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Heritable variation underlies behavioural types in the mating context in male bluefin killifish

Katie E. McGhee^{a,*} and Joseph Travis^b

^aSchool of Integrative Biology, University of Illinois at Urbana-Champaign, Urbana, IL, U.S.A

^bDepartment of Biological Science, Florida State University, Tallahassee, FL, U.S.A

Abstract

In many species, consistent behavioural differences among individuals are linked to fitness variation. Determining the environmental and genetic factors that mould these behavioural types is crucial to understanding how behaviours might respond to selection. Male bluefin killifish, *Lucania goodei*, show extensive consistent behavioural variation in their levels of courtship, male-directed aggression and female-directed aggression, resulting in a range of fitness-related behavioural types coexisting within a population. To determine whether the behavioural components underlying a male's stable behavioural type in the mating context are heritable and genetically correlated, we performed paternal half-sib crosses. Using animal models, we found that all three of these mating behaviours were moderately heritable ($h^2 = 0.17\text{--}0.29$) and courtship behaviour was also heritable as a binomial trait (court yes/no: $h^2 = 0.50$). Including effects of dam identity/common rearing environment experienced by full sibs decreased model fit, suggesting that early social interactions might contribute to behavioural types. In addition, we found evidence consistent with the possibility that the positive phenotypic correlations among mating behaviours are underlain by positive genetic correlations. Thus, it is possible that the seemingly maladaptive aggression that males direct towards females during social interactions persist due to genetic constraints and direct selection on both male-directed aggression and courtship behaviour.

Keywords

aggression; behavioural correlation; courtship; genetic variation; heritability; *Lucania goodei*; personality; sexual selection; social interaction

Unlike the case with their morphological and life history traits, individuals can often alter their behaviour in seconds in response to changing conditions. However, it is increasingly recognized that this behavioural plasticity can be limited. For example, some individuals tend to be consistently more aggressive, bold or exploratory than other individuals and these consistent behavioural types, or personalities, can extend across entirely different functional contexts (Sih et al. 2004a, c). That suites of behaviours are stably correlated with one

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*Correspondence: K. E. McGhee, School of Integrative Biology, University of Illinois at Urbana-Champaign, 433 Morrill Hall, 505 S. Goodwin Ave., Urbana, IL 61801, U.S.A. kemcghee@illinois.edu (K. E. McGhee).

Supplementary Material

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another (i.e. behavioural syndromes) opens the possibility that behavioural reactions to different stimuli are not independent of one another and thus that any individual's range of behaviours might be constrained (Sih et al. 2004a, c; Sih & Bell 2008).

Discerning how much of the phenotypic variation reflects underlying genetic variation is important to our inferences about how behavioural types might respond to selection (Dochtermann & Roff 2010; Dochtermann 2011). While a number of studies have found evidence for genetic variation in behavioural types (Dingemanse et al. 2009; Réale et al. 2009; Schielzeth et al. 2011; reviewed in: van Oers et al. 2005; Réale et al. 2007), stable behavioural tendencies can also be influenced by environmental conditions (Stamps & Groothuis 2010a, b). For example, behavioural types can be affected by abiotic environmental factors early in development (e.g. Carere et al. 2005; Arnold et al. 2007; Chapman et al. 2010) as well as by contemporary environmental conditions (e.g. Bolhuis et al. 2006; Biro et al. 2010; Pruitt et al. 2011). Similarly, there is accumulating evidence that behavioural types can be influenced by social experiences during development and in the recent past (e.g. Frost et al. 2007; McGhee & Travis 2011; Naguib et al. 2011) as well as by the current social environment (e.g. Travis & Woodward 1989; Schuett & Dall 2009; Piyapong et al. 2010; Morand-Ferron et al. 2011). The social environment in particular could exert powerful but subtle effects on behavioural types via dominance interactions and winner–loser effects (Hsu et al. 2006), information transmission (Earley 2010) and position within a social network (Krause et al. 2010).

