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Learning and context-specific exploration behaviour in hatchery and wild brown trout

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ABSTRACT

In this study we investigate whether rearing environment (wild vs. hatchery) affects the ability of brown trout parr (*Salmo trutta*) to learn two foraging tasks. Hatchery- and wild-reared brown trout were trained in two different foraging tasks: locating food hidden in a maze and finding a cryptic prey, and their performance within and across tasks was compared. Fish reduced their search time for cryptic prey, but not maze search time, by learning. In contrast to most previous studies hatchery-reared trout generally tended to be more successful feeders and showed faster learning than wild trout when foraging on cryptic prey. This appeared to be due to motivational effects rather than based on cognitive skills. In addition, we examine whether exploration behaviour in brown trout is repeatable across time and context (i.e. reflecting a behavioural syndrome). Individual exploration tendency was repeatable within tasks, suggesting the occurrence of personality in brown trout. However, individuals that were fast explorers in the cryptic prey task were not necessarily fast to explore the maze. Thus, a context-specific behavioural syndrome was found to best explain exploratory behaviour for both hatchery and wild trout. However, repeatability of exploration behaviour within tasks differed between hatchery and wild trout, where wild trout were found to be more consistent in their exploration strategy.

1. Introduction

Individual variation in behaviours such as learning or risk-taking have recently become of interest in fish farming and welfare (Brännäs and Johnsson, 2008; Huntingford and Adams, 2005). Releasing programs of captive-bred or translocated animals rely upon the assumption that animals can rapidly adjust to a wide diversity of novel challenges upon release. Unfortunately, however, many captive breeding programs fail to raise individuals with natural behaviour, with high mortalities upon release as a result (Araki et al., 2008). Recent experiments on fish show that the lack of stimulus variation in captive rearing conditions will influence the phenotype at many different levels, ranging from physiology, neurology to behaviour (reviewed by Brännäs and Johnsson, 2008; Huntingford, 2004; Olla et al., 1998). Sundström and Johnsson (2001), for instance, showed that hatchery reared brown trout require more time than wild reared conspecifics to learn to forage on a novel prey item.

Life-skill training has been suggested as a method to counter poor post-release performance of hatchery release programs (Brown and Laland, 2001; Griffin et al., 2000). However, the sensitivity to life-skill training may differ between different personality types (Sih and Bell, 2008). Consistent personality traits have been found in many species (Gosling, 2001; Wilson et al., 1994), and are related to the concept of behavioural syndromes, describing a suite of correlated behaviours across multiple functional

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contexts (Sih and Bell, 2008; Sih et al., 2004). One major axis of personality, the shyness–boldness continuum, has been shown to differ between hatchery and wild fish, where hatchery selection often results in more bold personality traits across different situations than in wild trout (Huntingford, 2004; Sundström et al., 2004b).

Personality traits can relate to learning skills in different ways. A higher tendency to explore new environmental stimuli may, for instance, result in faster learning in bold than in shy individuals (Sneddon, 2003). Yet, other studies suggest that bold individuals are only better in routine tasks, whereas shy individuals are more sensitive to changes in the environment (Benus et al., 1990; Verbeek et al., 1994). In addition, learning may also affect the repeatability of personality traits. For example, experience may create a positive feedback loop on previously performed behaviours, thereby increasing their consistency (Wolf et al., 2008) or, alternatively, learning can break up consistency when behavioural types are not affected equally by experience (Sih et al., 2004). When behaviour is consistent across individuals, personality traits may be *context-general*, i.e. consistent across different situations, or *context-specific* and change according to experience or context (Coleman and Wilson, 1998). One aim of personality research is to understand why individuals behave consistently in some situations and more flexibly in others (Dingemanse et al., 2009).

