APC001

Personality

Individual humans show consistent differences in their behavioral tendencies. […] In humans, these differences have been termed personality types (Pervin and John 1999). In other taxa, they have been referred to as coping styles, temperaments, behavioral tendencies, strategies, syndromes, axes, or constructs (Gosling 2001). From an ecological and evolutionary view, an underlying theme of these related concepts is that they refer to suites of correlated behaviors that can include those expressed either within a given behavioral context (e.g., foraging behaviors in different habitats) or across different contexts (e.g., feeding, antipredator, mating, contest, and dispersal contexts). […] we refer to suites of correlated behaviors as behavioral syndromes.

To quantify a behavioral syndrome, we need at least two observations of behaviour (preferably in different contexts or situations) for each of a set of individuals. With these data we can quantify two distinct aspects of a behavioral syndrome: *within*-individual versus *between*-individual consistency in behavior. Within-individual consistency refers to the tendency for any given individual to exhibit consistent behavior across observations (e.g., for an individual to be generally aggressive). […] Between-individual consistency refers to consistent differences among individuals in behavior (e.g., rank order consistency in aggressiveness) expressed statistically as a *behavioral correlation*. If the study involves repeated observations of the same type of behavior in the same context and situation, we refer to behavioral consistency as *repeatability* (Boake 1994). A *behavioral syndrome* is a suite of correlated behaviors across multiple (two or more) observations—most interesting, if it involves multiple contexts or situations. Within the syndrome, each individual has a *behavioral type* (e.g., more versus less aggressive individuals).

The existence of between-individual consistency need not imply within-individual consistency or limited plasticity. It is possible, for example, for individuals to differ consistently in mean aggressiveness, but for all individuals, including those that are more aggressive, to be highly plastic in their aggressiveness across contexts. If, however, individuals show limited behavioral plasticity, we refer to this as a *behavioral carryover* or *spillover*.

Personality trait

Within the syndrome, each individual has a *behavioral type* (e.g., more versus less aggressive individuals).

Repeatability

If the study involves repeated observations of the same type of behavior in the same context and situation, we refer to behavioural consistency as *repeatability* (Boake 1994).

**APC002**

Personality

Recently, repeatability estimates became highly relevant in the growing field of animal personalities that focus on consistent between-individual differences in behaviour. A meta-analysis of repeatabilities for animal behaviour demonstrated that many behavioural types are more predictable (i.e. more consistent within individuals) than previously assumed (Bell, Hankison & Laskowski, 2009).

Personality trait

Repetability

Repeatability, an index for quantifying the accuracy and consistency of phenotypic measurements. […] We encourage the use of repeatability estimates as a means of quantifying the flexible properties of a range of phenotypes as well as the accuracy of measurements […] Repeatability […] is an important concept to assess the accuracy of measurements. It expresses the proportion of the total variation that is reproducible among repeated measurements of the same subject or group (Lessells & Boag, 1987; Shrout & Fleiss, 1979). Consequently, the difference between unity and the repeatability, 1 − R, can be interpreted as the proportion of variance in a particular series of measurements associated with measurement error and phenotypic flexibility. Although 1 − R will always contain measurement error, it can also be studied as a measure of phenotypic flexibility [...] A meta-analysis of repeatabilities for animal behaviour demonstrated that many behavioural types are more predictable (i.e. more consistent within individuals) than previously assumed (Bell, Hankison & Laskowski, 2009). […] Repeatability […] can be interpreted as the expected within-group correlation among measurements (Sokal & Rohlf, 1995). […] Repeatability is a function of both the within-group variance and the between-group variance. Therefore, individual consistency will only be evident in the repeatability if there is between-individual variation in the population. It is important to bear in mind that the repeatability can be low for two reasons: high within-individual variation or low between-individual variation. […]

**APC003**

Personality

*Definition of personality.* The first task is to determine what is meant by "personality." Most theoretical and empirical research on personality has been done in the human domain. Humanpersonality psychologists come in a variety of orientations and often differ in the personality constructs they emphasize. The phenomena studied by personality psychologists include temperament and character traits, dispositions, goals, personal projects, abilities, attitudes, physical and bodily states, moods, and life stories (Angleitner, Ostendorf, & John, 1990; John & Gosling, 2000; Little, 1996; McAdams, 1996). There is no one specific definition of personality that would satisfy all personality psychologists. Only a very broad (and thus somewhat vague) definition would satisfy most. For example, personality can be defined as those characteristics of individuals that describe and account for consistent patterns of feeling, thinking, and behaving (Pervin & John, 1997), a definition broad enough to capture most phenomena studied by personality psychologists. […] It would seem that animal researchers come to use personality constructs to refer to consistent individual differences in animal behaviour in much the same way that humans use personality constructs to describe one another. For example, researchers working with hyenas might describe individuals that consistently use novel ways to approach situations and address problems (e.g., by finding many different ways to escape their enclosures) as more creative than hyenas that do not behave this way. […] The most systematic study to validate personality ratings with behavioral codings was performed on 42 male captive rhesus monkeys (Capitanio, 1999). The goal of the study was to test the predictive validity of personality ratings, that is, the degree to which the measures could predict conceptually related, subsequent outcomes. Specifically, Capitanio (1999) attempted to determine whether personality dimensions, identified in adult monkeys living in half-acre cages, predicted behavior in situations different from the one from which the dimensions were originally derived at time points up to 4.5 years after the original assessments.

Personality trait

*Rating traits.* The second method for studying animal personality involves observers as data recording instruments. Historically, data obtained from observers have been derided as subjective and inappropriate for the objective requirements of scientific measurement. However, Buirski et al. (1978) claimed that when applied to animals, terms such as " 'gregarious,' 'timid,' 'depressed,' and 'aggressive' are fundamentally no more subjective or less useful than most terms currently used in psychology or ethology" (p. 127). Block (1961) argued that aggregated observations composed of ratings by several independent observers meet the standards required of any measurement instrument; that is, aggregates composed of multiple observers are reliable and are largely independent of the idiosyncrasies of individual observers (see also Epstein, 1983). Indeed, in research on human personality, consensual observer ratings are often considered to be the sine qua non of personality traits (Hofstee, 1994; McCrae, 1982; Wiggins, 1973).

Repetability

**APC004**

Personality

In recent years evidence has been accumulating that personalities are not only found in humans1 but also in a wide range of other animal species. Individuals differ consistently in their behavioural tendencies and the behaviour in one context is correlated with the behaviour in multiple other contexts. […] Empirical findings in more than 60 species, ranging from primates to ants, suggest that animal behaviour is much less flexible than previously thought. Individuals consistently differ in whole suites of correlated behaviours and these differences are often heritable. At present, the existence of such personalities (also termed behavioural syndromes, coping styles or temperaments) is puzzling in several respects. First, why do different personality types stably coexist? Second, why is behaviour not more flexible but correlated across contexts and through time? And third, why are the same types of traits correlated in very different taxa? […] whenever individuals differ in their fitness expectations, we should expect stable individual differences and correlated behavioural traits: some individuals are consistently risk-prone whereas others are consistently risk-averse. […] We stress that, in principle, fully flexible behaviour could evolve in all our simulations. […] Yet, we find that selection gives rise to stable individual differences within the same game and correlated behavioural traits across different games (Fig. 3). […] Here superficial explorers evolve high levels of aggression in both games, whereas thorough explorers evolve to be consistently non-aggressive.

Personality trait

Some of the most prominent personality traits described in the literature can be categorized in terms of risk-taking behaviour. A good example is the correlation between aggressiveness towards conspecifics and boldness towards predators: individuals that risk more in intraspecific fights also risk more when confronted with a predator.

