



Early food and social environment affect certain behaviours but not female choice or male dominance in bluefin killifish

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Environmental conditions during development can have long-lasting effects on morphology, physiology and behaviour. In contrast to human personality, our understanding of how the early environment influences the development of animal personality is limited. In bluefin killifish, *Lucania goodei*, a male's mating behaviour is highly repeatable through time and across interactions. To examine whether these stable behavioural types are influenced by early nutritional and social conditions, we reared individuals on either high- or low-food levels in combination with either one adult male, one adult female or no adult. Individuals reared on high food were larger at the earliest measurements and remained so as adults. The high-food treatment also had the highest mortality, particularly if individuals were reared with an adult male. Despite these growth and survival consequences, the food and social treatments did not affect whether males were preferred by females or became dominant as adults. While the outcome of social interactions was not influenced by the early food and social environment, particular mating behaviours were; males reared on low food were more aggressive to females and showed more courtship, and males reared without an adult were more aggressive to females than those reared with either an adult female or male. Our results suggest that some of the behaviours that contribute to a male's behavioural type within the mating context and that influence mating success in this species are sensitive to aspects of the early environment.

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While there is often extensive behavioural variation among individuals within a population, individuals can be highly consistent in their behavioural tendencies (Sih et al. 2004a, b). For example, some individuals are consistently more prone to court females, more aggressive towards conspecifics, more bold towards predators, or more active in novel environments than others. An individual's behavioural type describes this behavioural consistency across time and/or contexts and contributes to their personality (Sih et al. 2004a, b; Réale et al. 2007; Sih & Bell 2008). In some cases there is evidence of a genetic basis for this behavioural consistency (reviewed in: van Oers et al. 2005; Réale et al. 2007). However, as with most phenotypic traits, it is often a combination of genetic and environmental factors that generates the variation we observe among individuals. This is the case for many alternative strategies (Gross 1996), and both the early abiotic and biotic environments can affect an individual's morphological and behavioural

trajectory (e.g. Emlen 1994; Bailey et al. 2010). However, studies of animal personality are primarily interested in the continuous rather than discrete behavioural variation among individuals within a population. While the influence of an individual's early environment on the development of particular axes of personality has been extensively studied in humans (e.g. Rosenman & Rodgers 2006; Clark et al. 2010), much less is known about the influence of ecologically relevant stressors on the development of animal personality (but see Carere et al. 2005; Chapman et al. 2008a, 2010; Stamps & Groothuis 2010a, b).

Environmental conditions during development can have long-lasting effects on morphology, physiology and behaviour. For example, nutritionally stressed individuals show slower somatic growth and reduced development of ornaments (Lindström 1999; Metcalfe & Monaghan 2001; but see Basolo 1998), are less likely to achieve dominant status (Richner et al. 1989; Royle et al. 2005), are less attractive to females (Scheuber et al. 2003; Spencer et al. 2005) and are less capable of learning (Arnold et al. 2007) compared to unstressed individuals. This can occur either due to, or in spite of, compensatory growth after conditions have improved (Metcalfe & Monaghan 2001; Ali et al. 2003). Experiencing different social interactions in ontogeny can also affect development. For example, rearing individuals in different social environments can affect

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a number of morphological (e.g. Hofmann et al. 1999; McGraw et al. 2003; Chapman et al. 2008b; Gonda et al. 2009; Magellan & Magurran 2009) and behavioural traits, including mate choice (Adkins-Regan & Krakauer 2000; Slagsvold et al. 2002), courtship (Rodd & Sokolowski 1995) and aggression and dominance status (Piper 1995; Sundström et al. 2003; Hansen & Slagsvold 2004; Newman et al. 2005; Price & Rodd 2006). The behavioural changes might be a consequence of a number of processes induced by the early environment, including changes to growth and metabolic rates (Stamps 2007; Criscuolo et al. 2008) as well as to neurological development (Nowicki et al. 1998; Gonda et al. 2009).

