Original Article

Population-level personalities in zebrafish: aggression-boldness across but not within populations

Emília P. Martins[a] and Anuradha Bhat[b]

[a]Department of Biology and Center for the Integrative Study of Animal Behavior, Indiana University, Bloomington, IN 47405, USA and [b]Indian Institute of Science Education and Research Kolkata, Mohanpur Campus, Mohanpur-741 252, India

Many animals exhibit personality types, for example, with some individuals being consistently both more aggressive and more willing to explore novel situations than others. Often those behavioral syndromes are shaped by pleiotropic genetic and physiological mechanisms or joint selective pressures that constrain variation within and between 2 seemingly different types of behavior. Here, we used wild zebrafish to ask whether the behavioral syndromes typically measured within populations also occur across populations, as might be expected for syndromes created by forces such as a hormone with multiple effects. We found major differences across populations in both aggression and boldness. Zebrafish captured in the wild from running streams in Northern India were both bold and aggressive, approaching predators and conspecifics more frequently than did zebrafish from slower moving irrigation canals or a large, still, lake near Kolkata, India. We did not find any sites that were bold, but not aggressive, or aggressive, but not bold, suggesting that these behavioral combinations are not physiologically possible or that they are eliminated by population-level selection. Within populations, however, we found evidence for an aggression-boldness syndrome within only 1 of 5 measured populations (from an irrigation canal). Zebrafish also became markedly more aggressive after 3 months in a laboratory environment. These results offer a natural example of population-level personality types in wild organisms and show that population-level patterns and environmental plasticity may be as important as within-population constraints. Our work also confirms that wild zebrafish offer promising insight into higher order phenomena such as clade diversification and selection.

Key words: **aggression, behavioral syndrome, boldness, evolution, population, zebrafish.**

INTRODUCTION

Although in many taxa, individuals exhibit consistently distinct behavior or "personality" types (see reviews by Bell 2007; Wolf et al. 2008; Conrad et al. 2011), in other taxa, personality types are characteristic of a group. For example, breeds of dogs exhibit distinct suites of behavior (e.g., Spady and Ostrander 2008; Careau et al. 2010) as do colonies of bees (Wray et al. 2011). Similarly, small fish from populations with high levels of predation tend to be bolder than fish from populations with low levels of predation (Fraser and Gilliam 1987; Brown et al. 2005; Chiba et al. 2007). Just as the study of individual behavioral syndromes has offered considerable fresh insight into the genetic and hormonal mechanisms underlying behavior, studies of natural populations that exhibit distinct behavioral phenotypes or tight relationships

between seemingly unrelated traits, can increase our understanding of higher order evolutionary phenomena such as species diversification and extinction. The consequences of behavioral syndromes can be profound (see review by Wolf and Weissing 2012), especially as they influence broad phenotypic features such as life history (Réale et al. 2010), dispersal (Cote et al. 2010), and sexual selection (Schuett et al. 2010). Here, we measure aggression and boldness of 5 populations of wild-caught zebrafish, asking whether the patterns of consistent individual differences and behavioral syndromes observed within populations translate into similar patterns across populations.

Within species, the relationship between aggression and boldness has been particularly well studied and may be the result of shared physiological mechanisms or environmental effects. Some steroid hormones and neurotransmitters (e.g., Cockrem 2007; Coppens et al. 2010; Norton et al. 2011) and certain pleiotropic genes (van Oers et al. 2005; Ducrest et al. 2008) may decrease behavioral inhibition and thereby make individuals simultaneously more

aggressive and bolder. Predation is an important factor shaping the aggression-boldness syndrome in natural populations of stickleback and guppies, where predators preferentially kill animals that readily approach predators but are nonaggressive (e.g., Bell and Sih 2007; Herczeg et al. 2009). Variation in developmental growth or metabolic rates can also shape covariation in aggression and boldness (e.g., Stamps 2007; Careau et al. 2008; Biro and Stamps 2010; Réale et al. 2010; Stamps and Groothuis 2010). Individual differences in expected future fitness may cause some fish to be more risk averse or risk prone (Wolf et al. 2008), and balancing selection may play a role when resources and environments shift often (Boon et al. 2007) or when individuals specialize to particular ecological or social situations (Bergmüller and Taborsky 2007; Bergmüller and Taborsky 2010). Animals may also evolve suites of behavioral traits that allow them to evade parasites or may produce linked behavior as a result of parasitic infection (Barber and Dingemanse 2010).

