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Personality traits predict hierarchy rank in male rainbowfish social groups

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KEYWORDS

behavioural syndrome, dominance, hierarchy, *Melanotaenia duboulayi*, personality, rainbowfish, sexual selection

ABSTRACT

Personality traits are becoming increasingly important in explaining adaptive individual differences in animal behaviour and probably represent a leading edge of the evolutionary process. Despite the newfound interest in animal personality among behavioural ecologists, fewstudies have investigated the link between personality traits and fitness measures. We examined this link using male rainbowfish, Melanotaenia duboulayi, as a model species and found that a range of personality traits (aggression, activity and boldness) covaried with a male's position in a hierarchy, which is directly related to reproductive success in this and many other species. Dominant fish were more aggressive, active, bold and also significantly larger than subordinate fish. Moreover, we found strong correlations between activity levels and boldness suggesting that selection may act on a suite of traits in concert (sensu behavioural syndromes). When taken together with previous research, our results suggest that the activityeboldness syndrome is likely to be domain specific. We suggest that multiple trait correlations may be generated by high levels of competition (e.g. sexual selection) in addition to predation pressure as identified by previous studies.

It is now well recognized that individuals differ consistently in their behaviour. One of the major axes describing differences in individual behaviour is the bold-shy continuum (Brown et al. 2005; Réale et al. 2007; Ioannou et al. 2008). Boldness is considered a major personality trait and has been linked to a number of fitness measures including condition factor, diet, exposure to predators and parasite load (Wilson et al. 1993; Brown & Braithwaite 2004; Brown et al. 2007). Differences in the degree of risk taking between individuals have been observed both within and between populations (Brown et al. 2007; Harris et al. 2010). But this divergence in individual behaviour also occurs in a number of other behavioural axes including parental care (Budaev et al. 1999), mating behaviour (Magellan & Magurran 2007), activity and aggressiveness (Huntingford 1976; reviewed in Budaev & Brown, in press). Furthermore, research into animal personalities has identified correlated behavioural axes, labelled syndromes. A syndrome is defined as a suite of correlated behaviours reflecting consistent individual differences in behavior across multiple situations (Sih et al. 2004). A population or species can exhibit a behavioural syndrome, but

individuals display a ‘behavioural type’ (Sih et al. 2004). Examples of syndromes have been found in several taxa including fish, birds, mammals, lizards and invertebrates concerning a range of different behaviours (Riechert & Hedrick 1993; Budaev 1997; Wilson 1998; Dingemanse et al. 2003; Bell & Stamps 2004; Bell 2005).

Interest in behavioural syndromes is growing because of its ecological origins and potential evolutionary implications. The existence of behavioural syndromes implies that behaviour is constrained and thus individuals may not be capable of displaying the degree of phenotypic plasticity expected under an adaptationist paradigm. In fact, syndromes could seem maladaptive in certain contexts and the correlation between behaviours may be indicative of underlying physiological constraints, pleiotropy or genetic linkage. In the psychology literature two alternative views regarding the development of individual behaviour have been suggested, the first of which is fairly compatible with the behavioural syndromes approach. The domain-general view suggests that personality traits are generally constrained and suites of traits are often correlated. In this case, populations of animals occupying different environments would show similar correlations between traits. Second, the domain-specific view, which is adaptationist in nature, suggests that individual traits are largely under independent selection; thus traits can become uncoupled and thereby permit a larger degree of phenotypic plasticity. Thus, domain-specific traits tend to be correlated only under certain contexts. In great tits, Parus major, for example, the link between exploratory behaviour and survival differs between the sexes and also with contemporary environmental conditions (Dingemanse et al. 2004)

