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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).

We examined body morphology and locomotor escape performance of adult zebrafish from bold and shy lines in the fourth ($N = 29$), fifth ($N = 29$) and seventh ($N = 67$) generations ($N_{total} = 125$; Supplementary Table S1). Zebrafish from each generation were age-matched across bold and shy lines and were similar in body size (mean ± SE for standard length: bold females 28.32 ± 0.75 mm, shy females 27.23 ± 0.65 mm; bold males 26.62 ± 0.53 mm, shy males 26.52 ± 0.54).

In the fourth and fifth generations, fish were moved to group tanks after the open field behaviour test, and so measurements of morphology and swimming performance could not be tied to individual behavioural measures. Thus, individual-level correlation analysis was not performed on the fourth and fifth generations. However, in the seventh generation, fish were tracked individually across all experimental components, permitting individual-level correlation analyses among stationary behaviour, body shape and fast-start performance. All fish were reared in a recirculating system at North Carolina State University on a 14:10 h light:dark cycle at 27.4 °C and fed dry flakes ad libitum.

Morphology

We used geometric morphometrics to measure the body morphology of all fish. We digitized 10 anatomical landmarks on lateral photographs of live individuals (Fig. 1a) using tpsDig2 (Rohlf, 2013). Landmarks were located on the anterior tip of the snout on the upper jaw, the back of the head (posterior aspect of the neurocranium), the anterior and posterior insertions of the dorsal fin, the anterior attachments of the dorsal and ventral insertions of the caudal fin, the anterior insertions of the anal and pelvic fins, the insertion of the operculum on the ventral lateral profile and the centre of the eye. We generated shape variables (relative warps) using tpsRelw (Rohlf, 2010). Prior to generalized Procrustes analysis in tpsRelw, we used tpsUtil (Rohlf, 2012) to perform the unbend function, which removes postural differences. Landmarks for unbending were located in the centre of the eye, the posterior midpoint of the operculum, the centre of the body between landmarks 3 and 7, and the base of the caudal fin between landmarks 5 and 6. Except for the eye landmark, these points were excluded from shape analyses because they are not anatomically homologous. We used centroid size (the square root of the summed, squared distances of all landmarks from their centroid) as an estimate of body size.

For analysis we retained 11 relative warps, explaining 95.5% of the shape variance. We tested for morphological differences between bold and shy lines using MANCOVA, with 11 shape variables (relative warps) as dependent variables, coping style line, sex and the interaction of sex and coping style line as independent variables, and generation and centroid size as covariates (the latter controls for multivariate allometry). We initially included all possible interactions, and excluded nonsignificant interaction terms in the final analysis.

To estimate the overall magnitude of shape differences between lines, we calculated Procrustes distance between line means for

