

Causes and consequences of contest outcome: aggressiveness, dominance and growth in the sheephead swordtail, *Xiphophorus birchmanni*

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Received: 9 February 2013 / Revised: 8 April 2013 / Accepted: 8 April 2013 / Published online: 23 April 2013
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Abstract Although our understanding of how animal personality affects fitness is incomplete, one general hypothesis is that personality traits (e.g. boldness and aggressiveness) contribute to competitive ability. If so, then under resource limitation, personality differences will generate variation in life history traits crucial to fitness, like growth. Here, we test this idea using data from same-sex dyadic interaction trials of sheephead swordtails (*Xiphophorus birchmanni*). In males, there was evidence of repeatable variation across a suite of agonistic contest behaviours, while repeatable opponent effects on focal behaviour were also detected. A single vector explains 80 % of the among-individual variance in multivariate phenotype and can be viewed as aggressiveness. We also find that aggressiveness predicts dominance—the repeatable tendency to win food in competition—and dominant individuals show faster post-trial weight gain (independently of initial size). In females, a dominance hierarchy predictive of weight gain was also found, but there was no evidence of variation

in aggressiveness. While size often predicts contest outcome, our results show that individuals may sometimes grow larger because they are behaviourally dominant rather than vice versa. When resources are limited, personality traits such as aggression can influence growth, life history, and fitness through impacts on resource acquisition.

Keywords *Xiphophorus* · Personality · Aggression · Dominance · Resource-dependence · Competition

Introduction

In animals, personality variation is defined by the expression of behavioural differences among individuals, which are repeatable across time and context (Sih et al. 2004; Réale et al. 2007; Biro and Stamps 2008). Major axes of personality such as shyness–boldness, aggressiveness, and sociability have been characterised in many taxa and are presumed to have major ecological significance (Réale et al. 2007; Smith and Blumstein 2008). There is also evidence that personality can be heritable in wild animal populations (van Oers et al. 2004; Dingemans et al. 2009; Wilson et al. 2009). Although there is increasing interest in how (genetic) variance of personality might be maintained in a population (Penke et al. 2007; Schuett et al. 2010), the relevance of this question presupposes that personality traits are under strong selection expected (at least naïvely) to erode variance. Although a number of studies have attempted to directly estimate selection on personality (Dingemans and Réale 2005), and meta-analysis suggests that relationships to fitness may be common (Smith and Blumstein 2008), comparatively little is known about the causal basis of personality–fitness covariance (Dingemans and Réale 2005; Dall et al. 2012).

One hypothesis is that personality traits (e.g. aggressiveness and boldness) are linked to resource acquisition under

Communicated by N. Dingemans

Electronic supplementary material The online version of this article (doi:10.1007/s00265-013-1540-7) contains supplementary material, which is available to authorized users.

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competitive conditions (Colleter and Brown 2011). If so, then personality differences could be an important source of variance for those resource-dependent life history traits (e.g. growth, fecundity, and survival) that determine lifetime fitness (Stamps 2007; Biro and Stamps 2008; Wilson 2013). For example, all else being equal, aggression is often a good predictor of social dominance which we define as an individual's repeatable tendency to win contests (Wilson et al. 2011b). Thus, we might predict that more aggressive individuals will be able to monopolise a limited food resource and will therefore exhibit faster growth than their less aggressive competitors.

An important caveat to the above argument is while behavioural aggression can be used to assert dominance, it is not the same as dominance (Francis 1988). Frequently competitors differ in aspects of morphology that are indicative of resource holding potential (RHP)—the ability of an individual to win a fight (Parker 1974). Assessment strategies are therefore expected to evolve, permitting individuals to adaptively moderate behavioural aggression and avoid engaging in costly fights they are unlikely to win (Arnott and Elwood 2009). As a commonly used indicator of RHP, there is considerable empirical evidence that size causally influences observed contest behaviour and outcome, with larger individuals tending to win (Huntingford and Turner 1987). Thus, while differences in aggressiveness are predicted to generate size variation (via effects on resource acquisition), size differences among competing individuals are also predicted to be a cause of behavioural variation. Here, we seek to disentangle these pathways experimentally in a study of aggression in sheepshead swordtail (*Xiphophorus birchmanni*), a freshwater poeciliid fish.

Aggression in *Xiphophorus* fishes has been extensively studied in the context of sexual selection, with males holding territories and defending themselves from rivals in order to gain mating opportunities (Franck and Ribowski 1993; Franck et al. 1998). However, food availability also influences contest behaviour, suggesting that male–male aggression also mediates competition over food resources (Magellan and Kaiser 2010). Previous work on this genus has highlighted how aggression and dominance can depend on prior experience (Beaugrand and Goulet 2000), social eavesdropping (Earley and Dugatkin 2002), and body and/or ornament size (Prenter et al. 2008). However, there is also increasing evidence that personality plays a role in determining contest success in animals generally (Mowles et al. 2012; Rudin and Briffa 2012). In recent study of male *Xiphophorus hellerii*, Wilson et al. (2011a) found evidence of repeatable among-individual differences in aggressiveness as indicated by a suite of agonistic behaviours. Although this study also found that focal individuals responded plastically to opponent size, for example smaller fish are less likely to attack a larger opponent (Wilson et al. 2011a),

repeatable behavioural variation could not be explained by size effects alone.

In what follows, we seek to disentangle the causal relationships between aggressiveness, resource acquisition, size, and growth. In particular, we ask whether the functional relationship between behaviour and morphology should properly be viewed as bi-directional. In other words, to what extent might among-individual differences in contest behaviour be a cause as well as a consequence of morphological variation? We address this question by applying a novel multivariate mixed model framework to data from dyadic interaction trials conducted using wild-caught *X. birchmanni*. Crucially, our modelling approach allows us to directly characterise the repeatable component of multivariate behavioural (co)variation in line with recent recommendations for studies of personality (Dingemanse and Dochtermann 2013) while also modelling contest behaviours (and outcomes) as being dependent on the phenotypes of both individuals in the dyad (Wilson et al. 2011a).

