Chapter 7

Personality Traits and Behaviour

Sergey Budaev and Culum Brown

7.1 Introduction

Individual differences in animal behaviour have been attracting the interest of researchers at least from the time of Darwin (Slater 1981; Caro & Bateson 1986; Clark & Ehlinger 1987; Sih *et al*. 2004; Réale *et al*. 2007). Such an interest is justified because individual differences represent the raw material of natural selection and evolution, the main cornerstone of modern biology. Furthermore, the individual is, after all, the main unit of selection (Maynard Smith 1982).

Within-population variation in alternative mating strategies, foraging tactics and other observed behaviours are now widely accepted in behavioural and ecological literature. Recent investigations, however, have revealed individual differences in behavioural traits that are consistent over time and across situations. Often, such variability cannot be easily described using observable behaviour and involves inference and interpretation in terms of internal physiological or psychological mechanisms such as fearfulness or aggressiveness. Essentially, such variation represents an analogue of human personality. Some people may accept personality in 'higher' animals such as primates or even in dogs, but seem to deny it in 'lower' species (such as fish) due to the underlying fear of anthropomorphism. Ironically, this is an example of anthropocentric thinking in terms of a 'Scala Naturae', which has long since been discredited (Hodos & Campbell 1991). Personality traits have now been identified in a variety of animals and in fact are actively manipulated by people working closely with them (e.g. police horses, guide dogs and domestic animals generally). A meta-analysis of the available animal literature suggests that about 35% of behavioural variability of single behavioural patterns can be ascribed to individuals (Bell *et al*. 2009). While there is still debate about the degree to which individual differences in behaviour are consistent across different situations (see Wilson *et al*. 1994; Coleman & Wilson 1998; Bell 2005; Wilson & Stevens 2005; Dingemanse *et al*. 2007), there is no doubt that consistency of behaviour exists within many situations.

Fishes have rapidly become one of the most widely studied animals with respect to personality largely because of the utility of housing and breeding them in the laboratory, but

Fish Cognition and Behavior, Second Edition. Edited by Culum Brown, Kevin Laland and Jens Krause.

also because they can be collected from a wide variety of habitats making them particularly amenable to evolutionary research (Magurran 1993; Wilson *et al*. 1994; Coleman & Wilson 1998; Budaev & Zworykin 2002). Substantial differences between conspecifics have been found in feeding, defensive, sexual, and other behaviours (see reviews by Ringler 1983; Magurran 1993; Budaev & Zworykin 2002). Individual fish substantially differ even within a shoal (Helfman 1984; Magurran 1993; Pitcher & Parrish 1993; Ward *et al*. 2004; Leblond & Reebs 2006), which has for a long time been considered the most homogeneous social structure in fishes (Radakov 1972). Even the classical example of many ethological textbooks, the stereotypic response of male three-spined sticklebacks (*Gasterosteus aculeatus*) to the red belly of an opponent is very pronounced in some individuals but absent in others: it is so variable that the classical concept of innate releasing mechanisms (sign stimuli) can be questioned (Rowland 1982; Baerends 1985; Bolyard & Rowland 1996).

Niko Tinbergen, in his classical work 'On the aims and methods of ethology' (Tinbergen 1963), outlined four questions that are fundamental for our understanding of any behaviour:

(1) Causation: What is the cause of the behaviour in question?
(2) Function: What is its survival value?
(3) Ontogeny: How does it develop?
(4) Evolution: How did it evolve?

These questions can also be asked about *individual differences* in behaviour as well as behaviour itself.

There is one important aspect of Tinbergen's classical paper that has largely been overlooked in modern interpretations. Tinbergen starts his seminal paper with a section entitled 'Observation and description', pointing to the importance of observation in tackling the unexplored world of natural behavioural patterns and the analysis of the whole landscape of behaviour. He warns against a tendency to skip this preliminary 'inductive' stage, which would easily result in losing touch with natural phenomena. Thus, analysis of individual behavioural patterns in isolation from one another may cause us to lose sight of a more holistic interpretation in which multiple behavioural traits become intercorrelated in various situations. Indeed, not only can an individual's behavioural patterns and strategies have proximate and ultimate causes, but so can the correlations and relationships between them.

In this chapter we review recent studies of individual differences in fish behaviour using this approach. We also provide a general methodological framework for the observation, description and analysis of fish individuality, which is based on the concept of personality. Such an approach allows the application of concepts and methods developed in human psychology, where individual differences have been the primary focus over the last 50 years. There is no need to reinvent the wheel in the animal field because human personality psychologists have solved many similar issues. The personality approach is useful because it allows to analyse generalised behavioural individuality in terms of unobservable psychological constructs, abstracting across the species and disciplines, thereby providing a single comparative and evolutionary framework that could potentially benefit behavioural ecology, evolution and personality psychology. In particular, such a general integrative approach is required if we aim to examine why personality patterns are similar (or dissimilar) across species and higher taxonomic groups.

7.2 Observation and description of personality

Biologists are accustomed to analysing differences between populations, species and other biological entities. Here, the basic unit of analysis is character. The concept of character includes any trait that can vary between species, populations or individuals (Michener & Sokal 1957; Langlet 1971; Réale *et al*. 2007). In the context of morphological and physiological variation, characters are rather easy to define and measure. In behavioural studies, however, this is often not an easy task. The behaviour of each individual depends on both its motivational state and the immediate environmental stimuli (i.e. context). Even under controlled experimental conditions it is almost impossible to create identical environment for all individuals. They often respond differently to identical stimuli due to different experience. For example, exposure to a predator behind a clear partition may be exceptionally stressful to individuals with personal experience of predation but may simply be a curiosity to predator-naïve individuals (Brown & Warburton 1999). Stochastic behavioural components represent a further caveat (Cooper & Kaplan 1982; Kaplan & Cooper 1984).

One of the greatest misconceptions regarding animal personalities is the fact that they are absolutely stable over time or across contexts. At the same time, however, all behavioural ecologists recognise that behaviour is highly plastic and animals frequently adjust their behaviour to suit the prevailing conditions. How can these two concepts be reconciled? The possibility of stable characteristics of personality in a constantly changing behaviour first appeared in psychology at the beginning of the twentieth century. While many researchers were happy with the concept of stable personality traits, it also attracted substantial criticism. Among the most influential critics, Mischel (1973) argued that personality does not really exist, suggesting that human behaviour is flexible. This personality-flexibility debate has largely been resolved over the last 40 years (Kenrick & Funder 1988; Fleeson 2004; Funder 2009). It is now accepted that behavioural plasticity and personality traits are not mutually exclusive, rather both are important in shaping human behaviour. Human behaviour displays enormous flexibility and personality cannot predict every isolated behavioural act or decision; nonetheless, stable personality traits really do describe and predict trends, typical ways of acting, and behaviour over longer periods of time (Fleeson 2004).

This general approach of inferring stable individual characteristics from a highly flexible behaviour can be applied to the study of non-human animal behaviour. Moreover, the concepts and techniques developed by human personality psychologists over a long period provide an ideal methodology for the description of the overall general landscape of animal individuality (see Gosling 2001; Budaev & Zworykin 2002; Réale *et al*. 2007; Vazire *et al*. 2007).

7.2.1 Current terminology

If the basic model describing human personality variation can be applied to animal individuality, what hinders us from using the term *personality*? Personality, conceived as a broad domain of behavioural individuality involving the widest range of consistent and enduring behavioural traits can be legitimately applied to a wide range of species. It does not necessarily involve emotions or advanced cognitive ability. Theoretically, personality can even be applied to bacteria.

Apart from applied research (Seaman *et al*. 2002; Svartberg 2002), application of the term personality to animals has been hampered by a widespread fear of anthropomorphism. Such a fear is largely unfounded, however, if animal personality is defined in descriptive, functional and motivational terms. Furthermore, when studying complex behaviour, some degree of frank anthropomorphism is inevitable (Dennet 1983). The best classical example is provided by Hebb (1946). When various behaviours were objectively recorded in chimpanzees, the resulting long list was virtually futile in predicting their behaviour: '*All that resulted was an almost endless series of specific acts in which no order or meaning could be found*.' In contrast, more subjective anthropomorphic descriptions like 'aggressive' provided '*an intelligible and practical guide to behavior*', which could be efficiently used even by persons inexperienced with the animals. In a similar vein, Konrad Lorenz, in his Nobel lecture, writes: '*When we speak of falling in love, of friendship, personal enmity, or jealousy in these or other animals, we are not guilty of anthropomorphism. These terms refer to functionally determined concepts* . . .' (Lorenz 1974).

To escape accusations in anthropomorphism, researchers tried to avoid personality by using a variety of presumably more 'objective' constructs like shyness–boldness (Wilson *et al*. 1994), behavioural syndrome (Sih *et al*. 2004), behavioural profile (Budaev *et al*. 1999a) or temperament (Francis 1990; Réale *et al*. 2007) and coping style (Huntingford *et al.* 2010). This had another unfortunate consequence, namely that the literature on individual differences in animal behaviour has quickly become fragmented. It is necessary, therefore, to create a framework which reunites the various concepts adopted. Here we briefly summarise the terminology commonly used in the animal personality literature.

7.2.1.1 Shyness–boldness

A variety of related concepts have been used to describe individual differences in behaviour that are consistent over time and across situations. Wilson *et al*. (1994) proposed that the *shy–bold continuum* – the propensity to take risks – is a fundamental axis of behavioural variation in various species. The concept of boldness has been frequently applied to fishes. For example, Wilson *et al*. (1993) used it to describe individual differences in risk taking in the pumpkinseed sunfish, *Lepomis gibbosus*. In this study, the shyness–boldness trait was measured as a propensity to approach a novel object such as a minnow trap and a measuring stick. The position of individuals on the shy–bold continuum was consistent, predicting diet, acclimation to the laboratory, habitat utilisation and parasite fauna.

The shyness–boldness continuum has been used in many subsequent studies. The tests and experiments used to measure boldness also varied substantially (Table 7.1). For example, researchers used empty novel environments (open field; higher locomotion indicative of boldness), novel objects, predator inspection (approach to predator or a novel object involves boldness), foraging in presence of a predator, latency to emerge into a novel environment from cover, time spent in open habitats and so on. In many studies, fishes behaved consistently when tested repeatedly over time and across situations (e.g. Huntingford 1976; Brick & Jakobsson 2002; Ward *et al*. 2004; Brown *et al*. 2007a; Wilson & Godin 2009), although this was not always the case (Coleman & Wilson 1998; Wilson & Stevens 2005; Dingemanse *et al*. 2007).

Table 7.1 A list of 'boldness' measures in fishes utilised by a range of authors.