The freshwater bluefin killifish, *Lucania goodei*, offers a striking example of fitness-related behavioural types and a system in which their origin is especially interesting. During the breeding season, males defend areas of aquatic vegetation from other males and spawning with females occurs in these territories (Foster 1967; Fuller 2001), but there is no evidence of parental care (Fuller & Travis 2001). Females are highly iteroparous and mate with multiple males daily throughout the breeding season (McGhee et al. 2007; K. E. McGhee, personal observation). Males show extensive behavioural variation in a competitive mating context, ranging from males that show intense aggressive and courtship behaviour to males that rarely show aggression and courtship in the presence of a rival male. These differences among males in their aggression and courtship levels are highly repeatable ($r = 0.61 - 0.72$) and lead to stable outcomes in dominance interactions (McGhee & Travis 2010). Most importantly, males that show high levels of aggression towards males and females, as well as high levels of courtship, have increased spawning success in the laboratory (McGhee et al. 2007) and in the field (Fuller 2001).

In this study we examined whether the behavioural components that contribute to a male's behavioural type within the mating context are significantly heritable and thus, might respond to selection. We also examined whether the strong phenotypic correlations among these behaviours might be underlain by similarly strong genetic correlations. To measure behaviours within the mating context, we assessed a male's response to both a female and a rival male presented simultaneously. Our aim was to create an ecologically relevant behavioural assay that captures the conflicting stimuli (i.e. potential mates versus rivals) that a male must deal with during the breeding season.

METHODS

Half-sib Breeding Design

We collected adult fish from the Upper Bridge site on the Wakulla River, FL, U.S.A., in March 2007 by dipnet and seine. We chose sires randomly with respect to colour pattern and size and paired each male with two randomly chosen dams (note: one sire was paired with three dams). Each dam was housed in a large 114-litre tank filled with well-water at a

greenhouse with natural light. Each tank had an external activated carbon bio-filter and two yarn mops, each one consisting of a floating yarn mop attached to a yarn mop on a sunken piece of PVC. We assessed the water quality in the tanks monthly and adjusted it as needed. We covered the sides of the tanks with sheets of aluminium foil to prevent behavioural interactions between tanks. We fed adults frozen *Artemia* and chironomids daily. We switched males between their two dam tanks every other day and collected eggs from the yarn mops daily. We reared 33 complete half-sib families ($N_{\text{sires}} = 33$, $N_{\text{dams per sire}} = 2$ except for one sire who was mated to three dams thus $N_{\text{dams total/full-sib families}} = 67$).

We put fertilized eggs in small plastic buckets with fresh well-water and several drops of methylene blue to prevent fungal growth. After hatching (10–14 days postfertilization), larvae were reared in small buckets and fed hatched *Artemia* nauplii for ~2 weeks. We put approximately 30 fry per cross (one sire X one dam) into fresh 114-litre tanks covered with aluminium foil on the sides. Fry tanks were randomly distributed with respect to family across tables throughout the greenhouse. In March 2008 we moved a subset of the largest fully mature fish (approximately six males and six females per rearing tank/full-sib family) to the laboratory for behavioural trials. This was to ensure that the fish for the behavioural assays were sexually mature and F1 not F2 offspring. In doing this, there is the possibility that we biased our sample to behavioural types with fast growth (Stamps 2007; Biro & Stamps 2008). Although offspring within a rearing tank differed by less than 7 mm in length on average (range of sizes across all rearing tanks = 19–40 mm), further examination of whether growth rates are associated with behavioural traits in this species are needed.

Offspring Behavioural Trials

While housed in the laboratory, we kept fish in brother–sister pairs (due to space limitations) in 19-litre tanks with a yarn mop and sponge filter. Opaque black plastic covered the walls to prevent behavioural interactions between neighbouring tanks. We fed fish frozen *Artemia* daily and maintained them at thermal (22 °C) and light (14:10 h light:dark cycle) regimes typical of the natural breeding season. For each behavioural trial, we tested three sons per full-sib family on average (range 2–4 sons, $N_{\text{total individuals}} = 192$), and thus we obtained behavioural measures on 4–8 sons per half-sib family. Males were tested randomly with respect to family, and thus siblings were not tested more closely in time than unrelated individuals.

