Comparative Personality Research: Methodological Approaches

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Abstract

In the broadest sense, personality refers to stable inter-individual variability in behavioural organisation within a particular population. Researching personality in human as well as nonhuman species provides unique possibilities for comparisons across species with different phylogenies, ecologies and social systems. It also allows insights into mechanisms and processes of the evolution of population differences within and between species. The enormous diversity across species entails particular challenges to methodology. This paper explores theoretical approaches and analytical methods of deriving dimensions of inter-individual variability on different population levels from a personality trait perspective. The existing diversity suggests that some populations, especially some species, may exhibit different or even unique trait domains. Therefore, a methodology is needed that identifies ecologically valid and comprehensive representations of the personality variation within each population. I taxonomise and compare current approaches in their suitability for this task. I propose a new bottom–up approach—the behavioural repertoire approach—that is tailored to the specific methodological requirements of comparative personality research. Initial empirical results in nonhuman primates emphasise the viability of this approach and highlight interesting implications for human personality research. Copyright © 2008 John Wiley & Sons, Ltd.

INTRODUCTION

Crossing the species borders inspires fascinating research questions about the nature and origins of personality. The shift in perspective from humans to the enormous diversity of today's species opens a huge field of research that allows profound and illuminative insights into personality. What is unique about *Homo sapiens* compared to all other species in the phylogenetic tree? What personality traits may have contributed to *Homo sapiens'*

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accelerated development in the most recent evolutionary past and to its unmatched success in conquering almost every habitat on earth? There is no better opportunity to understand the phylogenetic basis, adaptive significance and ecological relevance of personality and its role in speciation than studying the evolved diversity of species. Moreover, the greater possibilities for observation of naturalistic behaviour and experimental control made possible by shorter reproduction cycles and life spans make many nonhuman species good candidates for systematic studies of the genetic, biological and social basis of personality (Clarke & Boinski, 1995; Gosling, 2001; Gosling & Graybeal, 2007).

Comparative personality research in the broadest sense is the study of stable inter-individual variability in behavioural organisation in human and nonhuman species. It establishes general principles of the nature and origins of personality that are applicable to some or all of the species being compared. Its methodological strength relies on the possibilities to test and refine models, hypotheses and implications across many different populations. Comparative personality research is rooted in independent disciplines as different as animal personality psychology (Gosling, 2001), anthropology (Kottak, 2008), behavioural ecology (Sih, Bell, Johnson, & Ziemba, 2004), behaviour genetics (Plomin, DeFries, McClearn, & McGuffin, 2001), cross-cultural psychology (Berry, Poortinga, & Pandey, 1997), evolutionary biology (Futuyma, 1998), human personality psychology (Pervin, Cervone, & John, 2005), evolutionary psychology (Buss, 2005), livestock sciences (Grandin, 1998), neurosciences (Canli, 2006), theoretical biology (Dall, Houston, & McNamara, 2004; Wolf, van Doorn, Leimar, & Weissing, 2007), veterinary sciences or zoology (Svartberg & Forkman, 2002).

All these and other disciplines study personality variation, but an overarching theoretical and methodological framework is missing. The present work is an attempt to propose such a framework from a personality trait perspective that is generalised from the personality variation within human populations to nonhuman populations at various levels, including the level of species. The framework heavily draws on concepts and principles of cross-cultural psychology as far as it is concerned with cross-cultural differences in within-culture personality variation.

METHODOLOGICAL APPROACHES TO PERSONALITY DIFFERENCES WITHIN AND ACROSS SPECIES

In the broadest sense, personality refers to stable inter-individual variability in behavioural organisation within a particular population. It comprises behaviour regulating mechanisms within the individual conceived in trait psychological traditions as *personality traits* that can have genetic, neurobiological, cognitive, motivational and behavioural components, and that are thus higher-level phenomena than behaviour. Dynamic interactions between the individual's multiple trait dispositions with one another and with external situational features produce complex inter-individual differences in behaviour. Within nomothetic conceptions of personality, individuals differ continuously from one another in the degree to which they possess any particular personality trait. On the population level, traits are therefore conceived as latent dimensional variables that have the same meaning in all individuals, which permits comparing the relative positions of individuals to one another on these *trait dimensions*. Trait dimensions often covary empirically and can therefore be organised in hierarchical taxonomies that describe the *structure of personality differences* within a population. Narrow trait dimensions comprising more specific and homogeneous

trait domains are thereby subsumed within broader trait dimensions or trait factors comprising more general and heterogeneous trait domains (Allport, 1937; Matthews, Deary, & Whiteman, 2003).

The basic unit of analysis in personality research is the individual. It is studied from three interrelated viewpoints: uniqueness, comparability and universality. Uniqueness of the individual's behavioural organisation can only be quantified in relation to that of other individuals. This implies that individuals can be compared and that these comparisons depend on the reference population as the extended unit of analysis; both in turn determine quantifications of universality. Therefore, specifying the reference populations is vitally important (Matthews et al., 2003). For example, human personality psychology might use individuals sharing the same linguistic or cultural affiliation as a reference population. In nonhuman species, reference populations may share the same geographical distribution or habitat (King, Weiss, & Farmer, 2005), breed (Svartberg, 2006) or even cultural affiliation (Boesch & Tomasello, 1998; van Schaik, 2004). Going beyond that, comparative personality research can also define species as reference populations. Species are particularly interesting because they are supposed to represent the smallest biological populations that would not successfully interbreed due to intrinsic barriers such as genetic, morphological or behavioural differences, even in the absence of external, mainly geographical barriers (in contrast to subspecies or breeds; Campbell & Reece, 2005). Thus, species differ distinctively and not just continuously from another. The emphasis of this methodological discussion is therefore placed on species comparisons that can be drawn on different population levels nested in the biological classification such as within genera, families, order, classes or phyla.

The role of personality differences in evolution

Intra-species variation constitutes a variability reservoir for successful adaptations to environmental changes; it precedes speciation. As early as 1859, Darwin assumed that extreme within-species variation can trigger diversification of sub-populations that can evolve into new species. Different mechanisms of speciation are known. *Allopatric speciation* occurs when geographic barrier formation isolates sub-populations and hinders gene flow. *Parapatric speciation* occurs in continuously distributed populations living in adjacent habitats not separated by geographic barriers. Diversification happens because geographic neighbours are more likely to reproduce than random individuals, which also reduces gene flow. When adjacent habitats range along environmental gradients, varying selection pressures additionally increase the likelihood of localised adaptations that can generate disruptive selection. *Sympatric speciation* is supposed to occur within a single geographical area with unhindered gene flow because of genetic change and exploitation of new niches (Campbell & Reece, 2005; Doebeli & Dieckmann, 2003; Losos & Glor, 2003). These processes of speciation are often assumed to be slow and gradual, but alternative theories assume short periods of rapid and erratic change interspersed with long phases of equilibration (Bokma, 2002; Eldredge & Gould, 1972).

Although models and theories of speciation are mostly concerned with morphological traits, they may equally apply to personality traits. In fact, population differences in human personality seem to be related to active gene flow dynamics (Camperio Ciani, Capiluppi, Veronese, & Sartori, 2007). Behaviour and its dynamic organisation within individuals may play an important role in diversification and thus in speciation (Capitanio, 2004) because any behavioural advances increase the individuals' possibilities for responses to

and interaction with the environment that in turn can lead to neurological and morphological refinements. Behaviour is therefore considered a motor rather than a consequence of evolution (Piaget, 1978). Likewise, behavioural dispositions rather than size or reproductive capacity are assumed to be the key factors of artificial selection humans imposed on some species during domestication (Belyaev, 1969). In a 40-year experiment with farm foxes (*Vulpes fulvus*), strong selective breeding for tamability and against aggressiveness to humans was impressively shown to be associated with a host of changes in morphology, physiology and behaviour on which domesticated populations differ fundamentally from their wild forebears (Trut, 1999).

Because personality is assumed to be dynamic and multidimensional, small changes can result in significant differences in the behavioural output on which artificial or natural selection can act and trigger diversification (Capitanio, 2004; Hammock & Young, 2005). This also becomes apparent in variations in behavioural dispositions between breeds and in the pace of breeding new varieties in domesticated species. In dogs (*Canis familiaris*), for example, breed-typical behaviour seems to be much more strongly affected by the most recent selection than by past selection in the breeds' origin (Svartberg, 2006).

