

# Covariation between personalities and individual differences in coping with stress: Converging evidence and hypotheses

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**Abstract** In the past decade there has been a profusion of studies highlighting covariation between individual differences in stress physiology and behavioural profiles, here called personalities. Such individual differences in ways of coping with stress are relevant both in biomedicine, since different personalities may experience a different stress and disease vulnerability, and in behavioural ecology, since their adaptive value and evolutionary maintenance are the subject of debate. However, the precise way in which individual stress differences and personalities are linked is unclear. Here we provide an updated overview of this covariation across different species and taxa, consider its functional significance and present working hypotheses for how behavioural and physiological responses to stress might be causally linked, affecting life-history traits such as dispersal and life-span [*Current Zoology* 56 (6): 728–740, 2010].

**Key words** Animal personality, Coping style, Aggression, Stress response, Corticosterone, Glucocorticoids, Natural selection, Fitness evolution

## 1 Introduction

Accumulating evidence from a range of taxa shows that behaviour is not completely flexible. Individuals show differences in behaviour and physiology that are stable over time and across contexts, even among those of the same age or sex (e.g. Huntingford, 1976; Verbeek et al., 1994; Koolhaas et al., 2010; see Table 1 for an overview). Differences are particularly apparent when individuals face environmental challenges (Broom, 2001) or otherwise stressful situations, e.g. exploring a novel environment (Drent et al., 2003) or suffering social defeat by a conspecific (Koolhaas et al. 1999; Carere et al., 2001; reviews by Sih et al., 2004a,b; Carere and Eens 2005; Réale et al., 2007; Bell et al., 2009). Much of the literature from studies in captivity under standard conditions contrasts two alternative phenotypes, e.g. fast/slow, bold/shy, proactive/reactive, and indicates a clear genetic basis (Koolhaas et al., 1999; Drent et al., 2003; Veenema et al., 2003a; Groothuis and Carere, 2005; see Table 2), while in wild populations these are typically extremes of a continuous distribution (Réale et al., 2007). Notably, especially from an evolutionary point of view, such differences have clear fitness correlates, as exemplified by long-term studies in the great tit (*Parus major*; see Table 3). Throughout this article we will refer to these stable behavioural diffe-

rences as personalities.

Likewise, individuals show consistent differences in physiological indicators of stress, namely hypothalamic-pituitary-adrenal axis (HPA) reactivity (reviewed by Cockrem, 2007; Bonier et al., 2009, Koolhaas et al., 2010) and oxidative status (Costantini et al., 2008), as well as in the underlying neurobiology (Koolhaas et al., 1999; Feldker et al., 2003; Koolhaas et al., 2010). Such differences may reflect variation in condition or health (von Schantz et al., 1999; Romero, 2004; Cavigelli, 2005), though this is disputed (Bonier et al., 2009, 2010; Dingemanse et al., 2010).

Such individual differences in coping with stress are relevant both in biomedicine, since different personalities may experience different stress and disease vulnerability as well as different responses to medical treatments, and in behavioural ecology, since their adaptive value and evolutionary maintenance are the subject of debate and different phenotypes may have a different role in the population ecology of a given species (Réale et al., 2007). However, the precise way in which individual differences in stress coping and personalities are linked is unclear. The aim of this paper is to provide an updated overview of the biological basis of this covariation across vertebrate taxa (mainly birds and mammals) both at behavioural and physiological levels, discuss its functional significance and present working hypotheses

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for how behavioural and physiological responses to stress might be causally linked.

## 2 Correlated Variation in Physiological and Behavioural Responses to Stress: A Review of the Evidence across Vertebrates

### 2.1 Early studies

The link between behavioural and physiological traits was suggested by the work of Cannon (1915), who described how fighting or fleeing, as a result of feeling anger or fear, is coupled to a physiological activation of the sympathetic branch of the autonomic nervous system and consequent stimulation of the adrenal medulla to release adrenaline and noradrenaline into the bloodstream. In the 1970s, Henry and Stephens recognized the presence of two distinct physiological response patterns in mice *Mus musculus domesticus* on the basis of their behaviour in social conflict. Mice that tend to win fights are more prone to develop cardiovascular problems associated with strong sympathetic activation in terms of plasma noradrenaline and adrenaline, while mice that are subordinate tend to show strong activation of the HPA axis, with consequent high levels of blood corticosterone (Henry and Stephens, 1977). The latter physiological pattern was attributed to a more general strategy aimed at conservation/withdrawal, characterized by behavioural inhibition to counteract energy depletion through a homeostatic balancing mechanism (Engel and Schmale, 1972).