Repetability

**APC006**

Personality

Increasing evidence suggests that individ-ual animals differ in their average level of behaviour displayed across a range of contexts (animal ‘personality’), and in their responsiveness to environmental variation (plasticity), and that these phenomena can be considered complementary aspects of the individual phenotype [..] Animal personality: consistent differences between individuals in their behaviour across time and contexts [13]. This implies that interindividual correlations exist in behaviour across time or contexts (also referred to as ‘behavioural syndromes’ [5,6]). The term ‘animal personality’ used here has recently been coined by behavioural ecologists to describe a particular type of individual variation and does not imply a link with human personality [13], which has traditionally been quantified in other ways. […] Behavioural ecologists often assume that animal personality equates to the absence of plasticity, but such patterns illustrate that this is a misconception

Personality trait

Only in this way can future research tackle more challenging questions, such as why selection might favour speciﬁc links between personality type and level of plasticity or responsiveness [2,26].

Repetability

Repeatability: a standardised measure of the differentiation in average phenotype across individuals, defined as the proportion of phenotypic variance explained by differences between individuals [19].

**APC007**

Personality

Why do different individuals in the same population exhibit different behavior, and why is the behavior of a given individual consistent across time? […] In the context of animal personality, ‘consistency’ does not imply that an individual’s behavior is ﬁxed, but rather that its behavior in a given situation or context consistently differs from that of other individuals in the same population. […] Tradeoffs between growth and mortality might encourage the maintenance of individual differences in growth rates […] We ﬁrst present evidence supporting the view that consistent individual differences in productivity do exist, and consider reasons why rank-order consistency in LH productivity might exist. […] It is worth noting, however, that consistent individual differences in growth, fecundity or other LH traits are not the only reason why individuals might exhibit consistent variation in behavioral traits. For instance, individual consistency in social behavior (aggressiveness or sociality) might be maintained as a result of reinforcement by conspeciﬁcs, or because social skills developed early in life encourage continuity in social behavior later in life.

Personality trait

Animal personality traits such as boldness, activity and aggressiveness have been described for many animal species. However, why some individuals are consistently bolder or more active than others, for example, is currently obscure. Given that life-history tradeoffs are common and known to promote inter-individual differences in behavior, we suggest that consistent individual differences in animal personality traits can be favored when those traits contribute to consistent individual differences in productivity (growth and/or fecundity). […] Animal personality traits (PTs) can be defined as behavioral tendencies that affect behavior in several different contexts, vary across the individuals in a given population and are consistent within individuals across time [1,2]. From an ecological and evolutionary perspective, PTs are important because they represent consistent individual variation in behavior within populations, and account for apparently maladaptive behavior [1,2]. Because the literature on animal personality is still developing, and because it encompasses so many different types of animals, there is considerable confusion regarding appropriate definitions and terminology. Recently, Reale et al. [2] suggested that personality, temperament and individuality are equivalent terms, and went on to distill many of the terms used to describe PTs in animals into five general categories: activity, shyness or boldness (response to potentially risky situations), exploration (response to novel situations), aggressiveness and sociability [2]. Correlations among different PTs might exist, in which case the traits are said to form a behavioral syndrome (BS) […] More puzzling than inter-individual differences is why the behavior of an individual would be consistent across time, given abundant evidence that behavioral traits are often plastic, and readily adjusted to suit current conditions [1]. This second question is the focus of the current article. In the context of animal personality, ‘consistency’ does not imply that an individual’s behavior is fixed, but rather that its behavior in a given situation or context consistently differs from that of other individuals in the same population. For instance, rainbow trout Oncorhynchus mykiss all respond to predation risk by reducing their use of potentially risky habitats, but bold genotypes consistently show weaker anti-predatory responses than shy genotypes, both as juveniles and as adults [11,12]. […] Theory indicates that variation across individuals in productivity can be maintained by LH tradeoffs, for example between growth and mortality, or between fecundity and mortality. With this assumption in mind, we predict consistency within individuals in PTs when (i) productivity rank order is consistent across individuals and (ii) PTs are correlated with productivity across individuals.

Repeatability

**APC008**

Personality

In this paper, we propose that consistent behavioural differences among individuals, or personality, covary with life history and physiological differences at the within-population, interpopulation and interspecific levels. […] Individuals show consistent behavioural differences over time or across situations, in other words personality differences (Wilson et al. 1994; Gosling 2001; Sih et al. 2004; Reale et al. 2007). […] Recent work on personality has highlighted integrative aspects of research on the topic (Sih et al. 2004; Reale et al. 2007), in particular, how the concepts of personality and behavioural plasticity are tightly linked (Dingemanse et al. 2010) […] Because we are primarily interested in the presence of among-individual variance in the average level of behaviour, we will use the terms personality and behaviour interchangeably throughout the paper and will not be considering behavioural plasticity within individuals here.

Personality trait

First, personality traits are not systematically associ ated in a behavioural syndrome (Reale et al. 2007) […] Detailed investigation of the developmental aspects of personality traits, the effects of genotype by environment interaction, and of genotype/environment correlation on these traits have recently been advocated (e.g. Dingemanse et al. 2010; Stamps & Groothuis 2010a) […]The POLS perspective at the population level presented here extends ideas previously developed in life-history theory (i.e. r- and K-selection, fast-slow continuum) by proposing personality traits as a central element in the study of life-history strategies

Repeatability

**APC009**

Personality

Two findings promoted this shift. First, behavioural differences tend to be highly structured, that is, both stable over time and correlated across different situations and contexts […] Behavioral differences that are maintained through time and across contexts are termed ‘personalities’ in humans and, analogously, the term ‘animal personalities’ has been adopted in the literature […] Animal personalities: the phenomenon that individuals differ systematically in their behavioral tendencies; these differences are consistent over time (i.e., individuals that tend to score higher on a particular behavioral axis tend to score higher on that axis at later points in time) and correlated across different situations and contexts (e.g., individuals that tend to be more aggressive towards conspecifics also tend to be bolder in novel environments than less aggressive individuals). […] some individuals tend to be more aggressive than others (variation), these differences remain stable over longer periods of time (time consistency), and aggressiveness is correlated with boldness in that more aggressive individuals tend to be bolder in response to predators than less aggressive individuals (correlations across contexts).

Personality trait

In populations with personalities, individuals are said to have a personality or behavioral type (e.g., more aggressive types vs less aggressive types), behaviors that are involved in personality differences are termed personality traits (e.g., aggression and boldness)