Regardless of the specific mechanism, sensitivity to the early environment is likely to be particularly important for traits that have fitness consequences. Male bluefin killifish, *Lucania goodei*, collected from the field show extensive behavioural variation, ranging from males that show intense aggression and courtship behaviours to males that are never aggressive and rarely court females. 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). In addition, those 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 (Fuller & Travis 2001; McGhee et al. 2007) and in the field (Fuller 2001). Thus, there are clearly reproductive consequences of a male's behavioural type within the mating context and yet extensive behavioural variation persists within populations. Sensitivity to early rearing conditions might explain this behavioural variation despite the potential fitness consequences.

Here we examine whether the combination of nutritional and social conditions experienced early in life affects the development of adult behaviour, female preference, male attractiveness to females and male dominance status in the bluefin killifish. Specifically, during ontogeny we manipulated whether individuals received high- or low-food levels in combination with whether they were housed with an adult male, an adult female or no adult. We chose to manipulate food level because previous studies have shown that behavioural traits related to dominance are affected by food level (e.g. Royle et al. 2005). The rationale for our social environment manipulation was that juveniles would experience different levels of aggression (highest in the adult male treatment) during ontogeny. In nature, fry hatch on and move through male territories throughout the reproductive season (spring to autumn) and thus are likely to encounter adult males and females frequently. Juveniles do not shoal with adults, but are often caught in the same seine or dipnet (K. E. McGhee, personal observation), suggesting some spatial overlap. While there is extensive work on the separate effects of early food level and social environment on subsequent behaviour, an individual's early environment consists of both abiotic and biotic aspects with ample opportunity for interactions among resource and social factors to occur. For example, in the absence of a dominant adult, aggression among juveniles may only occur under low resource levels when individuals must compete for food. In the presence of a dominant adult however, all juveniles might be recipients of adult aggression regardless of the food level, with the influence of social environment trumping those of food level. Thus, behavioural differences between high-food and low-food individuals could potentially be exacerbated or reduced depending on early social environment.

The bluefin killifish is a sexually dimorphic fundulid found in springs and river drainages of the southeastern United States. Males defend areas of aquatic vegetation from other males, and spawning with females occurs in these territories (Foster 1967; Fuller 2001). Despite variation among males in colour and size, we have yet to find any morphological traits associated with female preference, male dominance or male mating behaviour in

this species (McGhee et al. 2007; McGhee & Travis 2010). Thus, the bluefin killifish is an excellent system in which to examine the influence of early experiences on the development of behavioural traits without having differences in morphology drive the outcome of social interactions.

METHODS

We collected fertilized eggs from 18 randomly matched field-collected adult pairs (collected from the Wakulla River, FL, U.S.A.). These eggs were pooled, and after hatching, fry were reared in large plastic buckets and fed live *Artemia nauplii* ad libitum. At 2 months' of age, we transferred fry to 38-litre 'rearing' tanks (length \times width \times height: 50 \times 25 \times 29 cm) with two yarn mops for shelter and a foam biological filter (range of standard lengths at 2 months: 9.5–12 mm). Juvenile males and females are indistinguishable until males begin to express colour, so we housed fry in groups of four individuals per rearing tank in anticipation of having both males and females in each tank. We covered the sides of the tanks with black opaque plastic to prevent behavioural interactions between fish from neighbouring tanks. We used thermal (22 °C) and light regimes (14:10 h light:dark cycle) characteristic of conditions in the natural growing season. Rearing tanks were randomly assigned to one of two food levels in combination with one of three social environment treatments. Individuals experienced either high or low levels of food until maturity (see below). Within each food treatment, individuals experienced one of three social environments: they were reared with one adult male, one adult female or no adult, producing six treatment combinations (HM = high food, adult male; HF = high food, adult female; HO = high food, no adult; LM = low food, adult male; LF = low food, adult female; LO = low food, no adult). Because we were unable to keep track of individuals in the rearing tanks, 'tank' was the unit of replication for the growth data (initial number of tanks per treatment: HM = 9; HF = 9; HO = 9; LM = 10; LF = 11; LO = 10).

We fed fish frozen adult brine shrimp (*Artemia*) supplemented until the fry were 5 months old with live *Artemia nauplii*. The high-food level was the maximum amount of food consumed by individuals in 5 min based on a pilot study and the low-food level was consistently half of the high-food treatment. We measured the amount of food with a pipette; a set amount of food (*A. nauplii* or frozen food) was added to a set amount of water and the slurry was pipetted out. We adjusted the food levels to account for the presence of an additional adult in four of the treatments and increased the levels through time to match growth. Uneaten food rarely accumulated but was removed as needed.