### 2.2 Mice and rats

This idea was extended by Koolhaas and colleagues to the concept of “coping styles”, based on detailed behavioural and physiological profiles of mice and rats and specifically considering their adaptive value in coping with a stressful situation (Koolhaas et al., 1999). In describing the individual variation in coping capacity they identified two main alternative strategies, which could be considered as basic personality styles. The “proactive strategy” consists of aggressiveness, boldness, inflexibility and is characterized by a general fight-or-flight behavioural response indicating a high emotional activation. The “reactive strategy” combines low aggressiveness, risk aversion, flexibility to changes and is dominated by freezing behaviour in response to stress (Table 2). Several studies covering a range of vertebrate species revealed that individuals adopting the proactive strategy show an enhanced sympathetic and

(nor-)adrenergic response to stress, while individuals with the reactive strategy show an enhanced parasympathetic activation and a high HPA response (Hessing et al., 1994; Fokkema et al., 1995; Sgoifo et al., 1996; Korte et al., 1999). Within the two branches of the autonomic nervous system, which together regulate the cardiovascular function, a shift towards sympathetic or parasympathetic activation explains a higher or a lower predisposition, respectively, to arrhythmias and long-term cardiovascular problems associated with coping styles (Sgoifo et al., 2005).

In male mice the coping styles have been studied using genetic selection lines for short and long attack latency (SAL and LAL), measured when a territorial male is introduced in the focal male's home cage. In addition to the differences in attack latency, SAL mice are more aggressive than LAL mice towards conspecifics of both sexes (van Oortmerssen and Busser, 1989; Benus et al., 1990; Caramaschi et al., 2008) and their aggression is directed towards vulnerable regions, so is more injurious (Haller et al., 2006). Defeated SAL mice have a greater tendency to flee, whereas LAL mice freeze more (Benus et al., 1992). In non-social situations SAL mice seem relatively unaffected by changes in the environment and are slow in reversal-learning tasks (Benus et al., 1990) and in actively coping with aversive challenges (Sluyter et al., 1996). LAL mice show more anxious behaviour and freezing in several paradigms (Hogg et al., 2000; Veenema et al., 2003a,b). The glucocorticoid response to ACTH, novelty and forced swim is significantly higher in LAL than in SAL mice (Veenema et al., 2004, 2005b). Chronic psychosocial stress induces a long-lasting increase in glucocorticoid production in LAL but not in SAL mice (Veenema et al., 2003a, 2005a). These data indicate that LAL mice are more responsive to stress in terms of glucocorticoid production than SAL mice (Veenema et al., 2004).

In rats, aggressiveness is positively correlated with proactivity in counteracting a mild adverse stimulus, specifically measured as the degree to which the animal buries a shock-prod in its cage after receiving a mild electric shock (de Boer and Koolhaas, 2003). Low aggressiveness is correlated with immobility. In physiological terms, aggressive animals display a higher reactivity of the sympatho-adrenomedullary pathway (autonomic nervous system), while less aggressive or passive animals show a marked increase in plasma corticosterone levels (Sgoifo et al., 1996) and a higher activation of the parasympathetic system, the other branch of the autonomic nervous system that counteracts the effects of

the sympathetic system. This evidence comes from comparing wild-type Groningen rats with Wistar rats and from examining individual differences between wild-type Groningen rats (Sgoifo et al., 1998). In laboratory Wistar rats, measurable aggression may be very low, rendering these types of studies difficult because of a lack of such behaviour in their agonistic repertoire (de Boer et al., 2003). However, two rat lines, the Roman-High-Avoidance (RHA) and Roman-Low-Avoidance (RLA) lines (Bignami, 1965), were established on the basis of their active/passive coping behaviour as measured in the shuttle-box test, a two-compartment box with one side able to deliver a shock and the other a "safe" side without shock. The RHA rats move quickly to the compartment without shock whereas the RLA rats remain in the compartment with shock but adopt an immobile state, either of which reduces the chances of receiving further shock. These Roman lines also show more general characteristics of high and low fearfulness, while their HPA reactivity correlates positively with the fearfulness exhibited by the RLA rats (Steimer et al., 1997). In another study, Sprague-Dawley rats were categorized as having either a neophobic style, characterized by cautious movements, or a neophilic style, characterized by ample locomotion and inspection. Neophobia and neophilia were lifelong stable traits in these rats. When exposed to a novel situation, neophobic rats exhibited a higher rise in plasma corticosterone, revealing a more responsive HPA axis and a general reactive phenotype (Cavigelli and McClintock, 2003).

### 2.3 Pigs

A similar picture emerges from work on farmed pigs *Sus scrofa* by Hessing and colleagues. Pigs were classified as having an active or a passive coping strategy based on aggressiveness and escape attempts in the back test (in which they were put on their back and restrained while supine). These behavioural traits are detectable early in piglets and persist into later life. When tested in an open field or in the presence of a novel object, active pigs made more escape attempts, vocalized less and approached the novel object earlier compared to the passive pigs, showing a fearless phenotype. As in the rodents, this behavioural phenotype was associated with the physiological response to stress, with the active copers having a higher sympatho-adrenomedullary pathway reactivity to stress and the passive copers having a higher HPA reactivity to stress (Hessing et al., 1994).