Similar forces may restrict behavior into consistent types and create strong relationships between traits at the level of breeds, populations, and species. For example, recent genomic comparisons of domesticated animals including dogs (Wayne and Ostrander 2007), chickens (Jensen and Andersson 2005), and honeybees (Wray et al. 2011) have identified specific genes associated with breed- or colony-specific behavioral types (e.g., tameness, foraging, aggression). Species comparisons of gene expression patterns have identified specific brain regions linking several forms of social and mating behavior (e.g., Nadler et al. 2006; Goodson and Kabelik 2009; Ross et al. 2009). Across natural populations, predation has been implicated as a major force influencing the presence or absence of distinct personality types in natural populations of stickleback, guppies, and spiders (e.g., Brown et al. 2005; Bell 2007; Chiba et al. 2007; Dingemanse et al. 2007; Herczeg et al. 2009; Conrad et al. 2011). Populations of animals living in different ecological contexts may also exhibit suites of metabolic, hormonal, and behavioral traits consistent with differences in life history (i.e., "Pace of Life" hypothesis as reviewed by Réale et al. 2010). Different species of *Danios* also exhibit differences in boldness and aggression (Kiesel et al. 2012). Comparisons of breed, population, and species differences in behavior offer powerful insight into the underlying genetic mechanisms and overlying selective factors that shape interactions between different types of behavior.

Very recently, researchers have described behavioral syndromes using a variety of quantitative genetic (Dochtermann and Roff 2010; Dingemanse et al. 2010a), reaction norm (Dingemanse et al. 2010b), and conceptual models (Dingemanse and Wolf 2010). Many of the genetic and physiological processes thought to underlie behavioral syndromes seem likely to produce consistent behavior across multiple contexts and correlations between unrelated behavioral traits at both individual and higher taxonomic (population or species) levels. For example, a genetic correlation or steroid hormone simultaneously influencing boldness and aggression might produce an aggression-boldness syndrome within each population, and also a relationship across population or species mean levels of aggression and boldness. However, if behavioral syndromes are the result of individual animals filling different social roles (e.g., leaders that are both more aggressive and more bold: Bergmüller and Taborsky 2010), we would expect a relationship between aggression and boldness within populations, but not necessarily across population or species averages. Conversely, heavy predation pressure or other population-wide environmental forces may result in some populations consisting entirely of highly aggressive and bold individuals, whereas other populations are entirely passive and shy, such

that within a population there is none of the variation among individuals typical of a syndrome. Given the potential also for gene by environment interactions and norm of reactions, all combinations of within- and across-population patterns seem possible.

Here, we compare the aggression-boldness syndromes occurring within and among 5 populations of wild zebrafish. Moretz et al. (2007b) describes significant differences across 3 laboratory strains of zebrafish in terms of their average levels of aggression and boldness, but found no evidence for an aggression-boldness syndrome within any of the 3, possibly because the aggression-boldness syndrome in fish appears to be linked to predation pressure (e.g., Bell and Sih 2007; Dingemanse et al. 2007; Dingemanse et al. 2009; Herczeg et al. 2009), a factor that is missing from domesticated laboratory zebrafish. In the current study, we collect wild fish from a range of habitats (an oxbow lake, 2 irrigation canals, 2 rocky streams) and measure their behavior in a common laboratory setting, testing whether zebrafish that have evolved in very different habitat types exhibit similar patterns of behavioral consistency and correlation within and across populations.

MATERIALS AND METHODS
Study species

Zebrafish are small cyprinids native to lakes and streams of Pakistan, India, and Bangladesh (Bhat 2004; McClure et al. 2006; Spence et al. 2006; Engeszer et al. 2007). In 2007, we collected adult zebrafish from 5 sites. Commercial suppliers shipped the fish to Indiana University-Bloomington, where we maintained them under standard laboratory conditions (21-L aquaria, 28 °C, 13:11 h light:dark cycle, filtered and aerated water, abundant food).

We collected PN zebrafish from a large, shallow, oxbow lake near Kolkata, India, and UT zebrafish from an irrigation canal about 65 km to the southwest. The remaining 3 sites were about 450 km north, near the borders of Nepal and Bhutan. We collected JO and DH zebrafish from rocky, hillside streams about 65 km apart, and PG zebrafish from an irrigation canal about 20 km from the DH site. Fish from our samples were included in a broad study of zebrafish population genetics (Whiteley et al. 2011). Using mitochondrial DNA and single-nucleotide polymorphism loci, Whiteley et al. (2011) found substantial genetic differentiation across the 450 km separating the Kolkata sites (PN and UT) from the 3 northern sites (PG, JO, DH), as well as evidence for limited gene flow among sites within each of these 2 groups during monsoon flooding of the Ganges river. Our populations thus represent a broad range of habitat differences and population substructure.