We test three specific hypotheses: (1) individual *X. birchmanni* shows repeatable patterns of (co)variation among agonistic behavioural traits consistent with an underlying personality axis of aggressiveness; (2) aggressiveness is positively correlated with dominance (independently of size), defined as the repeatable ability to acquire limited resources under competitive conditions; and (3) dominance predicts weight gain (independently of initial size), consistent with the expectation that those individuals best able to monopolise food resources will grow faster. Since competition for a food resource is not a sex-specific phenomenon, we test these hypotheses in both males and females. We note that much less is known about the prevalence and function of female aggression in *Xiphophorus*, although female–female aggression has been reported in some poeciliids (Magurran and Seghers 1991; Foran and Ryan 1994; Makowicz et al. 2010; Archard and Braithwaite 2011), as has the formation of female dominance hierarchies (Chen et al. 2011).

Methods

Livestock and husbandry

Mature adult *X. birchmanni* were collected using baited minnow traps from the Arroyo Coacuilco near the town of Coacuilco, municipality of San Felipe Orizatlán, Hidalgo, Mexico (elevation 314 m, latitude 21.099°, longitude –98.587°), with permission from the Mexican federal government. After importing to the UK in February 2010, they were maintained in a fish facility with water at 22–24 °C and a 12:12 light/dark cycle. Aquaria used for housing were enriched with rocks and plants, and the fish were fed twice daily with a standard ration of commercial flake

and frozen foods (brine shrimp, bloodworm, and daphnia). Individuals were not fed in the morning when they were to be used in a trial that day.

During the period of behavioural data collection (3 May to 10 June 2010), half of the fish (of each sex) were kept housed in small groups (comprising a single male with two to three females), while the half were kept individually. Those fish housed individually were kept in tanks partitioned into two sections using opaque dividers. Thus, each animal was kept physically and (partially) visually isolated from a single same-sex tank mate. Tank mates were assigned to different experimental blocks (see below) and so did not meet each other in trials. Flow-through filtration systems were used so there was no chemical isolation of fish. The alternative housing conditions were necessary for stock management in the context of controlled breeding for a separate study. While not directly relevant to any hypotheses tested here, differences in housing conditions are controlled for statistically in all analyses. At the end of the behavioural data collection, all fish were moved to group housing conditions (each group comprising a single male with three females) and maintained in this way over a 4-month post-trial period.

Dyadic trials of contest behaviour and outcome

Behavioural data were collected from a total of 224 same-sex dyadic trials (112 male–male and 112 female–female) conducted between 3 May and 10 June 2010. In each dyadic trial, behavioural data were collected for one fish only. We term this the *focal* individual, while the second fish is the *opponent*. Our experimental design was based on 32 fish (16 males and 16 females), each taking part in a total of 14 trials (7 as the focal and 7 as the opponent). For logistical reasons, the fish were assigned to blocks of eight individuals (i.e. 2 blocks per sex), and the trials were conducted using all possible within-block pairings. Trials were ordered such that all dyads comprised fish with equal experience (i.e. prior number of trials). The blocking and ordering ensured that all fish were rested for a minimum of 48 h between trials, a time period sufficient to minimise winner–loser effects (Prenter et al. 2008). Once all possible pairings within each block had been trialled, the dyads were repeated in a different (randomised) order, with the focal/opponent designation reversed. Thus, each fish met every other individual in its block on two occasions, once as focal and once as opponent. The time between two trials using a repeated pairing ranged from 18–21 days. We assume that behavioural data from these repeated pairings are independent (conditional on the focal and opponent effects as modelled; see below). The eventual data structure deviated from this design slightly due to mortality of three individuals during the testing period, which were replaced with stock fish.

Consequently, we actually used 35 individuals over the 224 trials (with an average of 12.8 trials per fish). All fish were individually identifiable based on a combination of home tank, natural colour markings, and gross morphology (i.e. size).

The trials were conducted in a glass aquarium (30×20 cm) filled to a depth of 8 cm with water at 25 °C (±1 °C) and partitioned into two equal volumes with an opaque polystyrene divider. The aquarium was visually screened from the experimenter and filmed using a Sunkwang C160 video camera mounted overhead. The fish were introduced on either side of the divider (with the focal on the left and opponent on the right) and allowed to acclimate for a period of 300 s. The divider was then removed, and the following period of 300 s (males) or 180 s (females) was recorded for behavioural analysis. The decision to use a shorter observation period in female trials was made following pilot work that indicated escalated agonistic interactions were unlikely to be observed between females (even given extended trials of up to 10 min). Although this potentially confounds any effects of total observation time with those of sex, male and female patterns of behaviour were so distinct as to make this a moot point (see “Results” section).

At the end of the observation period, the fish were subjected to a feeding trial in which prey items were introduced to the tank using a device comprising five plastic syringes inserted into a clear plastic tank cover (one in each corner and one in the centre). Each syringe was loaded with a single prey item (a previously frozen adult brine shrimp) in a small volume of water and connected via a manifold to an air pump. The cover was placed over the tank, and the camera was switched to a lateral view; after which, the experimenter retreated behind the visual screen and opened the manifold valves in a haphazard order. This resulted in prey items being introduced (at approximately 30-s intervals) in an unpredictable order with respect to spatial location. The number of prey items consumed by the focal individual was recorded and used as a measure of success in gaining resource (i.e. food) in a competitive context. Both fish were then returned to their respective home tanks, and the water was changed prior to starting the next dyadic trial.

After all trials were run, focal behaviours expressed during the dyadic observation period were scored from video using the keylogger software Jwatcher 0.9. Specifically, we recorded the (1) number of approaches to opponent, (2) number of lateral displays performed to opponent, (3) total time spent in lateral display, (4) number of attacks on opponent (characterised by a sudden forward acceleration towards the opponent that may or may not result in contact), (5) latency to attack (scored as trial duration if no attack was made), (6) number of retreats from opponent, and (7) number of flees from opponent. These behaviours are described in full in Wilson et al. (2011a) and were scored according to the ethogram presented there.

We square root-transformed all count data as well as time spent displaying to better meet the assumption of (multivariate) residual normality inherent in the modelling methods (described below). We also multiplied latency to attack by -1 such that a higher phenotypic value reflects a more escalated action. All (transformed) traits were then standardised to sex-specific unit variance to ease interpretation. Thus, unless stated otherwise, all results pertain to analyses of transformed traits expressed in sex-specific standard deviation units.