We measured standard length at 3, 4, 5 and 6 months and mass at 4, 5 and 6 months (mass was not measured at 3 months to avoid injuring fish). We stopped the social treatments and removed the extra adults (from the HM, LM, HF and LF treatments) at 5 months because some juveniles were nearing adult size and we did not want to confuse the 'focal fry' with the extra adult. At 6 months, when genders were distinguishable in all fish, we stopped the food treatments and moved fish into male–female pair tanks. Fish placed together as partners had experienced the same food and social treatments but had been housed in separate rearing tanks. We fed fish frozen adult brine shrimp ad libitum from this point onward.

We examined the effects of the food and social treatments on standard length (mm) at months 3–6 and on mass (g) and body condition at months 4–6 using repeated measures mixed models. Body condition was estimated for each individual using the residuals from a least squares linear regression of mass on standard length. We classified 'tank' (each with four fry) as the repeating subject. Thus, our size measurements are averages for all fish within a single rearing tank. In all analyses, we specified

a compound symmetry covariance structure, REML estimation method and Satterthwaite degrees of freedom estimation.

For all growth analyses, we excluded tanks that had fewer than three fry for a month due to mortality ($N = 4$). The number of rearing tanks included in the analyses varied through time because of total or partial tank mortality (at 3 and 4 months, $N = 58$ tanks; at 5 months, $N = 56$ tanks; at 6 months, $N = 52$ tanks; at 10 months, $N = 50$ tanks; Appendix, Table A1). We examined differences in juvenile mortality across food and social treatments by examining the proportion of the four fry in each of the rearing tanks that survived over the course of the rearing period. We used a generalized model to examine the effects of food and social treatments and their interaction on mortality. We specified a binomial distribution with a logit link function.

Behavioural Trials

At 10 months, when all fish were sexually mature, we performed two behavioural assays, one to quantify female choice and male attractiveness to females and another to quantify male dominance status. Males were paired randomly with a male of the opposite food treatment but within the same social treatment (HF versus LF, HM versus LM, H0 versus L0). Testing order was random with respect to social treatment. A single female was paired with the two test males. Females were chosen randomly with respect to their food treatment but had experienced the same social treatment as their test males. Females were isolated from males for about 48 h to ensure that they were gravid and were not tested with the males with whom they had been housed. Males and females were used only once. The two males and one female were kept in individual perforated, transparent containers within a large 114-litre testing tank ($L \times W \times H$: $75 \times 30.5 \times 45$ cm) with two yarn mops and gravel substrate and allowed to acclimate overnight. The male containers were on opposite ends of the tank (separated by ~ 40 cm), and the female container was in the centre of the tank. Males were assigned to their container by coin toss.

The following morning, we released the female and conducted a 15 min dichotomous choice trial. We recorded male activity during the choice trial as the number of times each male moved up and down in his container while facing the female. We videotaped the trials to determine the amount of time that the female spent within one body length (< 5 cm) and facing a particular male. We interpreted this 'female association time' as her level of preference for that male. Males with greater female association time were considered 'preferred'. Choice trials were excluded if the female did not look at each male during the trial ($N = 3$). In previous work we have shown that a female's association time in a dichotomous choice trial is significantly correlated with how quickly she spawns with a male (McGhee et al. 2007). Because both the female and the males in each choice trial had experienced a food and social treatment (although social treatment was the same for all individuals in a trial), we could examine (1) whether a male's food treatment affected his attractiveness to a female, (2) whether a female's food treatment influenced her choice and (3) whether their common social treatment affected these patterns.

We then released the males and allowed all three fish to interact freely for a 15 min male dominance trial. Male spawning success with a female is a result of an interaction between male–male competition and female choice (McGhee et al. 2007), and in nature, these processes occur simultaneously (Fuller 2001). Interaction with a female is necessary for bluefin males to show full aggressive interactions (McGhee et al. 2007), so we did not remove the female during male dominance trials. Because the choice trial immediately followed the dominance trial, males had the opportunity to observe each other across the tank as well as the female's response to each

male. However, we have found previously that neither male morphology nor female association time (even when observable by both males) predicts relative dominance status or eventual number of spawns (McGhee et al. 2007).