Behavioral assay

We measured the aggression and boldness of 360 wild-caught zebrafish, measuring half of the fish (18 males and 18 females from each of 5 sites) after a 2-week period and the remaining fish after they had spent 3 months in a common laboratory environment. Throughout their time in the lab, we housed the zebrafish in mixed sex groups, at roughly equal densities, and given abundant food. To conduct the assay, an observer placed 2 fish of the same sex, from the same population, and of approximately the same size into a divided 21-L testing arena (separated from each other by a tinted and perforated plastic divider), and then retreated behind a black sheet blind. After 3.5 h of acclimation, we removed the plastic barrier, video recording the interaction between the 2 fish. We later scored aggression from the recording as the number of

times each fish chased its partner in the first 5 min of interaction. After 20 min, we dropped a weighted, 15 mL centrifuge tube suddenly into the center of the testing arena (the centrifuge tube was dropped remotely from behind a blind and was intended to simulate an attack by a predator heron). Again from the video recording, we scored boldness as the number of times each individual approached to within one body length of the centrifuge tube in the first min after the centrifuge tube dropped.

Statistical analyses

To test for aggression-boldness syndromes, we examined relationships between aggression (number of same sex, conspecific chases) and boldness (number of times the fish approached a startling stimulus). Much as in Moretz et al. (2007b), we used general linear models and Pearson product-moment correlation coefficients to identify significant relationships between aggression and boldness both within and across populations (PN, UT, PG, JO, DH), while taking into account also acclimation time (2 weeks or 3 months). We also tested separately for the possible effects of 1) habitat (lake [PN], canal [PG, UT], stream [DH, JO]) and 2) genetic clade (Kolkata [PN, UT] vs. Northern [DH, JO, PG]). We found no evidence for sex differences in preliminary analyses, and thus did not include sex as a factor in our models. We examined residual plots from each model for assumption violations, but did not find any need to transform the data to obtain normal and homoscedastic residuals. All analyses were performed using SAS (2002).

As explained above, we paired 2 fish and measured the behavior of both in each assay. To avoid pseudoreplication, however, we included measures of only 1 of the 2 fish in each statistical test. Although partners were roughly size matched, there were small body size differences between the 2 fish in each pair, and we conducted separate statistical analyses considering only the slightly larger fish or only the slightly smaller fish in each assay pair. Although these absolute size differences were small (both "larger" and "smaller" fish encompassed the full range of available body sizes: 1.3–2.9 cm in standard length [SL]), this process allowed us to test also the importance of social context (i.e., being with a slightly larger or slightly smaller partner) in our assays. To confirm our results, we also ran limited analyses using the entire dataset (including measures of both fish in each trial) and using the behavior of the second fish as a covariate. Because the results were quite similar regardless of our approach, we report results only for analyses that included measures of only 1 fish from each trial.

RESULTS

Zebrafish from different wild sites exhibited markedly different behavioral profiles or personality types (Figure 1). Zebrafish from the northern DH stream were bold and aggressive, whereas fish from the more southern PN lake tended to be shy, only rarely chasing a conspecific or approaching a novel, startling stimulus (the dropped centrifuge tube). Fish from the other 3 sites were intermediate. Fish from the northern JO stream and PG irrigation canal sites frequently approached the simulated predator and chased conspecifics, whereas fish from the more southern UT irrigation canal site did both less often. There were no sites with fish that were bold but not aggressive, or aggressive without being bold. The result was a strong positive correlation across populations between the behavior shown toward conspecifics and that shown toward a simulated predator ($r = 0.91$; df = 3; $P < 0.05$; Figure 1). This relationship was confirmed by significant interaction effects between site and
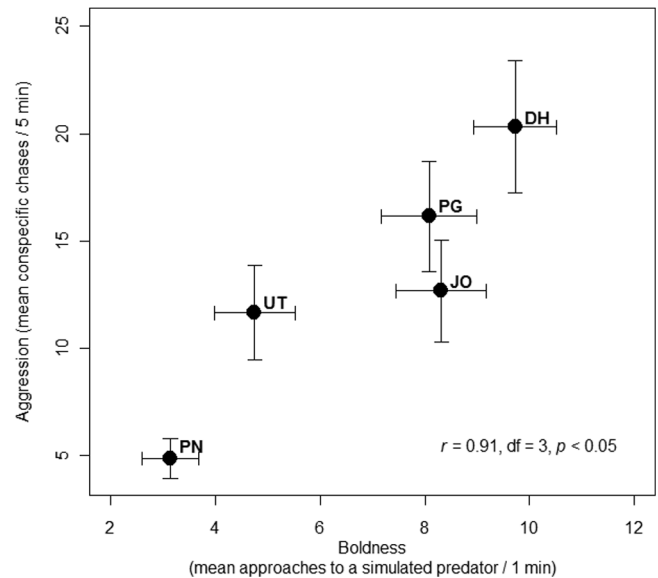

Figure 1

We found a strong, positive relationship between aggression and boldness across zebrafish from 5 wild populations ($r = 0.91$, df = 3, $P < 0.05$). Each point is the mean value (error bars show 1 standard error) for fish from 1 of the 5 sites. The statistical significance of the relationship was further confirmed by the regression models reported in Table 1 (see aggression × site and boldness × site interaction effects), which also take within-site variation into account. Although this plot depicts measures of only 1 fish in each trial (the slightly larger individual), a plot that included both fish in each trial would be quite similar.

aggression (or boldness) in predicting boldness (or aggression) in general linear models (Table 1, see below).