Repeatability

**APC011**

Personality

We specifically focus on three dimensions of personality: (1) contextual generality at a given age or time, (2) temporal consistency in behavioural traits and in relationships between traits, and (3) the effects of genes and experience on the development of personality at a given age or life stage. Individual differences in behaviour that are consistent across time and/or across contexts, as evidenced by the rapidly growing literature on animal personality, temperament, coping styles, and behavioural syndromes. […] ‘Personality’ is a term borrowed from psychology, where it refers to underlying behavioural tendencies that differ across individuals, that are consistent within individuals over time, and that affect the behaviour that is expressed in different contexts (Caspi, Roberts & Shiner, 2005; Reale *et al*., 2007). ‘Temperament’ and ‘coping styles’ are terms that initially developed in separate literatures, but whose meaning has recently converged with the definition for personality indicated above (Gosling, 2001; Caspi *et al*., 2005; Koolhaas *et al*., 2007; Reale *et al*., 2007). […] By contrast, the term ‘behavioural syndrome’ is currently defined as individual differences in behaviour patterns that are either correlated across time (e.g. aggressiveness of the same set of individuals before *versus* after sexual maturity), or across contexts (e.g. activity of the same set of individuals in their home cages *versus* in an open field) […] The second key criterion of personality traits is that they should be consistent within individuals for a period of time […] It should by now be apparent that the concept of animal personality is more complicated than intuition might suggest. The term ‘personality’ implies that individuals within the same group, sample or population express different levels of the same behaviour pattern, or different behaviour patterns, in the same context at a given age and time. In addition, personality assumes some degree of contextual generality: scores for the same behaviour expressed in two or more contexts, or scores for different behaviour patterns expressed in two or more contexts, should be correlated with one another across individuals or genotypes at a given age and time. […] Third, personality traits are assumed to be both differentially and structurally consistent across time. That is, personality not only requires that individual scores in a given context at one time be positively correlated with their scores in the same context at a later time (differential consistency), but also that correlations between the same behaviour in different contexts, or between different behaviours in different contexts, measured at one time will be maintained if the same behaviours in the same individuals are measured in the same contexts at a later time (structural consistency). Both types of temporal consistency need to be documented, since structural consistency can occur without differential consistency. Note that all of these criteria for personality (individual differences in behaviour, contextual generality, differential consistency and structural consistency) all apply at the group level. Regardless of whether or not behavioural traits satisfy all of these criteria, individual-level indices of behaviour (contextual reaction norms, individual stability) can still be useful for studying how different individuals or genotypes behave in different contexts at the same time, or how the behaviour expressed by individuals or genotypes in a given context changes over time. […]changes in personality within individuals are most likely to occur when those individuals shift from one physical or social environment to another, e.g., as a result of natal or breeding dispersal, migration, or recruitment to a new social group or neighborhood. […] Personality is a complicated concept, because although it requires repeated measurements of the same individuals at different times and in different contexts, the focus is actually on the behaviour of individuals relative to one another, not on the absolute levels of behaviour expressed by individuals or by groups of individuals. Indeed, as we discuss below, it is perfectly possible for personality to be stable over a period of time even if the scores of individual subjects, and/or the mean score for all of the subjects, change dramatically over that same period of time. This emphasis on the behaviour of individuals relative to others is reflected in the use of descriptive phrases such as ‘consistent individual differences’, and by the use of correlations across individuals in behaviour expressed in different contexts and at different times to measure personality traits. […] The second key criterion of personality traits is that they should be consistent within individuals for a period of time (Caspi *et al*., 2005; Reale *et al*., 2007). […] Anyone interested in the development of animal personality traits must consider temporal consistency over two different intervals: short intervals to determine whether behaviour is sufficiently consistent across time to be included in a study of personality, and longer intervals to determine how behaviour changes over the course of a lifetime.

Personality trait

Animal personality traits have been documented in many vertebrates […] First, information about the ontogenetic stages when personality traits are first expressed or change can provide valuable insights into the physiological processes that are responsible for the organisation and stability of personality traits. […] However, only a few researchers have described how correlations among different personality traits change across ontogeny (e.g. Dingemanse *et al*., 2002; Bell&Stamps, 2004; Carere *et al*., 2005*b*; Johnson & Sih, 2007; Weiss, King & Hopkins, 2007; Sinn, Gosling & Moltschaniwskyj, 2008), or have experimentally tested whether a specific type of experience at a given age affects correlations among personality traits later in life (e.g. Sluyter *et al*., 1996; Benus, 1999; Carere *et al*., 2005*a*; Bell & Sih, 2007; Frost *et al*., 2007). […] Two key attributes of personality traits: consistency in behaviour across contexts at a given time, and consistency in behaviour across time.

Repeatability

For current purposes, four of these terms are most relevant: ‘mean-level consistency’ (also called normative consistency), ‘differential consistency’ (also called repeatability), ‘structural consistency’, and ‘individual stability’. The first three of these terms summarize patterns of temporal consistency in behaviour for the members of a group; by contrast, individual stability describes the temporal consistency of behaviour at the level of the individual. […] Differential consistency describes the extent to which subjects maintain their behaviour scores in a given context across time, relative to the scores of all of the other individuals in the same study. High levels of differential consistency can occur even if the behaviour of every individual in the sample changes over time, since this term refers to the consistency of behavioural differences among individuals, not their absolute scores. High differential consistency can occur even if mean-level consistency is low (e.g. Fig. 3). Because differential consistency is computed using data collected on interval scales, this index not only indicates whether some individuals have higher or lower scores than others, but also the extent to which their scores differ from one another. Rank-order consistency is a special case of differential consistency. Because this index is based on an ordinal scale, it describes the extent to which the rank order of the scores of different individuals within the same sample is preserved over time, but ignores information about the extent to which their scores differ from one another. Differential consistency can be measured using indices of ‘repeatability’ in the broad sense of that term, where repeatability is measured by computing correlations across individuals for their scores on the same behaviour in the same context at different times. In the animal behaviour literature, the two most commonly used indices of repeatability are the product-moment correlation *r*, and the intra-class correlation *τ*, where *τ* is ‘repeatability’ in the narrow sense of the term, based on equations derived and used by quantitative geneticists (Lessells&Boag, 1987; Falconer&Mackay, 1996). However, since *τ* is very sensitive to changes in the mean value of traits in repeated samples (Hayes & Jenkins, 1997), *r* provides amore useful index of differential consistency than *τ* for inter-test intervals when mean-level consistency is low.

**APC012**

Personality

The study of behavioural syndromes (animal personalities) considers how limited behavioural plasticity, as well as behavioural correlations affects an individual’s fitness in diverse ecological contexts. […] Behavioural syndromes (a.k.a. animal personalities) that acknowledges that in many species, individuals exhibit both within-individual and between-individual consistency in behaviours across time or across ecological contexts (Sih et al. 2004; Dall et al. 2004; Sih and Bell 2008) […] […] Hallmarks of the behavioural syndrome concept include limited plasticity (relative to infinite, optimal plasticity) and behavioural correlations (carryovers across ecological contexts or across time). […] Recent work on behavioural syndromes emphasises that animals also often have less than optimal behavioural plasticity that has analogous effects.

Personality trait

We identify several general mechanisms for how population ecology phenomena can be influenced by a species or populations average behavioural type, by within-species variation in behavioural type, or by behavioural correlations across time or across ecological contexts. We note, in particular, the importance of behavioural type-dependent dispersal in spatial ecology. […] In many species, some individuals are consistently the more aggressive behavioural type (BT), whereas others are consistently less aggressive not just in competitive contests that involve aggression, but also in foraging, mating, parental and ⁄ or antipredator behaviour (Riechert & Hedrick 1993). Other documented BT axes include variation in boldness (Wilson et al. 1994) or sociability (Cote et al. 2010a). Although it has long been clear that humans differ in personality, and that a few other animals (e.g. primates, dogs, cats, laboratory rodents) exhibit consistent individual BTs, recent work suggests that behavioural syndromes apply across the entire animal kingdom (Gosling 2001). Behavioural syndromes are ecologically important because an individual’s BT can clearly affect its fitness

Repeatability

**APC013**

Personality

Personality will introduce variability in resting MR measures because individuals consistently differ in their stress response, exploration or activity levels. […] Recently, however, researchers from a broad array of ecological sub-disciplines […] have begun to consider inter-individual variation as an important ecological and evolutionary characteristic of wild populations. The burgeoning field of animal personality seeks to explain the maintenance of variation in numerous behavioural traits, including exploration, boldness, activity and stress response among others, by examining their fitness in a variety of ecological, developmental, and demographic contexts. […] However, a variety of individual behavioural traits such as activity levels and the type or strength of a stress response are repeatable and intrinsic attributes of individuals that we now refer to as personality. […] Personality refers to individual behavioural differences that are consistent – or largely maintained - over time and/or across situations (Reale et al. 2007). […] That individuals often differ consistently in how they behave has been reported for a variety of mammals (including humans, Nettle 2006), birds, fish, reptiles, amphibians, insects, spiders and cephalopods (Gosling 2001). […] Personality is considered an intrinsic characteristic of the individual and thus should not be confused with non-repeatable variation in behaviours that may be determined by recent experience or environmental (extrinsic) conditions, as is the case for social status. […] Individuals with different personalities will react differently to the same treatment […] Two fundamental questions in the study of animal personalities are: why do populations harbour more than one personality type? Why do animals exhibit behavioural consistency? In the following, we show why incorporating energy metabolism into theoretical and empirical studies of personality may give further insights of why individuals behave consistently over time and across contexts.

