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Behavioral plasticity in rainbow trout (*Oncorhynchus mykiss*) with divergent coping styles: When doves become hawks

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ABSTRACT

Consistent and heritable individual differences in reaction to challenges, often referred to as stress coping styles, have been extensively documented in vertebrates. In fish, selection for divergent post-stress plasma cortisol levels in rainbow trout (*Oncorhynchus mykiss*) has yielded a low (LR) and a high responsive (HR) strain. A suite of behavioural traits is associated with this physiological difference, with LR (proactive) fish feeding more rapidly after transfer to a new environment and being socially dominant over HR (reactive) fish. Following transport from the UK to Norway, a switch in behavioural profile occurred in trout from the 3rd generation; HR fish regained feeding sooner than LR fish in a novel environment and became dominant in size-matched HR–LR pairs. One year after transport, HR fish still fed sooner, but no difference in social dominance was found. Among offspring of transported fish, no differences in feeding were observed, but as in pre-transported 3rd generation fish, HR fish lost fights for social dominance against size-matched LR opponents. Transported fish and their offspring retained their distinctive physiological profile throughout the study; HR fish showed consistently higher post-stress cortisol levels at all sampling points. Altered risk-taking and social dominance immediately after transport may be explained by the fact that HR fish lost more body mass during transport than did LR fish. These data demonstrate that some behavioural components of stress coping styles can be modified by experience, whereas behavioural plasticity is limited by genetic effects determining social position early in life story.

Introduction

Within the last decade, it has been clearly established that individual animals of various species (vertebrate and invertebrate) differ in the nature of their response to challenges. Such differences may involve suites of correlated physiological and behavioural traits and are often referred to as “coping strategies” (Koolhaas et al., 1999). In mammals and birds, two distinct coping strategies can be distinguished. At one extreme, animals with a proactive coping strategy tend to show a fight-flight response, to be more aggressive and bold (in the sense of taking risks in a variety of dangerous situations), and to have low levels of plasma corticosteroids. In contrast, at the other extreme, reactive animals show a freeze-hide response; tend to be shy and less aggressive with a more flexible behaviour than proactive individuals. The physiological response to stress in reactive individuals involves relatively higher plasma cortisol levels, as well as differences in a number of other neuro-endocrine systems (Koolhaas et al., 1999; Korte et al., 2005).

In several species it has been shown additionally that such differences in physiological and behavioral stress responses are heritable (van Oers et al., 2005; Øverli et al., 2005; Koolhaas et al., 2007), which raise a question about how such variability is maintained within populations. The emerging consensus is that proactive and reactive animals flourish in different selective environments, possibly in a frequency-dependent manner. Some authors have likened proactive and reactive animals to the hawks and doves of classical game theory (see for example Korte et al., 2005). The existence of such adaptive individual differences within a population has evoked considerable scientific interest and has important consequences for disciplines as diverse as evolutionary ecology (Bolnick et al., 2003; Sih et al., 2004), animal husbandry (Cavigelli, 2005; Huntingford and Adams, 2005) and biomedicine (Korte et al., 2005).

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One outstanding question is the relationship between behavioural plasticity and underlying physiological mechanisms (Øverli et al., 2007). On the one hand, if behaviour is closely linked to strongly heritable physiological traits (as in Miller et al., 2004; Uhart et al., 2004; Serretti et al., 2006; Poirier et al., 2007), this may limit behavioural plasticity. On the other hand, some components of the neuro-endocrine machinery are rapidly modifiable by experience (e.g. Burmeister et al., 2005; Burmeister, 2007; Watt et al., 2007) and this is likely to be reflected in plasticity in associated behavioural traits. The results presented in this paper provide an example of flexible dissociation of behavioural and physiological components of the coping strategy, using an established fish model, the rainbow trout (*Onchorhynchus mykiss,* Walbaum, 1792).

A number of studies have documented the existence of co-varying behavioural traits in teleost fish (e.g. Bell and Sih, 2007; Wilson and McLaughlin, 2007). For example, a positive correlation between aggression towards conspecifics and risk-taking in various potentially dangerous situations has been described in three-spined sticklebacks (*Gasterosteus aculeatus*, Huntingford 1976, though see Bell and Stamps 2004), brown trout (*Salmo trutta*, Sundstrom et al., 2004), and grayling (*Thymallus thymallus*, Salonen and Peuhkuri, 2006). There is relatively little information on physiological correlates of such behavioural variability in fish, though Bell et al. (2007) report a correlation between individual risk-taking behaviour and brain biochemistry in sticklebacks. The rainbow trout provides an exception, in that a number of behavioural differences have been reported in strains of rainbow trout selected for high (high responsive, or HR-trout) and low (low responsive, LR) cortisol responsiveness to a standardized stressor (see reviews by Øverli et al., 2005; Schjolden and Winberg, 2007).