### 2.4 Non-human primates

In free-ranging rhesus monkeys *Macaca mulatta*,

longitudinal studies have distinguished between individuals that are highly reactive to the stress of social separation and those that are more stable (Suomi, 1997). In these studies personality is defined as 'temperament', meaning stable behavioural traits recognizable very early in life. In general, monkeys that underwent social separation in infancy developed a highly reactive behavioural profile and were characterized by high sympatho-adrenomedullary and HPA activation during a social encounter (reviewed by Suomi, 1997). In another study on non-manipulated subjects, the aggressive individuals showed both higher sympathoadrenal and HPA reactivity to stress (Higley et al., 1992). Other studies on rhesus monkeys have described an early detectable and consistent source of variation in anxious and fearful temperament related to extreme right- or left-brain frontocortical activity. In these monkeys the variation in temperament is associated with consistent individual differences in physiological activation of the HPA axis in situations of stress. Anxious monkeys show higher cortisol and corticotropine-releasing hormone levels than less anxious ones (Kalin and Shelton, 2003). In capuchin monkeys *Cebus apella*, high cortisol reactivity correlates negatively with subjectively rated personality traits such as aggressive, confident, curious, effective and opportunistic, and positively with apprehensive, fearful, insecure, submissive and tense (Byrne and Suomi, 2002). Taken together, such studies provide evidence for a close link between behavioural and physiological stress reactivity, with some similarities to the rodent studies.

### 2.5 Birds

In birds, much of the published work is based on two selection lines of great tits *Parus major*, which has recently stimulated research on several other species (Table 1). The great tit lines were selected from wild populations on the basis of their exploratory behaviour and labelled Fast and Slow to indicate the speed with which they explore a novel environment and approach a novel object (Drent et al., 2003). The lines were found to differ consistently in a range of behavioural contexts (Groothuis and Carere, 2005). For example, the Fast explorers tended to develop routines and were more risk-prone and aggressive than the Slow explorers. As in the rodent studies, the physiological response to stress was linked to these alternative behavioural profiles: Slow birds were more reactive in terms of HPA activation and body temperature in response to stress than fast birds (Carere et al., 2003; Carere and van Oers, 2004; Stöwe et al., 2010).

**Table 1** Overview of the species in which consistent individual differences in suites of (at least two) traits have been described at different levels of analysis

SPECIES	Behaviour	Physiology	Genetics	Fitness
House mouse <i>Mus musculus domesticus</i>	++	++	+	+
Great tit <i>Parus major</i>	++	+	++	+
Norway rat <i>Rattus norvegicus</i>	++	++	+	
Pig <i>Sus scrofa</i>	++	+		
Rhesus monkey <i>Macaca mulatta</i>	++	+		
Chimpanzee <i>Pan troglodytes</i>	++		+	
Dog/wolf <i>Canis lupus</i>	++	+		
Bighorn sheep <i>Ovis canadensis</i>	++			+
Stickleback <i>Gasterosteus aculeatus</i>	++	+		+
Atlantic Salmon <i>Salmo salar</i>	++		+	
Pumpkinseed sunfish <i>Lepomis gibbosus</i>	++			
Guppy <i>Poecilia reticulata</i>	++			
Octopus <i>Octopus sp.</i>	++			
Spotted hyena <i>Crocuta crocuta</i>	++			
Gorilla <i>Gorilla sp.</i>	++			
American mink <i>Neovison vison</i>	+	+	+	
Japanese quail <i>Coturnix japonica</i>	+	+	+	
White stork <i>Ciconia ciconia</i>	+	+		+
Marmot <i>Marmota vancouverensis</i>	+			+
Cattle <i>Bos primigenius</i>	+	+		
Tree shrew <i>Tupaia sp.</i>	+	+		
Chicken <i>Gallus gallus domesticus</i>	+	+		
Rainbow Trout <i>Onchorhynchus mykiss</i>	+	+		
Greylag goose <i>Anser anser</i>	+	+		
Baboon <i>Papio sp.</i>	+			
Vervet monkey <i>Chlorocebus pygerythrus</i>	+			
Domestic cat <i>Felis silvestris</i>	+			
Dumpling squid <i>Euprymna tasmanica</i>	+			
Zebra finch <i>Taeniopygia guttata</i>	+			
Chaffinch <i>Fringilla coelebs</i>	+			
Collared flycatcher <i>Ficedula albicollis</i>	+			
European kestrel <i>Falco tinnunculus</i>	+			
Common raven <i>Corvus corax</i>	+			
Water strider <i>Acquarius remigis</i>	+			
European house cricket <i>Acheta domesticus</i>	+			

The list is an update from Carere and Eens (2005) and does not pretend to be exhaustive. ++ means that at least two papers from different authors have been published for a given species.