We measured each male's behavioural reaction to a live female and a live male introduced simultaneously into the focal male's tank. Our aim in this assay was to simulate a potential mating opportunity in the presence of a nearby rival male similar to what occurs in nature when females swim through neighbouring male territories. We recorded the focal male's aggressive and courtship behaviour towards the female as well as their aggressive behaviour towards the rival male. We conducted these trials in a focal male's home tank but removed the female (sister) for > 24 h before the trial so that focal males were alone in their tank until the addition of a new female. In the afternoon on the day before the trial, we removed the filter and the yarn mop and put an unfamiliar gravid field-caught female in a transparent, porous container overnight in the focal male's tank. We began the trial the next morning. We released the female and added a field-caught stock male that was physically distinguishable from the focal male. Field-caught males were kept in a large stock tank and were likely reused across trials but they were not reused within 48 h.

Once the focal male encountered the female or rival male, we recorded all of the focal male's aggressive behaviours (fin flares, sigmoids, chases and attacks) and courtship behaviours (headflicks and courting circles) for 10 min (600 s). Fin flares consist of a male spreading both dorsal and anal fins at another individual. Sigmoids often precede an attack and consist of a male moving sideways towards another individual and curving its body in a

sigmoid shape. Chases consist of a male chasing another male with a brief burst of speed. Attacks consist of a male rapidly lunging at another individual and striking the individual with its head. Headflicks consist of a male rapidly flicking his head side to side under the abdomen of the female or directly in front of the female. Courting circles consist of a male slowly swimming in a looping circle either around, to the side or in front of the female. To reduce the number of behavioural variables, we calculated (1) the total number of aggressive behaviours directed towards the other male in the trial (sum of fin flares + sigmoids + chases + attacks), (2) the total number of aggressive behaviours directed towards the female (sum of fin flares + sigmoids + attacks), and (3) the total number of courtship behaviours directed towards the female (sum of headflicks + courting circles). We measured standard length of both the focal male and the rival male immediately after the assay.

Estimation of Variance Components

To estimate all variance components, we used the ‘animal model’ as implemented in the MCMCglmm R package (Hadfield 2010), which uses Bayesian statistics with Markov chain Monte Carlo (MCMC) simulations. Prior to analysis, behavioural data were mean-centred by subtracting the mean from each value, and the variance was set to one by dividing each difference (value – mean) by the standard deviation. To account for the possibility that the difference in size between the interacting males might influence their behavioural reaction to one another, we included the difference in size between the males (focal male standard length minus that of their rival) as a covariate in all analyses. We first assessed the additive effect of genetics (V_A), which in the ‘animal model’ is inferred from the pedigree information and includes both sire identity and dam identity (random effect of ‘animal’). We also assessed the effect of the common rearing environment (i.e. rearing tank); however, because full siblings were reared together until maturity, the effects of dam identity and common rearing environment could not be disentangled. Thus, in our models, dam/common environment effects ($V_{d/ce}$) are those effects that are in addition to the dam identity effects from the pedigree that contribute to V_A .

We used weakly informative priors in our models ($V = 1$, $N = 1.002$; see Supplementary material for all R code), and output was robust to slight changes to these priors. For each model, we ran the MCMC for 500 000 iterations (‘nitt’), dropping the first 50 000 iterations (‘burnin’) and storing one of every 100 iterations in memory (‘thin’). We determined whether our models had adequate mixing by examining the variance component plots, the levels of autocorrelation (ensuring it was <0.08 for each run) and the effective size (ensuring it was >4000 per run) (Hadfield 2010; Wilson et al. 2010; de Villemereuil 2012). To examine the extent to which behavioural variation was influenced by additive genetic effects (V_A) and dam/common rearing environment effects ($V_{d/ce}$), we compared four different candidate models that varied in whether V_A and $V_{d/ce}$ were included using deviance information criterion (DIC; Table 1). The model with the lowest DIC was selected as the most parsimonious model, and we used this particular model to estimate variance components and heritability for each behaviour.

Courtship had a large number of zero values, thus we also coded it as binomial and examined it as a threshold trait (yes/no) in an additional univariate model. For the binomial courtship data, we adjusted our prior to fix V_R to 1 (see Supplementary material), and in our model, we specified an ‘ordinal’ distribution that uses a probit link for the data (‘family’). We extended our MCMC and ran it for 5 000 000 iterations (‘nitt’), dropping the first 50 000 iterations (‘burnin’) and storing one every 1000 iterations in memory (‘thin’) (Wilson et al. 2010; de Villemereuil 2012).