The effects of personality differences on behavioural output may be particularly pronounced in traits related to social behaviour, which seems to evolve quickly given the diversity of social organisations even among closely related species (Capitanio, 2004; Hammock & Young, 2005). In Rhesus macaques (*Macaca mulatta*), the composition of groups in terms of their members' personality significantly influences behaviour at the group level; for example, greater variability in sociability is associated with more affiliative behaviours (Capitanio, 2004). This seems to reflect the importance of complementarity in social relationships (Hinde, 1997) and of intra-species niche picking (Buss, 1999; Sih et al., 2004). In fact, due to their greater proximity, individuals uniformly high in sociability may face stronger competition for food and for opportunities to affiliate and may therefore counter increased affiliation with increased aggression. By influencing dyadic and group dynamics, personality differences may play important roles in the development of species differences in social organisation (Capitanio, 2004). Recent findings from comparative genomics support this idea. In rodents and primates, for example, the vasopressine receptor gene V1a seems to offer a polymorphic genetic mechanism of continuous phenotypic variation in social behaviour on both the individual and the species levels (Hammock & Young, 2005).

Thus, understanding differences among populations—in particular among species—may be closely connected to understanding differences among individuals. Systematic empirical investigation of personality variation within and across species can therefore allow important insights into the mechanisms of speciation and the vital role personality plays therein (Capitanio, 2004).

Comparisons of individual trait scores within and across species: Positioning and patterning effects

The main emphasis in comparative personality research is comparability among individuals within and across different populations. Comparability among individuals from different species, for example, implies similarity in personality dimensions in terms of components, distributions and correlates across species. Such comparisons are often compromised by the fact that the distributions of trait scores within the species differ across species, particularly the species-specific means and variances, and that the correlates of the given trait dimension are different across species. Because there is a clear parallel to similar

problems in human cross-cultural research, concepts and methods from cross-cultural psychology can be applied to the above questions.

Concerning cross-species differences in trait distributions, the approach by Leung and Bond (1989) can be applied. They distinguished different types of trait dimensions with regard to the inter-individual variation within and across cultures. *Species-specific trait dimensions* are confined to a 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*, by contrast, are applicable to all individuals of all target species (the possibility of such a trait dimension in macaque species is discussed in Capitanio, 2004). They allow comparisons of individuals across species. If all species share the same mean and variance of the trait distribution, they are *weak universal trait dimensions*. Individuals of different species can be directly compared on these traits. If the species' means or variances show significant variation along these dimensions, they are *strong universal trait dimensions*. Such dimensions are also *species-comparative trait dimensions* that are useful to quantify species differences. In this case, individuals of different species can be also compared but relative comparisons can be made only after standardisation of the trait scores within each species so that each species has the same mean and variance (e.g., z-transformation of scores); without such standardisation, the trait scores of individuals of different species would confound within- and between-species differences. This is a critical case for comparative personality research.

Species can also differ in the *correlational structure* of the different trait dimensions, even in the case of weak universal dimensions where the trait distributions are identical across species. Similar to the above distinction of types of trait dimensions, three types of correlational analyses, including factor analyses of many different trait dimensions, can be distinguished. *Species-specific analyses* correlate different trait dimensions within only one species. *Universal analyses* are performed on all individuals of different species. Thus, the species membership of the individuals is ignored. This approach confounds correlates of personality traits with correlates of species differences in the trait means in the case of strong universal trait dimensions. Therefore it is again important in such cases to standardise the data within each species before they are pooled for direct inter-individual comparisons across species. *Species-comparative analyses* correlate the trait means of different species on strong universal trait dimensions. They inform about correlates of the rank-order of species in trait means, for example, in boldness depending on the degree of being predator or prey species. Consequently, a species is characterised by its personality structure that may comprise both species-specific and universal trait dimensions that are shared with other species and on which the target species may show a unique configuration of trait variances and means.

Leung and Bond (1989) called the effects of cultures on trait distributions, particularly trait means, the cultures' *positioning effects,* and their effects on correlational structure their *patterning effects*. When this terminology is applied to comparative personality research from a trait perspective, important goals of this research can be described as identifying positioning and patterning effects of populations, particularly species, on personality trait dimensions.

Further levels of analysis

This multi-level approach to trait dimensions can be applied to inter-individual comparisons on different population levels. For example, species can be compared

within and across different taxa such as genera, order, animal classes or even phyla. Likewise, different sub-species or breeds can be compared to one another. Cross-cultural psychology compares socially defined lower-level populations such as cultures or nations (Leung & Bond, 1989). On each population level, there may be again population-specific, weak and strong universal trait dimensions applicable to the considered populations, and their correlational structure can be determined.

Because universality is often considered an indicator of evolutionary origins of personality traits (Gosling & Graybeal, 2007), systematic investigations using this methodology would illuminate possible evolutionary origins of personality traits. If, for example, universal trait dimensions exist in the about 200 primate species comprising lemurs, monkeys, apes and humans, this fact would suggest a common evolutionary history of selection pressures operating on these trait dimensions. What differentiates these 'primate traits' from traits of species of other animal orders like carnivores, insectivores or rodents? In what ways do the species of the animal classes within the phylum chordata— that is fishes, reptiles, amphibians, birds and mammals—differ from one another? Is there a trait dimension that species of all vertebrate classes share? And how do vertebrate species differ from invertebrate species—and what do they share?

The possibilities for comparisons in the phylogenetic tree are almost unlimited (Gosling & Graybeal, 2007). Whereas human personality psychology is confined to within-species comparisons, evolutionary anthropology is particularly interested in species comparisons across the zoological family *Hominidae* comprising humans (*Homo sapiens*) and their closest living relatives—the great apes, bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo pygmaeus*). Identifying universality and uniqueness within this family is considered illuminative regarding human evolution (Maestripieri, 2003). Studying these and other parts of the phylogenetic tree can unravel which of the traits *Homo sapiens* is exhibiting today are in fact uniquely human, which ones are uniquely hominoid, uniquely primate, uniquely mammalian or uniquely vertebrate.

Methods of assessment

Except for self-report-based assessments, all methods of personality assessment known in human personality research are probably applicable to nonhuman species, although few are regularly used to study stable inter-individual behavioural variability and the reliability and construct validity of its assessments. Direct behaviour measures have high face validity and are used by all disciplines in all species; their reliability requires sufficient aggregation of observations over time. Ratings by knowledgeable informants on either behaviour-descriptive verbs or on trait-adjectives are reliable and valid at least in some nonhuman species (Uher, under review, Uher & Asendorpf, in press).

All methods are useful in studying the patterning effects of populations, such as by comparing the factor-analytic personality structures of species, but methods are not equally valuable in studying their positioning effects. Instead, relative personality assessments as in rating methods hinder position comparisons between species (Capitanio, 2004). To a much smaller extent, this problem may also arise in subpopulations within a species. Raters base their judgements on implicit comparisons with reference populations; presumably, they thereby refer to similar individuals they know. Because individuals from different species are less similar than same-species individuals, implicit reference populations are more likely to refer to same-species individuals if not to individuals from even more

homogeneous within-species populations. Absolute differences between species may therefore not be appropriately represented in relative data derived from ratings on individuals; only absolute behaviour measures permit direct position comparisons between species (Capitanio, 2004). This problem may also occur in comparisons between lower-level populations such as between subspecies, breeds or cultures (see for example the recent controversy in human cross-cultural personality psychology between Ashton, 2007; McCrae, Terracciano, Realo, & Allik, 2007a, b; Perugini & Richetin, 2007; Terracciano et al., 2005). These methodological differences strongly suggest a multi-method approach for comparative personality research.

Ecologically valid operationalisations

How can we operationalise trait dimensions comparably in species as different as squids, finches and chimpanzees? Personality traits are internal behaviour-regulating mechanisms; the specific behaviours they regulate, however, may vary across species. In fact, the diversity of species-typical behaviours suggests substantial variation in trait manifestations among species. But even within-species populations such as sub-species, breeds or cultures may vary in trait expression.

A similar phenomenon is known on the individual level in humans and in different nonhuman species. Even same-species individuals differ in how they externalise the same trait. Such individual response specificity leads to stable individual response profiles that result in low correlations between responses on the sample level. Traits are often expressed in various responses that are not necessarily shown by all individuals; restricting trait operationalisation to a few responses can therefore result in misclassifying those individuals who primarily react with responses that are not measured (Asendorpf, 1988; Lacey, 1950; Uher, under review; Uher, Asendorpf, & Call, 2008).

The same argument can be applied to species-specific externalisations of traits; just like individual response profiles, species-typical trait expressions characterise species over time and may result in low correlations between species. Because particular externalisations are not necessarily shown by all species, restricting trait measures to specific responses can result in misclassifying those species that externalise the trait differently. To obtain valid assessments, operationalisations must recognise the existing diversity of behavioural externalisations in different species; considering species-specific manifestations is vital for cross-species comparative personality research.