**Table 2** Overview of the overt behavioural and physiological traits that define proactive and reactive coping styles in mice and rats

PROACTIVE		REACTIVE
<i>Mice</i>		
high	Aggression	low
high	Routine formation	low
low	Flexibility	high
low	HPA activation	high
<i>Rats</i>		
high	Aggression	low
high	Sympathetic activation	low
low	Parasympathetic activation	high
low	HPA activation	high

Other avian studies, notably those on farmed poultry, have revealed a similar relationship between corticosterone and consistent behaviour. The duration of tonic immobility, reflecting “fearfulness”, was longer in white Leghorn chickens *Gallus gallus domesticus* than in brown Hy-line chickens, and the Leghorns also showed a greater corticosterone response to handling (Fraisse and Cockrem, 2006). White Leghorn chicken lines selected for high (HP) and low (LP) feather pecking consistently showed this difference soon after hatching (Blockhuis and Beutler, 1992; van Hierden et al., 2002a,b). In these lines, high levels of feather pecking were associated with more preening, tonic immobility in open field and struggling under restraint, indicating an aggressive and proactive, but cautious, coping style. In contrast, low levels of feather pecking were associated with more ground pecking, locomotion and vocalization in open field and higher speed in social competition tests, indicating a non-aggressive and reactive phenotype. As in mammals, the proactive and reactive chicken lines showed consistent physiological profiles, the HP line being characterized by a marked sympathetic, noradrenergic and tachycardic response to stress, the LP line being characterized by a pronounced corticosterone and parasympathetic response to stress (Korte et al., 1999). In all cases the physiological parameters, more than behaviour (see Groothuis and Carere, 2005), point to similarities between the avian and mammalian data, suggesting that HP birds are proactive and LP birds are reactive copers. In Japanese quails *Coturnix japonica*, a line selected for low corticosterone response showed less intense reactions to threat than a line selected for high corticosterone response (Jones et al., 1994a,b). Quail lines selected for low and high corticosterone responses have different behavioural profiles and can be consistently classified into proactive and reactive types

(Satterlee and Johnson, 1988).

### 3 Explaining Individual Differences in Behaviour: Ultimate Mechanisms

We have reviewed evidence across taxa that individuals differ consistently in their ways of coping with stress, both behaviourally and physiologically. Typically, individuals with a proactive, risk-prone, aggressive, bold personality respond to stress with a strong sympathetic activation and increase in noradrenergic stimulation, with side effects on the cardiovascular system. In contrast, individuals with a passive, risk-averse, non-aggressive, shy personality respond to stress with a strong HPA stimulation and a consequent increase in circulating glucocorticoids. This covariation between behaviour and stress physiology opens up the possibility that there may be mechanistic and functional links between the two. In this respect, Koolhaas and co-workers have recently suggested that the differential neuroendocrine characteristics are a consequence rather than the cause of the behavioural differentiation (Koolhaas et al., 2010, see section 4).

How can we explain from an ultimate point of view these consistent individual differences in behaviour and physiology? This question has recently attracted great interest from evolutionary biologists, seeking to understand how a mixture of behavioural phenotypes can be maintained in a population when natural selection should eliminate all but the fittest phenotype (e.g. Wilson, 1998; Dall et al., 2004; McElreath and Strimling, 2006; Stamps, 2007; Wolf et al., 2007, 2008; Biro and Stamps, 2008; Sih and Bell, 2008; McNamara et al., 2009; Schuett et al., 2010). Here we consider four basic explanations.

#### 3.1 Behavioural differences have no fitness consequences

Individual differences in behaviour could be maintained in a population if they have no major effects on fitness. That is, if natural selection does not distinguish between alternative behavioural responses to stress, these alternative responses could simply represent random, non-adaptive, neutral variation. This hypothesis could conceivably account for some instances of behavioural variation but is contradicted by long-term field studies on great tits and bighorn sheep *Ovis canadensis*, which have documented clear fitness differences between individuals showing different degrees of exploratory behaviour and boldness (Dingemanse and Réale, 2005; Table 3). A recent meta-analysis (Smith and

**Table 3** Overview of the fitness correlates of personality types in wild great tits

Fitness parameter	Fast vs Slow	Reference
Postfledging dispersal	F>S	Dingemanse et al., 2003
Dominance in territorial males	F>S	Dingemanse and de Goede, 2004
Dominance in non-territorial males	S>F	Dingemanse and de Goede, 2004
Offspring recruitment in poor years	FS=SF>FF=SS	Dingemanse et al., 2004
Offspring recruitment in a good year	FF=SS>SF=FS	Dingemanse et al., 2004
Female adult survival in poor years	F>S	Dingemanse et al., 2004
Female adult survival in a good year	S>F	Dingemanse et al., 2004
Male adult survival in poor years	S>F	Dingemanse et al., 2004
Male adult survival in a good year	F>S	Dingemanse et al., 2004
Reproductive success	FF=SS>SF=FS	Both et al., 2005
Laying date	F earlier than S	Groothuis et al., 2008

Except for laying date, all variables were recorded in captive birds from two selection lines; F = fast profile, S = slow profile (see text for a description of the selection lines). Assortative and disassortative pairs are included. The list is an update from Groothuis and Carere (2005).

Blumstein, 2008) also argues against a non-adaptive explanation, suggesting that bold individuals typically have greater reproductive success, while shy individuals tend to live for longer (see Fig. 2 for possible mechanisms). Similarly, a longitudinal study on laboratory rats found an association between exploratory tendency and survival, with neophobic individuals having a shorter lifespan than neophilic individuals (Cavigelli and McClintock, 2003).