Size and weight gain

To obtain an estimate of size with minimal handling stress, we measured live weight by placing each animal in a beaker of water set on a tared electronic balance at the end of each trial. We defined the post-experiment *weight gain* as the natural log of the ratio of a single weight measurement in early October of 2011 (approximately 4 months from the end of trials) to the mean weight of an individual during the trial period such that $\text{weight gain} = \text{Ln}(\text{WT}_{\text{Oct}}/\overline{\text{WT}}_{\text{trial}})$. Defined in this way, the relative post-trial weight gain should be statistically independent of absolute size (measured as weight during the trial period). Repeated measures of individual length were not made, and we must therefore remain agnostic about the relative contributions of skeletal growth and condition change to weight gain, but note that it may differ between the sexes: females show indeterminate growth, but males stop, or at least dramatically slow, their growth (as measured by length) at maturation (Meffe and Snelson 1989). As noted above, all fish used were mature (based on visual assessment) but of unknown age. Female weight is also expected to depend on reproductive status, though this source of uncontrolled variance is not expected to bias any analyses.

Data analysis and modelling

We modelled the data using linear mixed-effect models, following the general approach developed and presented didactically in Wilson et al. (2011a). Briefly, for the case of a single response variable, inclusion of individual identity as a random effect in a mixed model allows partitioning of observed variance into a repeatable (among-individual) component and an among-trial component. The among-individual variance quantifies the magnitude of consistent behavioural differences among individuals. The among-trial (or residual) variance component captures variation due to trial-specific effects and/or measurement error. For the case of dyadic interactions, we extend this approach by including random effects of both focal and opponent identities. We hypothesise that focal behaviours will be influenced by opponent phenotype, and we can test this by estimating the

among-opponent (as well as among-focal) variance component. We also explicitly model covariance that may be present between focal and opponent effects if, for example, a fish that consistently behaves aggressively as a focal individual also has a consistent effect on the behaviour of others when acting as the opponent (following Wilson et al. 2011a).

By analysing all the dyadic behaviours in a single multivariate model, we then partitioned not only the variance for each trait but also the covariance among behaviours. For a set of traits, the among-individual variation in the multivariate behavioural phenotype can be described by estimating the variance–covariance matrix among all repeatable focal and opponent effects. We subsequently refer to this matrix as **I**. Since the (transformed) behaviours were expressed in standard deviation units, the diagonal of matrix **I** actually contains the estimated repeatabilities (i.e. the proportion of phenotypic variance explained by individual identity). Note that for each dyadic behaviour, a focal (R_F) and an opponent repeatability (R_O) were estimated. The among-trait covariance structure of **I** was further explored by principal component analysis (eigen decomposition). This technique characterises the covariance matrix **I** as a set of uncorrelated, orthogonal axes of variation, each explaining a diminishing amount of variation. By doing this, we were able to assess whether the structure of **I** is consistent with a single major axis of variation in individual aggressiveness as hypothesised.

Additional (bivariate) mixed models were then used to test the hypothesised relationships between the repeatable components of individual contest behaviour and dominance, weight (during the trial period), and post-trial weight gain. We define dominance as the repeatable ability of an individual to do well in contests. This can be determined in practice as the random effect of focal identity on the number of prey items gained during the feeding trial. This is consistent with standard definitions, except that our measure of contest winning is quasi-continuous (a count) rather than binary (win/lose). As with the dyadic contest behaviours, we expect that opponent identity will also influence contest outcome. In fact, since a dominance phenotype that predisposes a focal individual to win necessarily predisposes to losing (and by an equal amount) when encountered in an opponent, it follows that focal and opponent effects on contest outcome have a perfect negative genetic correlation. This was ensured by constraining the model parameters such that, for contest outcome only, $V_{\text{FOC}} = V_{\text{OPP}} = -\text{COV}_{\text{FOC,OPP}}$ (see Wilson et al. (2011b) for a quantitative genetic formulation of this model). We assumed a normal error structure for models of contest outcome which cannot strictly be true since the response variable is a count. However, visual inspection of model residuals showed a strong central tendency and suggested that this assumption is not unreasonable.

In addition to random effects of individual identity, all models included fixed effects of the mean, *housing condition*

(a four-level factor defined by the interaction of focal and opponent conditions) and trial *order* (to account for any within-individual habituation). For analyses where male and female data were combined (see below), a fixed effect of *sex* was included, as well as its interactions with housing condition (*sex X housing condition*) and trial order (*sex X order*). Statistical inferences were based on conditional Wald *F*-tests for fixed effects and likelihood ratio tests (LRT) for random effects. For testing single variance components estimated from univariate models, we assumed the LRT test statistic was distributed as a 50:50 mix of χ^2_1 and χ^2_0 (following Visscher (2006)). Where nested multivariate models were compared, we took the more conservative approach of assuming a distribution of χ^2_n (where *n* is the number of additional covariance components in the more complex model). All mixed models were fitted by restricted maximum likelihood using ASReml version 3.

Results

Not unexpectedly, males and females showed very different patterns of agonistic behaviour during the dyadic trials (Fig. 1). Some behaviours were never observed in female trials (displays and flees), and others only very rarely (attacks). Approaches were observed in females (Fig. 1), though observed rates (estimated as count/trial length) were much lower than those in males (female median 0.33 approaches min^{-1} , male median 1.0 approaches min^{-1} , Wilcoxon rank test $W=9508.5$, $P<0.001$). Similarly, retreats

were observed in female–female trials but much less often than in males (female and male median rates of 0.33 and 0.80 retreats min^{-1} , respectively, $W=9064$, $P<0.001$). As a consequence of such large differences in average behaviour among the sexes and the lack of defined variance for female traits that were not expressed, we formulated sex-specific multivariate mixed models of the dyadic contest behaviours.

Among-male variation in contest behaviour

Univariate models supported the presence of repeatable focal variation in male agonistic behaviours. Across behavioural traits, estimates of focal repeatability (R_F) ranged from 0.078 to 0.474 and were statistically significant for all traits except fleeing ($R_F=0.078$ (SE=0.079), $P=0.104$) (Table 1). It is worth noting, however, that flees were rarely observed (Fig. 1), and even after square root transformation, the model residuals for this trait showed major deviations from assumed normality. As such, all statistical inferences related to this trait should be treated cautiously. Estimates of opponent repeatability (R_O) were generally lower, ranging from 0.023 to 0.271, but were nonetheless significantly greater than zero for the number of displays, time displaying, and retreats. Marginally non-significant opponent effects were also estimated for flees ($R_O=0.101$ (0.091), $P=0.054$). The univariate models also indicated significant effects of trial order on all agonistic traits (with a consistent tendency towards higher levels of aggression over the study), but not on retreating or fleeing. No significant effects of housing regime were found (supplemental Table 1).