Assumptions that trait operationalisations that are independent of species-typical manifestations facilitate species comparisons (Capitanio, 2004; Weiss, King, & Perkins, 2006) should therefore be considered with caution. Just as items of human personality inventories are translated into the languages of the studied populations, trait operationalisations must be adapted to the idiosyncrasies of different species (Gosling, 2001). For example, the dog's invitation to play resembles the cat's (*Felis silvestris catus*) threat to attack; this posture is no valid indicator of the same trait in both species. Instead, operationalisations should respect variations in the meanings and functions of behaviours across different species. This likewise applies to variations in trait expression that already occur on lower population levels. Humans, for example, differ on the national or cultural level not only in linguistic but also in behavioural expressions, especially in symbolic gestures that can sometimes have completely different or even opposite meanings, such as nodding versus head-shaking signalling agreement or disagreement.

Individual- or population-specific externalisations become manifest in specific habitual acts and trait-facets, which are located near to the bottom of hierarchies of trait dimensions. They are subsumed within broader personality factors located near to the top that are less specific and more heterogeneous (Costa & McCrae, 1995; Eysenck, 1990). Therefore, specific externalisations are less likely to emerge at more abstract levels of personality description, which suggests that more abstract operationalisations are also more comparable across populations. However, this should not obscure the fact that all operationalisations eventually refer to specific behavioural acts that are often individual- or population-specific. In fact, morphological differences result in differences in behavioural expression among individuals and even more among species. It is thus not sufficient to use abstract trait indicators; instead, relations to specific behaviours should be clearly defined. For example, operationalisations of aggressiveness in dogs versus cats should specify the different behavioural expressions of aggressiveness in these species; otherwise the assessments will be invalid.

This is important because abstraction is often done implicitly. In fact, although even same-species individuals do not show identical muscle activities and courses of movement, behaviours are often perceived in categories that apply to all individuals. Implicit abstraction for assessments in our own species that we access as conspecific insiders is less problematic than it may be for assessments in other species to which our access is limited because we are nonconspecific outsiders. One has to be, therefore, familiar with the meaning and function of specific behaviours to make valid personality assessments. Trait operationalisations are only ecologically valid and thus useful for comparisons across populations when they address the diversity in externalisations among them. Operationalisations used for multiple species thus require broader categories that refer to much more heterogeneous specific acts than those used for single species or particularly for more homogeneous populations within the same species.

Systematic studies of species-specific trait externalisations can identify *species-typical response profiles* that are comparable between species both in shape, which reflects a patterning effect of species, and in mean profile level, which reflects a positioning effect of species. This also allows grouping species with similar response profiles to identify profile types among species or classes of coherent responses that define lower-level trait dimensions on the species level. It is obvious that varying degrees of abstraction of the responses are needed to identify response profiles on different population levels. For example, more specific responses are required for breed-typical response profiles whereas more abstract responses are required for response profiles that characterise the species of particular genera.

Species and populations may also differ in how they perceive and respond to situations (Capitanio, 2004). For example, in standardised situations Rhesus macaques express more fearful responses than Hanuman langurs (*Presbytis entellus*; Singh & Manocha, 1966) and gibbons (*Hylobates lar, Hylobates pileatus*; Bernstein, Schusterman, & Sharpe, 1963). How can we ensure that situations represent comparable circumstances for different species to justify inferring species differences? What if Rhesus macaques respond more fearfully because they perceive the situations as more dangerous than do the other species?

Again, an analogous phenomenon is known on the individual level from within-species research: the much debated cross-situational consistency. Even same-species individuals differ in how they respond to situations; this individual specificity is often stable over time and results in only moderate cross-situational consistency on the sample level. Stable individual situational profiles were shown in human and nonhuman species (Mischel,

Shoda, & Mendoza-Denton, 2002; Uher et al., 2008; Uher, under review). They reflect interactions between individuals and situations; individuals high scoring on a trait dimension are either more sensitive to trait-relevant stimuli, or react to them more quickly or more intensely than other individuals (Tett & Guterman, 2000).

Analogously, species may respond differently to specific situations, with some species being more sensitive or more reactive to some situations than others. A patterning effect of the species shows up in the shapes of *species-typical situational profiles*; a positioning effect shows up in their mean profile levels across situations. Both permit comparisons between species as well as identification of situational profile types and lower-level trait dimensions on the species level. Differences between species can then be explored, for example, in ecological correlates such as predation risk that may be causally linked to differences in mean profile levels across species. Situational profiles can also be studied on other population levels such as in breeds.

Species-specific trait dimensions are probably easier to study with behaviour measures that are based directly on the species' behavioural repertoires than with trait ratings that additionally rely on the repertoire and meaning of human trait words (Uher & Asendorpf, in press). Such trait ratings entail two problems. First, using human language makes ratings prone to projections of human-like characteristics that may not exist in nonhuman species. And second, it is possible that some species show personality differences for which appropriate human-trait-descriptive words are lacking. Of course, any research ultimately depends on verbal descriptions. But we should be aware of the limits set by human language, in particular by the words that are valid indicators for human personality traits (Allport & Odbert, 1936; Goldberg, 1990). There is no reason to assume that humans have developed an equally systematic body of trait-related words to describe traits in nonhuman species with which they generally interact only rarely or not at all (Uher & Asendorpf, in press). For example, we know near to nothing about the infrared world of bats or the ultra-sound world of whales from everyday perceptions on which the lexica of human languages are built. The use of trait-descriptive words, which inherently describe human-specific trait externalisations but not necessarily those in other species, therefore requires systematic validation in each species.

Behaviour-descriptive items may provide an opportunity to circumvent these problems. In great apes, associations with manifest behaviour are much stronger for behaviour-descriptive verbs ($r = .56$) than for trait-adjectives ($r = .35$; Uher & Asendorpf, in press). Adjectives may be broader in bandwidth but behaviour-descriptive verbs may be more prototypical (Borkenau & Müller, 1991) and thus more suitable to meet the specific externalisations and trait domains in nonhuman species.

METHODOLOGICAL APPROACHES TO THE MAJOR PERSONALITY VARIATION WITHIN A POPULATION

Different populations, especially species, may vary not only in their patterning and positioning effects in domains of personality variation they share. Differences in phylogenetic origins, ecological adaptations and natural or artificial selection pressures actually suggest that some populations may also exhibit fairly different or even unique trait domains that they do not share with other populations. To guard against the danger of missing important trait domains, a methodology is needed that maps the behavioural variability in a population in ecologically valid and comprehensive ways.

Two bottlenecks: Exhaustive selection and systematic reduction to major traits dimensions

Mapping the enormous diversity of personality variability within and across species encounters two crucial bottlenecks: The selection of representative trait domains and subsequent reduction to underlying major trait dimensions. Both can cause the entire process of representative trait identification to succeed or fail because bias in either of them can lead to invalid conclusions regarding the populations' patterning and positioning effects. Without clear 'inclusion and exclusion criteria, personality research can appear directionless, with each investigator focusing on a favorite disposition or subset of dispositions' (Buss & Craik, 1985, p. 934). Reduction procedures are discussed widely in personality research (Allport & Odbert, 1936; Cattell, 1946; Saucier & Goldberg, 1998), but selection procedures receive little attention (Bell, 2007; Buss & Craik, 1985).

Selection procedures are all methods aimed at gathering a representative pool of trait domains and indicators for an empirical study. It is obvious that trait domains excluded in this step cannot be studied empirically and are thus not captured in the later derived trait structure. For this reason, selection must represent the existing personality variability appropriately, that is, be ecologically valid, and exhaustively, that is, be comprehensive (see also Gosling, 2001).

Reduction procedures are all methods used to identify major trait dimensions that summarise a large amount of shared variance in the studied pool of trait domains and indicators. Reduction can be either non-empirical, for example analysis of semantic similarity in the case of human traits, or empirical using statistical methods such as factor analysis. These kinds of reduction are often combined because non-empirical reduction reduces the complexity for empirical studies. Independent of how exhaustive the selection may have been bias in reduction can cause invalid conclusions on patterning and positioning effects. Non-empirical reduction procedures are prone to bias and require stringent rationales to reduce the selected material systematically to a set of traits or indicators that is representative of the original selection. Empirical reduction, by contrast, follows statistical criteria to reduce the data; decisions must be made on the statistical methods to be used and on how completely the data should be reduced (Carver & Scheier, 2000).

Taxonomy of current approaches to identify trait dimensions within a species

I propose a taxonomy that differentiates ten basic types of approaches that are used to identify trait dimensions in human and nonhuman species (ignoring theoretical approaches that start from intra-individual processes to derive personality traits). They are organised in five major groups that differ in starting points. Nomination approaches start from human perceptions of personality variation; adaptive approaches start from interactions between environment and personality variation; bottom–up approaches start from manifestations of personality variation in naturally evolved systems inherent to the species; top–down approaches start from findings on personality variation in another species and eclectic approaches capitalise on findings and/or methods of different approaches (Figure 1).