### 3.2 Selection pressures fluctuate in time or space

Directional selection or stabilising selection will generally eliminate behavioural variation, preserving only those types closest to the optimum. However, a mixture of behavioural types might coexist if environmental conditions change across time or space, favouring different types of individuals in different locations or at different points in time. For example, proactive individuals may outcompete reactive individuals when food is abundant because they selectively target the most profitable locations, whereas the latter may be more successful under conditions of food scarcity because they explore the environment more thoroughly (Marchetti and Drent, 2000; Korte et al., 2005). If individuals are not completely flexible in their behaviour and the local spatio-temporal conditions fluctuate unpredictably, selection could potentially preserve a mixture of proactive and reactive types, for example as outcomes of a 'bet-hedging' strategy (Seger and Brockmann, 1987). Whether fluctuating selection pressures can maintain behavioural variation in practice depends critically on various biological details of the population in question, for example the speed at which conditions change across space or time, the degree of generation overlap and the costs of behavioural plasticity (Wolf et al., in press). But there is at least some em-

pirical evidence in support of this idea. In great tits the direction of selection on exploratory tendency changed from year to year in relation to the crop of beech masts, an important winter food (Dingemanse et al., 2004). Exploratory tendency has a high heritability in this species (0.54; Drent et al., 2003) and it is therefore possible that fluctuating selection pressures maintain variation in the trait (Dingemanse and Réale, 2005).

### 3.3 Behavioural differences are related to underlying state differences

Several authors have suggested that stable individual differences in behaviour are related to underlying differences in state, for example the body size or health of an individual (e.g. Rands et al., 2003; Dall et al., 2004; McElreath and Strimling, 2006; Stamps, 2007; Biro and Stamps, 2008). Behaviour in many situations is state-dependent, because differences in state affect the costs and benefits of particular actions and therefore alter the optimal cost-benefit trade-off (Houston and McNamara, 1999). For example, hungry and well-fed individuals are expected to differ in their foraging effort because their current energetic requirements are very different (Dall et al., 2004). Therefore, if individuals exhibit stable differences in their underlying state, this could explain consistent individual differences in behaviour.

What could generate these stable state differences between individuals? One possibility is that they are non-genetic and arise purely from stochastic effects, especially when these occur in sensitive ontogenetic phases: some individuals suffer bad luck early in their development, experience poor nutrition and consequently end up in worse condition than those that were more fortunate. Thereafter, the best decision when faced with a given behavioural problem may well differ for

individuals in poor and good condition. In this way, proactive and reactive behaviour may both represent optimal solutions to the same stressful situation, but each may be appropriate only for individuals in a given state. Variation in the degree of proactive/reactive behaviour would then reflect stochastic variation in the conditions experienced by individuals during development. Note that there is no requirement for these behavioural variations to have equal fitness; it could be that individuals in poor condition have lower fitness prospects and the behaviour they display is a way of 'making the best of a bad job' (Krebs and Davies, 1993). However, similar fitness might also be achieved through different developmental histories and trajectories (Caro and Bateson, 1986; Carere and Eens, 2005).

Initial state differences, caused by stochastic influences on development, might be maintained or even exaggerated through positive feedback between behaviour and state (Sih et al., 2004a; Sih and Bell, 2008). For example, if individuals with a high energetic state do best by adopting aggressive, proactive behaviour, and this behaviour gives them a competitive edge over more passive, reactive individuals in gaining access to food, then their high energetic state should be maintained and the associated behavioural differences reinforced (Sih and Bell, 2008). Likewise, learning mechanisms improving behavioural performance might generate positive feedback loops that stabilise individual behavioural differences (Wolf et al., 2008).

Although stochastic influences on development provide a compelling explanation for many behavioural differences, current evidence suggests that genetic factors contribute to personality variation in several well-studied systems. Heritability estimates from breeding experiments under standardised conditions, which can control for environmental effects, show that personality traits often have a substantial genetic basis (reviewed by van Oers et al., 2005). In such cases, state-dependent behaviour cannot by itself account for the coexistence of different phenotypes; we need also to explain the maintenance of the underlying genetic variation. Either this variation is selectively neutral (explanation (i), above), which seems unlikely (Smith and Blumstein, 2008), or selection actively favours the coexistence of different genotypes, through spatiotemporal fluctuations (explanation (ii), above) or frequency dependence (explanation (iv), below).

### **3.4 Behavioural differences are maintained by frequency-dependent selection**

Consistent individual differences in behaviour could

arise even in the absence of state differences, if alternative behaviours are equally fit. Specifically, evolution might lead to a stable mixture of behavioural variants if selection is negatively frequency-dependent, with each variant favoured when it is rare (Maynard Smith, 1982). At evolutionary equilibrium, the fitness of alternative behaviours is equal, and it does not pay individuals to change their behaviour. A classic theoretical example to illustrate this is the so-called Hawk-Dove game (Maynard Smith and Price, 1973), in which two individuals contest a resource and each can adopt one of two behaviours, Hawk or Dove. Individuals that play Hawk will always escalate the conflict until they are injured or their opponent withdraws; Doves, in contrast, initially display but will withdraw immediately if their opponent attacks. When the cost of being injured outweighs the value of the resource, selection favours a mixture of Hawks and Doves: Hawks have an advantage when rare because they always defeat Doves, but Doves likewise have an advantage when rare because they avoid the injuries that Hawks inflict on one another.