Correlations among Behaviours

To examine the extent to which the phenotypic correlations within the mating context reflect underlying genetic correlations, we calculated the phenotypic correlations as well as the genetic covariances and correlations among mating behaviours (Falconer & MacKay 1996) with bivariate animal models as implemented in MCMCglmm. We used slightly stronger priors in our models ($V = \text{diag}(2)$, $N = 1.002$; see Supplementary material) and extended our MCMC to 800 000 iterations. Again, we determined whether our models had adequate mixing by examining the variance component plots, the levels of autocorrelation (ensuring it was <0.08 per run) and the effective size (ensuring it was >6000 per run) (Hadfield 2010; Wilson et al. 2010; de Villemereuil 2012). Similar to the univariate analyses, we compared four different models that varied in whether additive genetic effects and dam/common rearing environment effects were included using DIC (Table 1).

For each pair of behaviours, we estimated variances and covariances from the bivariate model with the lowest DIC scores. From these variances and covariances, we calculated the genetic correlations between traits (Falconer & MacKay 1996). To determine whether the covariance between behaviours was likely different from zero, we compared the DIC of each bivariate model where the covariance was free to vary (i.e. ‘random = ~us(trait):animal’) with the DIC of a model constraining the covariance to zero (i.e. ‘random = ~idh(trait):animal’). In all model comparisons, we used likelihood ratio tests of the DIC difference between the alternative models (delta DIC) with one degree of freedom.

All estimates reported are posterior modes with 95% highest posterior density intervals (95% HPDIs). We performed all analyses using the R package (version 3.0) and R code is available in the Supplementary material.

Ethical Note

While prolonged attacks and fights can result in torn fins and bruising, the trials were of short duration to ensure that males and females were not injured. Because these fish were laboratory reared, we could not release them into the field and all fish were euthanized with an overdose of MS222. This study was approved by the Animal Care and Use Committee at Florida State University (Protocol No. 0003).

RESULTS

On average, males showed 23.5 ± 2.2 (mean $\pm$ SE) aggressive behaviours to their rival male, 8.6 ± 0.8 aggressive behaviours to the female and 8.2 ± 1.7 courtship behaviours to the female during the 10 min trial. The number of the three behaviours shown within a trial was highly variable across families (range among half-sib families: male-directed aggression = 4.0–55.2, female-directed aggression = 1.0–21.8, courtship = 0–49.7). Interestingly, the level of these behaviours was slightly higher than those we have found previously in field-caught and laboratory-reared adults (Table 2).

On average, the focal male was 1.1 ± 0.2 mm larger than its partner, but this ranged from the focal male being 8.5 mm larger than its partner to the focal male being 8.0 mm smaller than its partner. All three mating behaviours were negatively related to the difference in size between the interacting males in the models (Table 3). Thus, the larger the focal male was relative to the field-caught rival with which he was paired, the less aggression and courtship he showed during the trial.

Inclusion of an additional random effect specifying dam identity/common rearing environment ($V_{d/cc}$) in our models substantially decreased model fit for all behaviours (Table 1). Thus, we excluded $V_{d/cc}$ effects in our estimates of variance components and used

the univariate Model 1.3 for all three behaviours and the bivariate Model 2.3 for each pair of behaviours (see Supplementary Tables S2, S3). Note that the genetic effect of dam was still retained in our estimate of V_A through its inclusion in the pedigree. Estimates of all variance components, heritabilities and genetic correlations with $V_{d/ce}$ effects included (Models 1.4 and 2.4) are in the Supplementary material (Tables S2, S3).

We found that all of the components of the behavioural type within the mating context were moderately heritable regardless of whether $V_{d/ce}$ was included (Table 3, Table S2). Courtship behaviour was heritable both when considered a continuous trait and a threshold trait (court: yes/no) (Table 3). While inclusion of additive genetic effects via the pedigree substantially improved model fit for female-directed aggression (Table 1a, Model 1.1–Model 1.3: delta DIC = 11.4, $P = 0.0007$) and courtship behaviour (delta DIC = 21.1, $P < 0.0001$), it only slightly improved model fit for male-directed aggression, and this improvement was not statistically significant (delta DIC = 1.1, $P = 0.294$).