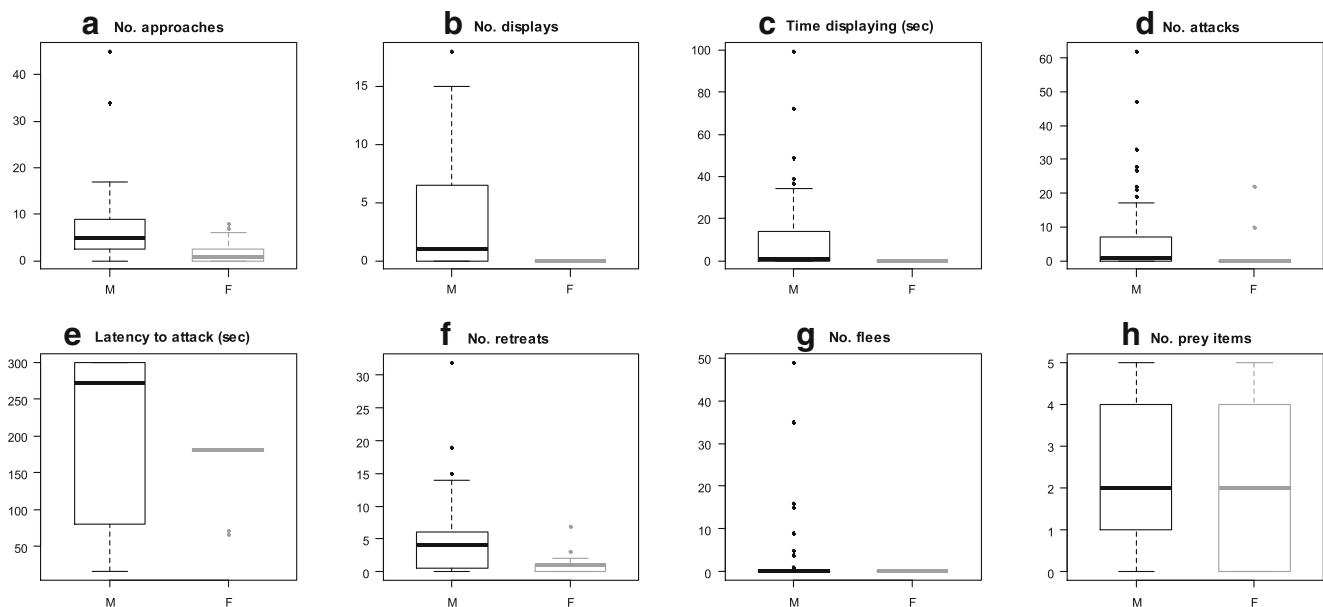


Fig. 1 Box plots showing distributions of observed (i.e. untransformed) focal traits in male (*M*, black) and female (*F*, grey) dyadic interaction trials. Note that female trials were of shorter duration than male trials, and no statistical comparison is intended here. Horizontal lines indicate the

trait median; boxes contain the inter-quartile range, and whiskers extend to the most extreme data point that is no more than the inter-quartile range from the box. Outliers beyond these whiskers are denoted by solid points

Table 1 Focal (R_F) and opponent (R_O) repeatabilities for (transformed) behaviours in same-sex dyadic trials

| Sex | Response | R_F (SE) | P | R_O (SE) | P |
|--------|-----------------------------------|---------------|--------|--------------------|--------|
| Male | $\sqrt{(\text{no. approaches})}$ | 0.459 (0.204) | <0.001 | 0.048 (0.052) | 0.119 |
| | $\sqrt{(\text{no. displays})}$ | 0.344 (0.166) | <0.001 | 0.111 (0.079) | 0.019 |
| | $\sqrt{(\text{time displaying})}$ | 0.252 (0.136) | 0.001 | 0.124 (0.088) | 0.020 |
| | $\sqrt{(\text{no. attacks})}$ | 0.442 (0.198) | <0.001 | 0.023 (0.046) | 0.301 |
| | $-(\text{latency to attack})$ | 0.474 (0.208) | <0.001 | 0.044 (0.050) | 0.152 |
| | $\sqrt{(\text{no. retreats})}$ | 0.155 (0.092) | 0.002 | 0.271 (0.134) | <0.001 |
| Female | $\sqrt{(\text{no. flees})}$ | 0.078 (0.079) | 0.105 | 0.109 (0.091) | 0.054 |
| | $\sqrt{(\text{no. approaches})}$ | 0.152 (0.104) | 0.014 | 0.064 (0.074) | 0.135 |
| | $\sqrt{(\text{no. attacks})}$ | 0.078 (0.078) | 0.100 | 0 (–) ^a | 0.500 |
| | $-(\text{latency to attack})$ | 0.096 (0.083) | 0.055 | 0 (–) ^a | 0.500 |
| | $\sqrt{(\text{no. retreats})}$ | 0.089 (0.091) | 0.112 | 0.003 (0.058) | 0.479 |

Estimates (with standard errors) are from univariate models, and the P values are based on one-tailed likelihood ratio tests (comparing full model to one in which the corresponding focal or opponent effect was omitted)

^aA parameter estimate was bound, and standard error is not estimable

Additional support for focal and opponent effects was provided by a series of multivariate models fitted to the male data. We first modelled \mathbf{I} as an unstructured matrix containing focal effects only (i.e. allowing focal repeatability and within-focal individual covariances). This model provided a significantly better fit to the data than a null model containing fixed effects only ($\chi^2_{28}=72.5$, $P<0.001$). Inclusion of opponent effects (including among-trait within-opponent covariance terms) resulted in a marginally non-significant improvement to model fit ($\chi^2_{28}=41.0$, $P<0.053$), though the likelihood ratio test applied is conservative (in that it is two-tailed with respect to variance, as well as covariance, components) (Visscher 2006). Taken together with the results from the univariate models, we view this as providing support for repeatable opponent effects on at least some aspects of the observed male behavioural phenotype.