In a wide range of species, individuals compete with one another for access to resources and competition often results in the formation of a hierarchy. Dominance has significant costs and benefits associated with it, but dominant individuals tend to have higher reproductive success. Some of the benefits of dominance include preferential access to sexual partners, shelter or food resources. Chase et al. (2002) suggested that an individual’s position in the hierarchy is the product of both individual characteristics (physical and behavioural) and dynamic social interactions. Although most research tends to focus on the influence of physical traits, suites of correlated behavioural traits may also play a key role in determining an individual’s position in the hierarchy. For example, less exploratory mountain chickadees, *Poecile gambeli*, were more dominant when paired with more exploratory conspecifics in pairwise encounters, but no link existed between exploration and boldness (Fox et al. 2009). In fishes, the opposite trend seems to exist, with highly active individuals being more aggressive (Huntingford 1976). Moreover, fish that show low-stress responses while exploring a new environment are more likely to become dominant (Schjolden et al. 2005). To appreciate fully the importance of personality traits from an evolutionary perspective, it is imperative that they are directly linked with individual fitness measures (Smith & Blumstein 2008). For example, bold geckos, *Lepidodactylus lugubris*, are less active but have higher foraging rates (Short & Petren 2008) and female guppies, *Poecilia reticulata*, prefer to associate with bold males (Godin & Dugatkin 1996). Links between personality traits and male reproductive success suggest that personality traits may be an important component of life history strategies (Reale et al. 2009).

A boldness-aggressiveness-activity syndrome has been identified in some populations of three-spined sticklebacks, Gasterosteus aculeatus (Huntingford 1976; Bell 2005; Dingemanse et al. 2007). For example, Bell (2005) found a correlation between the three traits in one population of sticklebacks but not in another. When data for both populations were combined, however, bold sticklebacks tended to be less aggressive than shy sticklebacks. In contrast, Huntingford (1976) found strong correlations between boldness and aggression in sticklebacks collected from a range of habitats that varied over the course of the breeding season but no population-level analysis was performed. Dingemanse et al. (2007) similarly investigated the relationship between activity, boldness and aggression in 12 populations of sticklebacks that varied in the level of predation pressure. A positive correlation was found only in those populations

subject to high predation pressure, suggesting that key environmental variables may drive the coevolution of a number of traits and that this syndrome may be domain specific. We extended this work by examining the potential influence of this syndrome on an important fitness component, that of male hierarchy formation.

In this study, we aimed to examine the link between aggressiveness, boldness and activity with individual rank in the hierarchy of male crimson-spotted rainbowfish, *Melanotaenia duboulayi*. Previous studies examining female mate choice in this species have shown that females exercise choice in a dichotomous chamber based on male size and display rate when males are held behind barriers. When males and the choosing female interact freely, however, the dominant male prevents subordinate males from approaching the female (Collins 1999). Thus male dominance in this species leads to a form of mate guarding and enhances male reproductive success (Young et al. 2010).

METHODS

Study Organism

The crimson-spotted rainbowfish is a freshwater fish occupying lakes and streams on the east coast of Australia from Coffs Harbour to Gladstone (Brown & Warburton 1999; Allen et al. 2002). In the wild, these fish form small shoals commonly consisting of one to six fish, but larger shoals also exist (Brown 2000). Their standard length reaches 80 mm after maturation and they seldom live beyond 2 years of age. This species is sexually dimorphic. Males are larger, more colourful and more aggressive than females. Both males and females form hierarchies within the shoal, but male-male competition is generally more intense than that among females. We used mature male fish that were 18 months old that had been laboratory reared for multiple generations (for details see Kydd & Brown 2009).

Experimental Design and Procedures

We studied the aggressiveness, boldness and activity levels of 28 males. The males were housed in four aquaria (92 × 36 cm and 50 cm deep) in social groups consisting of seven males and four females. Each aquarium was filled with tap water aged for 1 week prior to use and was furnished with river gravel, plastic plants and spawning nets. These elements created a seminatural environment, which encouraged relatively natural behaviour. The presence of male and female conspecifics facilitated shoaling behaviour and other social interactions including hierarchy formation. The water temperature was maintained at 23 °C, light was maintained on a 12:12 h light:dark ratio and the fish were fed every day with commercial flake food.

The 28 males allowed us to form seven groups of four unfamiliar males, each selected from different aquaria. All fish were tagged using Fluorescent Visible Implant Elastomer tags (Northwest Marine Technology Inc., Shaw Island, WA, U.S.A.). Two colours were used in four combinations of tag placement allowing us to distinguish between individuals. During the tagging procedure, each fish was lightly anaesthetized by placing it in 1 litre of tank water, containing 0.6 g of NaHCO3 and 0.3 g of MS222, for 30 s. After tagging, each fish was weighed, measured and then placed back in the housing aquarium. No mortalities occurred as a result of tagging and all fish recovered quickly. At the end of all the experiments all fish were rehomed with aquarium enthusiasts in accordance with our ethics licence. This research was conducted under an animal ethics licence from Macquarie University.