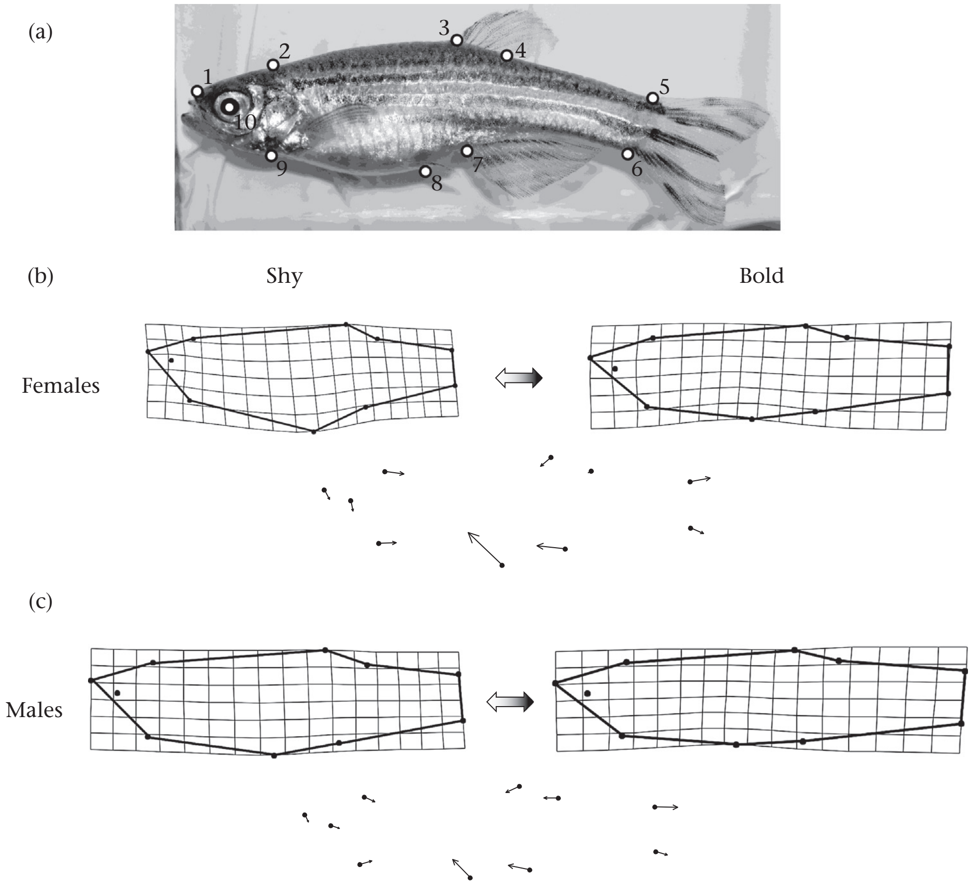

Figure 1. (a) Landmarks used for morphological analysis. Morphological differences between bold and shy phenotype lines of zebrafish (b) females and (c) males. Body shape variation along the shape index (see text) depicted with thin-plate spline transformation grids (no magnification; solid lines connecting outer landmarks are drawn to aid interpretation). Landmark vectors beneath each set of grids convey the direction and relative magnitude of change in the location of each landmark, pointing towards values characteristic of bold lines.

each sex using tpsSmall (Rohlf, 2003). Procrustes distance represents the standard metric of shape differences in geometric morphometrics (e.g. Bookstein, 1996), and is closely approximated by Euclidean distance between landmarks after generalized Procrustes analysis (Zelditch, Swiderski, & Sheets, 2012). To evaluate the nature of the shape differences between lines, we calculated a divergence vector (**d**) following Langerhans (2009b) and visualized this axis using thin-plate spline transformations. This divergence vector or 'shape index' represents a canonical analysis of the coping style term from the MANCOVA and describes the linear combination of shape variables that exhibits the greatest differences between groups, adjusting for other factors in the model, in Euclidean space.

Performance

Swimming-performance trials took place in a square arena (25.4 cm long × 25.4 cm wide × 6 cm deep) with a transparent Plexiglas base and opaque, black sides. Trials were recorded from below using a digital high-speed video camera (Model N4, Integrated Design Tools, Tallahassee, FL, U.S.A.) at 600 fps and 1016 × 1016 pixel resolution. For the seventh generation of zebrafish, we recorded videos at 400 frames/s. Tests were performed after fish were at least 7 months old. Testing order was randomized by individual (fourth and seventh generations) or systematically alternated between bold and shy lines (fifth generation). Water temperature was held constant (27.4 °C) for all trials. We changed the water after each trial to avoid accumulating any alarm cues.

After placing an individual in the arena and allowing it to come to a standstill, we startled each fish by waving a hand over the tank and recorded the fast-start response. In fish, a fast-start is a brief, stereotyped burst of acceleration that enhances survival during predator encounters (Langerhans, 2009a, 2010). We recorded two to four responses per fish and selected one for analysis based on a qualitative assessment of the maximal response, as we wished to estimate maximum fast-start capacity and avoid inclusion of trials where individuals performed at less than their maximal capabilities (Losos, Creer, & Schulte, 2002).

We measured fish displacement during the first ~70 ms of the fast-start response by digitizing the centre of mass in each video frame using tpsDig. Centre of mass was estimated for each individual based on the point along the centre longitudinal line of the body (viewed from below) that showed the greatest latency for displacement in space as the fish's body bent during initiation of the C-start (Tytell & Lauder, 2008). We smoothed displacement data using the mean-squared error quantic spline (Jeffrey A Walker, 1998), and used the smoothed data to calculate maximum velocity, average velocity, maximum acceleration and average acceleration. We measured turning angle and mean angular velocity during stage 1 of the fast-start by digitizing the centre of mass and the tip of the snout during the earliest part of the escape response, in which the fish's body bends into a tightly curved 'C' before moving forward (this was typically accomplished within the first 12 ms of the response).