Finally, we estimated \mathbf{I}_{male} as the full covariance matrix among all individual-level effects, such that covariance terms between focal and opponent effects (within and among-traits) were also modelled (Fig. 2). Unsurprisingly, given the enormous number of addition parameters required (49), overall fit was not significantly improved relative to the preceding models including opponent effects alone ($\chi^2_{77}=73.9$, $P=0.577$) or focal and opponent effects ($\chi^2_{49}=32.9$, $P=0.962$). However, inspection of approximate standard errors suggests that specific correlations between focal and opponent effects may well be significant (based on $|r_{FO}|>2$ SE) for a number of trait pairs (Fig. 2). Furthermore, since the full model gives the least assumption-laden estimate of \mathbf{I}_{male} , we use estimates from the full model to base our qualitative interpretations of the repeatable multivariate phenotype.

The overall structure of \mathbf{I}_{male} is consistent with a major axis of among-male variance in aggressiveness. There is a uniformly positive covariance/correlation structure among focal effects on traits expected to reflect aggression (e.g. $r_F=0.980$ (0.040) between $\sqrt{(\text{no. attacks})}$ and $\sqrt{(\text{no. displays})}$), while individuals

that attack more are also less likely to retreat or flee from an opponent (e.g. $r_F=-0.658$ (0.304) between $\sqrt{(\text{no. attacks})}$ and $\sqrt{(\text{no. retreats})}$). Eigenvector decomposition of the full variance-covariance matrix revealed that almost 80 % of the total variance in the repeatable component of behavioural variation was explained by the first vector (Table 2). This axis of among-individual variation is characterised by loading coefficients of equal sign (and similar magnitude) for focal effects on $\sqrt{(\text{no. approaches})}$, $\sqrt{(\text{no. displays})}$, $\sqrt{(\text{time displaying})}$, $\sqrt{(\text{no. attacks})}$, and $-(\text{latency to attack})$, while the loading coefficients for $\sqrt{(\text{no. retreats})}$ and $\sqrt{(\text{no. flees})}$ have opposing signs.

We therefore consider that the first eigenvector of \mathbf{I}_{male} can be viewed as aggressiveness. A more aggressive fish has a higher propensity to approach an opponent, displays more often (and for longer), attacks more often (and more rapidly), and is less likely to retreat or flee. Individuals that are more aggressive as focal fish also tend to cause more retreats and flees when acting as an opponent (Table 2). Interestingly, such individuals also tend to induce more displaying when acting as an opponent. We interpret this as being consistent with the observation that lateral displays are reciprocal behaviours (i.e. a display by one male frequently elicits a display). This view is consistent with the strong positive estimates of the focal-opponent effect correlations for $\sqrt{(\text{no. displays})}$ and $\sqrt{(\text{time displaying})}$ which were estimated as $r_F=0.852$ (0.290) and as $r_{FO}=0.896$ (0.370), respectively.

Among-female variation in contest behaviour

Modelling of female data was necessarily limited to those behaviours seen (approaches, attacks, latency to attack, and retreats). Univariate models provided support for significant among-focal individual variation in tendency to approach an opponent ($R_F=0.152$ (0.104), $P=0.014$), while the focal effect on latency to attack was marginally non-significant ($R_F=0.096$ (0.083), $P=0.055$). There was no evidence of

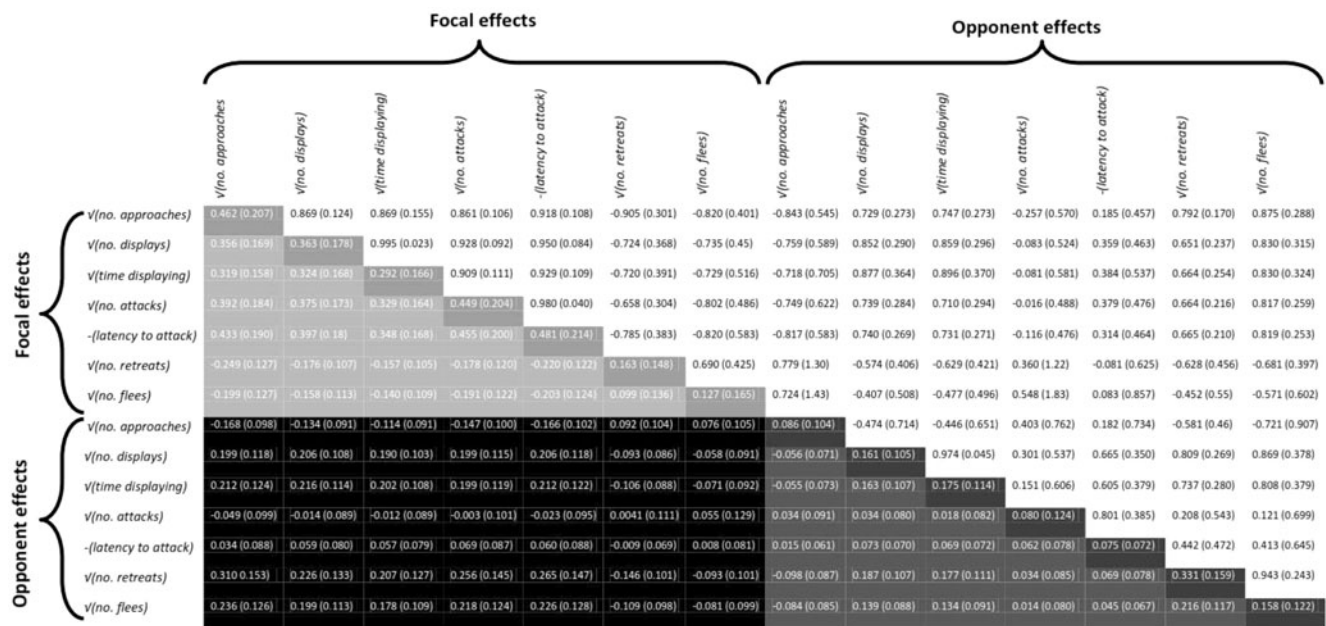


Fig. 2 Estimated variance–covariance matrix **I** for the repeatable component of male behavioural phenotype. Matrix sub-spaces are indicated for the focal effects (*light grey*) and opponent effects (*dark grey*), and for the sub-space containing elements corresponding to focal–opponent

effect covariances (*black*). Values on the *diagonal* represent trait-specific estimates of R_F and R_O . Corresponding correlation estimates are shown above the *diagonal*. Standard errors for all elements are indicated in *parentheses*

significant opponent identity effects, and indeed R_O estimates were actually fixed to zero for $\sqrt{(\text{no. attacks})}$ and $-(\text{latency to attack})$. Trial order effects show that attacks occurred more often and more rapidly in later trials