Reference	Measure	Species
Brown *et al*. (2007a)	Novel object inspection	*Brachyraphis episcopi*
Brown *et al*. (2007a, 2007b)	Open field	*B. episcopi*
Brown & Braithwaite (2004) and Brown *et al*. (2005a)	Latency to emerge from cover	*B. episcopi*
Bell & Stamps (2004)	Open field	*Gasterosteus aculeatus*
Bell & Stamps (2004) and Bell (2005)	Foraging under predation risk	*G. aculeatus*
Azuma *et al*. (2005)	Recovery from fright	*Oncorhynchus mykiss*
Brick & Jakobsson (2002)	Tendency to inspect mirror image	*Nannacara anomala*
Budaev (1997a)	Open field	*Symphodus ocellatus*
Budaev (1997b)	Open field	*Poecilia reticulata*
Budaev *et al.* (1999a)	Tendency to inspect novel fish	*Steatocranus casaurius*
Budaev *et al.* (1999a)	Open field	*S. casaurius*
Budaev *et al.* (1999b)	Open field	*Cichlasoma nigrofasciatum*
Budaev *et al.* (1999b)	Tendency to inspect novel fish	*C. nigrofasciatum*
Coleman & Wilson (1998)	Response to threatening stimuli	*Lepomis gibbosus*
Coleman & Wilson (1998)	Response to novel food source	*L. gibbosus*
Dugatkin & Alfieri (2003)	Predator inspection	*P. reticulata*
Dugatkin *et al*. (2005)	Predator inspection	*Danio rerio*
Fraser *et al*. (2001)	Tendency to cross open habitat	*Rivulus hartii*
Godin & Davis (1995)	Predator inspection	*P. reticulata*
Godin & Dugatkin (1996)	Predator inspection	*P. reticulata*
Huntingford (1976)	Response to predatory attack	*G. aculeatus*
Johnsson *et al*. (2001)	Response to predatory attack	*Salmo trutta*
Magnhagen & Staffan (2005) and Magnhagen (2006)	Foraging under predation threat	*Perca fluviatilis*
Schjolden *et al*. (2005)	Response to novel object	*Oncorhynchus mykiss*
Shaklee (1963)	Response to predators	Multiple species
Sneddon (2003)	Time spent in the open habitat	*O. mykiss*
Staffan *et al.* (2005)	Time spent in the open habitat	*P. fluvitilis*
Sundstrom *et al.* (2004)	Response to novel object	*S. trutta*
Ward *et al*. (2004)	Foraging under predation risk	*G. aculeatus*
Westerberg *et al*. (2004)	Time spent in the open habitat	*P. fluvitilis*
Wilson & Stevens (2005)	Latency to forage, pass through a net, feed under predation threat and open field	*O. mykiss*
Wilson *et al*. (1993)	Inspection of novel object; Open field	*L. gibbosus*
Wright *et al*. (2003, 2006)	Inspection of novel object	*D. rerio*
Yoshida *et al*. (2005)	Open field	*L. macrochirus*, *Carassius langsdorfii*, *C. auratus*

7.2.1.2 Coping styles

Another concept frequently used to investigate individual differences in fish behaviour is coping styles or strategies, which often represent bimodal clusters of individuals with a number of similar behavioural traits rather than continuously distributed traits or dimensions (Budaev 1997a; Brelin *et al*. 2005; Øverli *et al*. 2007). Two alternative coping styles are frequently distinguished: *proactive* and *reactive* (Benus *et al*. 1991; Koolhaas *et al*. 1999; Øverli *et al*. 2007). Proactive individuals are more active, aggressive, bold, tend to form inflexible routines and hence learn more slowly about small changes in the environment. When presented with novel stimuli, they explore them quickly and superficially. Reactive individuals, in contrast, are shyer, non-aggressive, more sensitive to environmental changes, explore novel stimuli slowly and thoroughly and tend to adapt to the situational demands.

7.2.1.3 Behavioural syndromes

The third concept frequently implicated in the study of animal personality is *behavioural syndrome*: a suite of correlated behaviours that are expressed either within a given context or across contexts (e.g. correlations between activity levels, boldness and aggression in foraging and antipredator contexts) (Sih *et al*. 2004). Sih *et al*. pointed to a few behavioural syndromes that may be of particular importance: the aggression syndrome, activity syndrome, boldness, fearfulness and reactivity. In this approach, correlations between different contexts and across different types of behaviour are most interesting because they could generate trade-offs between contexts or behavioural traits and thereby may play an important role in the evolution of behaviour. The primary value of the syndrome approach, therefore, is that it recognises that various behavioural traits may be correlated, potentially providing constraints on behavioural flexibility. The approach also helps explain why some behavioural traits appear maladaptive in some contexts. For example, a highly aggressive individual may be a very successful forager, but may incidentally attack potential mates. When considering mating behaviour in isolation, a high level of aggressiveness may seem to be maladaptive.

7.2.2 Objectivity

A further problem with previous research on animal personality is that instead of carefully exploring the whole landscape of behavioural individuality, many researchers start by concentrating on a limited set of specific behavioural patterns, domains of situations or behaviours. Often, to gain more objectivity, the researcher provides a very specific (and narrow) definition for the individual trait under the study and then proceeds in developing methods to measure it. While there is nothing wrong with deductive hypothesis-led research, hasting from the first descriptive step is a potentially dangerous deviation from the ethological paradigm, which historically led certain areas of psychology to lose touch with the real phenomena due to loss of context (Tinbergen 1963). Such a danger can be illustrated by analysing boldness. Boldness was originally defined as a propensity to take risks (Wilson *et al*. 1994; Wilson 1998) and experimentally operationalised as an approach to, or avoidance of, novel objects. However, the above definition of boldness could include virtually any behaviour. For example, locomotion is almost always risky because it would allow a potential predator to detect and discover the individual. Aggression is risky because it could result in physical injury and reduced attention to an approaching predator. Does it mean that all and any behaviour can be subsumed under the concept of boldness?

The second potential problem is more subtle: when the overall personality landscape is obscure, it is easy to confuse different underlying traits. Imagine there are two independent personality traits based on different neurophysiological, hormonal or cognitive mechanisms: (1) fearfulness-reactivity and (2) curiosity. Some individuals could display behaviours indicative of heightened fear in a range of situations; also individuals could be either curious or uninquisitive in different contexts. Now imagine a researcher who decided to study 'boldness' operationalised as the propensity to take risks. The researcher developed two tests for boldness measuring an approach response to the stimulus, one involving a dangerous stimulus (e.g. sight of a predator) and another, involving novel object. It is likely that the first test would involve fearfulness-reactivity whereas the second, curiosity. For our blindly operationalist researcher, however, boldness just turns out to be non-existent because different tests presumed to measure boldness fail to detect any correlation! If each of these two kinds of boldness turns out to be consistent over time, however, the researcher may decide that boldness is domain- or situation-specific.

The concept of behavioural syndrome may potentially have similar problems. Studies of behavioural syndromes often start from a hypothesis specifying the traits being correlated (e.g. boldness and aggression), whereas other possible relationships may be overlooked. Again, behavioural patterns that the researcher presumes to measure 'aggression' in two situations may in fact reflect different behavioural dimensions, motivational, cognitive and emotional mechanisms (e.g. aggression in one context but fear in another). On the other hand, it is possible that suites of traits correlate and form behavioural syndromes at two stages of the ontogeny (or just at two different moments of time) with little correlation across time.

Some studies have found correlations between activity and boldness (Fraser *et al*. 2001; Dingemanse *et al*. 2007; Moretz *et al*. 2007). However, closer examination of many of these studies reveals that the correlation between personality traits may simply be a reflection of the techniques and methods employed. Fishes that are highly active, for example, are more likely to spend more time exploring a novel object, a novel environment or in risky locations simply because they are more likely, by chance alone, to score highly in these traits. In other words, the tests of each personality trait (boldness and activity) may not be measured independently. Indeed, activity levels are better quantified in a non-experimental context, such as the home aquaria, than in a novel experimental arena because the latter is a standard test for boldness (open field test; Crabbe *et al*. 1999; Brown *et al*. 2007a). Furthermore, analysis of partial correlations may be very helpful in controlling the moderating effect of locomotion on subtle behavioural differences (see Budaev & Andrew 2009a).

Thus, studying animal personality inevitably involves certain psychological concepts that may be considered anthropomorphic. Avoiding anthropomorphism by using deliberately blind operational constructs may lead to even more serious problems. The putatively 'objective' labels applied to behavioural traits are often uninformative and at worst misleading with respect to their underlying mechanisms. It is hardly possible to completely avoid descriptive labels with a degree of subjective connotation. However, the concept of construct validity could be instrumental in minimising interpretational anthropomorphism.

7.2.3 Labelling personality traits; construct validity

Once a measure of personality is obtained, its interpretation is often non-trivial. The descriptive label attached to such a measure must correspond to a particular theoretical concept. For example, if a trait is interpreted as *fearfulness,* the researcher must provide evidence that it is closely linked with *fear* (an emotional and/or motivational construct), if it is interpreted as *curiosity*, there must be evidence that it is linked with a predisposition to obtain novel information. In more formal terms, validity is '*the degree to which the test actually measures what it purports to measure*' (Anastasi & Urbina 1997). The theoretical construct must specify concepts with which it *is* related (convergent validity) as well as those with which it is *not* related (discriminant validity) (Cronbach & Meehl 1955; Anastasi & Urbina 1997). The most popular approach to assess convergent and discriminant validity is the multitrait–multimethod matrix (Campbell & Fiske 1959). As its name suggests, this method involves correlation or factor analysis of a data matrix including several alternative measures of the construct under the study together with unrelated constructs. Then, convergent validity involves correlations between different measures of the same construct (ideally high) while discriminant validity involves correlations between measures of dissimilar constructs (ideally low). For example, in case of curiosity, convergent validity may require high correlations between tests involving responses to novel environment, novel object and novel food. Discriminant validity may involve the *absence* of high correlation between the tests for novelty and tangential measures such as locomotion or social tendency. In the field of animal behaviour, various experimental procedures and manipulations can be used to assess the validity of personality tests.

Construct validity is rarely addressed in the animal personality field. Typically, the investigator chooses the tests and measures of personality traits and ascribes descriptive and interpretative labels to them arbitrarily (like boldness, fearfulness, exploration, sociability, etc.), based on whether they just *appear* persuasive. An exception in fish research where both convergent and discriminant validities were appropriately shown is the recent study by Burns (2008). In this study, scores the guppies *Poecilia reticulata* obtained in different open field tests correlated with emergence tests (convergent validity). Also, activity scores did not correlate with open field or emergence test behaviours (discriminant validity). While ecological validity of tests and stimuli (dictating that they should be compatible with the natural environment and behavioural repertoire of the species, see Tinbergen 1963; Lorenz 1974) is often an important concern in animal behaviour and personality research (Réale *et al*. 2007), construct validity of tests that measure unobservable personality constructs is also crucial.

7.2.4 Objective and subjective measurements of personality

Even though behavioural consistency may seem a simple concept, measurement of consistent personality traits is usually a difficult task. First, such traits cannot be observed and measured directly and must be inferred from multiple measures. Second, the same trait may be measured in a number of ways, using different tests. Furthermore, a single behavioural test may measure several different personality traits simultaneously. Two general approaches have been used to assess personality in animals that avoid these issues: (1) objective behavioural measurements and (2) subjective trait assessment by human observers using rating scales.

The objective behavioural measurement method involves testing an animal in one or several tests (i.e. a test battery). A variety of behavioural measures could be recorded in each of these tests: latencies, durations and frequencies of various behaviours, locomotion scores and so on. A single measure or a combination of measures is then used to describe personality. For example, latency to approach a novel object is frequently used to measure boldness (Table 7.1). In the best scenario, several measures should be combined using the principal component or factor analysis or even just summed with unit weights. This approach is the one most commonly adopted by behavioural ecologists.

In the subjective assessment method, one or more human observers rate their impressions of the animals using a set of adjectives or other similar descriptions. The observer ascribes quantities to the expression of the trait, which may be either binary (present/absent) or numeric (e.g. 1 for the lowest expression to 5 for the highest expression). For example, a personality assay of spotted hyenas (*Crocuta crocuta*) used by Gosling (1998) included numerous descriptive expressions like: '*Bold, brave, not shy: Behaves in a positive, assured manner. Exhibits courage in the face of danger. Is daring, not restrained or tentative. Not timid, shy, or coy*.' (Gosling 1998, p. 117). To date, only the objective behavioural measurement method has been used to describe personality in fishes. Most studies of personality in primates (e.g. Stevenson-Hinde *et al*. 1980; King & Figueredo 1997; Capitanio 1999; King *et al*. 2005), and some studies of dogs (Gosling *et al*. 2003) and birds (Figueredo *et al.* 1995) used rating scales.

Many scientists would argue that the 'objective' nature of behavioural measurement would make them superior over the subjective rating scales. However, this is not necessarily true. First, a significant amount of subjectivity is involved in the 'objective' methods for personality assessment: the choice of tests, procedures, selection of measures to record and analyse, etc. Second, whereas subjective ratings are based on a generalised perception of personality over many occasions, situations and observations, each of the objective measures is scored in a single context and, therefore, reflects a very significant context-dependent component. Most researchers do not think it essential to describe the protocol used (e.g. how many observers coded behaviour, were they experienced or undergraduate assistants, whether and how they were trained, etc., see Vazire *et al*. 2007) because objective behavioural measures are usually considered infallible.

Reliability and stability of objective measures are usually rather low. However, the statistical power is significantly reduced with diminishing reliability of measurement. When single behavioural measures are used as a proxy for personality traits, large sample size is often necessary to detect moderate consistencies across situations, even when the measures are relatively reliable. Unfortunately, few researchers studying animal personality ever care about reliability. The average sample size used in studies of behavioural replicability was 39 (Bell *et al*. 2009), which is considered a relatively large number of subjects in behavioural research. With such a sample size, however, the minimum correlation coefficient detectable with the power 0.8 at $\alpha = 0.05$ is 0.43. But this minimum detectable correlation increases to 0.55 when the reliability of the measures equals to 0.8 and to 0.73 when the reliability is 0.6. Behavioural correlations across situations are rarely that strong and will remain undetected if the sample size is not very large and the measures are not perfectly reliable.

