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Correlated evolution of personality, morphology and performance

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Evolutionary change in one trait can elicit evolutionary changes in other traits due to genetic correlations. This constrains the independent evolution of traits and can lead to unpredicted ecological and evolutionary outcomes. Animals might frequently exhibit genetic associations among behavioural and morphological-physiological traits, because the physiological mechanisms behind animal personality can have broad multitrait effects and because many selective agents influence the evolution of multiple types of traits. However, we currently know little about genetic correlations between animal personalities and nonbehavioural traits. We tested for associations between personality, morphology and locomotor performance by comparing zebrafish (*Danio rerio*) collected from the wild and then selectively bred for either a proactive or reactive stress coping style ('bold' or 'shy' phenotypes). Based on adaptive hypotheses of correlational selection in the wild, we predicted that artificial selection for boldness would produce correlated evolutionary responses of larger caudal regions and higher fast-start escape performance (and the opposite for shyness). After four to seven generations, morphology and locomotor performance differed between personality lines: bold zebrafish exhibited a larger caudal region and higher fast-start performance than fish in the shy line, matching predictions. Individual-level phenotypic correlations suggested that pleiotropy or physical gene linkage likely explained the correlated response of locomotor performance, while the correlated response of body shape may have reflected linkage disequilibrium, which is breaking down each generation in the laboratory. Our results indicate that evolution of personality can result in concomitant changes in morphology and whole-organism performance, and vice versa.

Evolutionary response to selection depends not only on the strength and nature of selection, but also on the heritability of the trait in question and its genetic correlations with other traits (Agrawal & Stinchcombe, 2009; Falconer & MacKay, 1996; Lande, 1979). Because genetic correlations are common, selection on one trait often affects the evolution of other traits (Brodie, 1989; Ketterson, Atwell, & McGlothlin, 2009; Pigliucci & Preston, 2004). Understanding how and why this happens has received considerable attention in animal personalities, where behavioural traits covary to produce consistently distinct 'personalities', 'temperaments' or 'behavioural syndromes' (Réale, Dingemanse, Kazem, & Wright, 2010; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). However, we know little about whether animal personalities have genetic associations with nonbehavioural traits, even though such associations should be expected and could have major ecological and evolutionary implications (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012). We suggest that animal personalities may often exhibit genetic correlations (i.e. heritable nonrandom associations among traits) with seemingly disparate nonbehavioural traits due to (1) correlational selection on behavioural and nonbehavioural traits or (2) pleiotropic effects of the genes and physiological mechanisms that underlie animal personalities.

First, correlational selection may often occur in nature since selective forces can influence both behavioural traits and nonbehavioural traits, such as morphology and physiology (Dewitt, Sih, & Hucko, 1999; Endler, 1995; Ketterson et al., 2009; Schluter, 2010; Sinervo & Svensson, 2002; Vervust, Grbac, & Van Damme, 2007). Correlational selection describes cases where the fitness effect of

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one trait depends on the value of another trait. For instance, certain behaviours may produce high fitness only when combined with specific morphologies. This frequently produces genetic correlations (Cheverud, 1984; Jones, Arnold, & Bürger, 2003; Lande & Arnold, 1983; Lynch & Walsh, 1998; McGlothlin, Parker, Nolan, & Ketterson, 2005; Phillips & Arnold, 1989; Roff & Fairbairn, 2012; Sinervo & Svensson, 2002), as in garter snakes, where correlational selection on colour pattern and predator-escape behaviour results in covariance among these traits (Brodie, 1992).

Correlational selection on personality traits and nonbehavioural traits may be more common than we realize, since certain behaviours should vary in fitness depending on other traits. For instance, risk-prone, aggressive individuals may require great strength, speed or large size to achieve high fitness. Correlational selection can produce genetic correlations through pleiotropy (where genes affect multiple traits), genetic linkage (where genes are located nearby on a chromosome) or linkage disequilibrium (where separate traits exhibit associations due to correlational selection or nonrandom mating; Falconer & MacKay, 1996; Lynch & Walsh, 1998). Regardless of the source of genetic correlations, understanding the existence and strength of these associations is important for understanding adaptation. In reality, traits do not adapt to environments independently; rather, selection acts on whole-organism phenotypes, resulting in organisms with evolved adaptations that reflect integrated suites of traits (Ghalambor, Walker, & Reznick, 2003; Murren, 2012; Pigliucci & Preston, 2004; Réale, Garant, et al., 2010; Santos & Cannatella, 2011).