Both habitat and genetic clade were significant predictors of boldness, but not aggression (Table 1). The northern stream fish (DH, JO) were bolder than were canal fish (PG, UT), which were in turn bolder than were the more southern lake fish (PN). Aggression was better predicted by acclimation time: wild-caught fish were much more aggressive after 3 months in the laboratory environment than they were after only 2 weeks of acclimation (Table 1). Neither aggression ($r = 0.21$) nor boldness ($r = 0.14$) was strongly correlated with body size (SL).

The cross-site correlation between aggression and boldness was not supported by a similar relationship within sites (Figure 2, Table 1). Only zebrafish from the PG irrigation canal exhibited a within-population aggression-boldness syndrome with a distinct range of aggression and boldness (Figure 2b, $r = 0.6$; df = 34; $P < 0.05$). There was slight evidence for weak relationships between boldness and aggression in zebrafish from the southern PN lake and northern DH stream sites ($r = 0.1$ and 0.2, respectively; df = 34; $P > 0.05$), but no suggestion of even a weak relationship in zebrafish from the northern JO stream and more southern UT canal sites ($r = 0.0$; df = 34; $P > 0.05$).

Social context was also quite important. The above results are for zebrafish in the context of being paired with a slightly smaller conspecific. Zebrafish paired with slightly larger conspecifics in the behavioral assays only rarely chased their partners or approached the startling stimulus, leading to less measurable behavior and explainable variation and thus fewer statistically significant results. Correlation coefficients measuring the relationships between aggression and boldness for zebrafish paired with slightly larger conspecifics were weak ($r < 0.3$ both within and across populations),

Table 1

General linear models showing a significant relationship between aggression and boldness across populations (interaction effects between aggression/boldness and population)

	df	Mean squares	P
Y = boldness			
X =			
Aggression	1	64.1	0.08
Assay time (2 weeks vs. 3 months)	1	0.0	0.97
Population (nested within habitat	2	3.8	0.84
or genetic clade)	3	68.8*	0.02
Habitat	2	234.4*	<0.01
or genetic clade	1	267.6*	<0.01
Aggression × population	4	55.9*	0.04
Full model (r^2 = 27%)	10	132.8	<0.01
Error	165	21.3	
Y = aggression			
X =			
Boldness	1	618.5	0.07
Assay time (2 weeks vs. 3 months)	1	923.3*	0.03
Population (nested within habitat	2	295.2	0.21
or genetic clade)	3	467.8	0.06
Habitat	2	434.7	0.10
or genetic clade	1	81.9	0.51
Boldness × population	4	454.2*	0.05
Full model (r^2 = 21%)	10	826.4	<0.01
Error	165	185.7	

The relationship between aggression and boldness was not statistically significant within populations (main effects of aggression on boldness and boldness on aggression). Fish from the northern streams were bolder than fish from irrigation canals and more southern lakes. Fish also became more aggressive over time as they acclimated to laboratory conditions. This table includes results for separate analyses nesting population either within habitat or genetic clade. Results presented here are for analyses including only 1 fish in each trial (the slightly larger individual). Asterisks denote factors that were statistically significant at α = 0.05 level.

and general linear models fit the data poorly. Nevertheless, as above, habitat also predicted boldness ($F_{2,166}$ = 4.51, P = 0.012) but not aggression ($F_{2,166}$ = 0.14, P = 0.873) of zebrafish in the context of being paired with a slightly larger conspecific.

DISCUSSION

Our study finds evidence that the zebrafish aggression-boldness syndrome is shaped by forces acting at the population, rather than the individual, level. Zebrafish from northern streams and irrigation canals fearlessly chased conspecifics and approached potential predators, whereas fish from the more southern irrigation canals and oxbow lake tended to be nonaggressive and shy. We did not find any populations composed of shyly aggressive, or boldly nonaggressive zebrafish. We also did not find the same pattern of distinct personality types among individuals within 4 of the 5 measured populations. Instead, levels of aggression and boldness were relatively fixed within most populations, showing less variation within each population than across populations. The result is similar to the personality types of domestic breeds, where strong artificial selection has produced entire populations that are relatively fixed for desired behavioral types.