Personality trait

Individuals may consistently differ in one or more personality traits, such as boldness, aggressiveness, reactivity, sociability, exploration or activity levels (Reale et al. 2007). The so-called ‘‘laid back, relaxed, placid, or calm’’ vs ‘‘high-strung, restless, jumpy, or nervous’’ natural dispositions of animals referred to by physiologists (Mueller and Diamond 2001) actually represent personality traits. […] Differences in personality traits or combinations of traits have been shown to have consequences for individual fitness through their effect on predation rates (Reale and Festa-Bianchet 2003, Bell and Sih 2007), the form and outcome of competition for females and food (Dingemanse et al. 2004), or the response to social challenges (Dingemanse and Reale 2005, Sinn et al. 2006). […] Ignoring personality traits may create serious methodological issues on measures considered important by ecologists.

Repeatability

**APC014**

Personality

Behavioural ecologists have started to study from an adaptive viewpoint (i) why individuals are repeatable vs. flexible, (ii) which conditions favour between-individual vs. within-individual variance (Glossary) or between-individual vs. within-individual correlations (Glossary), and (iii) how evolution evolutionary and ecological processes are affected by individuality […]First, behavioural consistency, for example in avian provisioning rates, has been proposed as a quality indicator trait under sexual selection (Schuett, Tregenza & Dall 2010). The hypothesis predicts that males show lower within-individual variance compared with females. Published empirical tests of the proposed hypothesis typically quantify whether males have lower repeatability compared with females, which constitutes an inappropriate test because the hypothesis concerns within-individual variance not necessarily repeatability. […] Personality: Variation among individuals in the intercept of their behavioural reaction norm (Dingemanse et al. 2010).

Personality trait

Social interactions have been proposed to induce selection for different behavioural types, for example a mix of individuals that are relatively bold vs. relatively shy.

Repeatability

Individual repeatability: The proportion of phenotypic variance that is attributable to differences between individuals, where phenotypic variance represents the sum of the between- and within-individual variance (Falconer & Mackay 1996).

**APC015**

Personality

Individual behavioral characteristics appear to be consistent over time and across situations. [..] Since the times of the Greek philosophers, scientists have tried to categorize individual variability in behavior and underlying physiology into distinct personalities or temperaments. Currently, the general view is that trait characteristics should be stable over a considerable period of time and should be consistent across situations. […] Behavioral ecology has adopted the term behavioral syndrome indicating that trait characteristics should involve suits of correlated behaviors [100,111]. This more neutral term may apply for any set of correlated behaviors that shows consistency over time and across situations. In the biomedical research field the term coping style is commonly used for these individual trait differences. […] Coping styles may be defined as alternative response patterns in reaction to a stressor. The concept is based on the observation that the individual variation in offensive aggressive behavior is stable over time and related to the response pattern in a variety of other challenging conditions. […]The consistency of aggression as an expression of coping style across situations can be best demonstrated in tests that allow the animal a choice of different response patterns. […]This demonstrates the consistency of individual variation in behavior across situations, i.e. the aggressive response to an intruder in the home cage predicts an active behavioral response in this non-social burying paradigm. Other examples of this consistency in response pattern to challenging situations can be found in nest building behaviour [115], active avoidance behavior [9] and in the forced swim test [135].

Personality trait

Various terms are used to categorize the extremes of the individual variation such as shy versus bold, active versus passive, proactive versus reactive, and hawk versus dove.

Repeatability

**APC016**

Personality

Consistent differences in behaviour between individuals […] To date, the few available naturalistic studies have addressed the functional consequences of animal personality by describing how selection operates on single components of animal personality (e.g., exploratory behaviour of novel environments as a measure of 'avian personality' in great tits; Dingemanse et al., 2002). Our second aim is to point out that, ultimately, such studies cannot provide functional explanations for the existence of animal personality per se, as this would require insight in why individuals show consistency in their behaviour, either across time, generations, contexts or situations (Dall et al., 2004; Sih et al., 2004a). We outline both direct and indirect approaches to study suites of correlated traits from an adaptive perspective. […] When quantitative genetic parameters have also been quantified ( i.e., heritability of and genetic correlations between components of personality traits), one can make an informed evaluation of the evolutionary consequences of the imposed selective regime (Falconer & Mackay, 1996; Roff, 1997; Lynch & Walsh, 1998), including the evolution of genetic correlations between behavioural traits (Roff, 1996), i.e., animal personality.

Personality trait

Behavioural flexibility is often regarded to be unlimited, immediate, and reversible (Sih et al., 2004a,b), allowing individuals to maximize their fitness in the many different environments they encounter during life. Contrary to this notion of behavioural plasticity as the major adaptive cause of phenotypic variation in behaviour (Houston & McNamara, 1999; Dall et al., 2004; Neff & Sherman, 2004), animals often show very limited behavioural plasticity (Sih et al., 2004a, b) and commonly differ consistently in their reaction towards the same environmental stimuli (Clark& Ehlinger, 1987; Wilson et al., 1994; Boissy, 1995; Wilson, 1998; Gosling, 2001; Greenberg & Mettke- Hofmann, 2001). These individual differences in behaviour are, moreover, frequently expressed across a wide range of contexts and situations: individuals commonly differ consistently in whole suites of functionally-distinct behavioural traits (Sih et al., 2004a, b). For instance, in birds (Verbeek et al., 1996), rodents (Koolhaas et al., 2001), and fish (Huntingford, 1976), animals that are relatively aggressive towards conspecifics are also bolder in exploring novel environments and predators. These individual differences in suites of correlated traits have been named behavioural syndromes (Sih et al., 2004a, b), coping strategies (Koolhaas et al., 2001), temperament (Boissy, 1995; Clarke & Boinski, 1995) or animal personality traits (Buss, 1991; Gosling, 2001). […] Variation in personality has received considerable attention from the mechanistic viewpoint; the emerging pattern is that individual differences in single components of animal personality (e.g., aggressiveness) are moderately heritable and relatively stable over the entire life of the individual (Boissy, 1995; Koolhaas et al., 1999; Bouchard & Loehlin, 2001) and that phenotypic correlations between components of personality (e.g., between aggressiveness and boldness) often originate from strong underlying genetic correlations (Bakker, 1994; Bult & Lynch, 2000; van Oers et al., 2004a; Bell, 2005). […] Thus providing first detailed descriptions of how and when natural selection may operate on animal personality […] Taking these long-term fitness consequences into consideration, adult males may have maximized their fitness by means of adaptive mate choice: adult males of extreme phenotype were mated disassortatively with respect to personality type (Dingemanse et al., 2004).

Repeatability

**APC017**

Personality

Consistent individual differences (CIDs) in a wide array of behaviors are surprisingly widespread in animals [1–4]. CIDs are individual differences in phenotype that are maintained over time (e.g. as measured by repeatability). Why then should behavior be temporally consistent, given the abundant evidence that behavior can quickly change in response to changes in the environment or internal state? In recent years, a number of hypotheses have been advanced to explain why behavioral traits might differ across individuals, but be temporally consistent within individuals [5–10]. […] In addition, personality itself can vary as a function of temperature: the rank order of individual scores for activity, aggressiveness and boldness changed when tested across temperatures <3 8C apart [66].

Personality trait

Careau and colleagues [11] discussed more generally why individual differences in RMR might lead to differences in personality traits such as activity, and how personality might affect measures of RMR.