Negative frequency-dependent selection is central to two recent mathematical models by Wolf and colleagues (Wolf et al., 2007, 2008), which attempt to explain the evolution of stable differences in behaviour. Negative frequency-dependent selection first promotes the coexistence of superficial and thorough explorers (Wolf et al., 2007) or responsive and unresponsive individuals (Wolf et al., 2008), and this then leads to the evolution of various correlated traits (Wolf et al., 2007) and, through positive feedback loops, consistency in behaviour (Wolf et al., 2008). The advantage enjoyed by each behavioural type when it is rare ensures that no single strategy can dominate and go to fixation.

An influential review by Korte et al. (2005) summarised the evidence that 'Hawk' and 'Dove' behavioural types exist in real animal populations, and the extent to which these are associated with physiological differences. This is a misrepresentation of the original purpose of the Hawk-Dove model, which was a simple game-theoretical tool used to illustrate the principle that all-out aggression would not necessarily be favoured by individual-level selection (Maynard Smith and Price, 1973). The Hawk and Dove types implemented in the model were caricatures used to simplify the logic of animal contests and clarify the evolutionary forces involved, rather than accurate representations of the range of aggressive types that might be encountered in real systems. In wild populations, we typically see a continuous range of behavioural phenotypes (Réale et al.,

2007), with Hawk- and Dove-like individuals, if they exist at all, occupying the extremes. A more distinct dichotomy, with two alternative behavioural types, would be characteristic of selection lines in which individuals are selectively bred in opposing directions (e.g. for high versus low aggressiveness; van Oortmerssen and Bakker, 1981).

Which of these accounts is most likely to explain the maintenance of consistent individual differences in behaviour? It is difficult to give a definitive answer to this question at present, given that the functional analysis of animal personalities is a relatively new field and detailed studies are rare, particularly in wild populations. It is possible that each of the four explanations outlined above may be valid in particular cases. However, as behavioural biologists we feel that marked behavioural differences are unlikely to be selectively neutral in most instances, a suspicion backed up by Smith and Blumstein's (2008) meta-analysis. We therefore lean towards the adaptive explanations.

The importance of spatiotemporal variation is difficult to determine. In evolutionary ecology, field studies spanning multiple years frequently find evidence of fluctuating selection pressures (e.g. Grant and Grant, 2002; Chaine and Lyon, 2008). However, whether such fluctuations can account for the consistent individual differences found in particular populations is a different matter. Assessing this requires detailed statistical models of selection based on measured fitness effects (e.g. Dingemanse et al., 2004) and heritability estimates (e.g. Dingemanse et al., 2002; Drent et al., 2003), which in most studies of personality traits are lacking.

State differences may account for many of the individual behavioural differences in wild populations. Stochastic influences on development are many and varied and will often favour alternative actions for individuals in different states (Houston and McNamara, 1999). On observing pronounced behavioural variation within a population, the critical next step is to determine whether this variation is associated with measurable state variables, for example age, body size or parasite infestation. Even in laboratory studies, where the experimenter commonly attempts to control for state differences by matching individuals, personality may be related to unobservable state variables (Wolf et al., in press). Our suspicion is that state-dependent behaviour is a major cause of personality differences in wild populations. However, for personality traits that show significant heritability (reviewed by van Oers et al., 2005), any underlying state differences may be partly due to ge-

netic factors. State-dependent behaviour then offers only a partial explanation, since we are left to explain how the genetic variation is maintained.

We find frequency-dependent selection the most intriguing explanation, since it suggests that personality differences may be maintained even in the absence of initial state differences. The logic behind this idea has been given solid mathematical support by the recent models by Wolf et al. (2007, 2008), but as yet it has not been confirmed empirically. The challenge now is to determine the true role of frequency-dependent selection in promoting the coexistence of personality types in real populations. Alongside empirical work, existing theory needs to be extended to ascertain whether frequency-dependent selection can favour not just two alternative strategies but a continuum of behavioural types, as is common in nature (Réale et al., 2007). In this respect, the role of environmental factors during ontogeny may be crucial to shape a range of phenotypes (Carere et al., 2005; Stamps and Groothuis, 2010).

#### 4 Explaining Individual Differences in Stress Physiology: Proximate Mechanisms

Given the observed covariation between physiology and behaviour, the above explanations for individual differences in behaviour might be key to understanding individual differences in stress physiology. From a proximal level, there are three basic possibilities that might link the two: (i) stress physiology determines behaviour; (ii) additional factors jointly determine stress physiology and behaviour; (iii) behaviour determines stress physiology. Below we consider these possibilities in detail by taking as an example the hallmark of the stress response, the secretion of glucocorticoids in response to a stressor.