Experiment 1: Hierarchy Establishment

In this experiment, we aimed to establish new hierarchies in each group of four males, which also provided information regarding their level of aggression. In addition, we were interested to learn whether

a female audience would alter the nature of the aggressive interactions between individuals (i.e. a mild change of context) as observed in previous studies (Dzieweczynski et al. 2005). Groups of familiar males have well-established hierarchies; thus agonistic interactions occur relatively infrequently and are difficult to assess. Therefore, individuals were taken from different aquaria to ensure they were not familiar with one another, so as to maximize the interactions between the fish during hierarchy formation. Moreover, hierarchy position in small groups tends to be maintained even after subgroups are merged (Earley & Dugatkin 2006). Thus staging dyadic interactions allowed us to maximize the extraction of behavioural data while providing useful information about the relative hierarchy position of males within each group.

Six trials were run in every group of fish allowing for dyadic interactions between all individuals (i.e. 1 versus 2, 1 versus 3, 1 versus 4, 2 versus 3, 2 versus 4, 3 versus 4). The order of the interactions was randomized and a single contest within each group was staged one after the other. The minimum separation between trials using the same individuals was 7 days. This approach helped minimize potential winner/loser effects (Hsu et al. 2006). The experimental arena was furnished in a fashion similar to the home aquaria, including the provision of aquatic plants to provide refuge so fish could escape and hide from aggressors. In addition, a clear divide could be added and removed as necessary. For half of the trials, two males were placed directly in the experimental arena without the divide and their behavior was observed for 30 min. Subsequently, the males were removed for 20 min and a transparent divide was added to create a small compartment (20 cm in length) and a larger compartment (70 cm in length). An unfamiliar female was placed in the smaller of the two compartments and allowed to settle for 15 min. The males were placed back in the large compartment and their behaviour was observed for a further 30 min. For the other half of the trials, we repeated the procedure but in reverse order: the males were first observed with a female present and then in the absence of the female. During our observations the following behaviours were documented using Etholog 2.2 (Ottoni 2000): lateral displays, head displays, fins up, bite, charge, chase/flee and hide (for descriptions see Table 1). Rainbowfish are insectivorous and have small mouths, so bites cause no serious harm to conspecifics. Moreover, fish had the opportunity to flee and hide if necessary. If fights became overly aggressive we planned to intervene, but this step was never necessary. For every pair there was a clear winner by the end of the contest. By examining the winners in all dyadic interactions, individual fish were assigned ranks within their respective groups (dominant rank 1 to subordinate rank 4).

Table 1. A brief explanation of the primary behaviours displayed by male rainbowfish during agonistic interactions

Behaviour	Description
Lateral display	Fish swims laterally alongside the other fish with fins extended
Head display	Fish puts its head up, tail down, forms an S shape with the body while extending the first dorsal fin
Bite	Fish bites the other fish
Charge	Fish swims rapidly in direction of the other fish's flank
Chase	Fish rapidly follows the other fish which tries to escape
Fins up	Fish opens mouth and extends dorsal fins
Hide	Fish hides in the refuge out of view

Experiment 2: Measuring Boldness

The boldness experiment was conducted 2 weeks after the conclusion of experiment 1. In this experiment, we established a boldness-shyness classification for each of the 28 males. The experimental apparatus consisted of an aquarium (33 × 90 cm and 38 cm deep) with the addition of a transparent divide placed 20 cm from one end of the tank. This divide was equipped with a rectangular trapdoor (15 × 20 cm) which could be opened remotely by an observer. A novel object (a coke can) was placed at the other extremity of the tank. A grid was constructed over the top of the tank and the behaviour of the fish was recorded on a video camera mounted overhead. Each fish was placed in the start compartment for 5 min with the trapdoor closed. During this time the fish recovered from handling and explored the start compartment. It could also view the novel object from afar. After 5 min, the trapdoor was opened allowing the fish to emerge from the compartment, explore the novel environment and approach the novel object. We analysed the progress of the fish for 15 min using Etholog 2.2 while watching the video on a remote computer monitor. The test aquaria and the coke can were rinsed with tap water between trials. The time to emerge from the small compartment and the time spent close to the novel object during the first 5 min (both measures of boldness) were recorded.