Nomination approaches
Nomination approaches build on the human ability to perceive personality variation in a species and to develop pertinent concepts and implicit theories based on these perceptions.

A Taxonomy of Approaches to Identify Trait Dimensions in the Species

Nomination approaches

Build on the human ability to develop concepts and implicit theories about personality variation in a species based on pertinent perceptions

Adaptive approaches

Start from interactions between environment and personality variation

Ecological approaches
Use details of the species' current ecology to identify traits based on their current fitness consequences in natural environments

Evolutionary approaches
Use adaptive problems of the evolutionary past to identify traits as evolved mechanisms that could have solved them

Bottom-up approaches

Start from naturally evolved, complex systems inherent to the species, such as neuro-biological, behavioural or language systems, that are measurable or observable to identify personality variation

Endophenotype approaches
Assess inter-individual differences at the level of underlying neurobiological mechanisms that are quantifiable and that mediate between genes and more complex or abstract traits

Lexical approaches
Use trait-related words in the lexicon as trait indicators to derive fundamental dimensions of human personality; are based on the sedimentation hypothesis that confines its validity to humans

Behavioural approaches
Derive trait dimensions from their manifestations in observable or measurable behaviour

Selective behavioural approaches
Study inter-individual variability in selected be-haviour domains to derive single trait dimensions

Behavioural repertoire approach
Starts from the species' universal behaviours and related situational features to systematically identify potential trait domains that are studied empirically for stable inter-individual variability to derive underlying major trait dimensions

Top-down approaches

Apply trait dimensions and indicators found in one species to other species and look for similarities and dissimilarities in their patterning effects

Candidate approaches
Examine and quantify relationships between indicators of single trait dimensions that were already shown to be important in another species

Model approaches
Adapt a set of broad trait dimensions and their indicators from one species to other species to study differences in their patterning effects

Eclectic approaches

Draw on trait dimensions and indicators (sometimes across different species) and/or methodologies from various types of approaches without holding to a single approach.

Replications

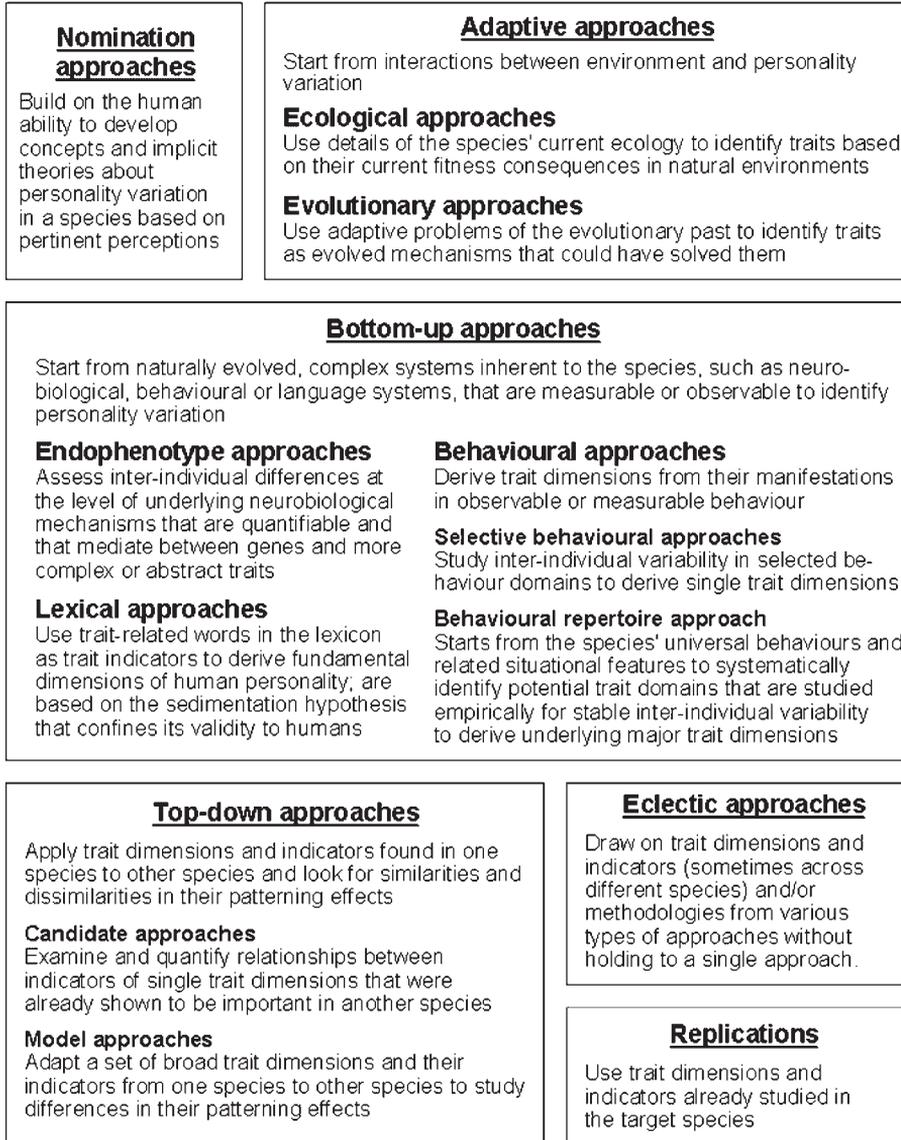Use trait dimensions and indicators already studied in the target species

Figure 1. Taxonomy of strategies in personality research to identify trait dimensions.

They require substantial knowledge about the meaning and function of a species' specific behaviours. Nomination procedures vary in degree of structure and the nominators' expertise. Examples of nomination procedures are open-ended descriptions of inter-individual differences (e.g. Stevenson-Hinde & Zunz, 1978), multi-stage nomination procedures and some psychological methods such as the repertory grid technique (Dutton,

Clark, & Dickins, 1997). In nonhuman studies, they commonly use only a few nominators (Gosling, 2001), who may be zookeepers or trained observers.

Adaptive approaches

Adaptive approaches identify trait dimensions based on their current fitness consequences in natural environments or on their possible adaptive significance in the species' evolutionary pasts. *Ecological approaches* use particular details of a species' current ecology to identify trait dimensions, their underlying mechanisms and means of maintenance such as fitness-relevant inter-individual differences in response to high-predation risk (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). *Evolutionary approaches* try to identify past adaptive problems to derive traits as evolved psychological mechanisms (EPMs) that could have solved them. For example, the challenges and benefits produced by group living and intra-specific competition could have led to the evolution of inter-individual differences in status striving and coping with stress (Buss, 1999). A related approach in biology uses a seemingly maladaptive behaviour running counter to general ecological or evolutionary explanations to infer a trait that is strongly cross-situationally consistent (spills over across contexts). For example, precopulatory sexual cannibalism in female fishing spiders (*Dolomedes triton*) is hypothesised to result from high and non-discriminate aggressiveness that is advantageous for foraging in these ambush predators but sub-optimal for reproduction (Bell, 2007).

Bottom–up approaches

To identify personality variation, bottom–up approaches start from naturally evolved, complex systems inherent to the species that are measurable or observable such as neurobiological, behavioural or language systems. *Endophenotype bottom–up approaches* assess inter-individual differences at the level of underlying neurobiological mechanisms that are quantifiable and that mediate between genes and more complex or abstract traits such as neurotransmitter or endocrine systems (Bell, 2007; Cannon & Keller, 2006). For example, the regulatory polymorphism of the vasopressine receptor gene V1a is associated with inter-individual differences in receptor distribution patterns and in social behaviour (Hammock & Young, 2005). *Behavioural bottom–up approaches* derive personality dimensions from their manifestations in observable behaviour, for example social impulsivity from social and aggressive responses to an intruding stranger (Fairbanks, 2001). *Lexical bottom–up approaches* use the natural system of human language to derive dimensions of human personality. They rely on the assumption that the most important traits are perceived in social interaction and encoded in human language (Allport & Odbert, 1936; Goldberg, 1990), which confines its validity to humans.

Top–down approaches

Top–down approaches apply trait dimensions and indicators found in one species to other species and look for similarities and dissimilarities in their patterning effects. *Candidate approaches* study relationships between indicators of single trait dimensions that were already shown to be important in another species such as correlations between exploratory and aggressive behaviour indicating an underlying reactive-proactive dimension in some species (Bell, 2007; Sih et al., 2004). *Model approaches* adapt a set of broad trait dimensions and their indicators top–down to other species such as work applying the human Big Five model to nonhuman species (King & Figueredo, 1997; Weiss et al., 2006).

Eclectic approaches

Eclectic approaches draw on trait dimensions and indicators (sometimes even across different species) and/or methodologies from various approaches without holding to a single approach. This distinguishes them from mere replications that apply a set of trait dimensions or indicators to the species for which they were originally developed. For example, Rouff, Sussman, and Strube (2005) selected trait dimensions and indicators from different models of human personality and previous studies in different nonhuman species.