Personality describes global individual differences, overall trends and predispositions that generalise across observations, measures and contexts. Therefore, single behavioural measurements are often too poor an approach for measuring personality. We argue that many reports that failed to find significant cross-situational consistency in fish boldness and behavioural syndromes (e.g. Wilson *et al*. 1994; Coleman & Wilson 1998; Bell 2005; Wilson & Stevens 2005; Dingemanse *et al*. 2007) may have been unable to do so because they used isolated behavioural measures with low reliability. Indeed, many studies of boldness and behavioural syndromes used only one or two measures of these behavioural constructs.

To improve the reliability and relevance of personality measurement, psychologists often aggregate behavioural measures over time, situation, observers, etc. Such data aggregation reduces unstable situationally specific behavioural components, improves reliability and increases correlation coefficients measuring consistency (for more discussion, see Epstein 1983; Rushton *et al*. 1983; Funder 1995; Pruessner *et al*. 1997). A similar aggregation approach has been used in studies of personality in rats (Ossenkopp & Mazmanian 1985) and fishes (Budaev 1997a). However, sometimes multiple testing of the same individuals may also be difficult or even impossible; in addition to being costly and time-consuming, it may involve habituation, learning, high stress, and other undesirable effects.

It has been shown that, when carefully designed, subjective rating scales have high inter-rater agreement, do not reflect anthropomorphic projections and usually agree with objective behavioural measurements (Vazire *et al*. 2007; Uher & Asendorpf 2008). However, subtle human cognitive biases cannot be ruled out. For example, humans can have specific adaptive cognitive mechanisms for rapid assessment of the human personality. The assessors could then match strangers, animals and even inanimate objects with a set of hardwired cognitive personality templates. Because the templates are species specific, they will not result in disagreement across observers so that subjectivity would not be easily noticed. This becomes increasingly problematic as we move further away from species closely related to ourselves (e.g. primates) towards the taxa with intuitively less familiar behaviour (e.g. fishes and invertebrates).

Thus, while isolated behavioural measures are usually too poor an instrument for assessing animal personality, aggregation of many measures would improve personality assessment. Furthermore, subjective rating-bases assessment sometimes provides the most efficient (in terms of time and cost) approach to measure personality. Although human observers are likely to find it more difficult to rate fishes on subjective scales, such scales could still be used in studies of fish personality. When applied to measure personality in fishes, subjective rating scales should be validated using objective behavioural measures in the first instance. Ideally, if a smaller sample experiment using both objective measures and rating scales can be designed, then rating scale assessment could be used for rapid assessment of personality of a larger sample of fish.

7.2.5 Modern terminology and statistical approaches

In order to appreciate the fact that animal personality traits are not incompatible with behavioural plasticity, it is important to adopt terminology developed in the human personality literature and apply modern statistical analyses. Two different aspects of stability are usually distinguished in psychology (Eysenck 1970; Eysenck and Eysenck 1985): (1) 'stability' and (2) 'consistency'. *Stability* usually means that the absolute level of the behaviour in question does not change. *Consistency*, on the other hand, refers to predictability (or correlations) during repeated measurement of the same individuals in the same situation or across various situations (Nunnally 1967; Ozer 1986; Réale *et al*. 2007). For example, an individual exhibiting higher level of aggressiveness than other individuals in one situation could also be more aggressive than others in another situation even if the absolute level of aggression measured for that individual changes from one situation to the next. Thus, the concept of stability involves the absolute value of a particular behavioural measure whereas consistency involves correlations and relative values within a population of individuals. The level of variability is another concept independent of the first two. Variability involves behavioural scatter in one situation relative to another situation. In effect, the behaviour can be situation-specific while individual differences are consistent. Further, the behaviour can be extremely variable in some situations while individual differences remain consistent (Fig. 7.1).

This model can be reformulated in an ANOVA-like way, which is perhaps more familiar to biologists. We can consider two sources of variability: (1) 'individual' (random factor because we potentially have an infinite number of 'random' individuals) and (2) 'situation' (either fixed or random repeated measurement factor). In this way of thinking, consistency means that the individual factor accounts for a significant proportion of the total variance.

Recently, Dingemanse *et al*. (2009) have proposed the concept of a behavioural reaction norm linking individual differences and behavioural plasticity. This approach accounts for individual behavioural response over an environmental gradient (stimulus value, predation

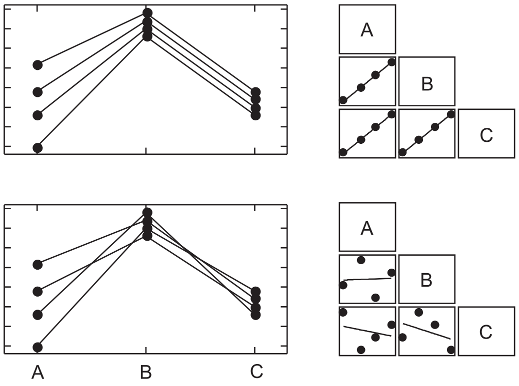

Fig. 7.1 Stability, consistency and variability in behavioural traits. Here the connected points on the left panel depict behavioural profiles of four individuals over three situations A, B and C; the right panel presents scatterplots of correlations between the behaviour scored in these situations. Low average level and high variability of the behaviour is observed in the situation A, high average level and low variability in the situation B and low average level and low variability in C. However, individual differences may be consistent (upper panel, strong correlations between situations) or inconsistent (lower panel, no correlations).

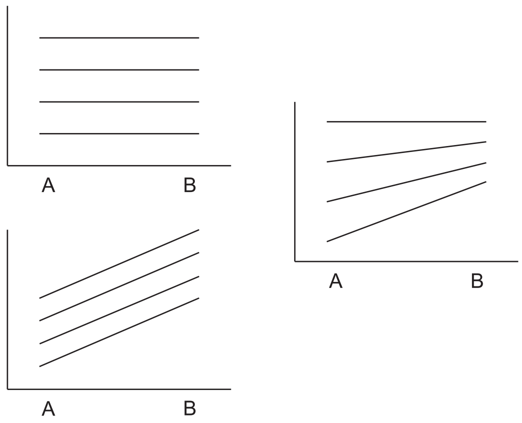

Fig. 7.2 The concept of behavioural reaction norm linking individual differences and phenotypic plasticity (after Dingemanse *et al*. 2009). The behaviour can be measured over multiple environmental gradients (here A and B). The upper left panel shows consistent individual differences with zero plasticity represented by a collection of horizontal regression lines (slope = 0). Lower left panel displays consistent individual differences with identical plasticity described by parallel regression lines with the same slopes. The right-hand panel shows more complicated patterns involving correlation between elevation and slope, when shy individuals show higher plasticity.

risk, food availability, temperature, etc.). Individual behaviour is described by a *linear regression line* linking the response with the environmental condition rather than just the response value. Two aspects of the regression are then considered: (1) Elevation describing the average individual level of the behaviour and (2) slope describing individual degree of plasticity (Fig. 7.2). Linear mixed models (random regression model) can be used to estimate parameters of the individual responses, link them together (correlate the elevation and the slope) and with external variables, for example, indicators of fitness.

The main advantage of the reaction norm approach is that it allows us to analyse individual differences and plasticity within the same adaptive framework. However, there are limitations. A single trait (measure) is usually analysed, making it less appropriate for the analysis of *multivariate* personality traits. Individuals are described by linear models requiring multiple measures for reliable parameter estimation (otherwise the standard errors of individual elevation and slope would be very large). Linearity is also not always a realistic assumption. While non-linear and multivariate models can be used, they increase complexity enormously. Furthermore, to achieve reasonable statistical power, random regression models require huge sample sizes (usually $N > 200$, Martin *et al*. in press).

7.3 Proximate causation

If suites of correlated behavioural traits are observed, a reasonable hypothesis is that these correlations reflect specific genetic and physiological mechanisms that constrain behavioural variability. For example, genetic correlations could be brought about by pleiotropy (multiple action of a particular gene to more than one phenotypic trait) or linkage disequilibrium (non-random association of alleles at different loci, e.g., by physical linkage) (Falconer 1981). The simple existence of a phenotypic correlation could often suggest, not necessarily however, that a genetic correlation could also be present between these traits (Falconer 1981; Cheverud 1988; Bakker 1994; Roff 1996). Several studies explored heritability of personality as well as genetic and phenotypic correlations between personality traits in humans (Livesley *et al*. 1998), dogs (Saetre *et al*. 2006) and birds (van Oers *et al*. 2004).

Fish personality traits may also have a heritable component. Brown *et al*. (2007b) compared boldness scores in laboratory-raised offspring taken from two populations of a tropical poeciliid fish, *Brachyraphis episcopi*, with contrasting predation pressures. Fishes descended from high-predation populations were bolder than those descended from low-predation population. Furthermore, the differences between the two groups of laboratory-reared fishes were of a similar magnitude as observed in the parental populations. Similarly, Wright *et al*. (2003) found differences in boldness in zebrafish, *Brachydanio rerio*, descendants from four wild populations.

Some studies have attempted to obtain a measure of personality heritability. Bell (2005), for example, found that heritability estimates of boldness and aggression in two populations of sticklebacks, *G. aculeatus*, were rather low (<0.2), indicating that there may be a very strong selection depleting additive genetic variance or these traits are mostly under an environmental control. Similarly, Dingemanse *et al*. (2009) tested sticklebacks originating from high- and low-predation environments. Some of the fishes were also subjected to repeated predator experience allowing assessment of the experience effect. In this case, heritability of personality traits such as novel environment exploration, activity, sociability and boldness ranged from 0.06 to 0.32 and in most cases was higher in population sympatric with predators.

The study of personality in fishes is frequently linked with the response to stress. Individuals that are relatively bold also show attenuated stress responses (Brown *et al*. 2005b); thus, there may be a link between personality traits and the expression of underlying hormones such as cortisol. Correlation between boldness and stress responses has been identified in several species of fishes (Koolhaas *et al*. 1999; Øverli *et al*. 2005; Schjolden *et al*. 2005). Recent studies have also shown relationships between stress responses and coping styles in carp (Huntingford *et al*. 2010). Metabolic rate was significantly higher in bold than in shy fishes, while expression of the cortisol receptor gene, plasma lactate and glucose concentrations was lower. Similar relationships between boldness and background blood cortisol concentrations have been observed in mulloway, *Argyrosomus japonicus*, where bold fishes have significantly lower cortisol concentrations than shy fishes (Raoult *et al.*, in press). Moreover, fish lines selected for high- and low-stress responses differ in a range of behavioural tests, including dominance and boldness (Øverli *et al*. 2005). Such effects often distinguish hatchery-reared and wild fishes (Lepage *et al*. 2000; Sundström *et al*. 2004), which is likely a reflection of the vastly different rearing conditions (Brown & Day 2002).

A selection programme was conducted on the rainbow trout, *O. mykiss*, where two lines of fishes were selectively bred for either high- or low-stress response (high- and low-plasma cortisol responsiveness, HR, i.e. high-response and LR, i.e. low-response lines). Subsequent studies indicated that these lines differ in numerous behavioural and physiological characteristics (Øverli *et al*. 2007). For example, the HR fishes demonstrated stress-induced anorexia: they did not eat during a stressful experimental period, whereas about 44% of

LR fishes ate (Øverli *et al*. 2002). LR trout were more aggressive and dominant than HR (Pottinger & Carrick 2001). Learning experiments indicated that LR trout were characterised by significantly longer extinction of a conditioned stress response than HR (Moreira *et al*. 2004). Thus, LR fishes show bold, active and inflexible behaviour characteristic of active coping style, almost exactly as previously found in mammals (mice, Benus *et al*. 1991; pigs, Bolhuis *et al*. 2005) and birds (tits, Groothuis & Carere 2005).