Once the males had encountered one another in the dominance trial, we recorded all male aggressive behaviours (fin flares, chases and attacks) and courtship behaviours (headflicks and courting circles). Fin flares consist of a male moving sideways towards another individual, often curving the body, while spreading both dorsal and anal fins. 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 other individual with his head. Headflicks consist of a male rapidly flicking his head side to side under the female's abdomen or directly in front of her. Courting circles consist of a male slowly swimming in a looping circle around, to the side or in front of the female. To reduce the number of behavioural variables, we calculated the total number of aggressive behaviours directed towards the other male in the trial (sum of fin flares + chases + attacks), the total number of aggressive behaviours directed towards the female (sum of fin flares + attacks), and the total number of courtship behaviours directed towards the female (sum of headflicks + courting circles).

The three types of behaviour shown in the mating context (aggression to males, aggression to females and courtship behaviour) are positively correlated with one another both in the laboratory (McGhee et al. 2007; McGhee & Travis 2010) and in the field (Fuller 2001). Using principal components analysis to combine these three types of behaviours generates a summary score (PC1) that can be interpreted as a male's behavioural type within the mating context. This measure of behavioural type corresponds to a male's behavioural activity within the mating context, ranging from males that are highly aggressive towards both males and females and that court intensely to males that rarely display aggression or courtship behaviours. A male's behavioural type is repeatable through time and across interactions ($r = 0.75$), as are the component behaviours ($r = 0.65$ – 0.72) (McGhee & Travis 2010). In this study, because our treatments may have influenced different behaviours in different ways and changed how the behavioural type (PC1) was constructed, we concentrate on the three types of behaviour separately.

Dominance status was determined by the outcome of aggressive interactions and circle fights rather than the number of aggressive behaviours. We considered a male dominant when the flaring of his dorsal and anal fins and curving of his body towards the second male caused the second male to lower his fins and/or retreat. We also considered a male dominant when he attacked the second male, resulting in this second male retreating. Finally we considered a male dominant when he won circle fights that ended with the second male retreating with fins lowered. Circle fights consist of males lining up head to tail and rapidly lunging at each other while moving towards the surface. Trials with no aggressive interactions were repeated at a later time. If dominance status did not stabilize in a single trial, dominance status was counted as a tie and excluded from the statistical analyses of dominance ($N = 1$). After completion of a trial, we weighed both males out of water and measured their standard length (tip of head to end of caudal peduncle) to the nearest 0.5 mm. Because both the female and the males in each dominance trial had experienced a food and social treatment (although social treatment was the same for all individuals in a trial), we could examine (1) whether a male's food treatment affected his behaviour and dominance status, (2) whether a female's food treatment influenced male behaviour and (3) whether their common social treatment affected these patterns.

Because we paired high-food males against low-food males within a social treatment, we used a type of repeated measures

analysis in which each pair of males was nested within the trial. While repeated measures analyses are familiar as methods for longitudinal analyses of individuals, they can be used whenever there is repeated testing of individuals within the experimental unit or 'subject' (multilevel analyses). This type of analysis has been advocated for dyadic trials because it (1) deals with the issue of nonindependence associated with dyadic data, (2) can examine whether partner behaviour influences focal individual behaviour and (3) takes advantage of the paired design approach leading to greater statistical power (Campbell & Kashy 2002; Briffa & Elwood 2010). This type of analysis can be used for both continuous and dichotomous response variables (Campbell & Kashy 2002; Flom et al. 2007). We chose to use this type of repeated measures analysis in a generalized linear mixed model (GLMM) framework to specify the distribution of the response variable rather than attempting to transform our non-normal count data to normality (Bolker et al. 2008).

To determine whether females preferred high-food males versus low-food males when given the choice, we examined preference as a discrete variable: a male was or was not the preferred male in the trial. To determine whether high-food males or low-food males were more likely to become dominant when interacting with one another, we examined dominance as a discrete variable: a male was or was not the dominant male in the trial. For both of these analyses, we included the main effect of male food treatment as well as two types of relevant interactions: social treatment \times male food treatment and female food treatment \times male food treatment. We specified a binomial distribution with a logit link function.