Suitability to map the populations' major personality variations

All approaches are valuable within the boundaries of the research questions for which they were developed. Their particular research foci, theoretical backgrounds and rationales, however, qualify only a few of them as suitable to map the populations' personality variabilities.

Nomination approaches are prone to biased selection because experts may be more likely to nominate those traits that are salient to human observers and may pay less attention to other traits, which limits the possibilities for exhaustive selection. This is probably less problematic for nominations in humans than it is for nominations in nonhuman species to which our access as nonconspecific outsiders is limited (Uher & Asendorpf, in press). We do not know whether humans rely in part on their implicit theories of their own species' personality differences when they start forming personality impressions of nonhuman individuals. We do not even know whether humans are generally able to perceive traits that exist in nonhuman species but not in humans; assuming they are, we do not know whether the trait-related words of the human lexica are appropriate to describe them precisely. Present results of ratings using trait-related words suggest that humans can perceive differences in the patterning effects of nonhuman species (Gosling, 2001), but these perceptions may be confined to trait domains covered by the human lexica. Perhaps using only behaviour-descriptive verbs would be a suitable alternative for nonhuman studies, but to my knowledge published nomination approaches rely largely on ratings of trait-adjectives.

Adaptive approaches have strong potential for representative trait selections that can be complemented with statistical reduction. They require stringent rationales to select the most important ecological details or adaptive problems that are then used to identify the most important trait domains; selections in evolutionary approaches are mostly theory-driven and must remain partly speculative, which may limit their ecological validity and comprehensiveness.

Bottom–up approaches start from measurable trait manifestations in natural systems inherent to the species and have therefore the greatest potential among all approaches to identify ecologically valid trait dimensions. Most studies using a bottom–up approach analyse selected trait domains in great detail. In those studies aiming at a trait taxonomy, limitations for comprehensiveness probably do not arise from their rationales but from their practical feasibility. This obviously depends on the effort invested, as the lexical approach impressively shows (Allport & Odbert, 1936). The complexity of potential trait domains and indicators may also require efficient non-empirical reduction strategies prior to empirical reduction, but these may be prone to bias (see, e.g. De Raad & Barelds, 2008).

Adaptive and bottom–up approaches study personality variation from inside the species, largely uninformed by findings from other species. They are thus analogous to 'emic approaches' in cross-cultural psychology that rely on trait indicators derived within each

culture. Top–down approaches, by contrast, draw on findings from other species' personality variations, from which they import trait dimensions and indicators to look for differences in the species' patterning and positioning effects. They are analogous to 'etic approaches' in cross-cultural psychology that apply the same trait dimensions and indicators to different cultures (Church, 2001; Weiss et al., 2006). Nominations in nonhuman species may be indirectly informed by knowledge of other species' personality variation, for example, through the nominators' implicit theories or explicit knowledge of human personality.

It is possible that etic top–down approaches facilitate direct comparisons between cultures because they are limited to comparisons among same-species populations, but they are less able to identify culture-specific trait dimensions (Church, 2001), which may bias inferences on the cultures' patterning effects. Differences between species are much larger than differences between cultures within the same species, which poses a serious challenge to top–down approaches. Sometimes trait dimensions and indicators that may not be applicable and that consequently fail to meet ecological validity may be forced on a species (Gosling, 2001). Moreover, confining the scope of trait domains to that of the original species may ignore important species-typical trait domains (Uher & Asendorpf, in press), which limits the potential of top–down approaches for comprehensive selections. Top–down approaches may permit first explorations in so far unstudied species but require inevitably empirical convergence with results from systematic bottom–up approaches to ensure ecological validity and comprehensiveness (Uher, under review).

The potentials and limitations inherent in these approaches apply to eclectic approaches that capitalise on findings (even across species) and methodologies of multiple approaches. Even though the major aim of eclectic approaches often is achieving comprehensiveness (Gosling, 2001), the possibility for representative selection obviously depends on those of the original approaches and on the rationale used to select and combine their findings and methods.

It seems that not a single nonhuman species has been studied using all approaches; probably the greatest methodological variety was achieved in nonhuman primates. A substantial body of research in these species is based on subsets of trait domains selected using endophenotype or behavioural bottom–up approaches, but only a few studies have been concerned with trait taxonomies developed using nomination, top–down and eclectic approaches. Obviously still lacking in nonhuman primate personality research are ecological and evolutionary approaches and systematic endophenotype bottom–up approaches; a systematic behavioural bottom–up approach is proposed below. Although there are often only a few studies available for any given species, the existing empirical studies allow some tentative first comparisons.

One of the most frequently used sets of trait indicators, the Stevenson-Hinde and Zunz's (1978) adjective list developed for Rhesus macaques by expert nomination yielded the factors confidence, sociability and excitability in that species. The list yielded the same factors when applied top–down to stumptail macaques (*Macaca arctoides*, e.g. Figueredo, Cox, & Rhine, 1995), pigtailed macaques (*Macaca nemestrina*; Caine, Earle, & Reite, 1983) and chimpanzees (Murray, 1998). Gorilla studies (e.g. Gold & Maple, 1994) and some Rhesus studies (e.g. Capitanio, 1999) additionally found aggressiveness; another chimpanzee study added curiosity/intelligence and protectiveness (Martin, 2005). Further Rhesus studies could replicate only sociability and excitability from this list, but found aggressiveness and curiosity/playfulness (Bolig, Price, O'Neill, & Suomi, 1992). The fact that the factors sociability and excitability were found in all cited studies suggests that at

least these factors may be universal trait dimensions in these species. Direct between-species comparisons to study their positioning effects on these dimensions (i.e., whether they are weak or strong universals) are still missing.

Apart from between-study differences in interrater agreement and sample size (ranging from 10 to 298 subjects), the selection of the traits was problematic because the original list used in all these studies was derived by expert nomination and may therefore be limited to traits that are easily perceivable for humans. Moreover, the same trait indicators (albeit minor modifications) may not be equally valid for species with different behavioural, social and ecological systems such as Rhesus macaques, gorillas and chimpanzees. For example, in adapting the Rhesus adjective list, the gorilla study (Gold & Maple, 1994) 'did not include items that could potentially load on openness to experience or conscientiousness and...hence...could not show whether gorillas exhibited' such traits (Weiss et al., 2006; p. 503). In fact in chimpanzees, an adjective list adapted from a human Big Five adjective list (Goldberg, 1990) could reveal conscientiousness and openness (e.g. King & Figueredo, 1997), whereas the Rhesus adjective list could reveal curiosity/intelligence in only one of two studies, but not conscientiousness; a corresponding study in gorillas is still missing. These findings suggest that the scope of the expert-nominated Rhesus adjective list may not identify all trait domains found in chimpanzees using a human Big Five adjective list. The problem here is that applying the same set of trait indicators across species often confounds effects of the species' personality variations with those of the content and scope of the used trait indicators.

If we applied the Rhesus adjective list top–down to humans, very probably we would find trait domains like excitability/neuroticism, sociability/extraversion and aggression/agreeableness but not conscientiousness. How representative can a top–down approach from a human Big Five adjective list to nonhuman species be? In orangutans, it revealed the factors extraversion, dominance, neuroticism, agreeableness and openness (Weiss et al., 2006) and in chimpanzees it additionally revealed conscientiousness (King & Figueredo, 1997). After several successful replications in the latter species (e.g. King & Landau, 2003; King et al., 2005; Pederson, King, & Landau, 2005), the factors neuroticism and openness could not be replicated from this list in a recent study using two large samples (Weiss, King, & Hopkins, 2007). The rating lists applied in all these chimpanzee studies (King & Figueredo, 1997) contained trait-adjectives that with two exceptions were taken from a human Big Five taxonomy (Goldberg, 1990). Recall that trait operationalisations must appropriately meet species-typical trait externalisations to avoid misclassifying individuals and species, and recall furthermore that trait-descriptive adjectives from human personality inventories may increase bias, such as halo-effects or anthropomorphism, in ratings.

A first study on empirical relations to observable behaviour in chimpanzees supports assumptions about the validities of the factors derived with these human adjective items (Pederson et al., 2005). The inconsistencies in replicating the factors neuroticism and openness in chimpanzees, however, suggests that the ecological validity of these adjective items could be improved. The authors' conclusion that these results indicate a 'need to sample more adjectives' that represent the non-replicated factors (Weiss et al., 2007, p. 1264) also suggests that adjective items that are appropriate for humans may not be sufficiently appropriate to operationalise the same factors in chimpanzees. Problems in the ecological validities of rating items may also be responsible for the mixed results reported from validation studies of other item pools (see Gosling, 2001).