The neuroendocrine differences between the HR and LR lines of trout include monoaminergic activity and metabolism (Øverli *et al*. 2001). Both the synthesis and metabolism of brain serotonin, norepinephrine and dopamine following stress were significantly more elevated in HR than in LR lines. LR fishes were characterised by increased level of 5-HIAA (serotonin metabolite) and MHPG (norepinephrine metabolite) in the hypothalamus and also had a significantly higher baseline 5-HIAA/5-HT ratios in the telencephalon. Overall, these patterns are similar to those found in mammals (see Øverli *et al*. 2007 for more discussion).

The limbic system, including hippocampus, amygdala, hypothalamus and a few other nearby structures, plays an important role in controlling personality and emotions in humans and other mammals (Gray 1987; Lautin 2002). Even though the organisation of the brain in fishes is significantly different (Chapter 15), certain forebrain areas – lateral and medial telencephalic pallia – are considered homological to the mammalian limbic system (Flood *et al*. 1976). They also control similar behavioural mechanisms and processes, such as emotional learning (Broglio *et al*. 2005; Portavella & Vargas 2005). However, how these structures are involved in fish personality remains unknown.

Recent studies on zebrafish highlighted a possible involvement of certain epithalamic structures, especially the habenula, in personality and laterality (for a full discussion, see Chapter 16). The habenula is a major component of the dorsal diencephalic conduction pathway connecting the limbic forebrain with midbrain and hindbrain (Sutherland 1982; Bianco & Wilson 2009). In fishes, it is asymmetric, the left lateral habenula significantly exceeds the right (see Bianco & Wilson 2009 for a review). Interestingly, spontaneous reversal of the habenular asymmetry in a selected zebrafish line resulted (along with reversed laterality) in heightened boldness (Dadda *et al*. 2010). Similarly, development of zebrafish embryos in darkness during early ontogeny, presumably affecting the habenular development (Budaev & Andrew 2009b), also results in differences in boldness (Budaev & Andrew 2009a). This is not surprising because the habenula is heavily involved in behavioural inhibition, pain, fear, anxiety and depression through modulation of the brain dopaminergic system (Shepard *et al*. 2006).

Despite the body of research conducted to date, the genetic, neurophysiological and neuroanatomical causes of individual differences in fish personality remain poorly understood. Whereas there is a substantial interest in neurophysiology of personality in mammals, especially humans (e.g. Eysenck & Eysenck 1985; Gray 1987; Zuckerman 1994), fish provides an ideal model system for studying the role of single genes in the development of personality. For example, polymorphism of the *D4* dopamine receptor (*D4DR*) gene expressed in the limbic areas of the brain in mammals predicts extraversion and novelty seeking in humans (Benjamin *et al*. 1996; Ebstein *et al*. 1996, 1998). A similar reduction of behavioural response to novelty was found in knockout mice, lacking the *D4DR* (Dulawa *et al*. 1999) and great tits, in which *D4DR* polymorphism predicts early exploratory behaviour (Fidler *et al*.

2007). A similar analysis can be conducted on zebrafish or sticklebacks, whose genomes have been sequenced. The gene sequence of *D4DR* is highly conserved across a wide range of vertebrates and a BLAST (Basic Local Alignment Search Tool) search of the stickleback genome reveals a strong match on chromosome 19 (the stickleback sex chromosome). It is a commonly observed phenomenon across vertebrates that males are more prone to risk taking than females (Wilson & Daly 1985; van Oers *et al*. 2005; Brown *et al*. 2007b in fishes, birds and humans, respectively) so the link to a sex chromosome is not surprising. This observation also warrants closer examination in fishes, especially considering the wide range of sex determination mechanisms.

In the genomic era it should be possible to identify the genes contributing to heritable personality traits. For example, a quantitative trait loci analysis of boldness scores in zebrafish revealed regions on chromosomes 9 and 16 significantly linked with boldness and a suggestive association with chromosome 21 showing signs of dominance and additive effects, respectively (Wright *et al*. 2006). To date, however, no further studies have attempted to identify the genes involved in fish personality traits.

7.4 Ontogeny and experience

As we have highlighted, personality traits are not entirely fixed for life, rather they are susceptible to adjustment through significant life experiences and developmental shifts. Only a handful of studies, however, have investigated the ontogeny of personality in fishes. Budaev *et al*. (1999b) analysed how behavioural consistency changes across the ontogeny in an African cichlid, *Steatocranus casuarius*. The fishes were tested for their responses to a novel environment, a novel fish, and a mirror (aggression test) at 4, 4.5, 12 and 13.5 months of age. Whereas the behavioural measures were not consistent in juveniles (4 and 4.5 months of age), consistency appeared in adult fishes (12–13.5 months).

Behavioural consistency was found very early in newly emerged and larval fishes (Budaev & Andrew 2009a; Conrad & Sih 2009). Such early consistency could also be induced by exposure to predator and probably other environmental stimuli (Budaev & Andrew 2009a). Personality can be significantly modified by factors such as exposure to light (Budaev & Andrew 2009a), acting very early in the ontogeny and becomes more consistent during the individual's development, which agrees with the data obtained in mammals (e.g. Loughry & Lazari 1994), including humans (see Roberts & DelVecchio 2000 for a review).

Individual experience can significantly affect boldness. For example, differences between shy and bold pumpkinseed sunfish were significant in the field, but disappeared after a period of isolation in the laboratory (Wilson *et al*. 1993). Simulated predator attacks (repeated chasing with a net) increased boldness in captive bred *B. episcopi* originating from both high- and low-predation populations (Brown *et al*. 2007b).

Magnhagen & Staffan (2005) found that changing group composition could significantly affect the behaviour of shy juvenile perch (*Perca fluviatilis*) and to a lesser degree, intermediate and bold perch. Shy fish, for example, become bolder when placed in a group of shy fishes. Bold individuals in a bold group tend to reduce their levels of boldness, whereas intermediate individuals did not change behaviour. Similar effects were confirmed by Magnhagen (2007): the correlation between risk taking (time spent in open water) and exploration (entrance to novel environment) was significant only when the behaviour of other group members was taken into account. Experience of winning and losing a contest and simply observing a shy or bold conspecific could alter boldness in the rainbow trout, *O. mykiss* (Frost *et al*. 2007). The sex of the schoolmates may also significantly affect individual boldness. For example, male guppies are bolder after a simulated aerial predator attack when shoaling with males than with females (Piyapong *et al*. 2010). Such strong social influences on the expression of personality traits are expected in fishes that spend a considerable amount of their lives in schools (Brown and Laland 2002; Chapters 10 and 11). The pattern of social interactions can be significantly affected by personality traits, creating a further level of complexity. For example, social networks of Trinidadian guppies are characterised by significant assortment and shyer guppies have higher numbers of network connections (Croft *et al*. 2009).

In addition to prior experience, fish personality could be affected by various physical factors. Ambient temperature, significantly affecting metabolism, would be one of the most important factors for fishes and other ectothermic animals. Even moderate changes in temperature could significantly affect boldness, aggressiveness and activity levels of damselfish, *Pomacentrus moluccensis* and *P. bankanensis* (Biro *et al*. 2009). Whereas correlations between personality traits were stable across temperature levels, individuals differed in their degree of plasticity. While some individuals significantly increased activity at higher temperature, others were more stable.

Thus, as with the vast majority of traits, fish personality is not entirely genetically fixed, rather it can be affected during early ontogeny and modified by later experience. Furthermore, it is possible that the degree of flexibility and susceptibility to experience is itself a consistent individual trait affected by various developmental events and selection pressures within a particular population.

7.5 Is personality adaptive?

The starting point for the theory of evolution by natural selection is that the traits being selected have some genetic basis. We have seen above that this is likely to be true for personality traits in fishes as well as in many other species. The next question is: Are such consistent differences across many contexts, over time and developmental stages simply non-adaptive noise around a single adaptive mean? Can natural selection produce and maintain variation? Will natural selection also support correlations across behavioural domains and contexts? That is, is personality adaptive?

7.5.1 Frequency- and density-dependent selection

Early game theory models tended to neglect any variability except alternative strategies. It was accepted that two or more strategies could be evolutionarily stable (mixed strategies, see Maynard Smith 1982) when fitness of a strategy depends on the frequency of the alternative strategy. However, no assumption was made about correlation and consistency. For example, it was accepted that natural selection will produce aggressive ('hawk') and non-aggressive ('dove') strategies within a single population, but it was not clear whether the particular individuals would use the same strategy consistently or switch randomly between them.

Later models slowly began to incorporate individual differences. In a seminal paper on shyness and boldness, Wilson *et al*. (1994) provided a simple account for the existence of the shy–bold continuum in various species based on frequency- or density-dependent selection. Here, the optimal behaviour depends on the frequency or density of conspecifics displaying each trait. For example, it may be more adaptive to be shy and occupy safe habitats; however, when the density of such shy individuals is sufficiently high, the safe habitat becomes overcrowded. At some point, the fitness cost of competition within the safe habitat exceeds the predation risk in the risky habitat and some individuals start using the risky habitat (see Wilson *et al*. 1994). In a later paper, Wilson (1998) extended this framework: when the population exploits several habitats, a range of resources, etc., natural selection could maintain multiple-niche polymorphisms and stable personalities. However, such models still do not account for consistency: why should one individual be bold consistently in various contexts rather than have a broad adaptive norm of reaction? To explain consistency, it is assumed that phenotypic plasticity is limited by various genetic and epigenetic mechanisms and incurs significant fitness costs (see DeWitt *et al*. 1998; Sih *et al*. 2004).

Many fish studies are consistent with such models. For example, a shyness–boldness continuum was found in wrasses, *Symphodus ocellatus*. In this species, fishes significantly differ in activity within a novel environment. Shy individuals (which do not explore novel environments) tended to stay in shoals and occupy relatively safe weeded habitats, whereas bold individuals (which are active in novel environments) were typically found in more dangerous open habitats and did not join shoals (Budaev 1997b). Similar patterns were found in bluegill and pumpkinseed sunfish (e.g. Ehlinger & Wilson 1988; Wilson *et al*. 1993). Feeding specialisations and alternative foraging tactics that may involve exploitation of distinct food resources and sub-niches by different individuals have long been reported in fishes (Bryan & Larkin 1972; Ringler 1983; Smith & Skulason 1996).

While the early models explaining personality variation based on frequency- and density-dependent selection look convincing in many cases, they have difficulty in accounting for consistency over time and across situations: such consistency is still considered to result from constraints on adaptation. At the basic level, they are not different from the 'hawk–dove' game.

7.5.2 State-dependent models

More recent models have used a dynamic programming approach, where the pay-off of every behaviour is calculated iteratively and depends on the state of the animal, including energy reserves, territory size, etc. (Mangel & Clark 1988). It would be adaptive to avoid exposure to excessive predation risks if an animal has good energy reserves, but if such reserves are close to depletion (e.g. the animal is close to starvation) the potential benefits of obtaining food may outweigh the risk of being eaten (see Clark 1994; Dall *et al*. 2004). For example, sticklebacks characterised by higher weight loss following a 2-day food deprivation tended to emerge earlier from a refuge (Krause *et al*. 1999). Quite simple models predict consistency if the state and the history of behaviour over time are taken into account (see Dall *et al*. 2004 for more discussion). Consistent differences in risk taking could be maintained within a foraging group if individuals differ in energy reserves and such differences are sustained by environmental factors (see Rands *et al*. 2003; Dall *et al*. 2004). Furthermore, when the individuals' states are changeable but information about the world is uncertain, it may become adaptive to just ignore environmental cues and behave consistently. Consequently, environmental noise is predicted to facilitate consistent personalities (McElreath & Strimling 2006).

Recent theoretical advances have emphasised the role of life-history trade-offs in generating consistent personalities (Stamps 2007; Biro & Stamps 2008). For example, Wolf *et al*. (2007) developed a series of state-dependent models based on a trade-off between current and future reproduction. Individuals with high expectations of future reproduction, who have much to lose, would be shy whereas those with low expectations would be bold. This is the case of a more general 'asset protection principle' (Clark 1994), stating that the larger the current reproductive asset, the more vital it becomes to avoid risks threatening reproduction. Therefore, accumulation of reproductive assets (body size, territory size, etc.) would lead to risk aversion (Brown & Braithwaite 2004).