One key question is whether consistent profiles arise from a common architectural basis governing different behaviours, e.g. the effect of pleiotropic hormones or genes that control multiple behaviours (Sih et al., 2004a; Bell, 2005). A common physiological mechanism might imply that correlated responses cannot evolve independently. Selection favouring one type of behaviour will then influence the whole physiological package, with knock-on consequences for a range of behaviours (Stamps, 1991; Ketterson and Nolan, 1999). Thus, correlated behaviours may result from pleiotropic effects of a single mediating factor in response to stimuli from various eco-ethological situations. Pleiotropy may also

occur via the physiological control of responsiveness, which determines the degree to which individuals perceive different stimuli as a threat (Sapolsky, 1994; Koolhaas et al., 1999; Wolf et al., 2008). Some individuals are highly responsive to environmental challenges and rapidly adjust their behaviour to prevailing conditions, while other individuals remain less responsive, guided by internal mechanisms and forming more routine-like behaviours in different contexts.

Glucocorticoids, and their neuroendocrinological substrates, are likely mediators of personalities. How these hormones are involved in the stress response has been investigated extensively in birds and mammals (e.g. Wingfield and Romero, 2000; Orchinik et al., 2002). Any exposure to a stressful stimulus leads to an activation of the HPA axis, which in turn induces a series of physiological and behavioural changes to promote the restoration of homeostasis (Sapolsky et al., 2000). Physiological responses involve the regulation of fuel metabolism during environmental challenge, while many aspects of behaviour, such as foraging or general activity, also change in response to glucocorticoid elevation (Silverin, 1997; Belthoff and Dufty, 1998; Saldanha et al., 2000). The glucocorticoid response has a partly genetic basis, as demonstrated in captive species by its significant heritability (Satterlee and Johnson, 1988; Odeh et al., 2003), and can therefore be shaped by natural selection. The repeatable and heritable individual variation in glucocorticoid responses suggests a link with personalities, which rely on individual consistency and determine how individuals cope with environmental demands at the behavioural level (Carere et al., 2003; Kralj-Fiser et al., 2007; Schoech et al., 2009). Accordingly, several studies, mainly on birds, have revealed a relationship between corticosterone and the behavioural traits commonly regarded as components of animal personality (Carere et al., 2003; Veenema et al., 2003b; Stöwe et al., 2010). The general pattern is that high response levels are associated with shy/slow/passive/reactive behavioural types, while low levels are typical for bold/fast/active/proactive profiles (Cockrem, 2007).

Despite this well-documented pattern of covariation, the precise role of glucocorticoids in mediating a stress response across multiple behaviours remains unclear. In accordance with pathways (i)–(iii) above we propose three possible mechanisms, each with different implications:

(i) *Stress physiology determines behaviour.* Glucocorticoids may be causally involved in the modulation of multiple behaviours that form an integrated package or may organize the perception of stimuli, thus modu-

lating responsiveness and its variation across individuals (Koolhaas et al., 1999; Kralj-Fiser et al., 2007). This would imply that either baseline or stress-induced glucocorticoid levels have a pleiotropic effect and as such are responsible for behavioural correlations.

(ii) *Additional factors jointly determine stress physiology and behaviour.* Individual differences in the performance of behaviours may be determined by “constitutional” characteristics (i.e. state differences, whether genetically or environmentally determined) that simultaneously affect responses to various challenges (Cockrem, 2007). This mechanism does not require a causal link between hormones and behaviours, instead producing a correlation through pre-determined individual types. Glucocorticoid levels would not determine personalities, but due to constraints established by the same proactive/reactive profile they could correlate with many behavioural traits. In this case glucocorticoid levels should be treated as response levels that are elevated by socio-ecological challenges.

(iii) *Behaviour determines stress physiology.* Behaviours could influence hormone levels if they affect the extent to which individuals actively seek out stimuli and situations that stimulate stress. For example, intraspecific social interactions can be an important source of stress (Koolhaas et al., 1999) and may cause aggressive and bold individuals to experience repeated hormonal pulses during periods of heightened social activity, such as the reproductive season (Mateos, 2005). Thus, individual differences in the glucocorticoid response may reflect differential stress exposure resulting from underlying differences in behavioural activity.

From an ultimate perspective, stress physiology and behaviour might have co-evolved with each other because of correlational selection pressures, and therefore correlation is probably a more comprehensive way of seeing their link than a cause-effect relationship, and individual animals can be viewed expressing different sets of behavioural and physiological traits in response to a given situation.