In this way we obtained six performance variables from each video sequence: maximum velocity, average velocity, maximum acceleration, average acceleration, turning angle and mean angular velocity during stage 1 of the fast-start. We conducted principal components analysis (PCA) on these six performance variables using the correlation matrix in order to reduce data dimensionality, and retained only those PCs that explained more variance than expected by broken stick criterion (three PCs). PC1 explained over 40% of the variance and captured a major axis ranging from high-performance fish (high values for maximum velocity, maximum acceleration, average velocity and rotational velocity) to low-performance fish (low values for those four variables). PC2 described variation in turning angle, and PC3 captured some of the variation in average acceleration (Table 1).

We tested for differences in fast-start performance between phenotype lines by running three general linear models, with each PC as the dependent variable and with coping style line, sex and their interaction as independent variables, and centroid size and generation as covariates. We originally tested for all other possible interactions but excluded them due to nonsignificance. To provide an assessment of the magnitude of differences between coping style lines, we report standardized effect sizes (Cohen's *d*, describing the difference between means in standard deviation units; Cohen, 1988).

Finally, to examine how the three traits of personality, morphology and performance might be correlated among individuals raised in a common environment, we conducted two sets of analyses using fish from the seventh laboratory-raised generation. First, we performed a general linear model with stationary time as the dependent variable and the following as explanatory variables: shape index, the three performance PCs, centroid size and sex. We excluded all nonsignificant terms. This model tested for direct associations between stationary behaviour and either morphology or performance or both, while controlling (i.e. adjusting) for potentially confounding variables. That is, this analysis tests for behaviour–morphology and behaviour–performance associations that are independent of any other measured variable (simple correlation if only one term is included; partial correlations if multiple terms are included). Second, we performed three separate general linear models, each model using one performance PC as the dependent variable, and shape index, centroid size and sex as explanatory variables. We again excluded all nonsignificant terms. These analyses tested for direct associations between performance and morphology, while again adjusting for possible confounding variables. That is, these analyses test for morphology–performance associations via simple correlation or partial correlation.

Ethical Note

The experiment was approved by the Institutional Animal Care and Use Committee of North Carolina State University (protocol 14-029-0). Fish were maintained in standard aquarium conditions and appeared to recover quickly after handling. No adverse effects on the overall health of the fish were apparent as a result of testing. The animals were later humanely euthanized in accordance with the approved animal care and use protocol (an overdose of tricaine methyl sulfonate).

RESULTS

Body morphology showed statistically significant differences between bold and shy zebrafish lines (Table 2). Average Procrustes

Table 1
PC loadings for kinematic variables used to measure locomotor performance

Performance variable	PC1	PC2	PC3
Maximum velocity	**0.93**	−0.13	−0.15
Maximum acceleration	**0.67**	−0.08	−0.59
Average velocity	**0.79**	−0.18	0.29
Average acceleration	0.06	−0.57	**0.64**
Turning angle	0.11	**0.83**	0.29
Rotational velocity	**0.75**	0.35	0.31
%Variance explained	41.84	19.85	17.59

PC1 captured most of the variation in velocity and maximum acceleration; PC2 largely described variation in turning angle; PC3 partially captured average acceleration. Values greater than |0.60| are shown in bold.

Table 2
Results of MANCOVA examining how body shape varies with coping style line (bold/shy), sex and size

Source	*F*	*df*	*P*
Coping style line	2.37	11, 108	0.0115
Sex	7.80	11, 108	<0.0001
Sex∗coping style line	0.73	11, 108	0.7052
Centroid size	4.88	11, 108	<0.0001
Generation	3.66	22, 216	<0.0001

distance between bold and shy lines was 0.017 for females and 0.009 for males. Fish from the bold line exhibited a more elongate body with larger caudal regions and shallower mid-bodies than fish from the shy line (Fig. 1). The shape index (visualized using thin-plate spline transformations in Fig. 1), as well as Procrustes distances, suggested that females showed a greater magnitude of morphological difference between bold and shy coping styles than males (Fig. 2), although we cannot reject the null hypothesis of no sex-dependent differences (i.e. nonsignificant interaction term between sex and coping style). Not surprisingly, we uncovered strong effects of allometry and sexual dimorphism on body shape (Table 2). There were also significant effects of generation; the fifth generation had a relatively longer body with a shallower mid-section, and the seventh generation had a longer anal-fin insertion.

