



Plasticity of boldness in rainbow trout, *Oncorhynchus mykiss*: do hunger and predation influence risk-taking behaviour?

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ABSTRACT

Boldness, a measure of an individual's propensity for taking risks, is an important determinant of fitness but is not necessarily a fixed trait. Dependent upon an individual's state, and given certain contexts or challenges, individuals may be able to alter their inclination to be bold or shy in response. Furthermore, the degree to which individuals can modulate their behaviour has been linked with physiological responses to stress. Here we attempted to determine whether bold and shy rainbow trout, *Oncorhynchus mykiss*, can exhibit behavioural plasticity in response to changes in state (nutritional availability) and context (predation threat). Individual trout were initially assessed for boldness using a standard novel object paradigm; subsequently, each day for one week fish experienced either predictable, unpredictable, or no simulated predator threat in combination with a high (2% body weight) or low (0.15%) food ration, before being reassessed for boldness. Bold trout were generally more plastic, altering levels of neophobia and activity relevant to the challenge, whereas shy trout were more fixed and remained shy. Increased predation risk generally resulted in an increase in the expression of three candidate genes linked to boldness, appetite regulation and physiological stress responses – ependymin, corticotrophin releasing factor and GABA_A – but did not produce a significant increase in plasma cortisol. The results suggest a divergence in the ability of bold and shy trout to alter their behavioural profiles in response to internal and exogenous factors, and have important implications for our understanding of the maintenance of different behavioural phenotypes in natural populations.

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Introduction

Boldness defines how individuals respond to risk and novelty: bold animals are generally more active, more likely to explore novel objects or environments and spend more time in the open compared with shy conspecifics (Sih et al., 2004; Sneddon, 2003), and this variation exists along a continuum from bold to shy. Whilst many behaviours are, at least partly, heritable (Giles and Huntingford, 1984; van Oers et al., 2004), they can also be shaped by experience and animals may vary their degree of boldness according to extrinsic (environmental; e.g. Chapman et al., 2010; Frost et al., 2007) or intrinsic (age, size, etc.; Bell and Stamps, 2004; Brown and Braithwaite, 2004) factors. Since boldness influences decision making, the fitness consequences of bold or shy behaviour may be determined by the immediate environment (for example, where territory or food is limited, bolder animals may be more successful due to higher aggression and exploration tendency; Dingemans et al., 2004); the ability to alter behaviour therefore has important implications for fitness, particularly

in a fluctuating environment, since an individual may be able to adapt to the environmental conditions. The present study tested this behavioural plasticity by determining the degree to which bold or shy behaviour changes in the context of extrinsic (risk, measured as predation threat) and intrinsic (nutritional status) factors.

The wrong behavioural choices when exposed to predation threat can lead to mortality, but the optimal behavioural strategy to deal with this threat remains unclear: whilst high threat may encourage risk-taking behaviour to forage (Brown et al., 2005b), a shy strategy limits exposure through reduced activity and exploration (Archard and Braithwaite, 2011; Brydges et al., 2008). The most appropriate behavioural response may depend on additional factors such as habitat stability (Brydges et al., 2008), age (Magnhagen and Borcherding, 2008), size (Werner et al., 1983) and food availability (Borcherding and Magnhagen, 2008). Exposure to predation threat can drive the expression of boldness (Bell and Sih, 2007), but little is known as to how this process may be modulated by individual hunger levels in prey. Nutritional status is an important determinant of activity levels since animals with low energy reserves need to increase activity to forage (Borcherding and Magnhagen, 2008; Vehanen, 2003). Like predator threat, foraging profitability varies spatiotemporally; animals therefore need to adjust foraging rates and activity dependent on both profitability

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(Croy and Hughes, 1991) and prevailing predation risk (Lima and Bednekoff, 1999; Metcalfe et al., 1987; Vehanen, 2003; Werner et al., 1983), and it is likely these decisions may be modulated by an individual's propensity for taking risks.

The stress response in fish is controlled through activation of the hypothalamo-pituitary-interrenal (HPI) axis, resulting in the release of cortisol (Wendelaar Bonga, 1997). Likewise, much of the control of food intake takes place in the hypothalamus (Kalra et al., 1999), and utilises some of the same biochemistry. Predation threat necessarily invokes a stress response and thus may evoke a reduction in feed intake both through physiological (Scheuerlein et al., 2001) and behavioural (Metcalfe et al., 1987) changes to reduce feeding rates in the presence of a predator. Coping style theory predicts that bold (proactive) and shy (reactive) animals respond to stress with low or high HPI activity, respectively (Koolhaas et al., 1999; Øverli et al., 2002; Pottinger and Carrick, 2001), and previous studies using lines of rainbow trout, *Oncorhynchus mykiss*, bred for divergent stress responses revealed significantly different patterns of gene expression between low and high stress responsive fish (Backström et al., 2011; Johansen et al., 2011; Thomson et al., 2011). However, how individual differences in HPI activity and coping style reflect antipredator and foraging strategies remains relatively under-studied.