Similar considerations involving trade-offs have also been used to account for consistent individual differences in decision making. Specifically, a trade-off between speed and accuracy could lead to individual differences in impulsiveness: some individuals make fast and inaccurate decisions whereas others are careful but slow (Chittka *et al*. 2009). Guppies (*P. reticulata*) consistently differ in their 'hastiness' in a spatial memory maze task (with female as reinforcement): some individuals tend to make quick decisions with many errors while others are slow but accurate (Burns & Rodd 2008).

Trade-offs between growth and mortality (Stamps 2007) and productivity and mortality (Biro & Stamps 2008) may be among the most important mechanisms maintaining consistent personality variation. In essence, the growth-mortality hypothesis argues that correlations between behaviours in various contexts may arise when these behaviours affect growth and mortality. Many fishes and other animals show consistent individual differences in growth rate (Biro *et al*. 2006; Stamps 2007). Personality traits such as risk taking and aggressiveness often affect both growth and mortality rates. Aggressiveness could increase growth rate by improving access to food resources, but would also increase the risk of injury and non-detection of a predator. Boldness in foraging context would also increase food intake, but simultaneously increase the risk of being eaten by a predator (Stamps 2007; Biro & Stamps 2008). From a more general perspective, any life-history trade-offs may be important: consistency appears when the behavioural tendencies contribute to individual differences in life-history productivity (Biro & Stamps 2008).

The hypothesis developed by Biro & Stamps (2008) has serious limitations by assuming a simple positive relationship between personality (boldness or aggressiveness) and access to resources or food intake. Some studies reported a positive correlation between boldness and body mass in fishes (e.g. Magnhagen & Borcherding 2008), some reported no relationship (Kobler *et al*. 2009) while others documented a reverse relationship (e.g. Brown & Braithwaite 2004; Millot *et al*. 2009), which is indeed expected in many state-dependent models involving the asset protection principle (Clark 1994). Furthermore, there is no clear relationship between aggressiveness and social dominance (e.g. Bakker 1986; Francis

1988; Colleter & Brown 2011), and dominance and growth rate can also be unrelated (e.g. Harwood *et al*. 2003).

Individual experience or similar mechanisms provide another important, although often neglected by evolutionary biologists, ingredient making individual differences consistent. A model developed by Wolf *et al*. (2008) accounts for consistent differences in responsiveness to environmental stimuli, with 'responsive' strategy assessing such stimuli and 'unresponsive', behaving rigidly. In addition to frequency-dependent selection (responsiveness pay-off reduces with increasing frequency of responsive individuals), it adds a *positive feedback* mechanism: responsiveness is less costly for individuals that were responsive before. It turns out that even a small positive feedback induces stable correlations between behavioural choices made at consecutive iterations. Such a feedback is realistic if responsive individuals are more efficient at discovering food with experience.

Thus, personality is shaped by natural selection. The most basic ingredient usually invoked to account for alternative strategies, behavioural polymorphisms and personalities is frequency- and density-dependent selections. Other mechanisms predicting adaptive individual differences, for example involving optimal decisions in unpredictable conditions ('adaptive coin-flipping', Cooper & Kaplan 1982; Kaplan & Cooper 1984), have been given surprisingly little attention, even though they may be more general. Furthermore, consistent individual differences are likely to arise when individuals can exploit several resources, habitats and sub-niches. A variety of other mechanisms, including environmental noise, protection of reproductive assets, accumulation of individual experience and life-history trade-offs, would facilitate consistency over time and across contexts. All these ingredients are typically found in many fish species and populations, making consistent personality the 'null hypothesis'. Nonetheless, in spite of the recent theoretical advances, our understanding of the adaptive factors contributing to the maintenance of consistent personalities and polymorphisms remains scant. The various existing models are often too simplistic and sometimes contradict each other and the empirical data. Thus, while the main adaptive factors producing personality in fishes are known, the exact mechanisms involved still remain a puzzle.

7.6 Evolution

Even though it is now clear that adaptive individual differences can be maintained by natural selection, very little is known about the phylogeny of personality. Because very similar personality factors have been found in a wide variety of vertebrates (Budaev 1998; Gosling & John 1999), they could represent a shared heritage involving homologous brain systems (for similar views, see Eysenck and Eysenck 1985; Gray 1987). This view depicts personality as a consequence of *constraint* on evolution. Alternatively, personality could be shaped by common adaptive mechanisms independently in each species or even in different populations; this view depicts personality as an *adaptation*. Further, if common adaptive factors are operating in a variety of species, we may expect similar patterns of personality to evolve (i.e. convergent evolution). Understanding the evolution of behaviour usually involves analysis of the patterns of similarities and differences across related species to elucidate the history of their appearance and divergence throughout the phylogeny. In a sense, evolution of behavioural traits should be studied comparatively as is the case with the evolution of morphology and physiology; behavioural patterns here represent taxonomic traits similar to morphological characters (Tinbergen 1963) to which various methods of cladistic analysis are applicable (Brooks & McLennan 1991).

It is tempting to use the same approach to animal personality. However, personality is extremely difficult to organise in such a phylogenetic framework. Personality traits and dimensions that appear as a result of correlation analysis are different from morphological characters and fixed behavioural patterns. Personality traits are artificial descriptive constructs, which have no 'real' physical existence and explanatory power (Revelle 1983; Eysenck & Eysenck 1985). Furthermore, there is no single optimal hierarchical level for personality traits. It is possible to define more narrow or more context-specific traits or fewer broader traits. In human personality research, second-order factor analysis has become popular (e.g. Cattell 1956; Digman 1997). Personality traits, dimensions and factors can be blended or split in various species or populations depending on characteristics of the sample of individuals, domains of situations, types of measures, characteristics of raters and various other causes. Such blending or splitting cannot be easily translated to any specific evolutionary events. Personality traits resulting from factor analysis can be rotated differently: the same correlation matrix may be equally well represented by an infinite number of factor loading patterns.

In human personality psychology there is no single universal species-specific personality structure. The dominant Big Five model (postulating that human personality variation is encompassed by five basic dimensions: (1) extraversion, (2) neuroticism, (3) agreeableness, (4) conscientiousness, and (5) openness to experience) is merely a point of consensus as an optimal research framework (Digman 1990), and is not the only possible species-specific pattern for humans (McAdams 1992). It is possible to extract more narrow personality factors instead of fewer broader ones. Indeed, splittings (16 factors, Cattell 1973) and lumpings (two or three factors: Eysenck 1970; Eysenck & Eysenck 1985; Cloninger *et al*. 1991; single general personality factor: Rushton *et al*. 2008) as well as alternative rotations (e.g. Gray 1982; Zuckerman *et al*. 1993; Caprara and Perugini 1994; Budaev 1999) of the human Big Five personality dimensions have been proposed as alternative models.

A further problem is that the dimensions presumed to be common in different species are not necessarily comparable. Comparison of personality in different species is totally based on the researcher's intuitive interpretation in each case. For example, the researcher may interpret some behaviours as indicative of 'boldness' in one species. In a different species, ecological validity may dictate a different set of tests and measures but again a 'boldness' trait could be defined. The researcher then argues that 'similar' boldness traits are found in both species. This is, however, incorrect because what is compared here is intuitive interpretation of behaviours rather than behaviours themselves. Again, we emphasise that the labels ascribed to behavioural traits are often arbitrary and non-informative. While informal comparisons of personality dimensions across different species may be very helpful (see Gosling & John 1999), they cannot be used for formal phylogenetic analysis. The study of the evolutionary history of personality variations requires a new approach.

7.7 Wider implications

7.7.1 Fish production and reproduction

Personality and especially coping styles may have several important implications for aquaculture and conservation of fish stocks based on artificial rearing. Comparisons of wild and hatchery-reared fishes of several species reveal many important behavioural and physiological differences (e.g. Brown & Day 2002; Huntingford 2004; Huntingford & Adams 2005). For example, hatchery-reared brown trout, *Salmo trutta*, are significantly bolder and more aggressive (e.g. Sundström *et al*. 2004) and tend to dominate wild fishes (e.g. Sundström *et al*. 2003). These differences between the wild and domesticated fishes are heritable and result from deliberate selection for fast growth rate as well as from indirect selection of fishes best adapted to intensive high-density aquaculture (Huntingford 2004; Huntingford & Adams 2005).

Possible implications of these personality differences for the welfare of farmed fishes have been considered by Huntingford & Adams (2005). Shy and non-aggressive fishes turn out to be disadvantaged in many high-density production systems, negatively affecting their welfare. Pre-screening, increasing the cost of fighting and competition by increasing the water current, more even distribution of food avoiding its monopolisation, the use of smart automatic feeders and other measures have been proposed (see Huntingford & Adams 2005 for further discussion).

Restocking natural habitats with hatchery-reared juveniles has been used to replenish declining wild populations of various fishes, especially salmonids (Brown & Day 2002; Myers 2004; Bell *et al*. 2006). Restocking is very expensive (Beck *et al*. 1994) and its efficiency remains controversial. Most farm fishes die soon after release (Brown & Laland 2001) and some research suggests that the presence of hatchery-reared fishes in natural habitats may in fact facilitate extinction of wild stocks (e.g. McGinnity *et al*. 2003, 2009). Personality can be an important mediating factor here. Hatchery-reared fishes are more aggressive, bold, dominant and outcompete the wild fishes (Sundström *et al*. 2003, 2004; Huntingford 2004; Huntingford & Adams 2005). On the other hand, higher growth rate and the propensity to take risks would make them significantly more vulnerable to predators (Biro *et al*. 2004). Restocking natural environments with hatchery-adapted fishes, therefore, would depress rather than replenish the natural populations: hatchery fishes would competitively depress the wild fishes but would not contribute to reproduction due to increased mortality through predation.

7.7.2 Personality and population dynamics

Even though populations with contrasting predation regimes are frequently compared in fishes (e.g. Bell & Stamps 2004; Brown *et al*. 2007a, 2007b; Dingemanse *et al*. 2007), most studies of personality in animals strongly focus on individuals. Personality is, obviously, an attribute of the individual rather than the group. However, patterns of personality within a population may significantly affect higher order processes such as population dynamics. It has long been known that within-population variability in various traits, such as growth rate and body size, can increase the population stability, persistence and resistance to extinction (see Łomnicki 1988; Uchmański 2000; Grimm & Uchmański 2002). Such population models historically concentrated on individual variation in morphological and life-history traits. However, they can involve behavioural variability linked with competitive ability, resource utilisation and life-history traits (e.g. Biro & Stamps 2008; Colleter & Brown 2011).

The presence of individual variation within competing species can facilitate their coexistence. For example, Begon & Wall (1987) developed a simple model based on the classical Lotka–Volterra equation to describe competition between two species. In the classical model without individual variability, the competitively superior species rapidly excluded the inferior competitor to extinction. However, when individuals of both species differ in competitive ability, species with different competitive ability can easily coexist.

A few recent models investigated population effects of consistent personality traits. Petrovskii & Blackshaw (2003; see also Petrovskii *et al*. 2008) considered a population in a homogeneous environment under favourable environmental conditions. At some moment, the environment suddenly becomes harsh, causing environmental fragmentation (conditions are favourable within fragments but not in the rest of the environment) and significant mortality. Interestingly, if consistency is added to the model (the same individuals play fixed strategies, either aggressive or non-aggressive), the population density decreases significantly more slowly than in populations where all individuals play randomly.

These studies have important implications for conservation by suggesting that personality variation represents a very important yet neglected dimension of biodiversity. In some cases, personality could be the key factor in maintaining the population stability, especially when the population size is small, such that stochastic oscillations or catastrophic events could bring the population to extinction.

7.8 Conclusions

For some time individual differences in behaviour have been ignored by ethologists and behavioural ecologists and ascribing personality traits them has been highly controversial. It is becoming increasingly apparent, however, that rather than representing annoying noise in population data sets, they represent the leading edge of evolution. Much could be gained by adopting game theory models. Both Darwin and Tinbergen recognised the importance of understanding individuality and the latter in particular cautioned against taking too narrow a view when studying animal behaviour. By taking a holistic view of behaviour, we begin to see important relationships between behavioural traits and, in some instances, recognise potential constraints and trade-offs that may limit plasticity.

The study of fish personality is still very much in its infancy and suffers from a divided literature. There is a clear need to strengthen experimental methodology by taking advantage of the well-established human personality literature. We also recognise the importance of remaining faithful to the classical ethological framework. While some work has been directed at addressing ultimate questions, much remains to be done in terms of examining proximate causes of fish personality. It is clear that personality is subject to natural selection and research using fishes as model organisms has revealed that personality traits show a great deal of variability within populations, have fitness consequences and are heritable. In the genomic era it may be possible to pinpoint the exact genes responsible for personality traits and identify underlying hormone cascades that may link behavioural traits.

