Maternal inheritance and exploratory-boldness behavioural syndrome in zebrafish

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Summary
Correlated behavioural traits (behavioural syndromes) influence ecological interactions and, in turn, how natural selection shapes the evolution of behaviour. A major axis of intraspecific behavioural variation is the exploratory-boldness behavioural syndrome. Here, we describe how we sorted wild-caught zebrafish (Danio rerio) for increasing exploratory tendency using a serial open field maze. We then transferred test fish to a predator-inspection apparatus. Highly exploratory individuals spent more time near a novel predator than non-exploratory individuals, showing behavioural consistency indicative of an exploratory-boldness behavioural syndrome. We then bred the zebrafish to create F₁ offspring from four crosses: (1) exploratory × exploratory, (2) non-exploratory × non-exploratory, (3) exploratory females × non-exploratory males and (4) non-exploratory females × exploratory males. F₁ offspring were tested in a miniature serial open-field maze similar to the one used to sort the adults. Offspring of exploratory females were always highly exploratory regardless of the behavioural traits of the father suggesting that maternal effects may influence expression of exploratory-boldness behavioural syndrome in zebrafish.

Keywords: zebrafish, behavioural syndrome, exploratory behaviour, boldness, open field test, maternal inheritance.

1. Introduction
Correlated behavioural traits, or behavioural syndromes (Sih & Bell, 2008), can explain trait covariance in natural populations and the potential for correlated evolution of trait complexes. While consistent individual differences

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in behaviour have been known for some time (e.g., Huntingford, 1976; Benus et al., 1991; Magurran, 1993; Wilson et al., 1993) there has been renewed interest in correlated behavioural traits among behavioural ecologists (Sih et al., 2004a,b; Groothuis & Carere, 2005; Réale et al., 2007; Sih & Bell, 2008). It is now well documented that the exploratory-boldness behavioural syndrome is a major axis of behavioural variation within many animal taxa (see, for reviews: Gosling, 2001; Sih et al., 2004a,b; Dingemanse & Réale, 2005; Groothuis & Carere, 2005; Réale et al., 2007). This variation is important to behavioural ecologists because it affects the evolution of behaviour. For example, a suite of traits may serve an individual well in the context of foraging or courtship but be maladaptive in the context of predator avoidance. In this scenario, selection on foraging and reproductive behaviour would co-vary with temporal and spatial variation in predation risk. It is, therefore, of particular interest to study patterns of heritability of behavioural syndromes to gain a better understanding of the evolution of correlated behavioural traits (Lande & Arnold, 1983). Behavioural correlations such as that between the tendency to explore novel areas and boldness in the face of predation risk likely reflect shared, genetically-based proximate causations (van Oortmerssen & Bakker, 1981; Dingemanse et al., 2002; Armitage & van Vuren, 2003; Drent et al., 2003; van Oers et al., 2004a,b; Bell, 2005; Sinn et al., 2006). There is also emerging evidence for a role for non-additive genetic effects in shaping the formation of behavioural syndromes (van Oers et al., 2004b).

The underlying proximate mechanisms of behavioural syndromes remain largely unexplored and will likely be the focus of much future work (van Oers & Mueller, 2010). A promising candidate study organism to uncover the molecular genetic processes that give rise to behavioural phenotypes is the zebrafish (*Danio rerio*). Zebrafish exhibit behavioural syndromes (Moretz et al., 2007) and are the subject of intense research activity in molecular genetics (Grunwald & Eisen, 2002). Here, we use a modification of the open field test (Walsh & Cummings, 1976) in the form of a serial maze (Figure 1) to rank wild-caught zebrafish along a gradient of increasing exploratory tendency. We then show that individuals designated as highly exploratory are, on average, bolder in a predator inspection apparatus than individuals with low exploratory tendencies, thus establishing the existence of an exploratory-boldness behavioural syndrome.