Our results suggest that in zebrafish, external factors such as water flow and amount of vegetation may influence boldness, although studies of additional replicate populations are needed to confirm this point. Others have found population differences in fish
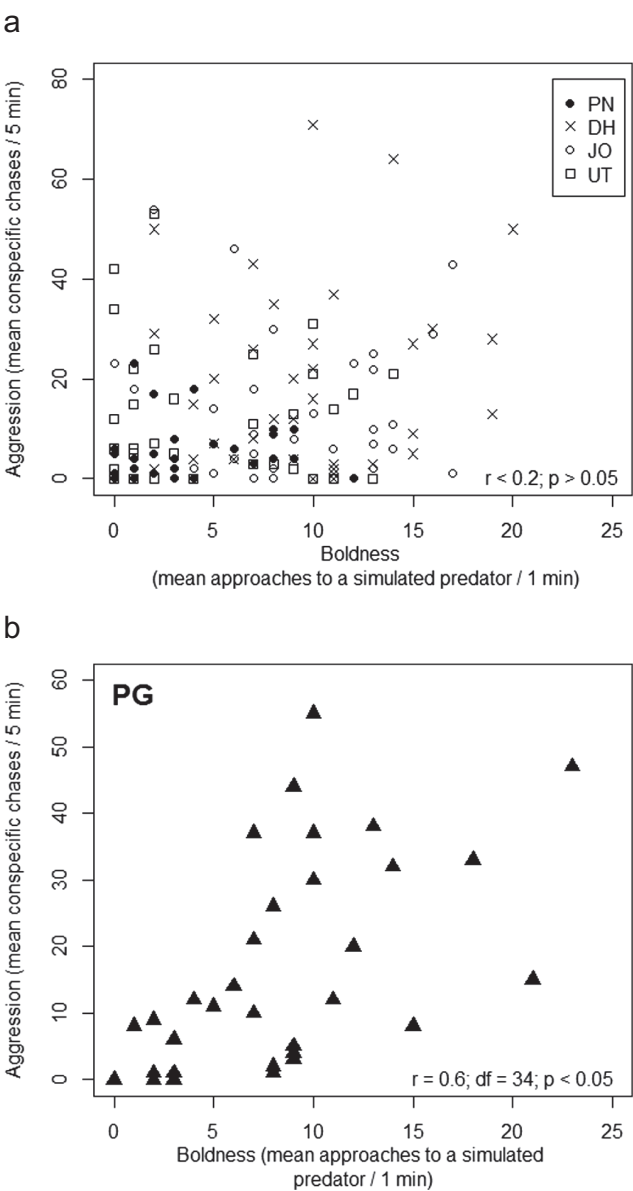
Figure 2
We found little evidence for a zebrafish aggression-boldness syndrome within 4 of the 5 wild populations (a: $r < 0.2$; $P > 0.05$ in all cases). (b) The exception was for fish from the northern PG irrigation canal, which showed a positive relationship between aggression and boldness ($r = 0.6$; df = 34; $P < 0.05$). Although these scatterplots depict measures of only 1 fish in each trial (the slightly larger individual), plots that include both fish in each trial would be quite similar with identical estimates of the correlation coefficients.

boldness due to aspects of the physical habitat (pond vs. marine 9-spined stickleback: Gonda et al. 2009; Herczeg et al. 2009; e.g., benthic vs. limnetic 3-spined stickleback: Larson 1976). For example, 3-spined stickleback (*Gasterosteus aculeatus*) that co-occur with large, piscivorous fish tend to exhibit strong within-population correlations between different measures of boldness (Dingemanse et al. 2007) as well as between boldness and aggression (Bell 2005). Moreover, Bell and Sih (2007) showed experimentally that exposure to predators can lead to the phenotypic correlation between

aggression and boldness. Detailed field and lab studies are needed to measure predation pressure, water flow, and degree of vegetation in different zebrafish habitats and to determine which, if any, of these forces are important in determining mean population levels of boldness and the across-population relationship between aggression and boldness. Zebrafish boldness can also be moderately heritable ($h^2 = 0.76$; Ariyomo et al. 2013), as evidenced now in multiple contexts (Robison and Rowland 2005; Wisenden et al. 2011).

Social factors are also likely to be important, especially in shaping zebrafish aggression. Both aggression and boldness in fish groups are influenced by the presence, familiarity with, and relative size of conspecifics (see Ward et al. 2009; Conrad et al. 2011 for reviews). Group size (Magurran and Seghers 1994; Webster et al. 2007) and whether shoals are composed of males or females (Piyapong et al. 2010) are also important. Zebrafish lab strains and wild populations differ significantly in their degree of sociality (Moretz et al. 2007b), the effects of recent social experience on aggression (Moretz et al. 2007a), and the degree to which individuals adopt particular social roles and recover from social disturbance (Vital and Martins 2011). Intriguingly, in the current study, we found an increase in aggression after 3 months in the lab, probably due to confinement at relatively high densities in aquaria. This result adds support to recent studies that suggest that adult zebrafish can respond flexibly to their circumstances (e.g., Oswald and Robison 2008) and may show similar changes in aggression and boldness in the wild, perhaps seasonally as bodies of water merge and separate with the monsoons.