Table 2 Loading coefficients for the first three eigenvectors of I_{male} , which explain 79.7, 9.1, and 5.5 % of the total variance, respectively

| Response | Eigenvector | | |
|-----------------------------------|-------------|-------|-------|
| | 1 | 2 | 3 |
| Focal effects | | | |
| $\sqrt{(\text{no. approaches})}$ | 0.39 | −0.18 | −0.37 |
| $\sqrt{(\text{no. displays})}$ | 0.35 | −0.02 | 0.30 |
| $\sqrt{(\text{time displaying})}$ | 0.32 | 0.02 | 0.25 |
| $\sqrt{(\text{no. attacks})}$ | 0.38 | −0.09 | 0.33 |
| $-(\text{latency to attack})$ | 0.41 | −0.18 | 0.21 |
| $\sqrt{(\text{no. retreats})}$ | −0.20 | 0.18 | 0.31 |
| $\sqrt{(\text{no. flees})}$ | −0.17 | 0.33 | 0.00 |
| Opponent effects | | | |
| $\sqrt{(\text{no. approaches})}$ | −0.14 | 0.21 | 0.14 |
| $\sqrt{(\text{no. displays})}$ | 0.21 | 0.34 | 0.06 |
| $\sqrt{(\text{time displaying})}$ | 0.21 | 0.28 | 0.08 |
| $\sqrt{(\text{no. attacks})}$ | −0.01 | 0.45 | 0.15 |
| $-(\text{latency to attack})$ | 0.06 | 0.38 | 0.20 |
| $\sqrt{(\text{no. retreats})}$ | 0.28 | 0.40 | −0.58 |
| $\sqrt{(\text{no. flees})}$ | 0.22 | 0.19 | −0.21 |

(as with males). No significant housing effects were detected (see [Supplemental materials](#)).

Multivariate models added little further insight into female behavioural patterns. Focal effects on the multivariate phenotype as defined by the four observed behaviours were not statistically supported ($\chi^2_{10}=8.97, P=0.535$), while subsequent addition of opponent effects led to problems of model convergence that could only be overcome by constraining R_O and associated covariance terms to equal zero for $\sqrt{(\text{no. attacks})}$ and $-(\text{latency to attack})$ (consistent with univariate estimates). This did not significantly improve model fit relative to inclusion of focal effects alone ($\chi^2_3=2.39, P=0.494$). Based on these results, we conclude that statistically supported among-female variance in behaviour is limited to the trait of $\sqrt{(\text{no. approaches})}$ and do not present or further interpret I_{female} .

Behavioural and morphological correlates of dominance

Analysis of the *number of prey items* provided evidence of a dominance hierarchy in both sexes. In males, this measure of contest success was found to be significantly repeatable ($R=0.217 (0.098), P<0.001$). Our results were also consistent with the prediction that there would be positive relationships between aggressiveness and dominance and between aggressiveness and size, although statistical support varied among specific comparisons made. Thus, significant positive estimates of r_F were found between (no. prey items) and

$\sqrt{(\text{no. displays})}$, $\sqrt{(\text{time displaying})}$, $\sqrt{(\text{no. attacks})}$ and $-(\text{latency to attack})$ (Table 3). Though not statistically significant, correlations with focal tendency to approach and retreat were also qualitatively consistent with the expected aggressiveness–dominance relationship (Table 3). While weight is positively associated with aggressiveness overall, pairwise estimates of r_F again lack statistical significance for some behavioural traits (Table 3).

For males, a moderate positive within-individual correlation between weight and dominance was found, but it was not statistically significant (bivariate model of focal weight and (no. prey items), $r_F=0.480$ (0.276), $P=0.134$). Similarly, a linear effect of focal weight was not significant when added to the model of contest outcome (univariate model of (no. prey items); $\beta=0.124$ (0.090), $F_{1, 74.3}=1.9$, $P=0.175$) and resulted in little change to the repeatability estimate ($R_F=0.195$ (0.090), $P<0.001$). Thus, while the data show that heavier males do win more prey items on average (Fig. 3), this relationship is not statistically supported, and variation in size (weight) does not account for individual dominance status.

In females, contest outcome was also repeatable (univariate model of no. prey items, $R=0.128$ (0.068), $P<0.001$). Although the slightly lower estimate could indicate that the dominance relationships are less conserved across trials than those in males, the sex-specific estimates are not significantly different (likelihood ratio test, $\chi^2_1=0.568$, $P=0.451$). No significant correlations were found between dominance and focal effects on tendency to approach or flee (the only two behaviours characterised by R_F that were either statistically supported or close to being so; Table 3). The mixed model analysis yielded a within-individual correlation between dominance and weight ($r_F=0.004$ (0.334), $P=0.989$). As in males, focal weight did not predict contest outcome in a univariate model ($\beta=0.019$ (0.097), $F_{1, 86.1}=0.04$, $P=0.839$). Thus, weight does not explain dominance in females either.

Consequences of dominance status for post-trial growth

Fish of both sexes were on average heavier after the 4-month post-trial period (absolute mean weight changes of +0.553 and +0.330 g in males and females, respectively, both $P<0.01$ based on paired t tests). Males that were heavier during the trial period did gain weight more rapidly after, although this trend was marginally non-significant; regression coefficient=0.377 (0.186), $F_{1,12}=4.10$, $P=0.066$). In females, the corresponding regression was actually negative, though non-significant (regression coefficient=-0.125 (0.239), $F_{1,12}=0.27$, $P=0.610$).

We also found evidence that more dominant fish exhibited higher weight gain (Fig. 3a). Though not significant in females (based on estimated SE), estimates for the regression of growth on dominance were very similar in the two sexes ($\beta_{\text{male}}=1.635$ (0.667), $\beta_{\text{female}}=1.685$ (0.933)). We

therefore combined data from males and females to maximise our statistical power analyses, obtaining an estimate of $\beta=1.702$ (0.570) (reported above). As final check that size variation does not explain the observed relationship between dominance and post-trial weight gain, we re-estimated the regression of growth on dominance after conditioning both traits on size (mean weight during the trial period). This yielded an almost unchanged estimate of $\beta=1.817$ (0.609).