Repeatability

CIDs are individual differences in phenotype that are maintained over time (e.g. as measured by repeatability). […] Finally, we make a plea for future studies to employ mixed model analyses of their data, which can estimate repeatability of a given trait while simultaneously controlling for the effects of age, gender or temperature. […] In fact, recent reviews indicate that RMR is consistently different (as measured by repeatability) for a diverse array of animal taxa [29,30]. Most researchers have studied RMR over relatively short inter-test intervals [29]. However, signiﬁcant repeatability of RMR has been reported over six months in ﬁsh [31], and over multiple years for birds in the laboratory [32] and in the ﬁeld [33]. Field studies with small mammals also show repeatability of RMR up to 1.5 months in voles [34] and six months in squirrels [35]. Even though mean-level RMR gradually declined across the lifetime (ca. 5 y) of both male and female zebra ﬁnches, individual rank-order differences in RMR were largely maintained within each sex, and so RMR was repeatable [36]. Possible proximate reasons why RMR should be consistently different are addressed in Box 2. […] One potential explanation for temporal consistency in RMR within individuals over relatively short periods of time (e.g. days to weeks) is that changes in RMR are constrained by the time required to change the sizes of organs associated with energy metabolism. […] The reasons for temporal consistency in RMR over longer periods of time (e.g. months to years) are also currently obscure. However, a recent study hints that temporal consistency in experiential factors and/or reproductive state may encourage temporal consistency in RMR. Duarte and others [74] studied CIDs in RMR in female mice, and found significant repeatability of RMR across 110 d for a group of female mice that were individually housed as virgins, but not for a second group of females that were housed with another female and a male, allowed to raise a litter, and then housed with other females prior to the second RMR measurement [74].

**APC019**

Personality

Animal personalities: individual differences in behaviour (or suites of correlated behaviours) that are consistent over time or contexts. […] Individuals within single populations often differ consistently in their behavioural tendencies across time and contexts (Wilson 1998; Sih et al. 2004a,b; Reale et al. 2007). Male great tits (Parus major), for example, differ consistently in whole suites of correlated traits, with more aggressive individuals also tending to be more explorative towards novel objects and unfamiliar environments than less aggressive ones (Verbeek et al. 1996). […] The empirical literature on animal personality has reported three types of behavioural patterns that require adaptive explanation in the context of animal personality variation (Dall et al. 2004; Sih et al. 2004b; Dingemanse et al. 2010b). First, consistent individual differences exist in single behaviours. Second, consistent individual differences exist in suites of functionally distinct behaviours. Third, consistent individual differences exist in behavioural plasticity (also called responsiveness). In all cases, consistency refers to both stability over time (in terms of date or age) and/or contexts (environmental gradients, e.g. predation risk). Patterns consistent with consistent individual variation in a single behaviour are illustrated in figure 1a, which depicts behavioural phenotypes over time (or alternatively an environmental gradient) for each of three individuals (black, grey and white), where lines depict their reaction norms (sensu Sarkar 1999). The key feature here is that the rank order differences between individuals are maintained over time or contexts (Sih et al. 2004a,b; Bell 2007). In many species, individuals differ consistently not only in single behaviours but also these differences involve whole suites of behaviours (van Oers et al. 2005; Bell 2007; Reale et al. 2007), resulting in correlations across functionally distinct behaviours at the population level (figure 1b). […] Individuals differ not only in their average behaviour but also in their level of behavioural plasticity (responsiveness) (Boyce & Ellis 2005; Nussey et al. 2007; Smiseth et al. 2008; but see Martin & Re´ale 2008; Dingemanse et al. 2010b). This phenomenon is also illustrated in figure 1a, which depicts a scenario where individuals differ both in their behavioural mean and in their behavioural plasticity (e.g. black circle individuals are more responsive than grey circle individuals). […]Moreover, it has recently been suggested that individual variation in plasticity (also referred to as ‘behavioural flexibility’; Coppens et al. 2010) might be correlated across traits, i.e. certain individuals might be consistently more plastic in a variety of functionally distinct behaviours when compared with others (Boyce & Ellis 2005; Sih & Bell 2008), resulting in plasticity syndromes. There is further evidence suggesting that individual variation in plasticity may also covary with mean levels of behaviour (Dingemanse et al. 2010b) (as in figure 1a). In Ural Owls (Strix uralensis), for example, mothers that are on average aggressive in nest defence against humans show greater plasticity in aggressiveness when compared with mothers that are less aggressive

Personality trait

Over the last few years, the notion that such personality types, or behavioural syndromes, exist in a wide range of animal species has stimulated empirical research on the proximate and ultimate factors shaping such variation (Dingemanse & Reale 2005; Sih & Bell 2008; Stamps & Groothuis 2010a,b). […] We then review formal (and some verbal) models for adaptive personality differences (§3), where we focus on two main questions. […] Animal personality traits can be underpinned by heritable variation (Penke et al. 2007; Reale et al. 2007; van Oers & Mueller 2010), result from environmental factors (Quinn et al. 2009; Oosten et al. 2010) or be shaped by interactions between genes and environments (Carere et al. 2005; van Oers et al. 2005; Dingemanse et al. 2009).

Repeatability

**APC020**

Personality

A coping style (also termed behavioural syndrome or personality) is defined as a correlated set of individual behavioural and physiological characteristics that is consistent over time and across situations. […] Behavioural flexibility appears to be an important underlying attribute or feature of the coping style that might explain consistency across situations. […] This article summarizes some of the evidence that individual differentiation in behavioural flexibility emerges as a function of underlying variability in the activation of a brain circuitry that includes the prefrontal cortex and its key neurochemical signalling pathways (e.g. dopaminergic and serotonergic input). […] These studies are all based on two observations: (i) within an individual, behaviours are often correlated independent of the environmental situation and (ii) correlated behaviours result in only a limited number of phenotypes across individuals. Several terms are used for this phenomenon. Sih et al. (2004) used the term behavioural syndrome, whereas Groothuis & Carere (2005) preferred the term behavioural profile. […] Whatever term is used exactly, they all refer to alternative response patterns in reaction to challenges that are stable over time and across various situations (Koolhaas et al. 1999). […] Individual differences in reward processing and the underlying neurobiology are important components of animal personality and behavioural flexibility that might explain the consistency of individual trait characteristics across contexts. […] Since we focus on individual behavioural characteristics that are stable across situations, one has to look for variation in causal mechanisms or behavioural control functions that are activated in different contexts in one and the same animal. Inter-individual variations in behaviour in these contexts should consequently be reflected in a differential activation of the underlying causal mechanisms. […] We will rather explore the neurobiology of behavioural flexibility as an important underlying attribute or feature of general coping style that might explain consistency of individual behaviour across a wide variety of environmental conditions.

Personality trait

Naturalistic studies in a variety of animal species show that individuals can be categorized in distinct behavioural phenotypes. […] Rodent research distinguishes between proactive and reactive coping (Koolhaas et al. 1999) and researchers of fish and birds often use the terms shyness and boldness (Wilson et al. 1994). […] For example, animals characterized by a proactive coping style are offensive towards male conspecific rivals, are impulsive in decision-making, score high in frustration tests, take risks in the face of potential dangers and are novelty seekers (David et al. 2004; Groothuis & Carere 2005; Steimer & Driscoll 2005). […] The dimensions of personality are likely to reflect individual variation in the pattern of activity of underlying causal physiological mechanisms.