Experiment 3: Measuring Activity Level

Two weeks after the conclusion of experiment 2, the activity level of each male was determined. Activity is best examined in a familiar environment in which the animal does not feel threatened and thus displays its natural behavioural patterns. In this last experiment, we established an activity classification of each male fish in its home aquarium in the presence of its fellow shoalmates.

The four home aquaria were divided into six equal parts, each 15 cm long, by drawing on the glass using a marker pen. We hung a sheet 65 cm from the aquaria behind which an observer could hide. A rectangular hole (90 × 2 cm) was cut in the sheet to allow the observer to watch the fish. We allowed the fish 24 h to habituate to the presence of the sheet and then recorded the activity of each male for 10min. The level of activity was defined as the number of transects crossed during the observation period.

Statistical Analysis

We analysed the behavioural data from experiment 1 using a principal components analysis (PCA) to identify suites of traits that clustered together as identifiable behavioural dimensions. Principal components with eigenvalues greater than 1 were considered for further interpretation. The coordinates of the individuals in dimension 1 of the PCA were considered as the aggressiveness scores while PC2 represented sociality scores (see Results). These scores were then analysed together with boldness scores from experiment 2 and activity levels from experiment 3 using hierarchy position as the independent variable. The time spent hiding was log +1 transformed and the time spent close to the novel object was log (1 + x) transformed to normalize the distributions. Jonckheere's trend test was employed to examine the data because we had a specific hypothesis relating dominance rank to our dependent variables. Comparisons between ranks were further analysed using Fisher's protected least significant difference (PLSD) test (ANOVA Statview, SAS Institute Inc., Cary, NC, U.S.A.). The female observer effect on male aggressiveness was analysed using ANOVA. Although we attempted to match males for size, we also analysed male standard length as a dependent variable.

Finally, a linear regression was conducted examining the associations between the aggressiveness score, number of transects crossed (activity) and the time spent near a novel object during the first 5min (boldness) using R 2.8.0 (The R Foundation for Statistical Computing, Vienna, Austria).