Swimming performance also showed significant differences between bold and shy lines (Table 3, Supplementary Table S2). Based on standardized effect sizes, females showed greater performance differences between lines than males (PC1: 0.91 versus 0.23; PC2: 0.36 versus 0.27; PC3: 0.61 versus 0.27). The bold line had higher fast-start performance (captured by PC1) than the shy line, and this effect was stronger in females than males (Fig. 2). There was also a negative relationship between centroid size and performance (smaller fish had higher PC1 scores). Generation 4 had the highest performance and generation 5 had the lowest performance. For PC2, bold females tended to have higher turning angles than shy females (although this was not significant), while males showed the opposite pattern. Bold females had higher PC3 scores (average acceleration) than shy females, while males again showed the opposite pattern. Generation 4 had lower PC3 scores than the other two generations.

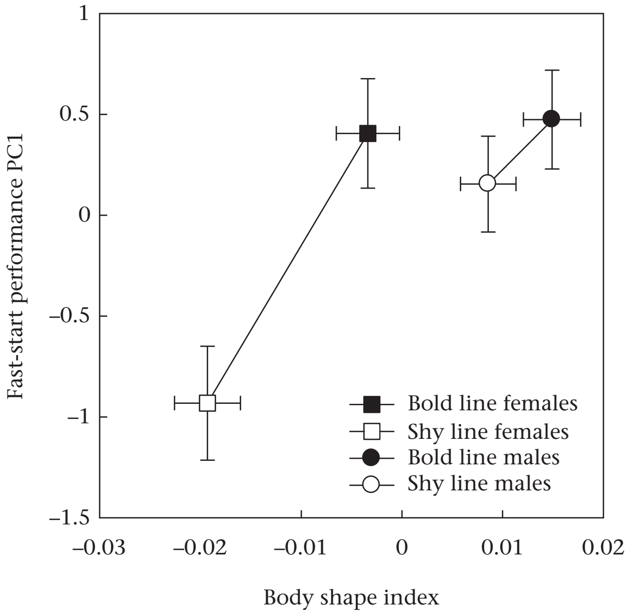

Figure 2. Variation in body morphology and fast-start performance (captured by PC1) between bold and shy coping style lines in female and male zebrafish.

By explicitly testing direct associations between stationary time, morphology and performance, we found that behaviour was directly correlated only with performance, not morphology or other potentially confounding variables. Thus, we did not find behaviour–morphology associations when statistically controlling for performance. Performance PC1 exhibited a significant association with stationary time (Pearson correlation: $r_{65} = -0.29$, $P = 0.0194$); the other two PCs did not. Only the shape index was significantly associated with performance PC1 ($r_{65} = 0.52$, $P < 0.0001$), indicating that fish with more elongate bodies and larger caudal regions exhibited higher fast-start performance. No model terms were significantly related to the other PCs. Based on these findings, we tested for an indirect association between stationary behaviour and body shape to quantify the potential strength of association owing to their shared relationships with performance PC1. Specifically, we calculated an indirect correlation coefficient as the product of the two simple correlation coefficients (correlation between PC1 and stationary time × correlation between PC1 and the shape index; equivalent to indirect effect tests of path models). Using 1000 bootstraps of the data set, we uncovered a significant indirect association between stationary time and shape index ($r_{65} = -0.15$, $P = 0.012$), mediated by their shared association with performance PC1. This indicated that individuals with more elongate bodies and larger caudal regions tended to exhibit lower stationary time in an open field test owing to the fact that these fish also tended to have higher fast-start performance PC1 values.