As we have found previously, the three components of a male's behavioural type within the mating context (male-directed aggression, female-directed aggression and courtship) were all positively correlated to one another (Fig. 1, Table 4). Consistent with the phenotypic correlations, we also found positive genetic correlations among all three mating behaviours (Fig. 1, Table 4; see Table S1 for genetic variances and covariances). Constraining the covariance between traits to zero decreased model fit for all pairs of behaviours (courtship and female-directed aggression: delta DIC = 9.352, $P = 0.002$; courtship and male-directed aggression: delta DIC = 5.853, $P = 0.016$; male- and female-directed aggression: delta DIC = 1.941, $P = 0.164$), but this decrease for the pair of male- and female-directed aggression was not statistically significant based on log-likelihood tests. In addition, due to our low sample size, the 95 % confidence intervals around our genetic correlation estimates were large and overlapped zero. Note that because $V_{d/ce}$ was not included in these analyses, a bias of genetic parameters from tank effects is possible (see Table S3 for genetic variances and covariances including the effects of $V_{d/ce}$).

DISCUSSION

We have previously found that the three behaviours contributing to a male's behavioural type within the mating context are strongly stable across time and interactions (McGhee & Travis 2010). The results from this study indicate that all three of these behaviours are moderately heritable. Courtship behaviour was significantly heritable both as a continuous trait ($h^2 = 0.29$) and as threshold trait ($h^2 = 0.50$). Although male-directed aggression was significantly heritable, the absence of a significant additive genetic effect with log-likelihood tests suggests that we had weak power to detect anything but the highest levels of additive genetic variation, and our results should be taken with caution. While studies in some species, such as great tits, *Parus major*, have found that a number of traits that contribute to a behavioural type are heritable, other studies have found mixed results depending on the particular behavioural context and species (reviewed in: van Oers et al. 2005; Réale et al. 2007). In general, conclusions about the developmental basis of behavioural types should be made cautiously and only after examining the genetic basis for the different behavioural components.

Interestingly, our model comparisons suggest that inclusion of effects due to the dam identity/common environment of the rearing tank ($V_{d/ce}$) substantially decreased the model fit for all behaviours. In most breeding studies, a common rearing environment tends to make relatives more similar to one another, but this may not be the case when one examines social behaviours. By rearing individuals in mixed-sex groups where social interactions could occur freely, early interactions might have affected our ability to detect additive

genetic variation. For example, social interactions might reinforce small initial behavioural differences among males, causing individuals to diverge behaviourally from one another over repeated interactions. The behavioural consequences of such early social interactions will inflate the residual variance and make siblings as different from one another as unrelated individuals. Thus, when examining social behaviours it might often be the case that additive genetic variance is difficult to detect without enormous sample sizes or modified rearing conditions, such as rearing individuals in isolation (which puts them at risk for poor social conditioning) or with unrelated individuals (which requires either individually marking fish or genotyping them afterwards). The reductions in model fit associated with the inclusion of dam identity/common rearing environment effects ($V_{d/c}$) for all behaviours are consistent with this possibility. In addition, we know that particular aspects of the early environment can influence mating behaviours in this species. For example, experiencing low food levels during ontogeny causes males to show higher levels of female-directed aggression and courtship as adults, and being reared in juvenile peer groups with no adult causes males to show higher levels of female-directed aggression as adults (McGhee & Travis 2011). It is likely that even within a rearing tank, individuals varied in the frequency of their social interactions and intensity of competition. The degree to which these early social interactions contribute to a male's behavioural type remain unclear and are an obvious direction for future studies (Moore et al. 1997; Stamps & Groothuis 2010a, b).