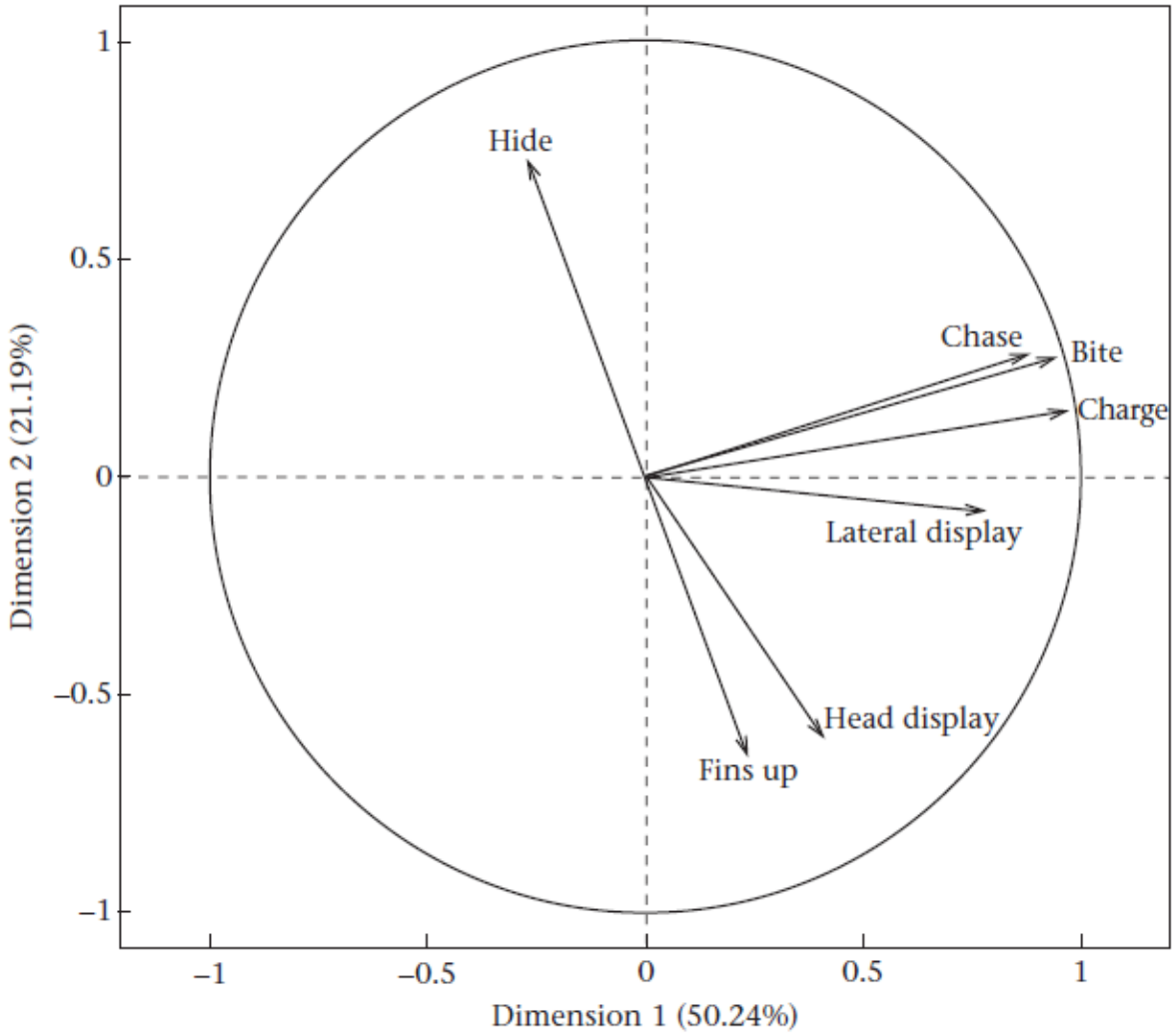

Figure 1. Variables factor map (principal components analysis) displaying the relationship between behaviours performed during agonistic interactions with respect to the first two principal components.

RESULTS

Experiment 1: Hierarchy Establishment

Each of the trials resulted in a clear winner and each social group of males displayed a clear and simple linear hierarchy. The variables factor map (Fig. 1) showed a strong relationship between the variables 'chase', 'bite', 'charge' and 'lateral display', all of which are characteristic of highly aggressive individuals in a range of fish species. Similarly, the variables 'fins up' and 'head display' were grouped together and probably represent general social displays. 'Hide', in contrast, was isolated by itself and diametrically opposed to the aggressive behaviours.

The first principal component explained 50% of the total variation (eigenvalue = 3.5) and from this analysis it was apparent that the first dimension exclusively expressed aggressive behaviours; therefore,

the component of each male in this dimension was used as the aggressiveness score for further analysis. The second principal component explained a further 24% of the variation (eigenvalue = 1.5) and comprised the variables 'hide' and 'head display'. These two variables were strongly negatively correlated (with N = 28, the minimum significant correlation r = 0.37; Table 2) and we interpreted this factor as a sociality score, 'hide' being an asocial response and 'head display' being a social signal. The third principal component explained 14% of the variance and comprised solely the variable 'fins up'. This factor had an eigenvalue just under 1 (0.97) and was therefore not considered in further analyses.

As expected, analysis of the aggressiveness score revealed that fish ranked higher in the hierarchy were significantly more aggressive than those ranked lower in the hierarchy (Jonckheere's trend test: S = 174, C = 4, N = 7, P < 0.01; Fig. 2a). Post hoc analysis (Fisher's PLSD) revealed a significant difference between the aggressiveness of the dominant fish and those ranked 3rd and 4th (P = 0.002 and P < 0.001, respectively). There were also significant differences between the second-ranked males and those ranked 3rd and 4th (P = 0.03 and 0.016, respectively). In general, the same was true for the sociality score. Highly ranked males were more social than lowly ranked males (Jonckheere's trend test: S = 106, C = 4, N = 7, P < 0.05; Fig. 2b). Specifically, fish from ranks 3 and 4 were less social than the fish from rank 1 (Fisher's PLSD: P = 0.007 and P = 0.034, respectively) and fish ranked 3 were less social than fish ranked 2 (Fisher's PLSD: P = 0.031; Fig. 2b).

Our observations during the experiment suggest that the dominant fish used different degrees of aggression in relation to the behaviour of the opponent fish. If the opponent was relatively meek, dominant fish had little need to be aggressive and brief displays were enough to settle the contest very quickly. If the opponent was very aggressive, on the other hand, the dominant male employed a series of aggressive behaviours to exert his dominance over the opponent and the length of the contest was extended. Moreover, subordinate fish sometimes initiated aggressive interactions with a series of displays but were eventually met with a single strong response from their dominant opponents, which ended the contest immediately. These general observations may explain the absence of significant differences between dominant and subordinates in some measures.

