijver, F. J. R., & Poortinga, Y. H. (2002). Structural equivalence in multilevel research. *Journal of Cross-Cultural Psychology, 141*, 141–156.
- van Oers, K., De Jong, G., Van Noordwijk, A. J., Kempenaers, B., & Drent, P. J. (2005). Contribution of genetics to the study of animal personalities: A review of case studies. *Behaviour, 142*, 1185–1206.
- van Oers, K., Drent, P. J., Dingemanse, N. J., & Kempenaers, B. (in press). Personality is associated with extra-pair paternity in great tits (*Parus major*). *Animal Behaviour*.
- van Oers, K., Klunder, M., & Drent, P. J. (2005). Context dependence of avian personalities: Risk-taking behavior is domain specific. *Behavioral Ecology, 16*, 716–723.
- Van Oortmerssen, G. A., & Bakker, T. C. M. (1981). Artificial selection for short and long attack latencies in wild *Mus musculus domesticus*. *Behavior Genetics, 11*, 115–126.
- van Schaik, C. P. (2004). *Among orangutans: Red apes and the rise of human culture*. Cambridge, MA: Harvard University Press.
- Vandello, J. A., & Cohen, D. (1999). Patterns of individualism and collectivism across the United States. *Journal of Personality and Social Psychology, 77*, 279–292.
- Vazire, S., Gosling, S. D., Dickey, A. S., & Schapiro, S. J. (2007). Measuring personality in nonhuman animals. In R. W. Robins, R. C. Fraley, & R. F. Krueger (Eds.), *Handbook of research methods in personality psychology* (pp. 190–206). New York, NY: Guilford Press.
- Verbeek, M. E. M., Boon, A., & Drent, P. J. (1996). Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour, 133*, 945–963.
- Voronov, M., & Singer, J. A. (2002). The myth of individualism-collectivism: A critical review. *Journal of Social Psychology, 142*, 461–480.
- Wagerman, S. A., & Funder, D. C. (January 2006). The Riverside Situational Q-Sort: A tool for understanding the psychological properties of situations. Poster presented at the *Annual Meeting of the Society for Personality and Social Psychology*, Palm Springs, CA.
- Wagerman, S. A., & Funder, D. C. (in press). Situations. In P. J. Corr, & G. Matthews (Eds.), *Cambridge handbook of personality*. Cambridge, UK: Cambridge University Press.
- Walsh, R. N., & Cummins, R. A. (1976). The open-field test: A critical review. *Psychological Bulletin, 83*, 482–504.
- Weiss, A., & Costa, P. T., Jr. (2005). Domain and facet personality predictors of all-cause mortality among Medicare patients aged 65 to 100. *Psychosomatic Medicine, 67*, 724–733.
- Weiss, A., King, J. E., & Hopkins, W. D. (2007). A cross-setting study of chimpanzee (*Pan troglodytes*) personality structure and development: Zoological Parks and Yerkes National Primate Research Center. *American Journal of Primatology, 69*, 1264–1277.
- Weiss, A., King, J. E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology, 90*, 501–511.
- Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution, 9*, 442–446.
- Wittmann, W. W. (1987). Foundations of successful psychological research: Multimodal assessment, multiplism, and multivariate theory of reliability and validity. *Diagnostica, 33*, 209–226.
- Wolf, M., van Doorn, S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature, 447*, 581–584.
- Wright, J. C., & Mischel, W. (1987). A conditional approach to dispositional constructs: The local predictability of social behavior. *Journal of Personality and Social Psychology, 55*, 454–469.
- Yamagata, S., Suzuki, A., Ando, J., Ono, Y., Kijima, N., Yoshimura, K., et al. (2006). Is the genetic structure of human personality universal? A cross-cultural twin study from North America, Europe, and Asia. *Journal of Personality and Social Psychology, 90*, 987–998.