Next, we examined the role of food and social treatments on the continuous behavioural measures. We examined whether behaviours in the choice trials (i.e. female association time and male up–down activity) and dominance trials (i.e. male aggressive behaviour towards both his male partner and the female, and male courtship behaviour) were influenced by a male's food treatment, the female's food treatment and the social treatment they had all experienced. Because female body condition may reflect her fecundity and a male's body condition may reflect his quality or stamina, we also included as a covariate a measure of the male's mass for his standard length relative to that of the female in the trial. Specifically, this measure was male body condition minus female body condition within a trial, with body condition being the residuals from a least squares linear regression of mass on standard length. Homogeneity of slopes was examined by testing for significant interactions between the covariate and the main effects (no significant interactions occurred).

For these analyses, we did not transform the data but instead specified a negative binomial distribution with a log link function. We specified a compound symmetry covariance structure for the nonindependence of dyad members and the Laplace likelihood approximation (Bolker et al. 2008). We included all main effects and their interactions and the covariate in the initial model. Terms were removed sequentially with interactions and the covariate with F values greater than 1 retained in the final model. The residuals were examined for each model to determine model adequacy. Sample sizes were slightly different between the choice and dominance trials because not all successful choice trials had successful dominance trials and vice versa.

While prolonged attacks and fights can result in torn fins and bruising, the trials were of short duration to ensure that no males or females were injured. In addition, all tanks had yarn mops and PVC tubes for shelter. Because these fish were laboratory reared, we could not release them into the field, so 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

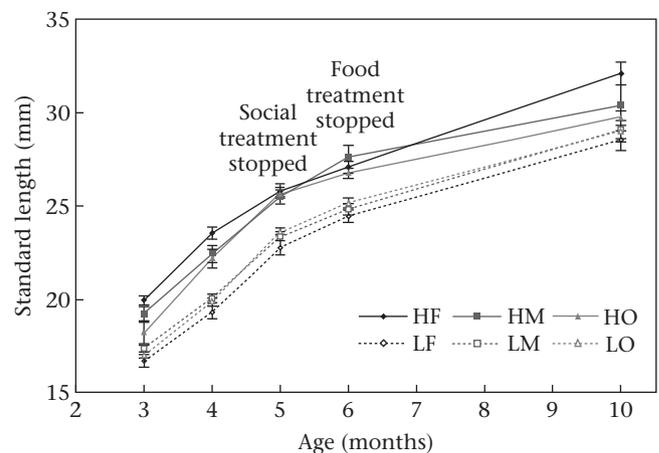


Figure 1. Mean \pm SE standard length of bluefin killifish in the six treatments over 10 months. HF: high food, female; HM: high food, male; HO: high food, no adult; LF: low food, female; LM: low food, male; LO: low food, no adult.

No. 0003). In all analyses, we report the unadjusted P values. We performed all analyses using SAS software, version 9.2 (SAS Institute, Inc., Cary, NC, U.S.A.), with the GLMMs performed in SAS 'Glimmix'.

RESULTS

Growth and Mortality

Beginning with the first measurements, fish that received the high-food level were consistently longer than fish that received the low-food level, and at the cessation of the food treatment (age 6 months), individuals that received high food were 9% longer than individuals that received low food (mean \pm SE standard length (SL): high food = 27.0 ± 0.2 mm; low food = 24.8 ± 0.2 mm; Fig. 1). Despite 4 months of being fed ad libitum, fish initially reared on low-food levels remained smaller than those reared on high-food levels at the time of behavioural testing (10 months of age), resulting in a significant main effect of food treatment (SL: high food = 30.5 ± 0.3 mm; low food = 28.7 ± 0.2 mm; Fig. 1, Table 1) and offering compelling evidence for a lasting effect of early food level on body size. While there was no detectable main effect of social treatment, there was a significant interaction between food level and social treatment, indicating that the effect of the social treatment depended upon which food level was experienced. This was due to individuals in the high-food-female (HF) treatment being longer than all others at particular time periods (Fig. 1). Mass and body condition showed similar patterns to body length (Appendix, Tables A2, A3). The high-food males used in the choice and dominance trials were significantly longer and heavier than

Table 1
Repeated measures mixed model results on standard length of bluefin killifish over time (months 3 to 10)

Effect	ndf, df	F	P
Food treatment (F)	1, 56.4	100.77	<0.0001
Social treatment (S)	2, 57.1	0.52	0.598
Time (T)	4, 910	867.80	<0.0001
F \times S	2, 54.5	5.28	0.008
F \times T	4, 908	3.10	0.015
S \times T	8, 909	1.57	0.131

Significant values are shown in bold. Rearing tank was the repeating subject. The three-way interaction had an F value less than 1 and was removed from the final model.