Male behaviour was also sensitive to the present context, which might have further inflated the residual variance. We found that all three behaviours were affected by the size difference between the focal male and his partner (included as a covariate). Specifically, the larger the focal male relative to his partner, the less aggression and courtship behaviour the focal male displayed during the trial. In addition, although the levels of phenotypic variance in behaviour are comparable to our other studies of bluefin killifish, the average values are slightly higher than those we have previously found for both field-caught and laboratory-reared adults. This increase in the number of aggressive and courtship behaviours shown is likely due, at least in part, to methodological differences between studies. In particular, males in this study were tested in their home tank rather than a new test tank, which likely resulted in residency effects. The size of the home tank was also much smaller than test tanks previously used (19 liters versus 114 liters in other studies), perhaps resulting in an increased encounter rate. Thus, although males are highly repeatable in their mating behaviours across multiple interactions (McGhee & Travis 2010), they are clearly adjusting their behaviour to the present context, emphasizing that the presence of behavioural types does not necessarily equate with the absence of behavioural plasticity (Neff & Sherman 2004; Sih et al. 2004b).

The clear distinctions between models with genetic correlations constrained to zero and the unconstrained models indicate that significant genetic correlations lay beneath at least two of the three phenotypic correlations (despite large confidence intervals). For females, there can be a direct cost of associating with a dominant male due to the high likelihood of being attacked and harmed by the male. The puzzle of female-directed aggression, particularly its association with high courtship behaviour, in this species might be partly explained by positive genetic correlations between behaviours. We had previously interpreted high levels of female-directed aggression as an unavoidable consequence of high levels of male-directed aggression (a 'spill-over' trait sensu Arnqvist & Henriksson 1997). However, the results from this study suggest that female-directed aggression to females might not be a 'spill-over' trait at all. While we estimated a positive genetic correlation between female- and male-directed aggression, a positive genetic covariance between these two behaviours was not statistically supported based on model comparisons. Thus, high levels of female-directed aggression might persist due to selection for greater levels of courtship rather than greater

levels of male-directed aggression. We know that female preference plays a role in determining mating success in this species, particularly since females cannot be forced to mate (McGhee et al. 2007). Female preference for greater levels of courtship might indirectly select for increased female-directed aggression due to genetic constraints. However, we also found evidence for a significant positive genetic correlation between male-directed aggression and courtship. Since both male–male and male–female interactions impact mating success (McGhee et al. 2007), the genetic relationship between male-directed aggression and female-directed courtship might positively link these different types of mating interactions. Additional studies are clearly necessary to explore not only the patterns of selection, but also whether aggression and courtship behaviour have a common hormonal regulation. Although our results should be interpreted with caution due to the large confidence intervals surrounding our estimates and may apply only to the population we examined, they do suggest that genetic correlations among mating behaviours are a potential explanation for the persistence of the seemingly maladaptive aggression directed at potential mates.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- We examined heritability of male mating behaviours in bluefin killifish using a half-sib breeding design.
- Courtship and male-directed and female-directed aggression were heritable.
- Our results indicate positive genetic correlations among mating behaviours.
- Early interactions could affect additive genetic variation of social behaviours.

Figure 1.

Half-sib family means ($\pm$ SE) for the number of behaviours within the mating context: A) male- and female-directed aggression, B) courtship and male-directed aggression and C) courtship and female-directed aggression. $N = 33$ half sib families; behaviours are on the log₁₀ scale for viewing ease.

Table 1

Deviance information criterion (DIC) scores for alternate univariate and bivariate animal models for bluefin killifish

Univariate models	Male-directed aggression	Female-directed aggression	Courtship
Model 1.1 $Y = \text{mean} + \text{covariate}^*$	537.9	542.7	546.5
Model 1.2 $Y = \text{mean} + V_{d/ce}^{\dagger} + \text{covariate}$	545.8	543.1	542.4
Model 1.3 $Y = \text{mean} + V_A^{\ddagger} + \text{covariate}$	536.8	531.3	525.4
Model 1.4 $Y = \text{mean} + V_A + V_{d/ce} + \text{covariate}$	544.0	535.3	532.5
<i>Bivariate models</i>	<i>Male/Female aggression</i>	<i>Male aggression/courtship</i>	<i>Female aggression/courtship</i>
Model 2.1 $Y = \text{mean} + \text{covariate}$	1011.3	1077.6	1084.0
Model 2.2 $Y = \text{mean} + V_{d/ce} + \text{covariate}$	1024.4	1083.1	1082.0
Model 2.3 $Y = \text{mean} + V_A + \text{covariate}$	997.8	1053.1	1043.0
Model 2.4 $Y = \text{mean} + V_A + V_{d/ce} + \text{covariate}$	1012.8	1066.8	1058.3

Models with the smallest DICs that were used to estimate variance components are shown in bold.