Instead of taking *items* directly from human personality inventories, generalizability studies could adapt the human Big Five *model* top–down to other species using

species-specific trait indicators operationalised in behaviour-descriptive verbs or direct behaviour measures. This could circumvent the problems inherent in trait-descriptive words because even 'clarifying definitions' that are frequently used to adapt human adjective items to nonhuman species may be insufficient to achieve ecological validity. Instead, they may actually induce bias. A recent systematic methodological study comparing direct behaviour measures, behaviour-descriptive verbs and trait adjectives in great apes showed that adjectives do not always have the theoretically expected empirical relations to observable behaviour (Uher & Asendorpf, in press). As such systematic validation studies are extremely rare, biases due to incongruities between the connotations of human adjectives and their explicit denotations for nonhuman individuals remain undetected. These kinds of incongruities could also account for differences in the patterning effects yielded by the Rhesus adjective list in different studies.

Apart from these difficulties in operationalisation, the utility of top–down approaches from the empirically well-documented human Big Five model as a systematic approach to nonhuman personality is often emphasised (John & Srivastava, 1999), pointing to the phylogenetic continuities between human and nonhuman species (for an alternative view stressing niche-differentiated adaptations that are species-unique; see Tooby & Cosmides, 1989). But even if the human Big Five factors are applicable to many nonhuman species, a top–down approach from these factors can only reveal empirical evidence for the existence or nonexistence of trait domains *within* their scope, but not beyond. It may thus ignore important species-typical trait domains that either do not exist in humans or that are underrepresented in human trait lexica or ignored by research in the lexical tradition. In fact, among those trait domains that were excluded in non-empirical reduction processes of Big Five traditions are some of high importance for nonhuman species such as physical size and strength as well as feeding- and sexuality-related trait domains (Saucier & Goldberg, 1998; Uher & Asendorpf, in press).

Even if top–down approaches started from the Big Five factors instead of relying on their human-specific indicators, they may be not able to identify the major trait domains in other species. For example, a study in liontailed macaques (*Macaca silenus*) used species-typical behaviour measures obtained through ethological observation to operationalise trait dimensions and indicators from different inventories of personality in humans (extraversion, neuroticism and agreeableness from the human Big Five factors; persistence and novelty seeking from Cloninger's Temperament and Character Inventory; Cloninger, Przybeck, Svrakic, & Wetzel, 1994) and other primate and nonprimate species (Rouff et al., 2005). The resulting trait domains, extraversion, aggressiveness and curiosity, included the imported trait dimensions, but yielded no additional dimensions.

That traits similar to some of the Big Five factors emerged repeatedly in a review of 187 nonhuman studies (Gosling, 2001) does not show that these trait domains represent the most important personality variations in all these different species. The Big Five factors may represent only those nonhuman trait domains that are shared with humans while ignoring those that humans do not show. This may apply particularly to species that are only distantly related to humans such as non-primate species or species that occupy different habitats with very different selection pressures such as the deep sea. Systematic and comprehensive future studies will shed more light on this question.

Thus, current approaches are not equally suited to identify ecologically valid and comprehensive trait dimensions that are needed to identify species-specific, strong and weak universal traits. Unfortunately, the most promising approaches—systematic bottom–up approaches—are underrepresented in primate personality research, which is

probably symptomatic of nonhuman personality research in general. I therefore propose a new behavioural bottom–up approach that may correct this imbalance.

Getting past the two bottlenecks: The behavioural repertoire approach

The behavioural repertoire approach (Uher, 2005) is a systematic behavioural bottom–up approach. It starts with a biological classification of the species' universal behaviours to systematically identify behavioural domains over which stable inter-individual variability can be studied psychometrically to identify underlying trait dimensions. Its primary objective is to map the major behavioural manifestations of personality variation for systematic studies on different population levels, in particular on the species level. The approach comprises procedures for exhaustive selection and systematic reduction to derive ecologically valid and comprehensive empirical representations that match the true patterning and positioning effects of populations as closely as possible. A peculiarity of this approach is its inherent multidisciplinarity; human personality and cross-cultural psychology provide the theoretical and methodological background, whereas behavioural biology contributes the expert knowledge on the species' behavioural systems.

Theoretical rationale

The theoretical rationale is rooted in the psychological trait paradigm but apart from that the approach makes no theoretical assumptions about underlying genetic, neurobiological or ontogenetic mechanisms, potential fitness-relevance or adaptivity. The trait paradigm conceives personality traits as internal, behaviour regulating mechanisms that can be inferred from observable behavioural regularities. Because trait-relevant behaviour emerges only in response to trait-relevant stimuli, personality traits are assumed to create stable relations between situations and the individual's responses across time (Funder, 2004; Mischel et al., 2002). This means that traits comprise specific behavioural tendencies that are related to specific situational stimuli; consequently, trait constructs can be derived from behaviour-situation units. Such units can be obtained systematically from the species' universal behaviours and the typical situations their members encounter. The biological classification of the species' universal behaviours needs not correspond to their underlying personality variation. In fact, personality traits comprising behaviours that are neither functionally nor mechanistically related on the phenotypic level are most intriguing cases (Bell, 2007).

Representative selection bottom–up from the species' behavioural repertoires

Trait identification starts with a broad and systematic review of the species' behavioural repertoires that are studied most comprehensively in behavioural biology—the discipline specialised in describing behavioural systems in different species. To avoid eclectic and biased selections of trait domains, only descriptions and categorisations of the species' observable or measurable behaviours are used. In contrast with other approaches, previous inferences of any internal, behaviour regulating mechanisms such as personality traits are excluded from the selection process because the approach is strictly restricted to the phenotypic behavioural variability.

In this review, broad and universal behavioural responses are listed together with general features of the typical situations to which they are related. For trait identification, it is not necessary to break down behaviours and situations to specific behavioural acts or specific situations. Instead, trait identification is facilitated by more abstract selection levels

because increasing detail requires greater empirical efforts, especially larger samples, to identify underlying trait dimensions and their basic structures. More specific behaviours or situational features are however important as trait indicators; they may therefore be listed separately under each universal behavioural domain. Using a matrix, all listed universal behavioural responses are then merged systematically with their associated general situational features into behaviour-situation units from which potential trait domains are derived. In this matrix, the same potential trait domains will emerge repeatedly from different parts of the behavioural repertoire. This is consistent with the conception of traits as internal mechanisms that regulate behaviour by integrating situational influences and that become therefore manifest in a wide range of behaviours.

Systematic non-empirical and empirical reduction
To reduce the complexity for empirical studies, the identified narrow trait domains may be reduced non-empirically by merging those that refer to the same behavioural responses but different situations. Trait domains that refer to behaviours of different quality, however, cannot be merged non-empirically. Whether this step is necessary depends on the degree of abstraction taken in the selection, on the number of potential trait domains identified and on the practical possibilities for empirical investigation. Notwithstanding this reduction to more abstract trait domains, more specific situations can be considered in studies of cross-situational consistency and in studies that identify subtraits.

   The bottom–up-derived potential trait domains derived so far do not necessarily reflect domains of high inter-individual variability in the considered species. Therefore, the degree of stable inter-individual variability in the identified potential trait domains has to be shown empirically, and domains with low inter-individual variability have to be discarded. Systematic factor analyses in large samples reveal the species' patterning and positioning effects in the identified trait domains.

Extension to other population levels
The behavioural repertoire approach can be refined by restrictions to lower-level populations, starting from more specific behavioural repertoires that cover, for example, breed-specific behaviours. Furthermore, it can be extended to species comparisons by considering the behavioural repertoires of different species. Multi-species studies can then identify species-specific, weak and strong universal trait dimensions.

Limitations
The behavioural repertoire approach relies on states of knowledge about the species behavioural repertoires that may not yet be complete for many species such as those living in habitats that are difficult to access. There may also be behaviours that are difficult to measure and that require technical devices so that humans can perceive them, for example, the ultra-sounds used for communication in whales. Moreover, behavioural systems are studied by behaviour scientists who decide on the categorisations and descriptions of other species' behaviours from their human observational perspective. The behavioural repertoires on which the approach is based are thus not completely free from bias. A further source of bias inherent in all bottom–up approaches derives from the practically unavoidable non-empirical reduction procedures, given the small samples that are often the only option for nonhuman species. Therefore non-empirical reduction must be done with great caution; if specific mergers of trait domains appear problematic or if first data on

situational or response profiles suggest the existence of possibly distinctive trait domains, they should be tested empirically.