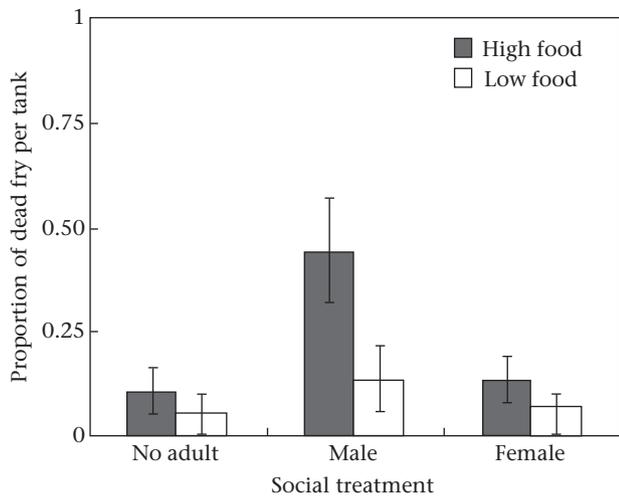


Figure 2. Mean \pm SE proportion of dead bluefin killifish fry out of the initial four in each rearing tank.

their low-food male partners, although they did not differ in body condition (SL: high food = 31.1 ± 0.4 mm; low food = 28.9 ± 0.4 mm; paired t test: $t_{26} = 3.6$, $P = 0.001$; mass: high food = 0.43 ± 0.02 g; low food = 0.35 ± 0.01 g; paired t test: $t_{26} = 3.1$, $P = 0.004$; body condition: high food = -0.0013 ± 0.007 ; low food = 0.0013 ± 0.005 ; paired t test: $t_{26} = -3.2$, $P = 0.75$).

There was greater mortality in the high-food treatments compared to the low-food treatments and this pattern was strongest in tanks with adult males (food treatment: $F_{1,50} = 7.53$, $P = 0.008$; social treatment: $F_{2,50} = 4.29$, $P = 0.019$; food \times social treatment interaction: $F_{2,50} = 0.49$, $P = 0.614$; Fig. 2).

Choice Trials

Females showed no preference for high-food or low-food males ($F_{1,24} = 0.08$, $P = 0.780$), with high-food males being preferred in 48% of the choice trials. The interactions between male food treatment and both social treatment and female food treatment had F values less than 1 and were removed from the model. The time that females spent associating with a male in the choice trial was not significantly influenced by the male's food treatment, the female's food treatment or the social treatment they had all experienced (Table 2). On average, within a 900 s trial, females spent 280 ± 54 s with the high-food male and 214 ± 49 s with the low-food male. Similarly, a male's activity level during the choice trial

Table 2
Repeated measures GLMM results for behaviours of bluefin killifish in the choice trial ($N = 25$)

Effect	ndf, ddf	F	P
Female preference time (s)			
Male food treatment (MF)	1, 24	0.64	0.433
Female food treatment (FF)	1, 24	0.06	0.806
Social treatment (S)	2, 24	0.10	0.901
Male up-down activity			
Male food treatment (MF)	1, 19	1.13	0.301
Female food treatment (FF)	1, 19	0.20	0.663
Social treatment (S)	2, 19	1.43	0.263
MF \times S	2, 19	1.58	0.231
FF \times S	2, 19	0.85	0.441
MF \times FF	1, 19	0.06	0.809
MF \times FF \times S	2, 19	1.54	0.240

Interactions and the covariate were sequentially removed from the model if their F values were less than 1.