Discussion

Our results provide broad support for repeatable behavioural variation in *X. birchmanni* and are consistent with the hypothesised causal links between aggressiveness and dominance, and aggressiveness and weight gain. This suggests that personality traits, such as aggressiveness, may be important for generating variation in resource-dependent traits such as size, fecundity, and survival. However, there are also major differences between the sexes, both in their patterns of behavioural expression and in the extent to which our a priori hypotheses are supported. In what follows, we therefore discuss the principal results for males and females separately before addressing several general issues and caveats relating to our interpretation of the data.

In males, there is strong evidence of repeatable among-individual (co)variation in contest behaviour across the suite of agonistic behaviours observed in the dyadic trials. Furthermore, almost 80 % of the repeatable behavioural variance estimated within \mathbf{I}_{male} can be explained by a single axis through multivariate trait space. While acknowledging that autocorrelation may arise from trait definitions in a few instances (e.g. time spent displaying will increase with the number of displays), this is not a generally sufficient explanation for the geometry of \mathbf{I}_{male} . Along the dominant eigenvector of this matrix, expression of the agonistic behaviours changes in an integrated manner such that, for example, males displaying more often than average also attack more frequently but retreat less often. We therefore interpret this vector as aggressiveness and consider it to be an axis of personality variation. This follows from our view that across-trial repeatability of behaviour satisfies the criteria of consistency in both behavioural context and time (Sih et al. 2004; Réale et al. 2007). We also found that more aggressive males tended to be dominant, acquire more food resource in competition, and showed higher weight gain. Importantly, these results are robust to conditioning analyses on pre-existing size variation at the time of behavioural trials. Our data are thus consistent with the hypothesis of a causal dependence of growth (i.e. weight gain) on personality (i.e. aggressiveness), via the influence of the latter on resource acquisition under competition (i.e. dominance).

Table 3 Estimated within-focal individual correlations (r_F) of dyadic behaviours with contest outcome and weight

| Sex | Response | Dominance | | Weight | |
|--------|-----------------------------------|------------------|----------|------------------|----------|
| | | Correlation (SE) | <i>P</i> | Correlation (SE) | <i>P</i> |
| Male | $\sqrt{(\text{no. approaches})}$ | 0.571 (0.275) | 0.097 | 0.741 (0.151) | 0.004 |
| | $\sqrt{(\text{no. displays})}$ | 0.835 (0.236) | 0.019 | 0.479 (0.256) | 0.112 |
| | $\sqrt{(\text{time displaying})}$ | 0.803 (0.283) | 0.043 | 0.436 (0.290) | 0.182 |
| | $\sqrt{(\text{no. attacks})}$ | 0.688 (0.253) | 0.044 | 0.508 (0.229) | 0.070 |
| | $-(\text{latency to attack})$ | 0.690 (0.250) | 0.041 | 0.667 (0.179) | 0.012 |
| | $\sqrt{(\text{no. retreats})}$ | -0.497 (0.364) | 0.239 | -1.01 (0.105) | <0.001 |
| | $\sqrt{(\text{no. flees})}$ | -0.189 (0.563) | 0.749 | -0.721 (0.413) | 0.106 |
| Female | $\sqrt{(\text{no. approaches})}$ | -0.050 (0.445) | 0.913 | 0.967 (0.178) | 0.002 |
| | $-(\text{latency to attack})$ | -0.081 (0.499) | 0.872 | 1.03 (0.281) | 0.006 |

Correlations were only estimated with those behavioural traits for which focal effects were statistically significant (or marginally non-significant) based on results presented in Table 1. Standard errors are shown in parentheses, and *P* values are obtained from likelihood ratio tests comparing an unconstrained bivariate model to one in which the corresponding correlation estimate is fixed at zero

We also found that male aggressiveness manifests not only as a tendency to behave consistently but also as a tendency to induce consistent behaviour in others. R_O estimates tended to be lower than R_F which is intuitive—an observed behaviour depends more strongly on the identity of the animal performing it than the identity of the social partner. Although opponent effects on agonistic behaviours are well documented, most studies have focussed on the plastic responses of individuals to opponent phenotype (see Earley (2006) for a review of work in *Xiphophorus*). Here, post hoc testing of male data is suggestive of some opponent-size effects. For example, on average, focal individuals approached opponents that smaller than themselves more often, while there was also a (non-significant) trend towards attacking smaller opponents

more (see Supplemental materials). Provided that size indicates RHP and that losing a fight is costly, then behaving less aggressively towards a larger opponent should be adaptive (but see, e.g. Just and Morris (2003) for counterarguments). However, our analysis of male contest behaviour reveals that opponent effects can also be repeatable and may be correlated with focal effects on observed behaviours. In other words, if observed contest behaviours depend on both focal personality (Wilson et al. 2011a) and plastic responses to opponent morphology (e.g. body size and dorsal fin size) (Fisher and Rosenthal 2006) and signalling (Morris et al. 1995), they can also depend on opponent personality. This demonstrates the importance of recognising that observed social behaviours are expressions of multiple interacting phenotypes (Moore et