This study investigates behaviour of hatchery and wild reared brown trout (*Salmo trutta*) in two different foraging tasks: (1) a spatial orientation task: locating food hidden in a maze and (2) a visual discrimination task: finding a cryptically coloured prey. In addition we study whether the tendency to explore a novel situation, a personality trait closely related to boldness (Réale et al., 2007), is consistent within and across tasks. Brown trout were used as a model species for this study. Since structural complexity is generally high in natural salmonid streams (Höjesjö et al., 2004; Orpwood et al., 2003), spatial orientation skills are expected to be critical for finding food. Moreover, young salmonids are opportunistic feeders which prey on a wide range of prey types (De Crespin De Billy and Usseglio-Polatera, 2002), some of which adjust crypsis and activity levels to avoid predation (Feltmate and Williams, 1989; Hargeby et al., 2004). A recent study further showed that prey crypsis reduces the foraging efficiency of wild brown trout parr which, however, are able to increase their foraging success by learning (Johnsson and Kjällman-Eriksson, 2008).

We addressed four related aspects of behaviour: *first*, we study the ability of brown trout to learn in both tasks. *Second*, we test two hypotheses concerning the foraging skills of trout: does development in a hatchery environment impair the (1) spatial orientation ability and (2) visual acuity/object discrimination ability of trout? These hypotheses predict that hatchery-reared fish should be less able (1) to find food hidden in a maze, and (2) to find cryptic prey, compared with wild conspecifics. *Third*, we investigate whether exploration behaviour is repeatable within and across tasks and forms an exploration syndrome. The structure of this repeatability was compared with existing syndrome hypotheses from the literature. *Fourth*, we test whether hatchery rearing affected the average exploration tendency of brown trout in these tasks, and/or the structure of the exploration syndrome thereby causing repeatability patterns of exploration behaviour to differ between hatchery and wild trout.

2. Materials and methods

During autumn 2004, eggs were collected from a batch of spawning brown trout from Norumsån, a small coastal stream in western Sweden (58°N 11°E), and transported to a nearby hatchery (E.ON Hatchery Laholm). After hatching (10–15 March 2005), trout were reared according to standard hatchery procedures (Pennell and Barton, 1996). On 24 August 2005 these fish, further called hatchery trout, were transported and transferred to a holding tank at the Department of Zoology (University of Gothenburg). On 7 September 2005 wild brown trout (age 0 yr) were caught in Norumsån by electrofishing and transported to another holding tank at the Department of Zoology. A semi-random sub-sample was taken from the total number of caught wild individuals to minimize effects of catching methods on behaviour (Wilson et al., 1993). Wild and hatchery-reared fish were kept at similar density (1.4 l/ind) and fed live maggots ('bronze pinkies', Fibe AB, Överkalix) and frozen chironomid larvae (commercial fish food supplier) at rates of 1% of their total wet mass.

After at least 19 days of acclimatization to laboratory conditions, 20 wild trout and 20 hatchery trout of similar fork length (mean ± SE = 56.3 ± 1.3 mm; *t*-test: $t_{38} = 0.03$, $P = 0.976$) were subjected in random order to an experimental sequence to measure their ability to learn to solve two complex foraging tasks: finding a foraging route in a maze and feeding on a cryptic prey. The number of trials ($n = 6$) and procedures chosen were based on previous experiments successfully using the maze (Johnsson and Sundström, 2007) and cryptic prey set-up (Johnsson and Kjällman-Eriksson, 2008) to study learning. To enhance foraging motivation, no food was provided to the focal fish on the day prior to start of the experimental sequence.

2.1. Maze solving

An opaque PVC maze structure (Fig. 1, Johnsson and Sundström, 2007) subdivided a flow-through tank into 4 rooms: a starting room (S), a "wrong side" room (W), a "right side" room (R) and a food room (F). From S, the fish could access the side rooms (W and R) through two circular entrances (30 mm diameter) with landmarks (Fig. 1). A third circular entrance (35 mm diameter) positioned 30 mm higher than the others connected the R room with the F room, which contained the water outlet and food. The W room led to a dead end. However, the PVC wall between the F room and the W room was perforated to enable chemical cues from the food to spread into both side rooms. The relative position of the W and R rooms was kept constant throughout trials on the same subject, but altered between subjects to account for any side biases affecting fish movement. Disturbance by movements from outside was minimized by covering the lateral sides of the tanks with black plastic. Observations were performed through