The first behavioural study conducted on these strains documented that fish from the LR strain become socially dominant over HR fish (Pottinger and Carrick, 2001). In addition, following transfer from group rearing to isolation in an unfamiliar tank, trout from the LR strain resumed feeding earlier than did fish from the HR strain (Øverli et al., 2002a). It was later shown that rapid resumption of feeding following transfer to a novel environment also predicts social dominance and level of aggression towards territorial intruders in non-selected aquaculture strains of rainbow trout (Øverli et al., 2004; Schjolden et al., 2005a). Most of the behavioural characteristics of the HR line are consistent with previously reported effects of the steroid hormone cortisol in non-mammalian vertebrates (Gregory and Wood, 1999; Øverli et al., 2002b; DiBattista et al., 2005). However, it seems unlikely that cortisol alone is responsible for controlling all behavioural aspects of stress coping style (Koolhaas et al., 2007; Øverli et al., 2007).

In this paper we present data indicating that cortisol responsiveness and behavioural profiles may be uncoupled. After 3 generations showing distinctive behavioural profiles, a batch of HR and LR rainbow trout were transported from their original rearing site (Windermere, UK) to Oslo, Norway. Unexpectedly, immediately after transport both strains switched behavioural profiles, with HR fish now being bolder in terms of rapid resumption of feeding behaviour after transfer to isolation and exhibiting social dominance over LR fish. The divergence in post-stress plasma cortisol concentrations between strains remained unchanged in transported as well as non-transported fish from the same generation. These data suggest a degree of plasticity in the behavioural aspects of coping style in fish that is independent of hypothalamus-pituitary-interrenal function.

Materials and methods

Outline of screening regime

Results presented here come from studies carried out on the third and fourth generations of LR and HR rainbow trout. Observations were made both at the original rearing site (CEH Windermere, UK) and after transport between this site and an experimental facility in Norway. Weights below are given as mean±S.E.M. Details of the selection programme used to generate the HR and LR strains have been described previously (Pottinger and Carrick, 1999, 2001), as has their typical behaviour (Pottinger and Carrick, 2001; Øverli et al., 2002a; Schjolden et al., 2005a; Schjolden and Winberg, 2007).

In the summer of 2005, adult 3rd generation HR (n=150, weight 493±12 g) and LR fish (n=150, weight 477±9 g) were fitted with Passive Integrated Transponder (PIT) tags and transported from the Windermere Laboratory of the UK Centre for Ecology and Hydrology (Windermere, UK) to the Norwegian Institute of Water Research Marine Research Station (Solbergstrand, Akershus County, Norway). Fish were deprived of food for 5 days prior to transport and then loaded in a tank truck equipped to transport fish (Donslund Special Transport, Hejnsvig, Denmark). Transported fish arrived 2 days later and no mortalities occurred during transport. Upon arrival in Norway all PIT-tags were registered, fish were weighed and screening for behavioural and physiological traits initiated. Individual identification of fish with PIT-tags permitted body mass loss during the 7 day period of transport to be assessed, since energetic status is a variable that may strongly influence risk-taking and social behaviour (e.g Johnsson et al., 1996; Damsgard and Dill, 1998); however, due to logistic reasons the body mass of some fish could not be measured.

Four sessions of behavioural testing were carried out. Immediately after transport adult HR (n=23 weight: 448±21 g) and LR fish (n=23 weight: 457±16 g) were tested for risk-taking (boldness). Data for this trait are not available for non-transported fish, but previous studies reported that adult LR fish resume feeding more rapidly than HR fish at the original rearing site (Øverli et al., 2002a). Social dominance and plasma cortisol following an acute stressor were also assayed in Norway. Simultaneously in Windermere UK, non-transported 3rd generation adult fish (n=16 weight: HR 742±41 g, n=16; LR 645±28 g) were tested for social dominance and post-stress plasma cortisol. In Norway, 1 year later in the summer 2006 a set of HR (n=18 weight: 1113±65 g) and LR (n=18 weight: 1108±61 g) fish, transported the year before, were screened for the same behavioural traits as in 2005. Finally, 8 months old 4th generation offspring (n=16 weight, HR 16.2±0.9 g, n=16; LR 16.4 ±0.9 g,) generated from transported F3 fish were screened for the same behavioural and physiological traits in August 2006.

Screening for boldness and social dominance

Prior to screening, fish were transferred from communal rearing tanks to 250 l (adult fish) or 12 l (offspring) glass aquaria, where they were held in isolation. Each observation aquarium was lined with black plastic on three sides and divided in two compartments by a removable opaque PVC wall, each section holding one HR or one LR fish in weight matched pairs. Prior to transfer from group rearing to social isolation each fish was anaesthetised, weighed, and for adult fish the PIT-tag was read. Offspring were fin clipped to distinguish between strains, by a small incision in the upper or lower section of the tail fin.

Fish were allowed to recover overnight and testing started the next day. For seven consecutive days, feeding was performed by dropping appropriate sized pellets where the fish was able to perceive them. Feeding was stopped either when the fish had refused to eat three

Table 1
Point scores to grade feeding behaviour in fish after transfer to social isolation (reprinted from Physiology and Behaviour)

Points	Behaviour
0	Fish does not respond to food
1	Fish eats only pellets that falls directly in front, and does not move to take food
2	Fish moves more than one body length to take food, but returns to original position in aquarium between each food item
3	Fish moves continuously between food items and consumes all food presented