Divergent bold/shy phenotypes reflect differences in how animals respond to threat, but whilst the strategies of bold and shy fish are established under risk or food-deprived regimes it remains unclear how animals exhibiting bold or shy strategies, and consequently differential physiological activity, respond to an interaction between risk and hunger. Individual genes are important in shaping behaviour (e.g. Greenwood et al., 2008; Sneddon et al., 2011), and to understand this relationship it is thus imperative to identify correlations between gene expression and behavioural or physiological responses to such challenges. The aim of this study was therefore to determine how behavioural decisions in bold and shy rainbow trout may be influenced by exposure to varying levels of predator threat and metabolic demand. Circulating plasma cortisol levels were assessed to determine variation in stress levels in these fish, and behavioural and physiological differences were related to the expression of three specific genes known to be involved in processes of behaviour, the physiological stress response and appetite regulation: ependymin, CRF and the GABA_A receptor (Table 1).

Table 1
Genes used in this study, their abbreviations and relevant roles.

Gene	Abbreviation	Role
Ependymin	Epd	A glycoprotein implicated in environmental adaptation, particularly linked to boldness ^a .
Corticotrophin Releasing Factor	CRF	A hypothalamic neurotransmitter hormone which activates the HPI axis by binding with CRF Type I receptors in the anterior lobe of the pituitary to stimulate the release of adrenocorticotrophic hormone ^b . Acts as an anorexigenic factor ^c .
γ-Aminobutyric Acid A Receptor	GABA _A	A receptor protein with diverse functionality, including roles in the control of ACTH release in the stress response ^d , the control of appetite ^e , and also linked with the expression of boldness (e.g. aggression ^f).
Glyceraldehyde 3-phosphate dehydrogenase	GAPDH	Reference gene

^a Sneddon et al. (2011).

^b Chrousos and Gold (1992).

^c Bernier and Craig (2005).

^d Makara and Stark (1974).

^e Pu et al. (1999).

^f Miczek et al. (2003).

Ependymin is involved in behaviours strongly linked with boldness, such as aggression (Sneddon et al., 2011) and behavioural plasticity and learning (Shashoua, 1991), but is also involved in responses to environmental stress (e.g. Tang et al., 1999). CRF plays an integral role in the corticosteroid response to stress, initiating the HPI axis through binding to CRF Type I receptors in the pituitary to stimulate the secretion of ACTH (Chrousos and Gold, 1992). CRF is also a critical hormone for the integration of sensory cues and dietary (or energetic) information with stress status, and translating this into orexigenic or anorexigenic signals (see Bernier, 2006, and references therein). Finally, the GABA_A receptor, and the GABA system in general, has broad functionality and has been linked with fearfulness (Caldji et al., 2000) and aggression (Miczek et al., 2003), both indicators of boldness and stress responsiveness or coping style (Koolhaas et al., 1999). Furthermore, evidence suggests GABA_A receptors may be linked with the control of appetite and feed intake (Wu et al., 2009). Divergent mRNA expression for each of these genes has previously been demonstrated in lines of rainbow trout bred for divergent stress responses (Backström et al., 2011; Thomson et al., 2011), and they are therefore excellent candidate genes to investigate links between boldness and stress responsiveness in unselected trout in the contexts presented.

Specifically, we hypothesised that (1) individuals would vary their behaviour according to prevailing risk, with the prediction that satiated fish would reduce risk-taking activity whilst food-deprived animals would take more chances; (2) fish under higher predation and/or restricted dietary regimes would experience elevated activation of the stress response, and alterations in the expression of three candidate genes implicated in feeding- and boldness-related behavioural processes.

Methodology

Test Animals

The following experiment was conducted under Home Office, UK, guidelines according to the Animal (Scientific Procedures) Act 1986, and following local ethics approval. Rainbow trout, *O. mykiss*, were maintained in stock tanks (2 × 2 × 0.5 m) with a semi-recirculating system on a 14:10 h light:dark cycle at 13 ± 1 °C, and fed 1% body weight per day on commercial trout feed (Skretting, UK). Experimental fish ($n = 75$, 93.48 ± 3.94 g) were caught at random and transferred to individual glass aquaria (90 × 50 × 45 cm) which were screened from visual disturbance, and maintained at 10 ± 1 °C with constant aeration. Fish were provided 1% body weight feed per day at the same time each day. The next day trout were netted, anaesthetised in 0.033 g l⁻¹, benzocaine (Sigma-Aldrich Co., UK) and weighed, and then returned to their individual aquaria and allowed to acclimate for at least one week or until the resumption of feeding. Fish that did not resume feeding after 14 days were not used in the study.

Novel Object Tests

Boldness was assessed using a standard novel object paradigm (Frost et al., 2007; Thomson et al., 2011) whereby a novel object was placed centrally into the tank and the behaviour was recorded for 10 min (after which the object was removed). Novel objects comprised an orange rubber stopper (7.1 cm mean diameter, 4.9 cm height) and a blue transparent box weighted with gravel (7.5 × 5.3 × 3.8 cm). We focussed on two key behavioural responses (see Thomson et al., 2011 for details): 1) latency to approach to within 5 cm of the novel object (s); and, 2) The duration of passive behaviour (s), which included the subject resting at the base of the tank, pivoting on its own axis, and drifting across the tank, but excluded swimming greater than one body length. Bold fish were defined as those approaching the novel object within 180 s ($n = 35$) and shy fish as those which did not approach within 300 s ($n = 36$); the remainder were classed as intermediate ($n = 4$) and discarded from further analysis. These were therefore clearly distinct

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