DISCUSSION

Wild-derived zebrafish selectively bred for divergent stress-coping styles did not merely evolve a set of behavioural differences, but also diverged in body morphology and locomotor performance. The correlated responses of body shape and fast-start performance to artificial selection on an animal personality trait demonstrates underlying genetic associations among the traits in this study. This means these traits probably cannot evolve independently, as the evolution of one can constrain the evolution of the others. Thus, seemingly unrelated traits like locomotor ability and personality can indeed coevolve. Overall, this study represents one of the earliest documentations of correlations between animal personalities and either whole-body morphology or locomotor performance (Ahlgren, Chapman, Nilsson, & Brönmark, 2015; Hulthén, Chapman, Nilsson, Hollander, & Brönmark, 2014; Müller & von Keyserlingk, 2006).

Compared to fish from the shy line, bold fish had enhanced fast-start performance and a more elongate body with a larger caudal region. This matches our a priori predictions for the phenotype combinations that should provide high fitness in the wild. The two selection lines examined in this study differed by as much as 2.1 standard deviation units in stationary behaviour, up to 0.9 standard deviation units in fast-start performance, and exhibited an average Procrustes distance as high as 0.017. This indicates substantial behavioural divergence, moderate shape differences and moderate-to-strong divergence in locomotor performance. For comparison, morphological differences between these zebrafish lines were considerably less than observed between populations of *Gambusia* fishes living with or without predatory fish (Procrustes distances = 0.030–0.046; Langerhans, Gifford, & Joseph, 2007; Langerhans & Makowicz, 2009; Langerhans, 2009b), but comparable to that seen in the rapid differentiation of a crater lake cichlid, *Amphilophus citrinellus* (Procrustes distance = 0.017; Elmer, Lehtonen, Kautt, Harrod, & Meyer, 2010).

Table 3
Results of general linear models examining variation in swimming performance (captured by PCs) between bold and shy zebrafish lines

Source	*df*	PC1		PC2		PC3	
		F	*P*	*F*	*P*	*F*	*P*
Coping style line	1, 118	10.88	**0.0013**	0.08	0.7716	1.05	0.3078
Sex	1, 118	4.94	**0.0281**	1.28	0.2608	1.54	0.2174
Sex∗coping style line	1, 118	4.05	**0.0464**	3.19	0.0768	6.32	**0.0133**
Centroid size	1, 118	4.76	**0.0310**	0.09	0.7588	0.03	0.8610
Generation	2, 118	11.46	**<0.0001**	1.37	0.2571	25.93	**<0.0001**

Statistically significant outcomes are shown in bold.

Based on work in other systems, we speculate that the genetic correlations in zebrafish stemmed from correlational selection in the wild via predation (Pruitt, Stachowicz, & Sih, 2012; Réale & Festa-Bianchet, 2003). Most natural fish populations are subject to predation, and the limited ecological data on wild zebrafish suggest they regularly encounter avian and fish predators (Bass & Gerlai, 2008; Engeszer et al., 2007; Spence et al., 2006). In the presence of predation, selection might favour both fast-and-bold phenotypes as well as shy-and-slow phenotypes, leading to correlation in these trait combinations. Bold, exploratory and risk-taking behaviours might offer a host of fitness advantages only when combined with greater acceleration, manoeuvrability and fast-start velocity. Larger caudal regions and increased fast-start performance can enhance survival during predatory encounters in fish (Langerhans, 2009a; Walker, Ghalambor, Griset, McKenney, & Reznick, 2005). Meanwhile, shy, slow individuals might represent an alternative high-fitness strategy by hiding from predators and experiencing greater longevity (Langerhans, 2006; Smith & Blumstein, 2008). Moreover, because of the physiological trade-off between fast-start performance and steady-swimming performance known for many fish, and expected in zebrafish, shy-slow individuals might exhibit higher steady-swimming abilities and thus greater energetic efficiency during routine activities such as foraging and station holding (Langerhans & Reznick, 2010; Langerhans, 2009b; Oufiero, Walsh, Reznick, & Garland, 2011; Plaut, 2001).