Surprisingly, the presence or absence of the female had limited impact on male behaviour. Our analysis showed some trends but no significant relationships (ANOVA: P > 0.05 in all cases).

Table 2. Pearson coefficients correlation matrix showing the relationship between behavioural variables during agonistic interactions in male rainbowfish

	Bite	Charge	Chase	Fins up	Head display	Hide	Lateral display
Bite	1.000	0.949	0.911	0.063	0.228	-0.051	0.682
Charge		1.000	0.898	0.180	0.254	-0.158	0.724
Chase			1.000	-0.070	0.282	-0.122	0.458
Fins up				1.000	0.226	-0.241	0.351
Head display					1.000	-0.424	0.194
Hide						1.000	-0.170
Lateral display							1.00

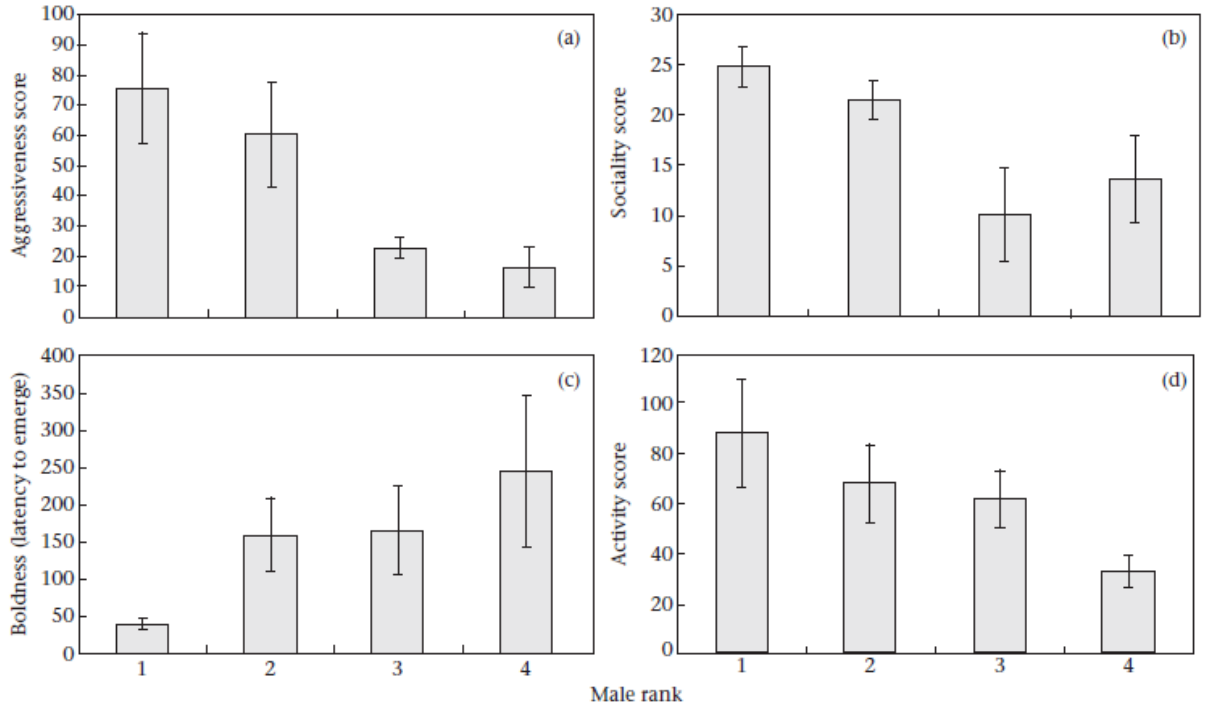

Figure 2. Mean ± SE (a) aggressiveness, (b) sociality, (c) boldness and (d) activity score for males ranked 1-4 in the hierarchy. All scores shown are raw data and statistics were performed on transformed data where appropriate. The aggressiveness and sociality scores are composite scores derived from a principal components analysis, the boldness score is the time to emerge from the start compartment and the activity score refers to the number of transects crossed.