Second, irrespective of correlational selection, prior work suggests that genes responsible for animal personalities may have widespread pleiotropic effects. The physiological mechanisms underlying animal personalities often pleiotropically affect traits such as dispersal behaviour, metabolic rate, immune capacity, life span, age at reproduction and growth rate (Biro & Stamps, 2010; Careau, Réale, Humphries, & Thomas, 2010; Réale, Garant, et al., 2010). These same factors could also affect other traits like morphology or whole-organism performance abilities (Bourdeau & Johansson, 2012; Dickey, McCarley, & Shenton, 2002; Johansson & Andersson, 2009; Selman, Lumsden, Bünger, Hill, & Speakman, 2001; Swallow & Hayes, 2009), yet few studies have examined whether animal personalities exhibit genetic associations with morphological-physiological traits. Considering what we know about hormone-mediated suites of traits (Adkins-Regan, 2005; McGlothlin & Ketterson, 2008), and given the diverse sets of trait correlations involved in pace-of-life syndromes (Careau et al., 2010; Réale, Garant, et al., 2010), we should expect to find a range of associations between animal personalities and morphological-physiological traits owing to shared genetic or physiological bases. Indeed, artificial selection on behaviour, such as during domestication, can result in changes in seemingly disparate traits such as colour, skull shape and seasonal reproductive patterns (Trut, Oskina, & Kharlamova, 2009; Trut, Plyusnina, & Oskina, 2004). Identifying such associations will help us understand the evolution of complex phenotypes and the limitations to adaptive evolution (since trait correlations can present trade-offs that bias the direction of evolution; Pigliucci & Preston, 2004; Pruitt & Riechert, 2012; Schluter, 1996). Here we use zebrafish to provide one of the first tests of the notion that animal personalities might exhibit genetic associations with morphological and performance traits.

Three general types of traits, behaviour (animal personality), morphology (body shape), and locomotor ability (fast-start swimming performance), could frequently show genetic correlation for a number of nonmutually exclusive reasons. First, changes in behaviour, metabolism or hormones might induce changes in morphology (Bourdeau & Johansson, 2012; Johansson & Andersson, 2009). Second, morphological changes should affect fast-start locomotor performance via trait codependence (sensu Dewitt et al., 1999), because swimming ability partially derives from the thrust generated by the caudal region of a fish (the two traits are mechanically linked). Furthermore, correlational selection might favour particular trait combinations such as (1) trait complementation, where boldness enhances foraging or mating only when combined with high fast-start performance, (2) trait cospecialization, where bold, fast individuals and shy, slow individuals have high fitness because their trait combinations influence different fitness components (e.g. the former may have higher mating success but low longevity, while the latter may have lower mating success but high longevity), or (3) trait compensation, where bold individuals encounter more predatory strikes but compensate with defensive morphologies or rapid locomotor escape abilities. Any combination of these underlying causes could lead to the evolution of genetic correlations among personality, morphology and performance (Wolf & Werner, 1994).

We investigated whether these three traits evolve independently or in concert using artificial selection with zebrafish (*Danio rerio*). We compared lines selected for bold or shy behaviour to determine whether body morphology or locomotor performance exhibited correlated responses to behavioural selection. If genetic correlations exist between animal personalities and these nonbehavioural traits, then body morphology and swimming ability should diverge between selection lines and appear as a correlated response to artificial selection (Carere & van Oers, 2004; Houde, 1994; Wilkinson & Reillo, 1994). We specifically predicted that artificial selection for boldness would elicit correlated evolutionary responses of larger caudal regions and higher fast-start escape performance (and the reverse for shyness).

While zebrafish are a well-established model laboratory organism (Norton & Bally-Cuif, 2010; Ribas & Piferrer, 2014; Ruzicka et al., 2015), less is known about their ecology in the wild. Zebrafish tend to inhabit shallow, slow-moving freshwater where they use the entire water column and occupy both vegetated margins and open areas (Spence et al., 2006). They respond strongly to predator cues (Dill, 1974), and their antipredator behaviour is heritable and tends to diminish in laboratory strains (Robison & Rowland, 2005; Wright, Nakamichi, Krause, & Butlin, 2006). Zebrafish face predation threats from multiple sources in the wild (Engeszer, Patterson, Rao, & Parichy, 2007), and appear to represent a likely candidate for experiencing correlational selection on behaviours and nonbehavioural traits in nature.

METHODS

Wild zebrafish from Gaighata, India were selectively bred in captivity for bold or shy personalities on the basis of stationary behaviour in a stressful environment (see Wong et al., 2012, for a complete description of the experiment). Briefly, during an open field test, zebrafish were introduced to a novel arena for 5 min, and the amount of time they spent stationary was recorded. Fish that exhibited at most 50 s of stationary behaviour were bred together to generate a bold line, and fish that exhibited at least 200 s of stationary behaviour were bred together to generate a shy line. The selective breeding programme began with F1 fish, and selection was repeated each generation. By the third generation, these two selection lines differed consistently not only in stationary time but also in six different measures of stress and anxiety-related behaviours (Wong et al., 2012). These sets of consistent differences in multiple behavioural stress responses are variously termed either proactive and reactive stress coping styles, or bold and shy behavioural phenotypes (Koolhaas, de Boer, Coppens, & Buwalda, 2010; Wong et al., 2012; Øverli et al., 2007).