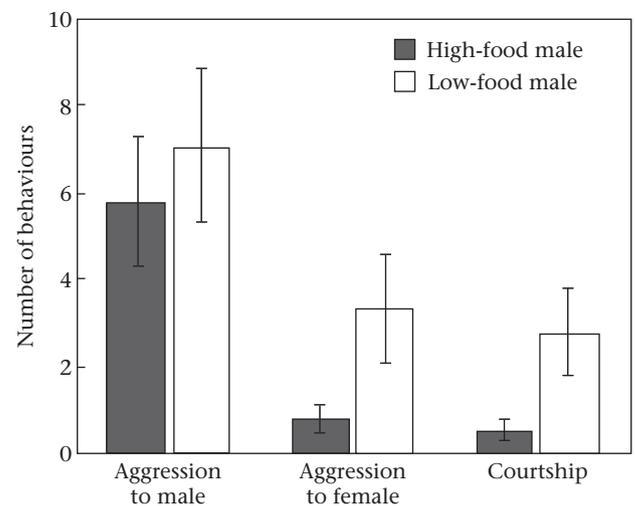


Figure 3. Number of behaviours performed by male bluefin killifish reared on high and low food in the dominance trial. Bars show adjusted least square means \pm SE.

(i.e. number of up-down movements performed in his container) was not significantly influenced by his food treatment, the female's food treatment or the social treatment they had all experienced (Table 2). Although low-food males tended to be more active during the choice trial (number of up-down movements: high food = 28.4 ± 5.4 ; low food = 40.0 ± 7.0), the difference was not statistically significant.

Dominance Trials

High-food and low-food males did not differ significantly in their likelihood of becoming dominant as adults ($F_{1,25} = 1.22$, $P = 0.280$), with high-food males becoming dominant in 58% of the dominance trials. The interactions between male food treatment and both social treatment and female food treatment had F values less than 1 and were removed from the model. Neither the social environment nor the food treatment that males and females experienced as juveniles significantly influenced the amount of aggressive behaviour a male displayed to his male partner (number

Table 3
Repeated measures GLMM results for behaviours of bluefin killifish in the dominance trial ($N = 27$)

Effect	ndf, ddf	F	P
Number of aggressive behaviours to male			
Male food treatment (MF)	1, 23	0.30	0.588
Female food treatment (FF)	1, 23	0.75	0.396
Social treatment (S)	2, 23	2.55	0.100
MF \times S	2, 23	1.89	0.174
FF \times S	2, 23	1.04	0.370
MF \times FF	1, 23	1.78	0.195
Number of aggressive behaviours to female			
Male food treatment (MF)	1, 24	5.82	0.024
Female food treatment (FF)	1, 24	0.27	0.607
Social treatment (S)	2, 24	5.57	0.010
MF \times S	2, 24	1.22	0.314
FF \times S	2, 24	1.30	0.299
Number of courtship behaviours			
Male food treatment (MF)	1, 25	6.09	0.021
Female food treatment (FF)	1, 25	2.54	0.124
Social treatment (S)	2, 25	1.68	0.208
Male condition–female condition	1, 25	9.04	0.006

Significant values are shown in bold. Interactions and the covariate were sequentially removed from the model if their F values were less than 1.

of aggressive behaviours towards male: high food = 7.3 ± 2.0 ; low food = 9.1 ± 2.9 ; Fig. 3, Table 3).

The social environment individuals experienced as juveniles significantly influenced how much aggression males showed towards females, with males reared with no adult displaying more aggression towards females regardless of the food level they had experienced (number of aggressive behaviours towards female: no adult = 6.1 ± 2.6 ; male = 1.6 ± 0.7 ; female = 1.8 ± 1.3 ; Table 3). In addition, males reared on low food showed greater aggression towards females than did high-food males regardless of the social environment they had experienced (number of aggressive behaviours towards female: high food = 2.2 ± 1.2 ; low food = 3.8 ± 1.5 ; Fig. 3, Table 3). Similarly, males reared on low food showed more courtship behaviours than those reared on high food regardless of the social environment they had experienced (number of courtship behaviours: high food = 1.2 ± 0.5 ; low food = 3.3 ± 1.0 ; Fig. 3, Table 3). However, courtship behaviour was also influenced by whether the female was heavier than the male, resulting in this covariate being statistically significant (Table 3). Specifically, when the female was heavier for her length than the male, the male courted in 50% of the trials (15 out of 30 males), and when the female was lighter for her length than the male, the male courted in 29% of the trials (7 out of 24 males).