Experiment 2: Boldness

Every male emerged from the start compartment within the allotted 15 min. Our analysis showed that male rank had an effect on boldness scores (Jonckheere's trend test: $S = 124$, $C = 4$, $N = 7$, $P < 0.01$; Fig. 2c). In general, the dominant fish emerged from the start compartment the most quickly followed by males ranked 2, 3 and 4. Fish ranked 1 emerged more quickly than those ranked 4 (Fishers PLSD: $P = 0.032$). Dominant fish (rank 1) also spent more time near the novel object during the first 5 min than all the other fish (Fisher's PLSD: 1 versus 2: $P = 0.038$; 1 versus 3: $P = 0.026$; 1 versus 4: $P = 0.030$). The trend test, however, was not significant because fish ranked 2-4 showed similar inspection levels (Jonckheere's trend test: $S = 8$, $C = 4$, $N = 7$, NS). When taken together, these two measures of boldness suggest that higher-ranked males had higher levels of boldness.

Experiment 3: Activity Level

Measurement of activity levels in the home tank showed a clear pattern. In general, the higher the rank of the fish in the hierarchy the higher its level of activity (Jonckheere's trend test: $S = 102$, $C = 4$, $N = 7$, $P < 0.05$; Fig. 2d). Fish from ranks 1 and 2 were significantly more active than fish ranked 4 (Fisher's PLSD: $P < 0.025$ in each case).

Morphology Measures

The analysis of the morphological measures showed a strong correlation between each of the variables (length, weight and body depth). Therefore we chose to conduct an ANOVA examining standard length and its relationship with fish rank. Despite trying to match the fish as much as possible in each group, size was still significantly related to dominance rank (ANOVA: $F_{3,24} = 3.792$, $P = 0.021$). Dominant fish were about 4 mm larger than subordinates (Fisher's PLSD: $P = 0.045$, 0.047 and 0.004 for fish ranked 2, 3 and 4, respectively), although no differences were observed in the standard length of fish ranked 2, 3 or 4. No significant correlations were found between the morphology traits and all the other behavioural traits.

Regression Analysis

Despite the link between activity, boldness, aggression and the position in the hierarchy, not all of these behaviours were correlated with each other. In fact, we only found a significant correlation between activity in the home aquarium and boldness scores (linear regression: t = 2.278, $P = 0.031$). Bolder fish were more active than shy fish. There were no significant relationships between activity and aggressiveness or boldness and aggressiveness ($t = 1.121$, $P = 0.136$ and $t = 0.937$, $P = 0.179$, respectively).

DISCUSSION

Personality traits are becoming increasingly important in explaining individual differences in the behaviour of animals (Wilson 1998; Gosling 2001). Almost by definition, personality traits represent a leading edge of the evolutionary process since natural selection acts directly on variation of individual phenotypes within populations. Surprisingly few studies have investigated the link between personality traits and fitness-related variables (great tits: Dingemanse et al. 2003; fish, *Brachyrhaphis episcopi*: Brown et al. 2007; sheep, *Ovis aries*: Reale et al. 2009). Here, we have shown that a range of personality traits (aggression, activity and boldness) all contribute to a male's position in a social hierarchy. Highly ranked individuals have the highest reproductive output because of their ability to dominate access to resources in social contexts (Ellis 1995; Young et al. 2010). Moreover, we have shown that activity levels in the home tank and boldness were significantly correlated suggesting that an activity-boldness-hierarchy rank syndrome exists in male rainbowfish. Our results suggest that personality traits predict the outcome of male-male competition that determines access to females and thereby male reproductive success. The correlations between these traits, therefore, may be the product of sexual selection (Wolf et al. 2007; Biro & Stamps 2008).

In male rainbowfish, we found a correlation between activity levels in the home aquaria and boldness as measured as the tendency to emerge into a novel arena and approach a novel object. Such correlations have been revealed previously in some populations of sticklebacks and zebrafish, *Danio rerio*, but not others (Huntingford 1976; Bell 2005; Moretz et al. 2007; Dingemanse et al. 2007). Both Huntingford (1976) and Dingemanse et al. (2007) suggested that variation in predation regime was driving the coevolution of certain traits, because correlations between activity and boldness only existed in populations subject to high levels of predation. Here, we have shown that co-evolution of these behavioural traits may also emerge in a completely different context, that of interindividual conflict. Competition for limited resources such as food and mates is often fierce among individuals. Although obtaining a high position in the hierarchy has multiple benefits in male fishes, competition is primarily over access to females, since males tend to be motivated by sex rather than by hunger (Griffiths & Magurran 1998). Thus, we suggest that correlations across personality traits can be driven by competition between conspecifics, potentially by sexual selection, and are therefore domain specific. Similar observations have been made in three strains of captive-reared zebrafish (Moretz et al. 2007) which suggests that such trait

correlations can be maintained even under captive conditions. Further work is clearly required to isolate the relative importance of natural versus sexual selection in shaping the evolution and development of correlated behavioural traits.