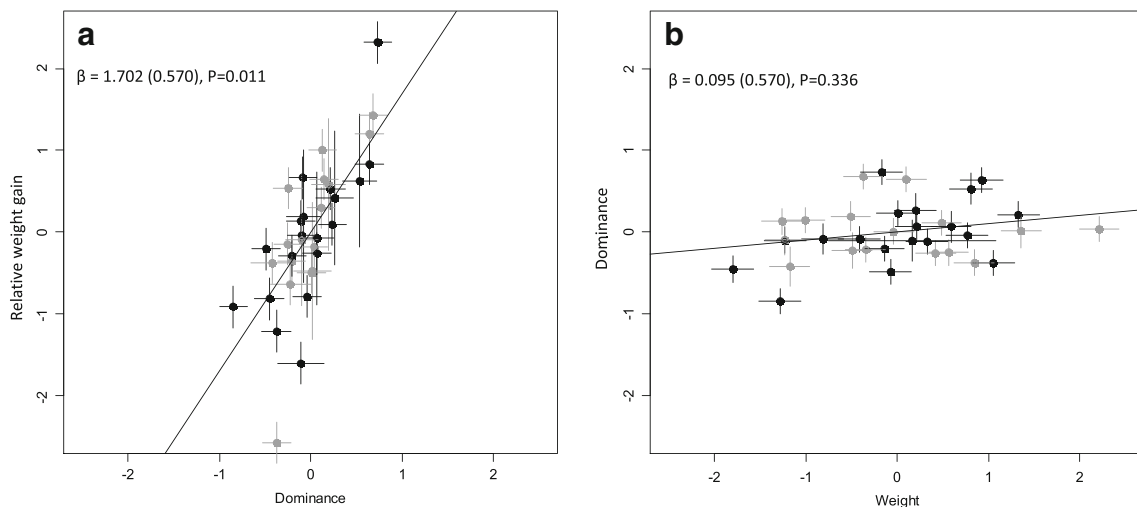


Fig. 3 Relationships between dominance, defined as the repeatable ability of an individual to win prey items, and both post-trial weight gain (**a**) and size (weight) during the trial period (**b**). *Black* (male) and *grey* (female) points show individual deviations from the fixed effect mean for each observed trait (in sex-specific standard deviation units).

Determined as the best linear unbiased predictions (BLUP) from a trivariate mixed model, these points are predicted with uncertainty. The bars show ± 1 standard error. Solid lines show the linear regressions of growth on dominance (**a**) and dominance on size (**b**) as estimated directly from the mixed model (not using the BLUP)

al. 1997) and by extension genotypes (Moore et al. 1997; Wilson et al. 2009).

In females, our data also provide evidence of a dominance hierarchy, and individuals able to acquire more food in dyadic trials gained weight more rapidly in the post-trial period. Dominance hierarchies have not been extensively studied in female poeciliids, though they are reported in some species (Foran and Ryan 1994; Chen et al. 2011). Here, we show that at least under laboratory conditions, dominance is likely to have downstream consequences for growth (i.e. weight gain). However, in females, we were not able to explain dominance status as a consequence of either size or aggressiveness. Clearly, the average level of contest escalation in female–female interactions is much lower than that in males (although attacks and flees are observed in our stock tanks). However, more pertinently, the failure of our experimental design to reveal substantial among-female behavioural variance makes it difficult to assess to what extent (if any) females vary in aggressiveness. Statistical support for behavioural repeatability was limited to the trait of (transformed) number of approaches. Though strongly correlated with more escalated aggression traits in males (e.g. displays and attacks), approaching behaviour in females could equally be viewed as indicative of boldness (i.e. willingness to approach novelty) or more general sociability (female swordtails show at least some degree of shoaling) (Wong and Rosenthal 2005). Regardless of how the approaching behaviour is interpreted—and we take no position on this—it does not predict dominance.

The above interpretation of our results makes two important assumptions that are worth drawing attention to. First, our inference of dominance assumes that food is limiting and that both individuals are motivated to consume it (or would be in the absence of the other). Across all trials, the number of uneaten prey items was low (median=0, mean=0.4 uneaten prey items), suggesting that this is not unreasonable. Second, our conclusion that dominant individuals gain more weight because they are better able to acquire food resource assumes that dyadic contest performance is a good measure of competitive ability in the larger groups in which fish were housed for the post-trial period. This may not always be the case, for example if complex social interactions such as coalition forming occur (Berghänel et al. 2011). Here, we were able to validate this assumption in a limited way using ad hoc observations of fish during routine feeding over the post-trial period. Specifically, by sequentially dropping five prey items into a home tank (at approximately 30-s intervals) and recording the number eaten by each fish, we were able to confirm that dyadic trials are at least predictive for performance in the mixed-sex post-trial housing groups ($r_T=0.756$ (0.263), $P=0.030$ from 96 observations of 16 individuals; full results not shown).

Overall, our results are certainly consistent with the view that variation in size (and/or condition) can be a consequence,

and not just a cause, of dominance. Similar findings have also been reported in juvenile Atlantic salmon, with relative weight failing to predict contest outcome after controlling for standard metabolic rate (which is correlated with dominance and aggression in this species) (Metcalf et al. 1995). In fact, despite the strong expectation from prior studies of *Xiphophorus* that bigger fish would be dominant (Earley 2006), we found only limited support for size-dependent contest success in our data. In females, there was no evidence of a positive relationship between size and dominance. In males, aggressiveness and size do positively covary in males, but the former is a better predictor of dominance than the latter. Thus, our results support the hypothesis that personality variation plays an important role in generating variance for fitness-related traits (Biro and Stamps 2008; Colleter and Brown 2011).

Factors causing variation in male aggressiveness found here are unknown but may ultimately include effects of age, experience or environment prior to capture, and genes. More proximately, behavioural variation between the sexes and among individuals could be driven by endocrine state (e.g. if more aggressive males have higher androgen levels). In the closely related pygmy swordtail, *Xiphophorus nigrensis*, variation in both male size and display behaviour is strongly associated with variation at the Y-linked *P* locus (Ryan et al. 1990; Lampert et al. 2010). Males with the “large” allele of *P* are much more likely to perform aggressive displays and initiate chases (Morris et al. 1992). Work to characterise the quantitative genetic basis of variation in the multivariate behavioural phenotype is ongoing for this specific population of *X. birchmanni*. Our study highlights one mechanism, whereby competition could induce a causal relationship between personality and fitness. However, quantifying the genetic basis of this relationship is necessary to fully understand its evolutionary consequences—both for the behavioural phenotype itself and for the evolution of resource-dependent life history traits.

Acknowledgments This work was funded by a BBSRC David Phillips Fellowship awarded to AJW. We thank the Mexican federal government for the permission to collect fish, and Holly Kindsvater, Olivia Ochoa, Gaston Jofre, and Palestina Guevara Fiore for their assistance with collection and transport. We also thank the technicians of the animal care facility at the University of Edinburgh for their assistance with husbandry.

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Ethics standards

All work described here was subject to approval by local ethical review (University of Edinburgh Local Ethical Review Committee) and conducted under the auspices of the Home Office (UK) under the Animals (Scientific Procedures) Act 1986. Criteria were in place to terminate any behavioural trial immediately in the event of physical injury or overt distress to any animal. This was not deemed necessary on any occasion, and no fish received physical injury during the experiments conducted.