Repeatability

**APC021**

Personality

Consistent individual behavioural tendencies, termed “personalities” […] We consider the evolution and maintenance of both main aspects of animal personality: inter-individual variation and intra-individual consistency […] Individuals often show very limited behavioural plasticity which can be manifest in consistent individual differences in behaviour (e.g. Benus *et al*., 1991; Boissy, 1995; Gosling & John, 1999; Koolhaas *et al*., 1999; Gosling, 2001; Groothuis & Carere, 2005;R´eale *et al*., 2007), also known as personality differences (Eysenck & Eysenck, 1985; Gosling, 2001; Dall, Houston & McNamara, 2004), behavioural syndromes (e.g. Sih *et al*., 2004*a*, *b*), coping styles (Benus *et al*., 1991; Koolhaas *et al*., 1999) or temperaments (Boissy, 1995). […] Individuals differ consistently in suites of correlated traits and along a subset of potential axes of behavioural variation […] If an individual is consistent in its behaviour over time, over different functional behavioural categories (contexts) and/or situations (*sensu* Sih *et al*., 2004*a*), it will appear to behave ‘‘maladaptively’’ in many situations. Consequently, the question arises why these personality differences exist; i.e. what is their evolutionary origin, and how are they maintained? More specifically: (1) why do individuals in the same population differ in their behavioural responses, even under the same environmental conditions, and (2) why are individuals consistent in their behaviour over time or space, even when ecologically significant factors change (Stamps, 2007)? The first question focuses on the reasons for the evolution of different levels of expression of a behavioural trait, i.e. inter-individual variation, whereas the second concentrates on reasons for the evolution of behavioural consistency, i.e. intra-individual stability (Stamps, 2007). As discussed further by Stamps (2007), one would either expect a combination of both low inter- and intra-individual variation in a population (if one behavioural pattern results in highest fitness) or a combination of both high inter- and intraindividual variation (if more than one behavioural pattern results in equal fitness); but instead high inter- and low intraindividual variation are often observed (e.g. Dall *et al*., 2004; Sih *et al*., 2004*b*; Dingemanse & Reale, 2005). […] Indeed, for personality differences to exist, mechanisms creating interindividual behavioural variation need to act together with mechanisms generating and maintaining intra-individual behavioural consistency. Explanations for the existence of intra-individual behavioural consistency include benefits of predictability (Dall *et al*., 2004; McNamara *et al*., 2009), constraints (costs or limits of flexibility, Sih *et al*., 2004*b*; noisy information, McElreath & Strimling, 2006) and positive feedback loops between state and behaviour (Dall *et al*., 2004; Sih *et al*., 2004*b*; Wolf *et al*., 2008). Another possibility, which has not received much attention, is a role of sexual selection in the evolution and maintenance of personality differences (both of inter-individual variation and intraindividual consistency), potentially acting together with some of the other evolutionary processes that have been hypothesised. […] Fig. 1

Personality trait

We provide an overview of how sexual selection could generate and maintain personality traits […] Also, the frequent use of self-reported questionnaires has been criticised where self-assessment may not reflect actual personality traits (see Penke, Denissen & Miller, 2007*a*) or where self-assessment ability may differ among people of varying personalities (see, for similar potential biases in animal studies, Biro & Dingemanse, 2009). […] Moral virtues are predicted to signal either genetic quality in that genes that are associated with generally higher fitness might be required for showing moral virtues like a ‘‘sophisticated, empathetic social intelligence’’; or to signal good parental abilities (which may have genetic and environmental components) which are predicted to be indicated by empathic personality traits as they could help during caring for offspring. […] Also, consistent behavioural differences in humour traits need to be demonstrated for classification as personality traits. […] From animal studies there is indirect support for the hypothesis that personality traits can signal male quality to a female from a study of collared flycatchers, *Ficedula albicollis,* (Garamszegi, Eens & Torok, 2008; Table 1). Risktaking and exploratory male collared flycatchers consistently sang from a lower song post when an observer was nearby than risk-averse or less exploratory males. These bold males singing from lower posts bonded relatively faster with a partner than individuals singing from higher posts. This could indicate (among other possibilities) that males on the lower posts were of superior quality or likely to commit more to raising offspring as risk-takers are likely to have lower prospects for future reproduction (Wolf *et al*., 2007; but see e.g. Nettle, 2005 for potential for reduced parental care by extraverts). […] It should be noted that both the female tendency to approach males (Forstmeier & Birkhead, 2004) and male song rate (as well as male aggression, Forstmeier, 2004, 2007; Forstmeier, Coltman & Birkhead, 2004) can be considered personality traits in zebra finches as individuals differ consistently from one another in these behaviours. […] Both Gonzaga *et al*.’s (2007) and Botwin *et al*.’s (1997) study also illustrate that humans actually prefer partners with personality traits that resemble themselves, instead of ending up with a similar partner just as a result of similar environmental and demographic backgrounds. […] Negative correlations between personality traits of partners are not only rarer in human partnerships, but they are also more distinctive in unstable partnerships than in stable ones (Vandenberg, 1972). […] If the personality trait (consistency or level) is an indicator of genetic quality, then this trait should exhibit some genetic variation and a positive genetic correlation with other fitness-related traits.

Repeatability

Roberts & DelVecchio (2000) identify different forms of consistency, two of which are relevant here. Intra-individual measures of consistency ask if an organism behaves in a stable manner over time or across different environments, whereas rank-order consistency refers to the relative placement of an individual within a group across behavioural tests. By analogy, consistency can be assessed either on a population level, often measured as repeatability (e.g. Sinn, While & Wapstra, 2008*b*, see Table 1) or as a rank correlation (rankorder consistency, e.g. Briffa, Rundle & Fryer, 2008; Sinn, Gosling &Moltschaniwskyj, 2008*a*); or it can be evaluated on an individual level, for instance measured as a coefficient of variation (Cummings & Mollaghan, 2006; Schuett, 2008; W. Schuett, S.R.X. Dall & N.J. Royle, in preparation). While repeatability is a population characteristic estimating how much of the behavioural variation is due to intra- and inter-individual variation, other individual-based consistency indices and statistical approaches can be used to test specifically for inter-individual variation in consistency or inversely for the degree of intra-individual consistency (see above, and also Asendorpf, 1990; Dochtermann & Jenkins, 2007; Sinn *et al*., 2008*a*; R´eale & Dingemanse, 2009).

**APC022**

Personality

We develop a conceptual framework for the understanding of animal personalities in terms of adaptive evolution. We focus on two basic questions. First, why do behavioural types exhibit limited behavioural plasticity, that is, behavioural correlations both across contexts and over time? Second, how can multiple behavioural types coexist within a single population? […] We emphasize differences in ‘state’ among individuals in combination with state-dependent behaviour. Some states are inherently stable and individual differences in such states can explain stable differences in suites of behaviour if it is adaptive to make behaviour in various contexts dependent on such states. Behavioural stability and cross-context correlations in behaviour are more difficult to explain if individual states are potentially more variable. In such cases stable personalities can result from state-dependent behaviour if state and behaviour mutually reinforce each other by feedback mechanisms. […] Individuals of the same sex, age and size differ consistently in whole suites of correlated behavioural tendencies, comparable to human personalities […] Consistent individual differences in behaviour have been termed animal personalities (also coping styles, Koolhaas et al. 1999; temperament, Reale et al. 2007; behavioural syndromes, Sih et al. 2004a). It should be stressed that the concept of personalities does not require that individuals are completely consistent in their behaviour but rather that individual differences are consistently maintained over time and across contexts. […] We now turn to the observation that behavioural types often exhibit (i) time-consistency of behaviour (i.e. stability through part of the ontogeny), and (ii) suites of correlated behavioural traits (e.g. types that are more aggressive towards conspecifics are also bolder when confronted with a predator). Both types of behavioural correlations indicate limited behavioural plasticity to a degree that is often surprising (Wilson 1998; Dall et al. 2004). […] If the state of an individual is stable over time, adaptive state-dependent behaviour will also be time consistent, that is, not easily changed on a short-term perspective. Moreover, if the same stable state affects the behaviour of an individual in multiple contexts, differences in inherently stable states can also explain adaptive behavioural correlations across contexts. Accordingly, differences in stable individual states provide an obvious and straightforward explanation for animal personalities. It is thus not surprising if large and irreversible state differences (e.g. male/female, different castes in social insects) result in stable and consistent differences in behaviour.