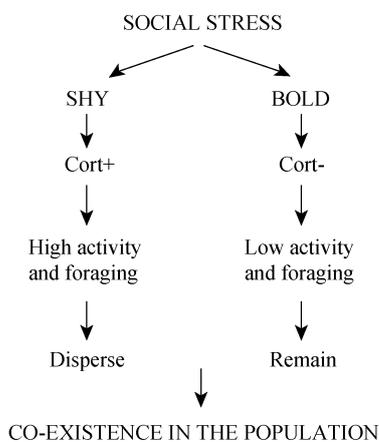
## 5 Two Concluding Hypotheses: Ecology of Dispersal and Differential Lifespan

The evidence we have reviewed here suggests that sensitivity to stressors shows stable variation between individuals, relating to behavioural differences with a genetic component maintained in wild populations (see also discussion in Schwabl, 1995). Under natural conditions, such variation in social stress may have important consequences for population dynamics. In birds, field

and theoretical studies suggest an ecological role for corticosterone in promoting dispersal via stimulation of locomotion and foraging activity (Silverin, 1997; Belthoff and Dufty, 1998). In the great tit, the Fast and Slow selection lines originate from a wild population where a coexistence of strategies does occur (Verbeek et al., 1994; Dingemanse et al., 2002). It can therefore be hypothesized that social stress has different effects on individuals adopting alternative coping strategies (Fig. 1, see legend for explanations).

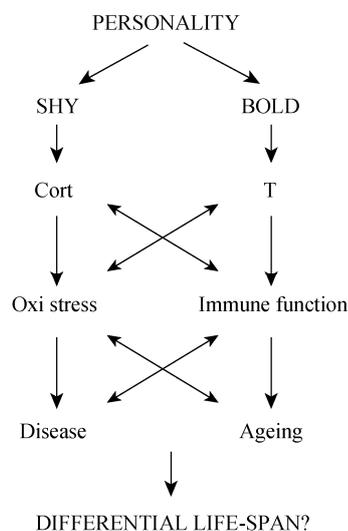
Another hypothesis builds upon the reported difference in lifespan between different personality types (Smith and Blumstein, 2008). Since the stress response may increase the production of reactive oxygen species (e.g. Costantini, 2008), this could lead to a difference in the basic and stress-induced oxidative status of individuals with different behavioural profiles. In recent work (Costantini et al., 2008) it was found that LAL mice have a higher serum anti-oxidant capacity than SAL mice. Moreover, in these mouse lines the amount of ROMs (reactive oxygen molecules) or oxidative stress was negatively related to body mass corrected for age. This indicates that variation in oxidative status is heritable and linked to personality, and suggests that

different behavioural profiles may be accompanied by differences in oxidative status, which in turn may predict differences in longevity (Costantini et al., 2008). As far as we know, this is the only study directly relating personality to oxidative status. However, one longitudinal study found that neophobic, shy rats had increased basal corticosterone levels throughout life and a 60% higher chance of death compared to neophilic, bold rats (Cavigelli and McClintock, 2003). These rats are comparable to the SAL-LAL mice in terms of glucocorticoid production and HPA reactivity. One potential explanation is that the higher glucocorticoid responsiveness of shy individuals could be associated with (or even induce) oxidative stress (Behl et al., 1997). In rats, for example, the stress response mediated by glucocorticoids increases oxidative stress (Sahin and Gümüşlu, 2007). Since oxidative stress is in turn related to a number of crucial life-history and physiological traits, including androgens and the immune system (Costantini, 2008), we propose a predictive model linking the different systems involved in ageing and lifespan (Fig. 2, see legend for further explanations). In this model it is assumed that bold individuals have an elevated testosterone secretion, which negatively affects their immune function



**Fig. 1 Hypothetical links between behaviour (social stress), physiology (HPA reactivity) and ecology (dispersal) in different avian personality types**

In birds the response to social stress activates differential corticosterone (cort) response patterns, which in turn elicit differential behavioural patterns (activity, locomotion, foraging) and eventually different dispersal strategies. Such physiological and behavioural differentiation, therefore translates into population ecology and might explain co-existence of different personalities. Note that this model is based on empirical data on the behavioural and physiological effect of social stress in adult birds (Carere et al., 2001, 2003) and does not fit with data on post-fledging dispersal in fast and slow great tits (Table 3). In post-fledging birds it is unlikely that social stress plays a role and thereby dispersal might be driven from factors not related to stress reactivity.



**Fig. 2 Potential factors and hypothetical links across different physiological systems underlying the lifespan of different personality types**

T = testosterone; cort = cortisol/corticosterone. In this picture shy individuals are initially expected to have shorter life-span than bold individuals because of their higher HPA reactivity, which in turn increases oxidative stress. Bold individuals on the other side, might have their immune system weakened by their higher levels of testosterone (T) and this might also decrease life-span expectancy. The crossing double arrows indicate connections across different systems for which the causal directions are not univocal. Therefore, at this level the potential differences might be buffered and eventually might disappear.

(e.g. Grossmann, 1985). Such assumption has not yet been directly supported by the growing research programme on animal personalities, but this may be due more to a lack of data than the lack of an effect. Extensive experimental studies conducted in the 1970s show that, both in birds and mammals, androgens are likely candidates for triggering persistent behaviour in several contexts and may therefore be associated with bold profiles (Andrews and Rogers, 1972; Archer, 1973).

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