* 'Focal male standard length minus partner male standard length' was used as a covariate in all models.

$^{\dagger} V_{d/ce}$ refers to the confounded effects of dam identity and common rearing environment (i.e. tank) not accounted for by the pedigree.

$^{\ddagger} V_A$ refers to the additive genetic effect contributed by both sire and dam via the pedigree ('animal').

Table 2

Average number of mating behaviours performed by bluefin killifish over 5 min intervals $\pm$ SE in the mating context assay (one female, two males) in this study and in previous studies

	This study [*] (lab-reared)	McGhee & Travis 2011 [†] (lab-reared)	McGhee & Travis 2010 [‡] (field-caught)	McGhee et al. 2007 [§] (field-caught)
Male-directed aggression	11.8 $\pm$ 1.1	2.7 $\pm$ 0.5	5.5 $\pm$ 1.4	2.4 $\pm$ 0.5
Female-directed aggression	4.3 $\pm$ 0.4	1.0 $\pm$ 0.3	1.3 $\pm$ 0.5	0.3 $\pm$ 0.1
Courtship	4.1 $\pm$ 0.8	0.8 $\pm$ 0.2	3.3 $\pm$ 1.3	2.2 $\pm$ 0.4

^{*} N = 192 males; ignoring relatedness; 10 min trials.

[†] N = 60 males; pooling all early food and social treatments; 15 min trials.

[‡] N = 16 males; average of seven interactions per male; 15 min trials.

[§] N = 46 males; 50 min trials.

Table 3
Behavioural trait means and estimates of their variance components and heritability for bluefin killifish

Trait	Mean [†] ± SE	Covariate [‡] (95% CI)	V _A [§] (95% CI)	V _R (95% CI)	h ² (95% CI)
Male-directed aggression	23.5 ± 2.2	-0.10 (-0.03, -0.13)	0.17 (0.07, 0.41)	0.81 (0.57, 1.01)	0.17 (0.07, 0.39)
Female-directed aggression	8.6 ± 0.8	-0.05 (-0.01, -0.10)	0.21 (0.08, 0.54)	0.72 (0.48, 0.98)	0.21 [*] (0.08, 0.49)
Courtship	8.2 ± 1.7	-0.05 (-0.01, -0.10)	0.29 (0.11, 0.62)	0.70 (0.43, 0.95)	0.29 [*] (0.11, 0.56)
Courtship (binomial: yes/no)	—	-0.03 (-0.02, -0.23)	1.00 (0.92, 1.10)	Fixed to 1	0.50 [*] (0.48, 0.52)

Variance components were estimated from models excluding the random V_{d/c}e effects (see Table 1, Model 1.3).

^{*} Indicates a significant additive genetic effect based on log-likelihood tests comparing deviance information criterion scores (delta DIC).

[†] Uncentred mean ± SE. N = 192.

[‡] Focal male standard length minus partner male standard length[†] was a significant covariate in all models (pMCMC < 0.03).

[§] Variance component and heritability estimates are posterior modes based on mean-centred data.

Table 4

Estimates of phenotypic correlations (upper off-diagonal) and genetic correlations (lower off-diagonal) for mating behaviours of bluefin killifish with 95% confidence intervals in parentheses

	Male-directed aggression	Female-directed aggression	Courtship
Male-directed aggression	—	0.55 (0.42, 0.63)	0.18 (0.05, 0.33)
Female-directed aggression	0.52 (−0.12, 0.80)	—	0.17 (0.04, 0.32)
Courtship	0.34* (−0.20, 0.77)	0.37* (−0.21, 0.78)	—

Estimates are based on the variance components estimated from models excluding the random $V_{d/ce}$ effects (see Table 1, Model 2.3).

* Indicates a significant genetic covariance (>0) based on log-likelihood tests comparing deviance information criterion scores (delta DIC) between a model with unconstrained covariance and a model with the covariance constrained to zero.