Most of the research to date has been conducted using the usual model organisms such as guppies and sticklebacks, but it is apparent that a better understanding of personality traits will have direct consequences for fisheries and aquaculture management. Thus, future studies are likely to be aimed at commercial and recreational species, such as salmonids, where selective manipulation of particular personality traits may significantly enhance productivity, as has been the case in terrestrial animal husbandry.

Acknowledgements

Sergey Budaev was supported by the EU Sixth Framework Programme grant, 'Evolution and Development of Cognitive, Behavioural and Neural Lateralization'. Culum Brown was supported by an Australian Research Fellowship from the Australian Research Council.

References

Anastasi, A. & Urbina, S. (1997) *Psychological Testing*, 7th edn. Prentice Hall, Upper Saddle River, NJ.

Azuma T., Dijkstra, J.M., Kiryu, I., Sekiguchi, T., Terada, Y., Asahina, K., Fischer, U. & Ototake, M. (2005) Growth and behavioral traits in Donaldson rainbow trout (*Oncorhynchus mykiss*) cosegregate with classical major histocompatibility complex (MHC) class I genotype. *Behavior Genetics*, **35**, 463–478.

Baerends, G.P. (1985) Do the dummy experiments with sticklebacks support the IRM-concept? *Behaviour*, **93**, 258–277.

Bakker, T.C.M. (1986) Aggressiveness in sticklebacks (*Gasterosteus aculeatus* L.): A behaviour-genetic study. *Behaviour*, **98**, 1–144.

Bakker, T.C.M. (1994) Genetic correlations and the control of behavior, exemplified by aggressiveness in sticklebacks. *Advances in the Study of Behavior*, **23**, 135–171.

Beck, B.B., Rapaport, L.G. & Wilson, A.C. (1994) Reintroduction of captive-born animals. In: P.J.S. Olney, G.M. Mace & A.T.C. Feister (eds) *Creative Conservation: Interactive Management of Wild and Captive Animals*, pp. 265–286. Chapman & Hall, London.

Begon, M. & Wall, R. (1987) Individual variation and competitor coexistence: a model. *Functional Ecology*, **1**, 237–241.

Bell, A.M. (2005) Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, **18**, 464–473.

Bell, A.M., Hankison, S.J. & Laskowski, K.L. (2009) The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, **77**, 771–783.

Bell, A.M. & Stamps, J.A. (2004) Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, **68**, 1339–1348.

Bell, J.D., Bartley, D.M., Lorenzen, K. & Loneragand, N.R. (2006) Restocking and stock enhancement of coastal fisheries: potential, problems and progress. *Fisheries Research*, **80**, 1–8.

Benjamin, J., Li, L., Patterson, C., Greenberg, B.D., Murphy, D.L. & Hamer, D.H. (1996) Population and familial association between the D4 dopamine receptor gene and measures of Novelty Seeking. *Nature Genetics*, **12**, 78–80.

Benus, R.F., Bohus, B., Koolhaas, J.M. & van Oortmerssen, G.A. (1991) Heritable variation for aggression as a reflection of individual coping strategies. *Experientia*, **47**, 1008–1019.

Bianco, I.H. & Wilson, S.W. (2009) The habenular nuclei: a conserved asymmetric relay station in the vertebrate brain. *Philosophical Transactions of the Royal Society B*, **364**, 1005–1020.

Biro, P.A., Abrahams, M.V., Post, J.R. & Parkinson, E.A. (2004) Predators select against high growth rates and risk-taking behaviour in domestic trout populations, *Proceedings of the Royal Society B*, **271**, 2233–2237.

Biro, P.A., Abrahams, M.V., Post, J.R. & Parkinson, E.A. (2006) Behavioural trade-offs between growth and mortality. *Journal of Animal Ecology*, **75**, 1165–1171.

Biro, P.A., Beckmann, C. & Stamps, J.A. (2009) Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B*, **277**, 71–77.

Biro, P.A. & Stamps, J.A. (2008) Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, **23**, 361–368.

Bolhuis, J.E., Schouten, W.G.P., Schrama, J.W. & Wiegant, V.M. (2005) Individual coping characteristics, aggressiveness and fighting strategies in pigs. *Animal Behaviour*, **69**, 1085–1091.

Bolyard, K.J. & Rowland, W.J. (1996) Context-dependent response to red coloration in stickleback, *Animal Behaviour*, **52**, 923–927.

Brelin, D., Petersson, E. & Winberg, S. (2005) Divergent stress coping styles in juvenile brown trout (*Salmo trutta*). *Annals of the New York Academy of Sciences*, **1040**, 239–245.

Brick, O. & Jakobsson, S. (2002) Individual variation in risk taking: the effect of a predatory threat on fighting behavior in *Nannacara anomala*. *Behavioral Ecology*, **4**, 439–442.

Broglio, C., Gómez, A., Durán, E., Ocaña, Jiménez-Moya, F., Rodríguez, F. & Salas, C. (2005) Hallmarks of a common forebrain vertebrate plan: specialized pallial areas for spatial, temporal and emotional memory in actinopterygian fish. *Brain Research Bulletin*, **66**, 277–281.

Brooks, D.R. & McLennan, D.A. (1991) Phylogeny, ecology, and behavior: a research program in comparative biology. Chicago, University of Chicago Press.

Brown, C. & Braithwaite, V.A. (2004) Size matters: a test of boldness in eight populations of bishop, *Brachyraphis episcopi*. *Animal Behaviour*, **68**, 1325–1329.

Brown, C., Burgess, F. & Braithwaite, V.A. (2007b) Heritable and experiential effects on boldness in a tropical peociliid. *Behavioral Ecology and Sociobiology*, **62**, 237–243.

Brown, C. & Day, R.L. (2002) The future of stock enhancements: lessons for hatchery practice from conservation biology. *Fish and Fisheries*, **3**, 79–94.

Brown, C., Gardener, C. & Braithwaite, V.A. (2005b) Differential stress responses in fish from areas of high- and low-predation pressure. *Journal of Comparative Physiology B*, **175**, 305–312.

Brown, C., Jones, F. & Braithwaite, V.A. (2005a) In situ examination of boldness-shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, **70**, 1003–1009.

Brown, C., Jones, F. & Braithwaite, V.A. (2007a) Correlation between boldness and body mass in natural populations of the poeciliid *Brachyrhaphis episcopi*. *Journal of Fish Biology*, **71**, 1590–1601.

Brown, C. & Laland, K. (2001) Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, **59**, 471–493.

Brown, C. & Laland, K. (2002) Social enhancement and social inhibition of foraging behaviour in hatchery-reared Atlantic salmon (*Salmo salar*). *Journal of Fish Biology*, **61**, 987–998.

Brown, C. & Warburton, K. (1999) Differences in timidity and escape responses between predator-naive and predator-sympatric rainbowfish populations. *Ethology*, **105**, 491–502.

Bryan, J.E. & Larkin, P.A. (1972) Food specialisation by individual trout. *Journal of the Fisheries Research Board of Canada*, **29**, 1615–1624.

Budaev, S.V. (1997a) "Personality" in the guppy (*Poecilia reticulata*): a correlational study of exploratory behavior and social tendency. *Journal of Comparative Psychology*, **111**, 399–411.

Budaev, S.V. (1997b) Alternative styles in the European wrasse, *Symphodus ocellatus*: boldness-related schooling tendency. *Environmental Biology of Fishes*, **49**, 71–78.

Budaev, S.V. (1998) How many dimensions are needed to describe temperament in animals: A factor reanalysis of two data sets. *International Journal of Comparative Psychology*, **11**, 17–29.

Budaev, S.V. (1999) Sex differences in the Big Five personality factors: Testing an evolutionary hypothesis. *Personality and Individual Differences*, **26**, 801–813.

Budaev, S.V. & Andrew, R.J. (2009a) Shyness and behavioural asymmetries in larval zebrafish (*Brachydanio rerio*) developed in light and dark. *Behaviour*, **146**, 1037–1052.

Budaev, S.V. & Andrew, R.J. (2009b) Patterns of early embryonic light exposure determine behavioural asymmetries in zebrafish: a habenular hypothesis. *Behavioural Brain Research*, **200**, 91–94.

Budaev, S.V. & Zworykin, D.D. (2002) Individuality in fish behavior: ecology and comparative psychology, *Journal of Ichthyology*, **42**(Supplement 2), S189–S195.

Budaev, S.V., Zworykin, D.D. & Mochek, A.D. (1999a) Individual differences in parental care and behavioural profile in the convict cichlid: A correlation study. *Animal Behaviour*, **58**, 195–202.

Budaev, S.V., Zworykin, D.D. & Mochek, A.D. (1999b) Consistency of individual differences in behaviour of the lion-headed cichlid, *Steatocranus casuarius*. *Behavioural Processes*, **48**, 49–55.

Burns, J. (2008) The validity of three tests of temperament in guppies (*Poecilia reticulata*). *Journal of Comparative Psychology*, **122**, 344–356.

Burns, J.G. & Rodd, F.H. (2008) Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. *Animal Behaviour*, **76**, 911–922.

Campbell, D.T. & Fiske, D. (1959) Convergent and discriminant validation by the multitrait-multimethod matrix. *Psychological Bulletin*, **56**, 81–104.

Capitanio, J.P. (1999) Personality dimensions in adult male rhesus macaques: Prediction of behaviours across time and situation. *American Journal of Primatology*, **47**, 299–320.

Caprara, G.V. & Perugini, M. (1994) Personality described by adjectives: The generalizability of the Big Five to the Italian lexical context. *European Journal of Personality*, **8**, 357–369.

Caro, T.M. & Bateson, P. (1986) Organization and ontogeny of alternative tactics. *Animal Behaviour*, **34**, 1483–1499.

Cattell, R. (1956) Second-order personality factors. *Journal of Consulting Psychology*, **20**, 411–418.

Cattell, R. (1973) *Personality and Mood by Questionnaire*. Jossey-Bass, San Francisco, CA.

Cheverud, J. (1988) A comparison of genetic and phenotypic correlations. *Evolution*, **42**, 958–968.

Chittka, L., Skorupski, P. & Raineet, N.E. (2009) Speed–accuracy tradeoffs in animal decision making. *Trends in Ecology and Evolution*, **24**, 400–407.

Clark, A.B. & Ehlinger, T.J. (1987) Pattern and adaptation in individual behavioral differences. In: P.P.G. Bateson & P.H. Klopfer (eds) *Perspectives in Ethology*, Vol. 7, pp. 1–47. Plenum Press, New York.

Clark, C.W. (1994) Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, **5**, 159–170.

Cloninger, C.R., Przybeck, T.R. & Svrakic, D.M. (1991) The Tridimensional Personality Questionnaire: US normative data. *Psychological Reports*, **69**, 1047–1057.

Coleman, K. & Wilson, D.S. (1998) Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, **56**, 927–936.

Colleter, M. & Brown, C. (2011) Personality traits predict hierarchy rank in male rainbowfish (Melanotaenia duboulayi) social groups. *Animal Behaviour*, in press.

Conrad, J.L. & Sih, A. (2009) Behavioural type in newly emerged steelhead *Oncorhynchus mykiss* does not predict growth rate in a conventional hatchery rearing environment. *Journal of Fish Biology*, **75**, 1410–1426.

Cooper, W.S. & Kaplan, R.H. (1982) "Adaptive coin-flipping": a decision-theoretic examination of natural selection for random individual variation. *Journal of Theoretical Biology*, **94**, 135–151.

Crabbe, J.C., Wahlsten, D. & Dudek, B.C. (1999) Genetics of mouse behavior: interactions with laboratory environment. *Science*, **284**, 1670–1672.

Croft, D.P., Krause, J., Darden, S.F., Ramnarine, I.W., Faria, J.J. & James, R. (2009) Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology*, **63**, 1495–1503.

Cronbach, L.J. & Meehl, P.E. (1955) Construct validity in psychological tests. *Psychological Bulletin*, **52**, 281–302.