The widespread appearance of the boldness-aggressiveness syndrome across a range of species has encouraged the search for a single underlying hormonal or genetic mechanism (Veenema et al. 2003). Boldness scores in males are typically higher than those in females across a range of species including humans (Wilson et al. 1994) and are related to testosterone levels (Daisley et al. 2005). Experimental enhancement of testosterone in dark-eyed juncos, *Junco hyemalis*, increased spatial activity and aggression relative to controls (Chandler 1994). Bolder male guppies are also more aggressive than shy males (Huntingford 1976; Bell 2005; Dingemanse et al. 2007). Not surprisingly, such traits are also linked to dominance status in social groups. Male rainbowfish are both larger and more colourful than females. During the breeding season, males are highly active, chase off rivals, pursue and display to females. Moreover, mate choice experiments show that male display rate, which is characterized by high levels of activity, is a good predictor of female preference and male quality in this and other fish species (Nicoletto 1993; Matthews et al.1997; Collins 1999). Females also prefer to mate with larger males and larger males are often the victor in male-male encounters (Collins 1999; Evans et al. 2010; Young et al. 2010). Thus it makes intuitive sense that activity, boldness and aggressiveness levels are a good indicator of a male's position in the hierarchy and elevated activity is probably indicative of underlying androgen levels. It is likely, therefore, that correlations between boldness and activity are driven by a common underlying hormonal mechanism. Thus there is emerging evidence that boldness, aggression and activity may all be linked to androgen levels across a range of taxa.

Intriguingly, aggression was not significantly correlated with activity levels or boldness despite the fact that all three factors explain some of the variation in male hierarchy rank. There are several possible reasons to explain this result. First, aggressiveness and activity were scored in the presence of conspecifics whereas the boldness measures were recorded in isolated fish. There is emerging evidence that the expression of personality traits varies with social context (Ward et al. 2004; van Oers et al. 2005; Webster et al. 2007). For example, pairs of bold fish might show signs of positive feedback thus causing them to behave more boldly when tested together, whereas pairs of shy fish show the opposite effect (Brown & Laland 2002). During our staged dyadic interactions, a relatively aggressive fish could face another aggressive individual, so both fish might escalate the conflict and express very high levels of aggression. Obviously, the opposite would occur if an aggressive individual confronted a nonaggressive individual. To counteract this potential problem to some extent, we recorded aggression across three interactions with different males. Nevertheless, one of our seven social groups showed very low levels of aggression across the board. The most aggressive male in this group displayed aggressive behaviours that were more symptomatic of fish ranked 3 and 4 in the other social groups. Previous authors have tested aggression by examining the number of displays to a mirror image or responses to model invaders (e.g. Peeke et al.1969; Clotfelter & Kuperberg 2007), but these methodologies, while testing individuals in isolation, still have problems with feedback loops. In addition, the composition of the shoal in the home tank from which the males were drawn could have had a strong impact on male aggressive behaviour owing to prolonged winning and losing effects (Hsu et al. 2006).

To conclude, once aggressiveness scores were assigned to individuals, we were able to illustrate how aggressiveness, boldness and activity levels co-varied with a male's position in the hierarchy. Dominant males were bolder, more active, more aggressive and slightly larger than subordinate males. While female rainbowfish are choosy if given the opportunity, males compete heavily for females and dominant males tend to monopolize access to females (Collins 1999; Young et al. 2010). In this way, male dominance leads to a form of mate guarding which increases their reproductive success (Birkhead 1987;

Warner et al. 1995; Reavis 1997). Like predation pressure, high levels of competition can have dramatic impacts on the evolution of behavioural traits (Hamilton 1964; West-Eberhard 1979). In the case of male rainbowfish it appears that intrasexual selection is the most likely driving force behind the coevolution of behavioural traits that comprise the boldness-activity syndrome. Clearly, further work needs to be conducted to illuminate the links between life history strategies and personality traits, and in particular, how they are shaped by natural and sexual selection.

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