Personality trait

Repeatability

**APC023**

Personality

Research on fishes, in particular, has contributed to the early documentation of individual consistency in behaviour (Huntingford, 1976; Wilson *et al*., 1993) and continues to pioneer new research avenues within the animal personality field […] The term animal personality (Buss, 1991; Gosling, 2001) is roughly synonymous with several other names used in the literature, such as temperament (Boissy, 1995; Clarke & Boinski, 1995), coping strategy (Koolhaas *et al*., 1999) and, more recently, behavioural syndromes (Sih *et al*., 2004*a*). Behavioural syndromes are specifically defined as suites of behavioural traits that co-vary across contexts or situations (Sih *et al*., 2004*a*). […] Behavioural syndromes are extremely relevant to ecology and evolution because they imply that plasticity in behavioural traits may be limited, thus constraining the ability of animals to behave in an optimal fashion in all situations. […] The behavioural syndrome framework presents the possibility that this variation may instead be systematic at the individual level: certain individuals are often more aggressive, or more active, than the optimal levels of aggression or activity would require, given the situation. Even when individuals adjust their BT across contexts or over time, their behavioural flexibility may be constrained by a population-level syndrome in which several aspects of behaviour are related (Bell & Stamps, 2004). […] One of the most intriguing questions about animal personality is whether it results in limitations on behavioural plasticity. A mechanistic understanding of animal personality traits is critical to determine the nature of these possible constraints on plasticity, or whether the mechanisms themselves may be predisposed to enhanced flexibility (*e.g.* rapid changes in neurotransmitter concentrations). Indeed, it is conceivable that some individuals may be consistently more plastic than others; thus, plasticity itself may be an aspect of personality (Sih & Bell, 2008; Dzieweczynski *et al*., 2010).

Personality trait

Such as the role of the selection regime in shaping personality traits (Bell & Sih, 2007; Dingemanse *et al*., 2007). […] Current knowledge of behavioural syndromes in fishes is reviewed with respect to five main axes of animal personality: (1) shyness–boldness, (2) exploration–avoidance, (3) activity, (4) aggressiveness and (5) sociability. […] Thus, within a syndrome of aggressiveness, individuals maintain a consistent behavioural type (BT), including consistent differences among individuals in their rank-order of aggression even as the environment changes. […] For example, a variety of experimental measures have been used to describe a single personality trait, or the same measure has been used to quantify different components of personality, such as the latency to emerge from shelter in an open field assay has been used as a measure of both exploratory tendency and boldness. […] Toms *et al*. (2010) have echoed this concern for studies on boldness in fishes, highlighting the fact that many studies claim to assess boldness, but not all methods capture an underlying personality trait of fearlessness […] Studies on aggression syndromes in fishes have predominantly investigated the correlation between aggression and other personality traits (Table II) rather than individual consistency in aggression alone

Repeatability

Logically, the implications of behavioural syndromes for individual fitness are more profound if personality traits are stable over longer periods of time. To date, however, relatively little work, in fishes or other taxa, has been done on the persistence of BTs through developmental changes or over significant periods of time relative to life span. A few studies have demonstrated stability in single behaviours; nevertheless, there is a need for more work to demonstrate how widespread stability is and what conditions favour stability of BTs. Aggression is stable through sexual maturation in *C. citrinellum* (Francis, 1990). In mature *L. goodei*, males are stable in their relative aggression levels over a 5 week period and through multiple instances of male–male competition for females (McGhee & Travis, 2010). Consistency in boldness levels over a five-week period have been shown in the African catfish *Clarias gariepinus* (Burchell) (van de Nieuwegiessen *et al*., 2010). In a mark–recapture study, Wilson & Godin (2009) found that shy-bold BTs in bluegill sunfish *Lepomis macrochirus* Rafinesque (Wilson & Godin, 2009) are repeatable over a one to three-month period in the natural environment. […] Stamps & Groothuis (2010) argue that adopting this developmental reaction-norm approach in combination with contextual reaction norms (in which behavioural trait expression is compared across contexts at a given age or time) will provide a holistic view of the relative influences of genotype, experience and their interaction in producing repeatable differences in behaviour between individuals over time, as well as stability in personality structure (*i.e.* behavioural correlations). […] Most telemetry studies, however, have not yet adopted an analysis that addresses whether observations of individual variation reflect the presence of different BTs (*e.g.* examine repeatability in movement patterns within individuals).

**APC024**

Personality

Consistent individual differences in behavioural traits […] Individual differences in a range of correlated behavioural traits have been labelled as temperament (Réale et al., 2000), coping strategies (Benus et al., 1991; Wechsler, 1995), coping styles (Koolhaas et al., 1999), behavioural syndromes (Sih et al., 2004a, b) or animal personalities (Dall et al., 2004; Gosling & John, 1999), comparable with human personalities (Eysenck & Eysenck, 1985; John, 1990; Zuckerman, 1991). The consistency of trait combinations and the resulting high level of correlation between behavioural traits allow this identification of animal personalities. […] Nevertheless, genetic studies on wild species investigating a set of consistent individual differences in behaviour are rare. […] These studies have given evidence for the existence of behavioural profiles or personalities. To investigate the genetic basis of a correlated set of personality traits a four-generation, two-way selection experiment for ‘fast’ and ‘slow’ early explorative behaviour was started in 1994 (Drent et al., 2003).

Personality trait

We will start with reviewing the evidence that shows how much variation in animal personality traits is genetic […] Bouchard & Loehlin (2001) reported broad-sense heritabilities for the Big-Five personality domains in humans (extraversion, agreeableness, conscientiousness, neuroticism and openness). […] Heritability estimates and the methods how they are derived from studies on personality traits on different animal species. […] This is confirmed in more recent laboratory studies on the genetic background of personality traits (Daniewski & Jezierski, 2003; Isles et al., 2004 […] Early exploratory behaviour is a combined score for two personality traits: boldness towards a novel object and exploration of a novel environment. In 2000, this was followed by a selection experiment using another behavioural trait: the latency to return to a feeding bowl after a mild startle (van Oers et al., 2004b). Realized heritabilities were 54*.*0 ± 5*.*0% (*V*P = 31*.*01, *V*E = 14*.*27) and 19 ± 3% (*V*P = 0*.*27, *V*E = 0*.*22*)* for early exploratory behaviour and risk-taking respectively (Table 1).

Repeatability

**APC025**

Personality

One intriguing possibility is that variation in cognition is functionally related to variation in personality. Here, we review some examples and present hypotheses on relationships between personality (or behavioural syndromes) and individual differences in cognitive style. […] Individual differences within species in animal personalities […] Individuals often exhibit consistent differences in boldness, aggressiveness, activity, sociability and/or exploratory tendency […] Suites of correlated behaviours across contexts have been termed behavioural syndromes, where individuals have a behavioural type (BT); here, we will use personality and BT interchangeably.