The responses of morphological and locomotor traits to selection on behaviour were particularly strong in female zebrafish: females tended to differ between lines more than males, and in more aspects of fast-start performance (multiple PCs). The cause of this is unclear: perhaps correlational selection in the wild is stronger for females than for males (e.g. selection in males may largely favour high fast-start performance regardless of stress coping style), or perhaps genetic and physiological differences between the sexes influence the expression of morphology and performance genes. Male zebrafish in this study and in the wild (Dahlbom, Lagman, Lundstedt-Enkel, Sundström, & Winberg, 2011; Wong et al., 2012) exhibit greater boldness than females, and male zebrafish also exhibit a more elongate body with a larger caudal region than females. It is possible that high fast-start performance phenotypes are more canalized in males than in females.

The ultimate and proximate causes of genetic associations between personality, morphology and performance and their prevalence in nature require further study. Our findings not only suggest that correlational selection might ultimately underlie the observed associations, but also that different proximate mechanisms might explain the correlated responses to selection on behaviour for the two nonbehavioural traits examined here. First, we found that after seven generations in the laboratory, zebrafish exhibited a significant and direct phenotypic correlation between personality (stationary time in an open field test) and locomotor performance (PC1 of fast-start performance). This is consistent with pleiotropy or physical gene linkage, where either expression of the two traits share some of the same genes or some independent genes that influence the two traits are proximally located on the same chromosome and are thus co-inherited. On the other hand, we found no evidence for a direct phenotypic correlation between personality and body shape after seven generations in the laboratory, even though body shape had diverged between selection lines. Instead, we only observed a significant indirect association between these two traits: personality was indirectly associated with body shape because (1) body shape and fast-start performance showed a strong phenotypic correlation, apparently reflecting biomechanical relationships where body shape partially influences locomotor performance (Domenici, Turesson, Brodersen, & Brönmark, 2008; Langerhans, 2009a, 2010; Swallow & Hayes, 2009) and (2) fast-start performance was significantly correlated with personality. These results suggest that the correlated response of body shape to selection on behaviour may have reflected linkage disequilibrium between genes that influence morphology and behaviour, built up by correlational selection in the wild. Without continued correlational selection, this kind of disequilibrium breaks down quickly under random mating, and is consistent with the lack of direct phenotypic correlation observed in the seventh generation of laboratory-raised fish in this study.

Although our results strongly suggest that genetic correlations among the traits caused correlated evolutionary responses to artificial selection on one trait, an alternative explanation is possible. That is, correlated responses could reflect socially induced phenotypic changes, where bold fish that only interact with other bold fish develop different body shapes and locomotor capacities than shy fish that interact only with other shy fish. In this scenario, social interactions, and not underlying genes per se, could create correlated responses to selection (Laskowski & Pruitt, 2014). Because the different selection lines were housed separately in this study, we cannot rule out this explanation. However, this interpretation seems less robust in light of the evidence for pleiotropy and in the absence of any previously demonstrated socially induced responses in zebrafish performance or morphology.

Owing to the rich resources available to zebrafish researchers and the ever-increasing use of zebrafish as physiological and behavioural genetic models, our results point toward promising future work in zebrafish that could provide insights into the genetic mechanisms underlying complex trait associations. Zebrafish research has already yielded information on genes and molecular pathways that influence locomotion, hyperactivity and morphological traits (Granato et al., 1996; Mabee et al., 2007; Norton & Bally-Cuif, 2010). Interactions among such genes are not well understood, nor are the interactions among behavioural, physiological and morphological genes or the pleiotropic effects of genes across these phenotypic domains. In light of our findings, genotype––phenotype studies focused on behaviour–physiology–morphology associations could represent a fruitful area of research. Because correlational selection on animal personalities and nonbehavioural traits might be common in the wild, and because personalities are underlain by mechanisms with broad phenotypic consequences, we might expect personality to often correlate with non-behavioural traits such as morphology and performance (Hulthén et al., 2014; Kim & Velando, 2015; Lacasse & Aubin-horth, 2012; Olmos & Turner, 2008). However, we currently know very little about these associations. If complex behaviours often coevolve with disparate traits like locomotion and morphology, not only will this alter our understanding of whole-organism adaptation and the role of evolutionary constraints among different types of traits, but we might also apply this knowledge to captive and domestic animal breeding and pest management, and understanding associations between human behaviours and other traits (Carré & McCormick, 2008; Zilioli et al., 2015). Results of this study suggest genetic associations exist between personality, morphology and performance; we now need additional research to understand their frequency and importance.

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Supplementary Material

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