Dadda, M., Domenichini, A., Piffer, L., Argenton, F. & Bisazza, A. (2010) Early differences in epithalamic left–right asymmetry influence lateralization and personality of adult zebrafish. *Behavioural Brain Research*, **206**, 208–215.

Dall, S.R.X., Houston, A.I. & McNamara, J.M. (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**, 734–739.

Dennett, D. (1983) Intentional systems in cognitive ethology: the 'Panglossian paradigm' defended. *Behavioral and Brain Sciences*, **6**, 343–398.

DeWitt, T.J., Sih, A. & Wilson, D.S. (1998) Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution*, **13**, 77–81.

Digman, J. (1990) Personality structure: the emergence of the Five-Factor model. *Annual Review of Psychology*, **41**, 417–440.

Digman, J. (1997) Higher order factors of the Big Five. *Journal of Personality and Social Psychology*, **73**, 1246–1256.

Dingemanse, N.J., Van Der Plas, F., Wright, J., Réale, D., Schrama, M., Roff, D.A., Van Der Zee, E. & Barber, I. (2009) Individual experience and evolutionary history of predation affect expression of heritable variation in fish personality and morphology. *Proceedings of the Royal Society B*, **276**, 1285–1293.

Dingemanse, N.J., Wright, J., Kazem, A.N., Thomas, D.K., Hickling, R. & Dawnay, N. (2007) Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, **76**, 1128–1138.

Dugatkin, L.A. & Alfieri, M.S. (2003) Boldness, behavioral inhibition and learning. *Ethology Ecology & Evolution*, **15**, 43–49.

Dugatkin, L.A., McCall, M.A., Gregg, R.G., Cavanaugh, A., Christensen, C. & Unseld, M. (2005) Zebrafish (*Danio rerio*) exhibit individual differences in risk-taking behavior during predator inspection. *Ethology Ecology & Evolution*, **17**, 77–81.

Dulawa, S.C., Grandy, D.K., Low, M.J., Paulus, M.P. & Geyer, M.A. (1999) Dopamine D4 receptor-knock-out mice exhibit reduced exploration of novel stimuli. *Journal of Neuroscience*, **19**, 9550–9556.

Ebstein, R.P., Levine, J., Geller, V., Auerbach, J., Gritsenko, I. & Belmaker, R.H. (1998) Dopamine D4 receptor and serotonin transporter promoter in the determination of neonatal temperament. *Molecular Psychiatry*, **3**, 238–246.

Ebstein, R.P., Novick, O., Umansky, R., Priel, B., Osher, Y., Blaine, D., Bennett, E.R., Nemanov, L., Katz, M. & Belmaker, R.H. (1996) Dopamine D4 receptor (D4DR) exon III polymorphism associated with the human personality trait of novelty seeking. *Nature Genetics*, **12**, 78–80.

Ehlinger, T.J. & Wilson, D.S. (1988) Complex foraging polymorphism in bluegill sunfish. *Proceedings of the National Academy of Sciences of the USA*, **85**, 1878–1882.

Epstein, S. (1983) Aggregation and beyond: some basic issues in the prediction of behavior. *Journal of Personality*, **51**, 360–392.

Eysenck, H.J. (1970) *The Structure of Human Personality.* Methuen, London.

Eysenck, H.J. & Eysenck, M.W. (1985) *Personality and Individual Differences. A Natural Science Approach.* Plenum Press, New York.

Falconer, D.S. (1981) *Introduction to Quantitative Genetics*, 2nd edn. Longman, London.

Fidler, A.E., van Oers, K., Drent, P.J., Kuhn, S., Mueller, J.C. & Kempenaers, B. (2007) Drd4 gene polymorphisms are associated with personality variation in a passerine bird. *Proceedings of the Royal Society B*, **274**, 1685–1691.

Fleeson, W. (2004) Moving personality beyond the person-situation debate. *Current Directions in Psychological Science*, **13**, 83–87.

Flood, N.B., Overmier, J.B. & Savage, G.E. (1976) Teleost telencephalon and learning: an interpretive review of data and hypotheses. *Physiology and Behavior*, **16**, 783–798.

Francis, R.C. (1988) On the relationship between aggression and social dominance. *Ethology*, **78**, 223–237.

Francis, R. (1990) Temperament in a fish: a longitudinal study of the development of individual differences in aggression and social rank in the Midas cichlid. *Ethology*, **86**, 311–325.

Fraser, D.F., Gilliam J.F., Daley, M.J., Le A.N. & Skalski, G.T. (2001) Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist*, **158**, 124–135.

Frost, A.J., Winrow-Giffen, A., Ashley, P.J. & Sneddon, L.U. (2007) Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proceedings of the Royal Society B*, **274**, 333–339.

Funder, D.C. (1995) On the accuracy of personality judgement: a realistic approach. *Psychological Review*, **102**, 652–670.

Funder, D.C. (2009) Persons, behaviors and situations: an agenda for personality psychology in the postwar era. *Journal of Research in Personality*, **43**, 120–126.

Godin, J.G.J. & Davis, S.A. (1995) Boldness and predator deterrence – reply. *Proceedings of the Royal Society of London Series B – Biological Sciences*, **262**, 107–112.

Godin, J.G.J. & Dugatkin, L.A. (1996) Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 10262–10267.

Gosling, S.D. (1998) Personality dimensions in spotted hyenas (*Crocuta crocuta*). *Journal of Comparative Psychology*, **112**, 107–118.

Gosling, S.D. (2001) From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, **127**, 45–86.

Gosling, S.D. & John, O.P. (1999) Personality dimensions in nonhuman animals: a cross-species review. *Current Directions in Psychological Science*, **8**, 69–75.

Gosling, S.D., Kwan, V.S.Y. & John, O.P. (2003) A dog's got personality: a cross-species comparative approach to personality judgments in dogs and humans. *Journal of Personality and Social Psychology*, **85**, 1161–1169.

Gray, J.A. (1982) A critique of Eysenck's theory of personality. In: H.J. Eysenck (ed) *A Model for Personality*, pp. 246–276. Springer, New York.

Gray, J.A. (1987) *The Psychology of Fear and Stress*. Cambridge University Press, Cambridge.

Grimm, V. & Uchmański, J. (2002) Individual variability and population regulation: a model of the significance of within-generation density dependence. *Oecologia*, **131**, 196–202.

Groothuis, T.G.G. & Carere, C. (2005) Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, **29**, 137–150.

Harwood, A.J., Armstrong, J.D., Metcalfe, N.B. & Griffiths, S.W. (2003) Does dominance status correlate with growth in wild stream-dwelling Atlantic salmon (*Salmo salar*)? *Behavioral Ecology*, **14**, 902–908.

Hebb, D.O. (1946) Emotion in man and animal: an analysis of the intuitive processes of recognition. *Psychological Review*, **53**, 88–106.

Helfman, G.S. (1984) Schooling fidelity in fishes: the yellow perch pattern. *Animal Behaviour*, **22**, 663–672.

Hodos, C.B.G. & Campbell, W. (1991) The Scala Naturae revisited: evolutionary scales and anagenesis in comparative psychology. *Journal of Comparative Psychology*, **105**, 211–221.

Huntingford, F.A. (1976) The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour*, **24**, 245–260.

Huntingford, F.A. (2004) Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *Journal of Fish Biology*, **65**, 122–142.

Huntingford, F. & Adams, C. (2005) Behavioural syndromes in farmed fish: implications for production and welfare. *Behaviour*, **142**, 1207–1221.

Huntingford, F.A., Andrew, G., Mackenzie, S., Morera, D., Coyle, S.M., Pilarczyk, M. & Kadri, S. (2010) Coping strategies in a strongly schooling fish, the common carp *Cyprinus carpio*. *Journal of Fish Biology*, **76**, 1576–1591.

Johnsson, J.I., Sernland, E. & Blixt, M. (2001) Sex-specific aggression and antipredator behaviour in young brown trout. *Ethology*, **107**, 587–599.

Kaplan, R.H. & Cooper, W.S. (1984) The evolution of developmental plasticity in reproductive characteristics: an application of the "adaptive coin-flipping" principle. *American Naturalist*, **123**, 393–410.

Kenrick, D.T. & Funder, D.C. (1988) Lessons from the person-situation debate. *American Psychologist*, **43**, 23–34.

King, J.E. & Figueredo, A.J. (1997) The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality*, **31**, 257–271.

King, J.E., Weiss, A. & Farmer, K.H. (2005) A chimpanzee (*Pan troglodytes*) analogue of cross-national generalization of personality structure: zoological parks and an African sanctuary. *Journal of Personality*, **73**, 389–410.

Kobler, A., Engelen, B., Knaepkens, G. & Eens, M. (2009) Temperament in bullheads: do laboratory and field explorative behaviour variables correlate? *Naturwissenschaften*, **96**, 1229–1233.

Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M.A.W. & Blokhuis, H.J. (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehaioral Reviews*, **23**, 925–935.

Krause, J., Loader, S.P., Kirkman, E. & Ruxton, G.D. (1999) Refuge use by fish as a function of body weight changes. *Acta Ethologica*, **2**, 29–34.

Langlet, O. (1971) Revising some terms of intra-specific differentiation. *Hereditas*, **68**, 277–280.

Lautin, A. (2002) *The Limbic Brain*. Kluwer, New York.

Leblond, C. & Reebs, S. (2006) Individual leadership and boldness in shoals of golden shiners (*Notemigonus crysoleucas*). *Behaviour*, **143**, 1263–1280.

Lepage, O., Overli, O., Petersson, E., Jarvi, T. & Winberg, S. (2000) Differential stress coping in wild and domesticated sea trout. *Brain Behavior and Evolution*, **56**, 259–268.

Livesley, W.J., Jang, K.L. & Vernon, P.A. (1998) Phenotypic and genetic structure of traits delineating personality disorder. *Archives of General Psychiatry*, **55**, 941–948.

Łomnicki, A. (1988) *Population Ecology of Individuals*. Princeton University Press, Princeton, NJ.

Lorenz, K.Z. (1974) Analogy as a source of knowledge. *Science*, **185**, 229–234.

Loughry, W.L. & Lazari, A. (1994) The ontogeny of individuality in black-tailed prairie dogs, *Cynomys ludovicianus*. *Canadian Journal of Zoology*, **72**, 1280–1286.

Magnhagen, C. (2007) Social influence on the correlation between behaviours in young-of-the-year perch. *Behavioral Ecology and Sociobiology*, **61**, 525–531.

Magnhagen, C. & Borcherding, J. (2008) Risk-taking behaviour in foraging perch: does predation pressure influence age-specific boldness? *Animal Behaviour*, **75**, 509–517.

Magnhagen, C. & Staffan, F. (2005) Is boldness affected by group composition in young-of-the-year perch (*Perca fluviatilis*)? *Behavioral Ecology and Sociobiology*, **57**, 295–303.

Magurran, A.E. (1993) Individual differences and alternative behaviours. In: T.J. Pitcher (ed) *The Behaviour of Teleost Fishes*, pp. 441–477. Chapman & Hall, London.

Mangel, M. & Clark, C.W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton, NJ.

Martin, J.G.A., Nussey, D., Wilson, A. & Réale, D. (in press). Measuring individual differences in reaction norms in field and experimental studies: a power analysis of random regression models. *Methods in Ecology and Evolution*, doi: 10.1111/j.2041-210X.2010.00084.x.

Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

McAdams, D.P. (1992) The Five-Factor model in personality: a critical appraisal. *Journal of Personality*, **60**, 329–361.

McElreath, R. & Strimling, P. (2006) How noisy information and individual asymmetries can make 'personality' an adaptation: a simple model. *Animal Behaviour*, **72**, 1135–1139.

McGinnity, P., Jennings, E., deEyto, E., Allott, N., Samuelsson, P., Rogan, G., Whelan, K. & Cross, T. (2009) Impact of naturally spawning captive-bred Atlantic salmon on wild populations: depressed recruitment and increased risk of climate-mediated extinction. *Proceedings of the Royal Society B*, **276**, 3601–3610.

McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., Maoiléidigh, N.O., Baker, N., Cotter, D., O'Hea, B., Cooke, D., Rogan, G., Taggart, J. & Crosset, T. (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society B*, **270**, 2443–2450.

Michener, C.D. & Sokal, R.R. (1957) A quantitative approach to the problem of classification. *Evolution*, **11**, 130–162.