Population-level syndromes can result from the same sort of shared underlying mechanisms or selective forces that are thought to produce within-population syndromes. Genes (e.g., Wright et al. 2006a, 2006b; Norton et al. 2011) or environmental factors (e.g., predation, as in references above) acting simultaneously on both aggression and boldness may make it impossible for populations of zebrafish that are aggressive toward conspecifics but wary of new environments (or nonaggressive yet bold) ever to arise. Although we would generally expect cross-population syndromes to be mirrored by a comparable pattern across individuals within each population (e.g., Pruitt et al. 2010), the within-population aggression-boldness syndrome in zebrafish may simply not be detectable because populations are essentially fixed in both aggression and boldness. This is consistent with recent quantitative genetic analyses (e.g., Walsh and Blows 2009) that suggest that the evolutionary processes underlying phenotypic adaptation are inherently complex and that we will not fully understand the system without measuring multivariate phenotypes and considering the impact of interacting traits at multiple levels.

Although selection and drift are the primary forces shaping evolution of behavioral phenotypes over relatively short periods of evolutionary time, higher order processes of clade diversification, persistence, and extinction can explain behavioral evolution over longer time periods or across broader groups of organisms (see review by Jablonski 2008). Thus, cross-population behavioral syndromes may also be the result of higher taxonomic phenomena such as clade diversification and extinction. For example, zebrafish populations that are both aggressive and bold may grow and colonize new areas more rapidly than do populations that are aggressive, but not bold. Similarly, zebrafish populations that are neither aggressive nor bold may persist over longer periods of evolutionary time than do populations that are not aggressive, but boldly confront novel situations. Over long periods of time, these macroevolutionary patterns would result in a population-level aggression-boldness syndrome. As reviewed by Jablonski (2008), these sorts of macroevolutionary

patterns appear to be most commonly associated with complex or "aggregate" traits. For example, insect flight and metamorphosis (both complex, "aggregate," traits) have contributed to the diversification of insect species (see review by Mayhew 2007). Similarly, warbler populations with polygynous mating systems (another aggregate trait) are expected to persist longer than monogamous populations (Saether et al. 2004). Thus, the degree to which individual populations exhibit aggression-boldness syndromes may influence their persistence and diversification from other populations. The study of behavioral syndromes at population and species levels thus offers unique insight into longer term evolutionary processes.

REFERENCES

Ariyomo TO, Carter M, Watt PJ. 2013. Heritability of boldness and aggressiveness in the zebrafish. Behav Genet. 43:161–167.

Barber I, Dingemanse NJ. 2010. Parasitism and the evolutionary ecology of animal personality. Philos Trans R Soc Lond B Biol Sci. 365:4077–4088.

Bell AM. 2005. Behavioural differences between individuals and two populations of stickleback (Gasterosteus aculeatus). J Evol Biol. 18:464–473.

Bell AM. 2007. Future directions in behavioural syndromes research. Proc Biol Sci. 274:755–761.

Bell AM, Sih A. 2007. Exposure to predation generates personality in three-spined sticklebacks (Gasterosteus aculeatus). Ecol Lett. 10:828–834.

Bergmüller R, Taborsky M. 2007. Adaptive behavioural syndromes due to strategic niche specialization. BMC Ecol. 7:12.

Bergmüller R, Taborsky M. 2010. Animal personality due to social niche specialisation. Trends Ecol Evol. 25:504–511.

Bhat A. 2004. Patterns in the distribution of freshwater fishes in rivers of Central Western Ghats, India and their associations with environmental gradients. Hydrobiologia. 529:83–97.

Biro PA, Stamps JA. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends Ecol Evol. 25:653–659.

Boon AK, Réale D, Boutin S. 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. Ecol Lett. 10:1094–1104.

Brown C, Jones F, Braithwaite V. 2005. In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. Anim Behav. 70:1003–1009.

Careau V, Réale D, Humphries MM, Thomas DW. 2010. The pace of life under artificial selection: personality, energy expenditure, and longevity are correlated in domestic dogs. Am Nat. 175:753–758.

Careau V, Thomas D, Humphries MM, Réale D. 2008. Energy metabolism and animal personality. Oikos. 117:641–653.

Chiba S, Arnott SA, Conover DO. 2007. Coevolution of foraging behavior with intrinsic growth rate: risk-taking in naturally and artificially selected growth genotypes of *Menidia menidia*. Oecologia. 154:237–246.

Cockrem J. 2007. Stress, corticosterone responses and avian personalities. J Ornithol. 148:169–178.

Conrad JL, Weinersmith KL, Brodin T, Saltz JB, Sih A. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. J Fish Biol. 78:395–435.