Personality trait

Fast–slow behavioural types (BTs; e.g. boldness, aggressiveness, exploration tendency) […] individual differences along the bold–aggressive–active–exploratory BT axis […] For personalities, many of the BT axes studied by behavioural ecologists (boldness, aggressiveness, activity, exploratory tendency, proactive–reactive) are associated with variation along a risk–reward axis [8,10]. […] BT axes (boldness, aggressiveness, activity, proactive and exploratory tendency)

Repeatability

**APC027**

Personality

In almost any species of animal studied, including humans, individuals differ consistently in numerous aspects of their behaviour. Behavioural differences between individuals that are consistent over time and across situations are referred to as personality by an increasing number of psychologists and biologists (Gosling 2001; Sih et al. 2004; Reale et al. 2007). […] The debate concerning the definition of personality has been a vigorous one in behavioural ecology over the past decade (Re´ale et al. 2007), and is similar to the types of discussion that have preoccupied differential psychologists for many years (Nettle & Penke 2010) After this first phase of discussion and reflection, two main definitions of personality now appear to coexist among behavioural ecologists. For some, personality simply corresponds to the presence of behavioural differences between individuals that are consistent and can involve any type of behaviour; we view this as the broad-sense definition of personality. Others have been interested in consistent individual differences in specific suites of behaviours, typically expressed in a novel or challenging context; we view this as the narrow-sense definition of personality. The former definition of personality is close to the notion of a behavioural syndrome (Clark & Ehlinger 1987; Sih et al. 2004), which does not make any assumption about the type of behaviour concerned, and addresses the study of correlations at the population level either between the same behavioural trait in two different environmental contexts or between two distinct behavioural traits. The broad-sense definition of personality has the advantage that any behaviour can be placed under the magnifying glass and scrutinized within a general evolutionary theoretical framework (see below). […] The second definition is closer to the one used in psychology (Gosling 2008; Nettle & Penke 2010) and behavioural physiology (where it is called coping style; Koolhaas et al. 1999; Coppens et al. 2010)

Personality trait

While the phenotypic approach can measure current selection on personality traits, they argue that to understand their evolutionary origins one needs to identify polymorphisms at the genomic level. New molecular techniques now allow us to study natural selection at the molecular level, gene interactions and pleiotropic effects, and how gene expression shapes personality phenotypes and the micro-evolutionary processes that maintain them. […] Extensive pedigree analysis of personality traits can, finally, help determine the level at which behavioural consistency occurs: a significant additive genetic variance or maternal genetic effects will, for example, indicate long-term effects (i.e. across generations) on individual consistency, whereas environmental maternal/paternal effects and permanent environmental effects can signal consistency that may be restricted to the individual level. […] Many personality traits are expressed within a social context (Reale & Dingemanse 2010)

Repeatability

**APC028**

Personality

The existence of ‘animal personality’, i.e. consistent individual differences in behaviour across time and contexts […] We discuss how animal personality research might benefit from insights into the study of alternative tactics and illustrate how selection can favour behavioural diversification and consistency […] Moreover, consistent individual differences in behaviour are often correlated across functional contexts. Such ‘personalities’, ‘behavioural syndromes’ or ‘coping styles’ are apparently ubiquitous in animals […] Animal personality: consistent differences between individuals in their behaviour across time and contexts [58]. Behavioural consistency: the behaviour of individuals remains stable over time in the sense that each individual does not express the full range of behavioural trait values present in its population [58]. This is reflected in an intra-individual correlation when subjects are measured repeatedly in the same context. As consistency is a relative measure applying to inter-individual comparisons it has also been referred to as ‘differential consistency’ [60]. […] Firstly, behaviour is generally expected to be flexible rather than consistent over time in order to allow appropriate responses to variation in environmental and social conditions. In contrast to this expectation, many studies have shown that behaviour is often remarkably consistent within individuals over time [2,5]. This is apparent especially if the behaviour of individuals relative to one another is concerned. In other words, the behaviour remains stable over time in the sense that each individual expresses only a part of the behavioural trait values present in a population, even if the absolute level of behaviour of an individual somewhat fluctuates [13]. […] However, frequency dependence can maintain either a situation where individuals perform alternative behaviours with certain probabilities (i.e. their behaviour is not consistent), or where certain proportions of individuals pursue divergent strategies consistently [11]. […] in contrast to the negative feedback mechanism favouring individuals that reduce the costs of conflict by adopting different social roles (character displacement and negative frequency dependence), a positive feedback mechanism can favour behavioural consistency of individuals due to the benefits of specialisation and the resulting costs of switching. Acting in concert these two feedback mechanisms might generate behavioural divergence and consistency. […] Hence, selection should favour individuals specialising by adopting a particular niche (Box 2), which will reduce interaction costs and at the same time create consistent individual differences. […] during early stages of development organisms are often flexible and susceptible to environmental influences. Environmentally mediated traits can be stabilised later in ontogeny, for instance through organisational effects of hormones or by a reduction of flexibility through learning processes with long-lasting effects [56]. […] Conclusions: The framework of social niche specialisation provides an adaptive explanation for the existence of animal personality differences among individuals in a social context based on the dynamic effects of interactions between individuals throughout life. It rests on the assumption that individuals increase their fitness by choosing behavioural strategies that reduce conflict with other members of the same population. Selection should favour traits providing effective solutions for social conflict. Behavioural consistency might serve to diminish conflict among conspecifics because it reduces niche overlap between individuals using the same resources, which is arguably the most important source of social conflict.

Personality trait

Recent research has revealed that individuals in a population frequently differ substantially in their behavioural type [1–3,5,51,81,82]. […] Empirical evidence suggests that individuals with particular behavioural tendencies adopt certain social niches. For instance, shy individuals (measured as exploration propensity in a novel environment) tended to be more gregarious when foraging than others in sheep (Ovis aries) [87]. In common lizards (Lacerta vivipara), independently measured variation of sociability of juveniles was associated with their dispersal behaviour [52]. […] intra- and inter-sexual selection can favour divergent behavioural types within a sex [34,35]. […] as yet research on animal personality has given little attention to the distribution of behavioural phenotypes within populations. Hence it is unknown in most cases whether personality types show a uni-, bi- or multi-modal distribution in a population, and the potential role of disruptive selection is obscure.

Repeatability

**APC029**

Personality

An individual may be constrained, and even behave sub-optimally, because of its personality type […] Animal personality refers to between-individual differences in behaviour that persist through time (Biro & Stamps, 2008; alternatively, behavioural type: Sih *et al*., 2004*b*). A related concept, behavioural syndromes, goes one step further, referring to individual-level differences in correlations between personality traits or behaviours (Table 1; see also Stamps & Groothuis, 2010). Here we will refer to animal personality in its broadest sense (as ‘behavioural variation between individuals’), encompassing the concept of behavioural syndromes throughout. […] Behavioural ecologists are currently asking three broad questions regarding animal personality: (*i*) why do individuals vary consistently in their behaviour, in some contexts to the point of sub-optimality; (*ii*) if selection ‘pushes’ behaviour towards one or more optimal strategies, how is further variation in animal behaviour maintained; (*iii*) why do crosscontext behavioural correlations (behavioural syndromes) occur?

Personality trait

Further, we use the term personality ‘trait’ in the behavioural ecological sense as a particular aspect of an individual’s behavioural repertoire, such as aggression or boldness (for a complete glossary of terms used in this article, see Table 1). […] A specific aspect of a behavioural repertoire that can be quantified and that shows between-individual variation and within-individual consistency (such as boldness, aggression, activity). […] Perhaps most telling is the confusion about how personality traits are defined and measured (see Section II). This confusion can lead to mislabelling traits and misinterpreting results, putting the development of animal personality theory at risk. […] Boldness is one of the most commonly measured personality traits […] Incorrectly labelling personality traits may be a common problem. […] ‘trait’. The term is used in behavioural ecology (and by us herein) to mean a measured aspect of an individual’s behaviour that is, usually, repeatable (e.g. the rate a behaviour is observed) while in psychology the use is more abstract and describes a construct […] ‘Big Five’ animal personality traits: boldness, exploration-avoidance, activity, aggressiveness and sociability

Repeatability

Reliability refers to the consistency of a measure through time, across contexts or across raters/observers. It estimates whether there is agreement between repeated tests of the same nature. Reliability differs from validity because a test may be reliable but not be valid. A common analogy used to demonstrate this difference (Nunnally, 1978) is an archer (the researcher) trying to hit a target (the trait) with a bow and arrow (the test). Validity refers to how close to the centre of the target the arrows land while reliability refers to how close together the arrows are clustered. Reliability is the first psychometric test employed in psychological research to assess a test’s performance (Gosling, 2001). In animal personality studies this approach is common practice, and is known as consistency or, more commonly, repeatability (Bell, Hankison & Laskowski, 2009). In fact, behaviours must be repeatable to be considered personality traits within behavioural ecology (Sih, Bell & Johnson, 2004*a*; Reale *et al*., 2007).