Millot, S., Begout, M.L. & Chatain, B. (2009) Risk-taking behaviour variation over time in sea bass *Dicentrarchus labrax*: effects of day-night alternation, fish phenotypic characteristics and selection for growth. *Journal of Fish Biology*, **75**, 1733–1749.

Mischel, W. (1973) Toward a cognitive social learning reconceptualization of personality. *Psychological Review*, **80**, 252–283.

Moreira, P.S.A., Pulman, K.G.T. & Pottinger, T.G. (2004) Extinction of a conditioned response in rainbow trout selected for high or low responsiveness to stress. *Hormones and Behavior*, **46**, 450–457.

Moretz, J.A., Martins, E.P. & Robison, B.D. (2007) Behavioral syndromes and the evolution of correlated behavior in zebrafish. *Behavioral Ecology*, **18**, 556–562.

Myers, R.A. (2004) Hatcheries and endangered salmon. *Science*, **303**, 1980.

Nunnally, J.C. (1967) *Psychometric Theory*. McGraw-Hill, New York.

Ossenkopp, K.-P. & Mazmanian, D.S. (1985) The principle of aggregation in psychobiological correlational research: an example from the open-field test. *Animal Learning and Behavior*, **13**, 339–344.

Øverli, Ø., Pottinger, T.G., Carrick, T.R., Øverli, E. & Winberg, S. (2001) Brain monoaminergic activity in rainbow trout selected for high and low stress responsiveness. *Brain Behavior and Evolution*, **57**, 214–224.

Øverli, Ø., Pottinger, T.G., Carrick, T.R., Øverli, E. & Winberg, S. (2002) Differences in behaviour between rainbow trout selected for high- and low-stress responsiveness. *Journal of Experimental Biology*, **205**, 391–395.

Øverli, Ø., Sørensen, C., Pulman, K.G.T., Pottinger, T.G., Korzan, W., Summers, C.H. & Nilsson, G.E. (2007) Evolutionary background for stress-coping styles: relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. *Neuroscience and Biobehavioral Reviews*, **31**, 396–412.

Øverli, Ø., Winberg, S. & Pottinger, T.G. (2005) Behavioral and neuroendocrine correlates of selection for stress responsiveness in rainbow trout – a review. *Integrative and Comparative Biology*, **45**, 463–474.

Ozer, D.J. (1986) *Consistency in Personality: A Methodological Framework*. Springer-Verlag, New York.

Petrovskii, S.V. & Blackshaw, R.P. (2003) Behaviourally structured populations persist longer under harsh environmental conditions. *Ecology Letters*, **6**, 455–462.

Petrovskii, S.V., Blackshaw, R.P. & Li, B.L. (2008) Consequences of the Allee effect and intraspecific competition on population persistence under adverse environmental conditions. *Bulletin of Mathematical Biology*, **70**, 412–437.

Pitcher, T.J. & Parrish, J.K. (1993) Functions of schooling behaviour in teleosts. In: T.J. Pitcher (ed) *The Behaviour of Teleost Fishes*, pp. 363–439. Chapman, Hall, London.

Piyapong, C., Krause, J., Chapman, B.B., Ramnarine, I.W., Louca, V. & Croft, D.P. (2010) Sex matters: A social context to boldness in guppies (*Poecilia reticulata*). *Behavioral Ecology*, **21**, 3–8.

Portavella, M. & Vargas, J.P. (2005) Emotional and spatial learning in goldfish is dependent on different telencephalic pallial systems. *European Journal of Neuroscience*, **21**, 2800–2806.

Pottinger, T.G. & Carrick, T.R. (2001) Stress responsiveness affects dominant-subordinate relationships in rainbow trout. *Hormones and Behavior*, **40**, 419–427.

Pruessner, J.C., Gaab, J., Hellhammer, D.H., Lintz, D., Schommer, N. & Kirschbaum, C. (1997) Increasing correlations between personality traits and cortisol stress responses obtained by data aggregation. *Psychoneuroendocrinology*, **22**, 615–625.

Radakov, D.V. (1972) *Schooling in the Ecology of Fishes*. Nauka, Moscow.

Rands, S.A., Cowlishaw, G., Pettifor, R.A., Rowcliffe, J.M. & Johnstone, R.A. (2003) Spontaneous emergence of leaders and followers in foraging pairs. *Nature*, **423**, 432–434.

Raoult, V., Brown, C., Zuberi, A. & Williamson, J.E. (2010) Personality traits are linked to stress hormones in a commercial marine fish species (*Argyosomus japonicus*). *Biology Letters.* (In press.)

Réale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. (2007) Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291–318.

Revelle, W. (1983) Factors are fictions, and other comments on individuality theory. *Journal of Personality*, **51**, 707–714.

Ringler, N.H. (1983) Variation in foraging tactics of fishes. In: D.L.G. Noakes (ed) *Predators and Prey in Fishes*, pp. 159–172. Junk Publishers, The Hague.

Roberts, B.W. & DelVecchio, W.F. (2000) The rank-order consistency of personality traits from childhood to old age: a quantitative review of longitudinal studies. *Psychological Bulletin*, **126**, 3–25.

Roff, D.A. (1996) The evolution of genetic correlations: an analysis of patterns. *Evolution*, **50**, 1392–1403.

Rowland, W.J. (1982) The effects of male coloration on stickleback aggression: a reexamination. *Behaviour*, **80**, 118–126.

Rushton, J.P., Bons, T.A. & Hur, Y.M. (2008) The genetics and evolution of the general factor of personality. *Journal of Research in Personality*, **42**, 1173–1185.

Rushton, J.P., Brainerd, C.J. & Pressley, M. (1983) Behavioral development and construct validity: the principle of aggregation. *Psychological Bulletin*, **94**, 18–38.

Saetre, P., Strandberg, E., Sundgren, P.-E., Pettersson, U., Jazin, E. & Bergstrom, T.F. (2006) The genetic contribution to canine personality. *Genes, Brain and Behavior*, **5**, 240–248.

Schjolden, J., Stoskhus, A. & Winberg, S. (2005) Does individual variation in stress responses and agonistic behavior reflect divergent stress coping strategies in juvenile rainbow trout? *Physiological and Biochemical Zoology*, **78**, 715–723.

Seaman, S.C., Davidson, H.P.B. & Waran, N.K. (2002) How reliable is temperament assessment in the domestic horse (*Equus caballus*)? *Applied Animal Behaviour Science*, **78**, 175–191.

Shaklee, A.B. (1963) Comparative studies of temperament – fear responses in different species of fish. *Journal of Genetic Psychology*, **102**, 295–310.

Shepard, P.D., Holcomb, H.H. & Gold, J.M. (2006) The presence of absence: habenular regulation of dopamine neurons and the encoding of negative outcomes. *Schizophrenia Bulletin*, **32**, 417–421.

Sih, A., Bell, A., Johnson, J.C. & Ziemba, R.E. (2004) Behavioral syndromes: an integrative overview. *Quarterly Review of Biology*, **79**, 241–277.

Slater, P.J.B. (1981) Individual differences in animal behaviour. In: P.P.G. Bateson & P.H. Klopfer (eds) *Perspectives in Ethology Journal of Genetic Psychology*, Vol. 4, pp. 35–49. Plenum Press, New York.

Smith, T.B. & Skulason, S. (1996) Evolutionary significance of resource polymorphisms in fishes, amphibians. *Annual Review of Ecology and Systematics*, **27**, 111–133.

Sneddon, L.U. (2003) The bold and the shy: individual differences in rainbow trout. *Journal of Fish Biology*, **62**, 971–975.

Staffan, F., Magnhagen, C. & Alanara, A. (2005) Individual feeding success of juvenile perch is consistent over time in aquaria and under farming conditions. *Journal of Fish Biology*, **66**, 798–809.

Stamps, J.A. (2007) Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters*, **10**, 355–363.

Stevenson-Hinde, J., Stillwell-Barns, R. & Zunz, M. (1980) Subjective assessment of rhesus monkeys over four successive years. *Primates*, **21**, 66–82.

Sundström, L.F., Lõhmus, M. & Johnsson, J.I. (2003) Investment in territorial defence depends on rearing environment in brown trout (*Salmo trutta*). *Behavioral Ecology and Sociobiology*, **54**, 249–255.

Sundström, F.L., Petersson, E., Höjesjö, J., Johnsson, J.I. & Järvi, T. (2004) Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. *Behavioral Ecology*, **15**, 192–198.

Sutherland, R.J. (1982) The dorsal diencephalic conduction system: a review of the anatomy and functions of the habenular complex. *Neuroscience and Biobehavioral Reviews*, **6**, 1–13.

Svartberg, K. (2002) Shyness-boldness predicts performance in working dogs. *Applied Animal Behaviour Science*, **79**, 157–174.

Tinbergen, N. (1963) On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, **20**, 410–433.

Uchmański, J. (2000) Individual variability and population regulation: an individual-based model. *Oikos*, **90**, 539–548.

Uher, J. & Asendorpf, J.B. (2008) Personality assessment in the Great Apes: comparing ecologically valid behaviour measures, behaviour ratings, and adjective ratings. *Journal of Research in Personality*, **42**, 821–838.

van Oers, K., de Jong, G., Drent, P.J. & van Noordwijk, A.J. (2004) A genetic analysis of avian personality traits: correlated, response to artificial selection. *Behavior Genetics*, **34**, 611–619.

van Oers, K., Klunder, M. & Drent, P.J. (2005) Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*, **16**, 716–723.

Vazire, S., Gosling, S.D., Dickey, A.S. & Schaprio, S.J. (2007) Measuring personality in nonhuman animals. In: R.W. Robins, R.C. Fraley & R.F. Krueger (eds) *Handbook of Research Methods in Personality Psychology*, pp. 190–206. Guilford, New York.

Ward, A.J.W., Thomas, P., Hart, P.J.B. & Krause, J. (2004) Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, **55**, 561–568.

Westerberg, M., Staffan, F. & Magnhagen, C. (2004) Influence of predation risk on individual competitive ability and growth in Eurasian perch, *Perca fluviatilis*. *Animal Behaviour*, **67**, 273–279.

Wilson, A.D.M. & Godin, J.-G. (2009) Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behavioral Ecology*, **20**, 231–237.

Wilson, A.D.M. & Stevens, E.D. (2005) Consistency in context-specific measures of shyness and boldness in rainbow trout, *Oncorhynchus mykiss*. *Ethology*, **111**, 849–862.

Wilson, D.S. (1998) Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London B*, **353**, 199–205.

Wilson, D.S., Clark, A.B., Coleman, K. & Dearstyne, T. (1994) Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution*, **9**, 442–446.

Wilson, D.S., Coleman, K., Clark, A.B. & Biederman, L. (1993) Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250–260.

Wilson, M. & Daly, M. (1985) Competitiveness, risk-taking, and violence: the young male syndrome, *Ethology and Sociobiology*, **6**, 59–73.

Wolf, M., van Doorn, G.S., Leimar, O. & Weissing, F.J. (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature*, **447**, 581–585.

Wolf, M., van Doorn, G.S. & Weissing, F.J. (2008) Evolutionary emergence of responsive and unresponsive personalities. Proceedings of the National Academy of Sciences of the USA, **105**, 15825–15830.

Wright, D., Butlin, R. & Carlborg, Ö. (2006) Epistatic regulation of behavioural and morphological traits in the zebrafish (*Danio rerio*). *Behavior Genetics*, **36**, 914–922.

Wright, D., Rimmer, L.B., Pritchard, V.L., Krause, J. & Butlin, R.K. (2003) Inter and intra-population variation in shoaling and boldness in the zebrafish (*Danio rerio*). *Naturwissenschaften*, **90**, 374–377.

Yoshida, M., Nagamine, M. & Uematsu, K. (2005) Comparison of behavioral responses to a novel environment between three teleosts, bluegill *Lepomis macrochirus*, crucian carp *Carassius langsdorfii*, and goldfish *Carassius auratus*. *Fisheries Science*, **71**, 314–319.

Zuckerman, M. (1994) *Psychobiology of Personality*. Cambridge University Press, Cambridge.

Zuckerman, M., Kuhlman, D.M., Joireman, J., Teta, P. & Kraft, M. (1993) A comparison of three structural models for personality: The Big Three, the Big Five, and the Alternative Five. *Journal of Personality and Social Psychology*, **65**, 757–768.