Coppens CM, de Boer SF, Koolhaas JM. 2010. Coping styles and behavioural flexibility: towards underlying mechanisms. Philos Trans R Soc Lond B Biol Sci. 365:4021–4028.

Cote J, Clobert J, Brodin T, Fogarty S, Sih A. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philos Trans R Soc Lond B Biol Sci. 365:4065–4076.

Dingemanse NJ, Dochtermann N, Wright J. 2010a. A method for exploring the structure of behavioural syndromes to allow formal comparison within and between data sets. Anim Behav. 79:439–450.

Dingemanse NJ, Kazem AJN, Réale D, Wright J. 2010b. Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol Evol. 25:81–89.

Dingemanse NJ, Van der Plas F, Wright J, Réale D, Schrama M, Roff DA, Van der Zee E, Barber I. 2009. Individual experience and evolutionary history of predation affect expression of heritable variation in fish personality and morphology. Proc Biol Sci. 276:1285–1293.

Dingemanse NJ, Wolf M. 2010. Recent models for adaptive personality differences: a review. Philos Trans R Soc Lond B Biol Sci. 365:3947–3958.

Dingemanse NJ, Wright J, Kazem AJ, Thomas DK, Hickling R, Dawnay N. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. J Anim Ecol. 76:1128–1138.

Dochtermann NA, Roff DA. 2010. Applying a quantitative genetics framework to behavioural syndrome research. Philos Trans R Soc Lond B Biol Sci. 365:4013–4020.

Ducrest AL, Keller L, Roulin A. 2008. Pleiotropy in the melanocortin system, coloration and behavioural syndromes. Trends Ecol Evol. 23:502–510.

Engeszer RE, Patterson LB, Rao AA, Parichy DM. 2007. Zebrafish in the wild: a review of natural history and new notes from the field. Zebrafish. 4:21–40.

Fraser D, Gilliam J. 1987. Feeding under predation hazard: response of the guppy and Hart's rivulus from sites with contrasting predation hazard. Behav Ecol Sociobiol. 21:203–209.

Gonda A, Herczeg G, Merilä J. 2009. Habitat-dependent and -independent plastic responses to social environment in the nine-spined stickleback (*Pungitius pungitius*) brain. Proc Biol Sci. 276:2085–2092.

Goodson JL, Kabelik D. 2009. Dynamic limbic networks and social diversity in vertebrates: from neural context to neuromodulatory patterning. Front Neuroendocrinol. 30:429–441.

Herczeg G, Gonda A, Merilä J. 2009. Predation mediated population divergence in complex behaviour of nine-spined stickleback (*Pungitius pungitius*). J Evol Biol. 22:544–552.

Jablonski D. 2008. Species selection: theory and data. Annu Rev Ecol Evol Syst. 39:501–524.

Jensen P, Andersson L. 2005. Genomics meets ethology: a new route to understanding domestication, behavior, and sustainability in animal breeding. Ambio. 34:320–324.

Kiesel AL, Snekser JL, Ruhl N, McRobert Scott P. 2012. Behavioural syndromes and shoaling: connections between aggression, boldness and social behaviour in three different Danios. Behaviour. 149:1155–1175.

Larson GL. 1976. Social behavior and feeding ability of two phenotypes of Gasterosteus aculeatus in relation to their spatial and trophic segregation in a temperate lake. Can J Zool. 54:107–121.

Magurran AE, Seghers BH. 1994. Predator inspection behaviour covaries with schooling tendency amongst wild guppy, *Poecilia reticulata*, populations in Trinidad. Behaviour. 128:121–134.

Mayhew PJ. 2007. Why are there so many insect species? Perspectives from fossils and phylogenies. Biol Rev Camb Philos Soc. 82:425–454.

McClure MM, McIntyre PB, McCune AR. 2006. Notes on the natural diet and habitat of eight danionin fishes, including the zebrafish Danio rerio. J Fish Biol. 69:553–570.

Moretz J, Martins E, Robison B. 2007a. The effects of early and adult social environment on zebrafish (*Danio rerio*) behavior. Environ Biol Fishes. 80:91–101.

Moretz JA, Martins EP, Robison BD. 2007b. Behavioral syndromes and the evolution of correlated behavior in zebrafish. Behav Ecol. 18:556–562.

Nadler JJ, Zou F, Huang H, Moy SS, Lauder J, Crawley JN, Threadgill DW, Wright FA, Magnuson TR. 2006. Large-scale gene expression differences across brain regions and inbred strains correlate with a behavioral phenotype. Genetics. 174:1229–1236.

Norton WH, Stumpenhorst K, Faus-Kessler T, Folchert A, Rohner N, Harris MP, Callebert J, Bally-Cuif L. 2011. Modulation of Fgfr1a signaling in zebrafish reveals a genetic basis for the aggression-boldness syndrome. J Neurosci. 31:13796–13807.