Contribution to personality research

Behavioural manifestations are only one piece in the puzzle of personality; its complexity often precludes straightforward inferences from behavioural manifestations to the basic mechanisms and processes governing personality phenomena (Matthews et al., 2003). But behaviour is a key piece in this puzzle because it represents an important interface between intra-individual processes and population-level phenomena of personality. A representative and comprehensive picture of the behavioural landscape can therefore meaningfully complement explorations of those mechanisms and processes that have shaped it. Associations to genetic, endophenotypic or ecological variability, for example, are particularly illuminating when studied with population-specific, population-comparative and universal correlations. Relating findings to other components of personality also breaks the circularity of inferring trait dimensions bottom–up from observable behaviour and using them in turn to explain behaviour. Fitting the different pieces together creates a more complex and bigger picture that permits profound insights into the mechanisms and origins of personality.

Example: The behavioural repertoire approach applied to the great ape species

The behavioural bottom–up approach has already been applied to the great ape species (Uher, 2005). I reviewed 16 extensive publications about bonobos (Kano, 1992; Susman, 1984), chimpanzees (Berdecio & Nash, 1981; de Waal, 1982, 1988; Goodall, 1986; van Hooff, 1973; van Lawick-Goodall, 1968), gorillas (Maple & Hoff, 1982; Meder, 1993; Robbins, Sicotte, & Stewart, 2001; Schaller, 1963) and orangutans (Jantschke, 1972; Kaplan & Rogers, 2000; Maple, 1980; Rijksen, 1978) in the wild and in captivity. This was complemented by review of additional 18 publications about more specific behavioural domains such as social behaviour, play behaviour, responses to change of environment, mating and breeding behaviour, communication systems and behavioural contrasts among species.

Universal behavioural responses and typical associated situational features were listed separately for each great ape species. Surprisingly, they showed strong similarities across these closely related species, which does not preclude species-specific behavioural acts within each behavioural category. The behaviours and situations were therefore pooled at the end of the review. The joint domains of universal great ape behaviours could be organised in six broad domains reflecting biological behaviour taxonomies: solitary behaviour, activity and ranging patterns, feeding behaviour, social behaviour, sexual behaviour and breeding behaviour (Figure 2). Interestingly, these domains could be related to adaptive problems discussed in evolutionary psychology (Buss, 1999).

All universal behavioural responses were then merged systematically with their related situational features into behaviour-situation units that were used to derive potential trait domains. For example, each of the behavioural responses listed in the nonsocial behavioural subdomain 'responses to animate and inanimate environment' (e.g. detection, approach, investigation, play, excitement, fear, attack) is merged with related situational features in which it is described to occur (e.g. encounter with unfamiliar objects). Detection of unfamiliar objects in the nonsocial environment may be related to a trait labelled vigilance; approach to an unfamiliar object may be related to a trait labelled curiosity and
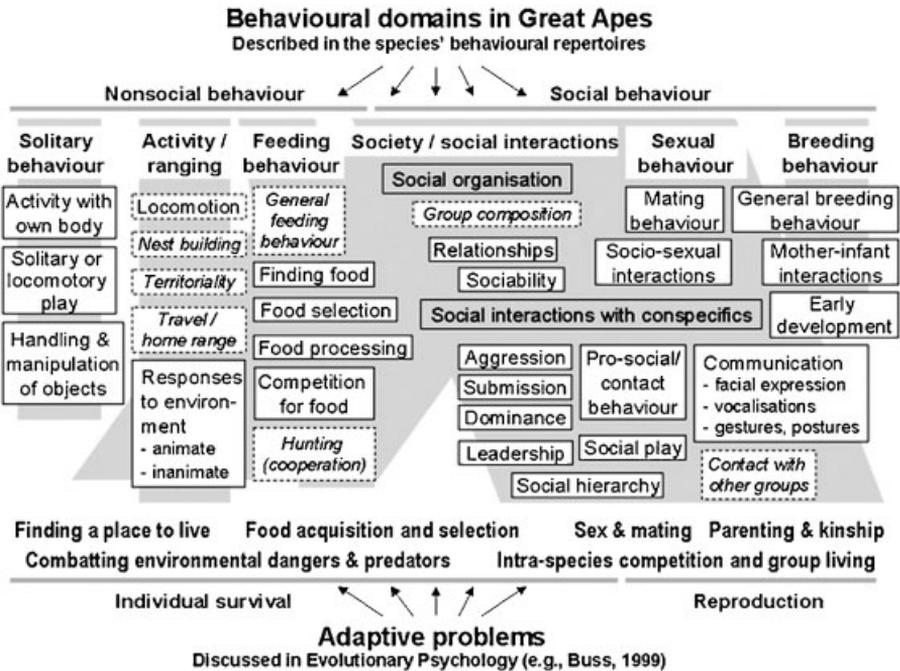
Figure 2.   Behavioural domains and subdomains described in the behavioural repertoires of the great ape species and associated adaptive problems discussed in evolutionary psychology.
Note: Domains in *italics* are only relevant in wild populations.

so forth. This procedure was applied to all behaviours and situations in all behaviour domains and subdomains shown in Figure 2; it sometimes yielded the same potential trait domains repeatedly in different parts of the behavioural repertoire. For example, detection of new environments (such as a new access to an adjacent habitat) could also be related to a trait domain-labelled vigilance. For a first empirical exploration in a captive sample of great apes, behaviours that only occur in the wild like travelling or territoriality were excluded. For example, investigation of new environments could yield a potential trait domain-labelled exploration. The comprehensiveness of the potential trait domains identified for this study is therefore limited to captive populations of great apes. Considering the importance of contacts with humans for captive apes, friendliness and aggressiveness were each sub-divided into directed at conspecifics versus directed at humans. Thus, the sets of potential trait domains that could be identified for captive and for wild populations differ slightly.

The potential trait domains that emerged repeatedly from the review (Figure 3) were studied in a sample of 20 zoo-housed great apes, five each of bonobos, chimpanzees, gorillas and orangutans. Three different assessment methods—behaviour measures, behaviour-descriptive ratings and trait-adjective ratings—expanded a nomologic network (Cronbach & Meehl, 1955) around each trait domain. Operationalisations were based on the specific behaviours and situations subsumed under the more abstract categories of the review used to derive the domains. Each individual ape was measured repeatedly in 76 manifest behaviour-situation units in 14 laboratory-based tests and two different group
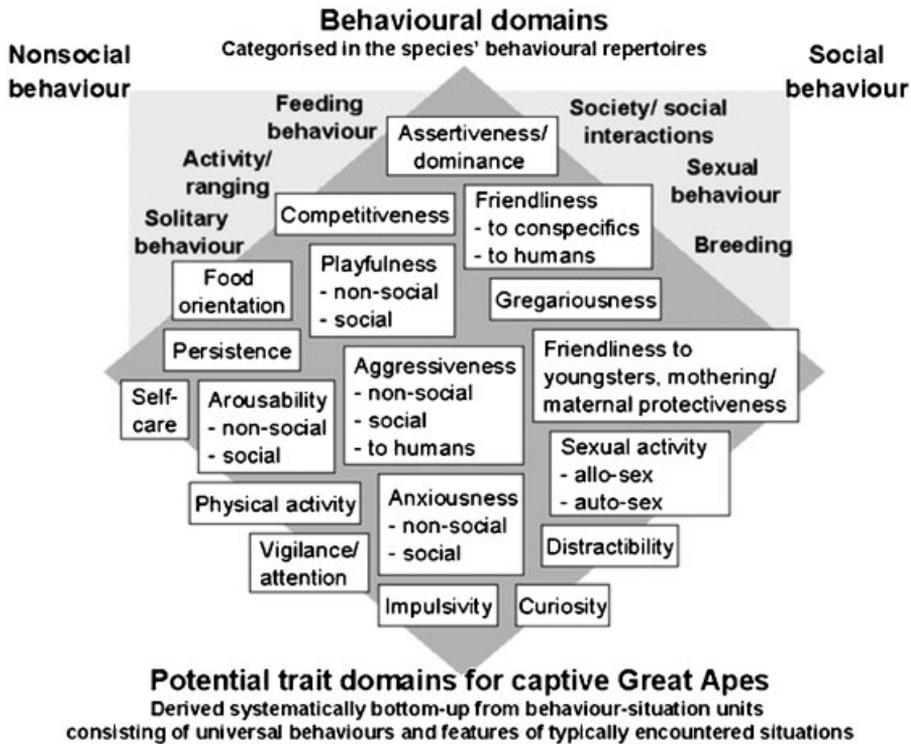
Figure 3. Potential trait domains derived bottom–up from behavioural domains in the behavioural repertoires of the great ape species.
Note: The arrangement of trait domains in the figure is random; it does not imply a hierarchy.

situations, and rated on 34 behaviour-descriptive and 17 trait-adjective items by four to five keepers. All three methods were reliable and yielded stable inter-individual variability at different levels of aggregation over a 50 day-period in both variable-centred and individual-centred analyses. Substantial cross-method coherence within nomological networks established construct validity for these bottom–up identified narrow trait dimensions (for details see Uher et al., 2008; Uher, under review; Uher & Asendorpf, in press). Empirical data for these species' patterning and positioning effects in these domains that could indicate broader underlying trait dimensions are still not available.