Oswald M, Robison BD. 2008. Strain-specific alteration of zebrafish feeding behavior in response to aversive stimuli. Can J Zool. 86:1085–1094.

Piyapong C, Krause J, Chapman BB, Ramnarine IW, Louca V, Croft DP. 2010. Sex matters: a social context to boldness in guppies (Poecilia reticulata). Behav Ecol. 21:3–8.

Pruitt JN, Riechert SE, Iturralde G, Vega M, Fitzpatrick BM, Avilés L. 2010. Population differences in behaviour are explained by shared within-population trait correlations. J Evol Biol. 23:748–756.

Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio PO. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philos Trans R Soc Lond B Biol Sci. 365:4051–4063.

Robison BD, Rowland W. 2005. A potential model system for studying the genetics of domestication: behavioral variation among wild and domesticated strains of zebra danio (Danio rerio). Canad J Fish Aqua Sci. 62:2046–2054.

Ross HE, Freeman SM, Spiegel LL, Ren X, Terwilliger EF, Young LJ. 2009. Variation in oxytocin receptor density in the nucleus accumbens has differential effects on affiliative behaviors in monogamous and polygamous voles. J Neurosci. 29:1312–1318.

Saether B-E, Engen S, Lande R, Møller AP, Bensch S, Hasselquist D, Beier J, Leisler B. 2004. Time to extinction in relation to mating system and type of density regulation in populations with two sexes. J Anim Ecol. 73:925–934.

SAS. 2002. SAS for Windows 9.1. Cary (NC): SAS Institute, Inc.

Schuett W, Tregenza T, Dall SR. 2010. Sexual selection and animal personality. Biol Rev Camb Philos Soc. 85:217–246.

Spady TC, Ostrander EA. 2008. Canine behavioral genetics: pointing out the phenotypes and herding up the genes. Am J Hum Genet. 82:10–18.

Spence R, Fatema MK, Reichard M, Huq KA, Wahab MA, Ahmed ZF, Smith C. 2006. The distribution and habitat preferences of the zebrafish in Bangladesh. J Fish Biol. 69:1435–1448.

Stamps J, Groothuis TG. 2010. The development of animal personality: relevance, concepts and perspectives. Biol Rev Camb Philos Soc. 85:301–325.

Stamps JA. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. Ecol Lett. 10:355–363.

van Oers K, de Jong G, van Noordwijk AJ, Kempenaers B, Drent PJ. 2005. Contribution of genetics to the study of animal personalities: a review of case studies. Behaviour. 142:1185–1206.

Vital C, Martins EP. 2011. Strain differences in zebrafish (*Danio rerio*) social roles and their impact on group task performance. J Comp Psychol. 125:278–285.

Walsh B, Blows MW. 2009. Abundant genetic variation + strong selection = multivariate genetic constraints: a geometric view of adaptation. Annu Rev Ecol Evol Syst. 40:41–59.

Ward AJW, Webster MM, Magurran AE, Currie S, Krause J. 2009. Species and population differences in social recognition between fishes: a role for ecology? Behav Ecol. 20:511–516.

Wayne RK, Ostrander EA. 2007. Lessons learned from the dog genome. Trends Genet. 23:557–567.

Webster MM, Ward AJW, Hart PJB. 2007. Boldness is influenced by social context in threespine sticklebacks (*Gasterosteus aculeatus*). Behaviour. 144:351–371.

Whiteley AR, Bhat A, Martins EP, Mayden RL, Arunachalam M, Uusi-Heikkilä S, Ahmed AT, Shrestha J, Clark M, Stemple D, et al. 2011. Population genomics of wild and laboratory zebrafish (*Danio rerio*). Mol Ecol. 20:4259–4276.

Wisenden BD, Sailer CD, Radenic SJ, Sutrisno R. 2011. Maternal inheritance and exploratory-boldness behavioural syndrome in zebrafish. Behaviour. 148:1443–1456.

Wolf M, van Doorn GS, Weissing FJ. 2008. Evolutionary emergence of responsive and unresponsive personalities. Proc Natl Acad Sci USA. 105:15825–15830.

Wolf M, Weissing FJ. 2012. Animal personalities: consequences for ecology and evolution. Trends Ecol Evol. 27:452–461.

Wray MK, Mattila HR, Seeley TD. 2011. Collective personalities in honeybee colonies are linked to colony fitness. Anim Behav. 81:559–568.

Wright D, Butlin RK, Carlborg O. 2006a. Epistatic regulation of behavioural and morphological traits in the zebrafish (*Danio rerio*). Behav Genet. 36:914–922.

Wright D, Nakamichi R, Krause J, Butlin R. 2006b. QTL analysis of behavioral and morphological differentiation between wild and laboratory zebrafish (*Danio rerio*). Behav Genet. 36:271–284.