These first empirical results show that the behavioural repertoire approach is not only theoretically valid but also empirically viable in identifying representative trait dimensions that are measurable with multiple methods including direct behaviour measures. This is important because the behaviour measures used as trait indicators were easily visible by trained observers and therefore minimally affected by their implicit personality theories. The study also demonstrates a suitable design of a multi-species study using multiple methods, which is particularly relevant for sound comparative analyses. When applied to larger samples, this design allows systematic factor analyses to reveal the patterning and positioning effects of the studied species to identify species-specific, weak and strong universal trait dimensions. It is also suitable for comparisons on any other population level.

Comparison to other approaches

The behavioural repertoire approach identified trait domains in great apes similar to those previously found in chimpanzees, gorillas and orangutans, such as gregariousness, friendliness to conspecifics, curiosity and aggressiveness. Beyond that, the approach yielded further trait domains that were not identified by previous approaches such as those tentatively labelled food orientation, sexual activity or friendliness to youngsters.

These findings suggest that by starting from the species' naturally evolved, complex systems, bottom–up approaches cover the diversity of personality variation in different species more appropriately than other approaches such as nomination or top–down approaches that may be easier to use. The manageable number of generated trait constructs and indicators even in highly developed species such as great apes shows that the behavioural repertoire approach as a systematic behavioural bottom–up approach is empirically viable. This is important because large-scale structural analyses are probably more difficult to realise with more molecular bottom–up approaches such as endophenotype approaches (Cannon & Keller, 2006). The empirical findings on stable inter-individual variability and on the reliability and construct validity of personality assessments in these domains also suggest that a biological classification of the species' universal behaviours excluding research on internal behaviour regulating mechanisms is a solid basis for systematic and representative trait identification.

The behavioural repertoire approach therefore constitutes an independent alternative to previous approaches. It would be highly interesting to compare results from different systematic bottom–up approaches to one another and to those derived from systematic adaptive approaches. Converging findings from different starting points establish strong evidence for the identified traits' ecological validity and comprehensiveness that are crucial for valid comparisons across different populations. Comparisons of these findings with those from top–down approaches will be methodologically illuminative and important given the roles these approaches play in nonhuman personality research.

IMPLICATIONS FOR RESEARCH ON HUMAN PERSONALITY

In humans, the most widely researched major personality dimensions, the Big Five, were derived with a lexical bottom–up approach. Its rationale relies on the hypothesis that the most important personality traits are coded in language (Allport & Odbert, 1936; Saucier & Goldberg, 1996), which entails two important implications. First, trait-related words can be considered ecologically valid trait indicators in humans; and second, the trait-descriptive words catalogued in the lexica constitute a comprehensive system of human trait indicators. A lexical bottom–up approach is thus suitable for representative selections of socially perceived human trait indicators.

The enormous complexity of selectable indicators requires efficient non-empirical reduction strategies (that are therefore sometimes incorporated in the selection strategy), which however are prone to bias. In fact, although all lexical studies base their selection on the lexicon, their non-empirical reduction strategies vary, yielding different solutions on the major personality domains even within one language (*cf.* Almagor, Tellegen, & Waller, 1995; Ashton & Lee, 2005; Cattell, 1946; Goldberg, 1990; Saucier & Goldberg, 1998). For this reason, non-empirical reduction strategies are intensely debated such as the utility of adjectives, verbs, nouns and adverbs as trait indicators (Saucier & Goldberg, 1996) or the

systematic exclusion of attitudes, values, physical and health- (Saucier & Goldberg, 1998) or sexuality-related trait indicators (Schmitt & Buss, 2000). The comprehensiveness of the Big Five factors is therefore repeatedly questioned (e.g. Ashton & Lee, 2005; Block, 1995; De Raad & Barelds, 2008; McAdams, 1992).

Limited comprehensiveness also affects top–down approaches from the human Big Five factors to nonhuman species. In fact, the trait domains revealed by the behavioural repertoire approach beyond those found with top–down approaches from the human Big Five adjective list covered domains that were systematically excluded in lexical studies such as feeding- or sexuality-related trait domains. One can argue about the reasoning behind systematic exclusions in humans, but it may not apply to nonhuman species in which the excluded trait domains are clearly relevant.

For humans, the behavioural repertoire approach is therefore worth consideration as an alternative to lexical approaches. Reviewing phenotypic classifications of the human behavioural repertoire as described for example in human ethology, biological anthropology and human behavioural ecology probably requires no more effort than scanning a lexicon of half a million entries. It could be stimulating for the controversies evolving around lexical approaches to compare their results with those yielded by other systematic bottom–up approaches such as the behavioural repertoire approach and systematic endophenotype approaches. Likewise, truly evolutionary or ecological approaches that are uninformed by previous findings on human personality—instead of *post hoc* theories about lexically derived traits—could be illuminative. Human personality research is not lacking 'any a priori rationale for selecting a set of variables to be factor-analysed' (Ashton & Lee, 2005, p. 21). Instead, many alternative approaches are available beyond lexical approaches.

Applying the behavioural repertoire approach to humans may also address some limitations inherent to the five-factor model (see McAdams, 1992). For example, being based on the observable behavioural system, the behavioural repertoire approach derives trait domains and indicators that are more closely bound to specific behaviours and situational contexts than the generic, rather nonconditional items used in lexical studies. Such constructs and indicators could limit translation inequivalences that may account for underestimations of cross-language congruence in lexically derived items (see John & Srivastava, 1999). Specifically, using behaviour-descriptors and manifest behaviour measures instead of trait-descriptors could perhaps improve predictions of manifest behaviour differences from ratings and reduce the difficulties in comparability entailed by language- and culture-specifics.

One may argue that social desirability tendencies are difficult to control in direct behaviour measures, but this also applies to ratings (see Crowne & Marlowe, 1960). Rather, direct behaviour measures are irreplaceable for some research questions. Recall that ratings are useful in studying patterning effects, but they do not appropriately represent positioning effects of populations because the comparative nature of ratings hinders direct comparisons between populations on shared dimensions. Mean trait levels based on personality ratings may be biased by reference group effects which, in turn, may also bias cross-cultural correlates of these mean trait levels (see, e.g. Terracciano et al., 2005). This renders the underlying scales incongruent and hinders direct cross-cultural comparisons—such comparisons however would be possible with absolute behaviour measures. Ultimately, multi-method studies are vital for comparative personality research. The behavioural repertoire approach represents a new alternative that permits using multiple assessment methods including direct behaviour measures.

CONCLUSIONS

Comparative personality research explores the evolved diversity of stable inter-individual variability in behavioural organisation in human and nonhuman species to gain fundamental insights into the nature and origins of personality. A comprehensive body of suitable methodologies is needed to study personality variability of populations within and across species. Regarding species, different types of trait dimensions are distinguished: species-specific, weak and strong universal trait dimensions, of which the latter also represent species-comparative dimensions. Their correlational structure then can be studied with three different kinds of analysis: species-specific, universal and species-comparative correlational analyses, including factor analyses. For universal trait dimensions, positioning and patterning effects of species can be empirically identified. This methodology can be extended to other population levels.

All methods of personality assessment are suitable for studying the positioning effects of populations but they are only unequivocally quantifiable with direct behaviour measures. This strongly suggests a multi-method approach for comparative personality research. Because populations, particularly species, may externalise traits differently, ecologically valid operationalisations must meet their specifics. For example, shape and mean profile level of species-typical response profiles permit comparisons across species. Similarly, the species' responsiveness to different situational features is studied and compared with species-typical situational profiles.

It is of vital interest for comparative research to identify the populations' major trait dimensions that together summarise a large amount of shared variance because ultimately all studies are based on the selection and definition of the traits they study. For representative trait identification, two crucial bottlenecks must be overcome: Exhaustive selection of potential trait domains and their systematic reduction to underlying trait dimensions. Previous approaches differ in their suitability for this task depending on their original purpose and rationale. Most promising are adaptive approaches and bottom–up approaches; their variety is however underrepresented in empirical comparative research. Instead, single approaches seem to dominate in nonhuman (top–down approaches) and human research (lexical bottom–up approaches) that thus miss the important possibility to establish convergent evidence from different starting points. The behavioural repertoire approach was proposed as a new behavioural bottom–up approach tailored to identify ecologically valid and comprehensive trait dimensions from the species' manifest behavioural systems.

Extending personality research to nonhuman species expands a huge field of research which is not only theoretically interesting, but also methodologically stimulating. It provides a proving ground to reconsider and sharpen theories, concepts and methodologies and to integrate new perspectives that allow gaining profound and illuminative insights into the nature and origins of personality.

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