Interestingly, these patterns did not seem to be driven by the final size of the male. When we replaced the early male food treatment with final male standard length (as a random factor) in the analyses, male standard length, female food treatment and social treatment did not emerge as significant predictors of any of the behaviours (results not shown). This suggests that early resource environment, rather than final size of a male, influenced male aggression towards females and male courtship patterns in our study.

DISCUSSION

It is becoming increasingly recognized that there is often consistent behavioural variation among individuals within populations (Sih et al. 2004a, b; Sih & Bell 2008). How sensitive these individual behavioural differences are to early experiences remains unclear (Stamps & Groothuis 2010a, b). Field-collected *L. goodei* males are highly repeatable in their mating behaviours through time and across interactions, resulting in predictable outcomes to dominance interactions (McGhee & Travis 2010) and prompting us to ask how individuals develop their particular behavioural trajectories. The results from this study suggest that some of these behaviours may be influenced by particular experiences during ontogeny.

Both our food and social manipulations were successful in influencing growth and survival (Figs 1, 2, Table 1). The effect of food treatment on body size was long-lasting and remained strongly evident at the time of behavioural testing, 4 months after the subjects had been fed ad libitum. Note that the low-food treatment was not a starvation treatment; the ranges of body size generated in this experiment were comparable to those seen in natural populations (this study: high-food males = 27.5–35.5 mm; low-food males = 25.5–33.0 mm; McGhee et al. 2007; field-collected males = 25.0–38.0 mm, $N = 68$). In addition, mortality was higher in the high-food treatment than in the low-food treatment. We removed uneaten food, so it is unlikely that the mortality was attributable to overfeeding and bacterial growth in the tank. It may be that higher food levels led to elevated encounter rates between individuals in the tank and greater aggression among fry or among adults and fry. We might have expected higher mortality of fry housed with adult males because adult males are highly aggressive towards other individuals. Interestingly, however, roughly half of the total mortality occurred after the adults were

removed from the tanks (in month 6; Appendix, Table A1). This suggests that the survival of fry reared in the male social treatment could have been affected by the adult male directly (e.g. as recipient of the adult male's aggression) or indirectly (e.g. aggressive interactions among fry resulting from the adult male aggression). While we did see both adult males and females behaving aggressively towards juveniles and juveniles behaving aggressively towards one another (e.g. chasing, attacking), particularly at feeding time, this was unfortunately not recorded systematically throughout development. Although we feel confident that mortality was a result of aggression among individuals, we do not know the importance of adult versus juvenile aggression. In addition, because individuals were not individually marked, it remains unknown whether aggression was more often directed at particular behavioural types and could have potentially resulted in a mortality bias (the behavioural consequences of such a bias are discussed below). Behavioural observations of individual fry throughout development would illuminate these issues.

Despite the long-lasting effects of the early food treatments on adult size, whether it had consequences for adult behaviour depended on the type of behaviour and its recipient. The behaviours shown in the choice trials (female association time and male up–down activity) as well as the outcome (preferred or not preferred) were not detectably influenced by the early food level experienced by males or females (Table 2). However, a male's behaviour towards a female was influenced by the food level that he had received as a juvenile, with males reared on low food showing increased levels of both aggression and courtship (Fig. 3, Table 3). In addition, whether a male courted a female was influenced by the female's size relative to that of the male. In contrast, a male's aggressive behaviour towards his male partner was relatively unaffected by his early food level, as was the outcome of these male–male interactions (dominant or subordinate) (Table 3).

Previous studies have found large behavioural effects associated with food level manipulations with an average effect size of 0.8 for aggression and dominance behaviours (estimated from: Royle et al. 2005; Kolluru & Grether 2005) and 0.5 for courtship and female preference behaviours (estimated from: Kolluru & Grether 2005; Fisher & Rosenthal 2006; Walling et al. 2007; Kolluru et al. 2009). We had ample power to detect similar effect sizes between high-food and low-food males with our sample size (power = 0.97 for dominance-related behaviours and 0.67 for courtship and female preference behaviours; calculation of effect sizes: Nakagawa & Cuthill 2007). Rather, the lack of statistically significant behavioural differences between high-food and low-food males in female preference, male attractiveness and male–male aggression suggests that our food manipulations did not result in a biologically meaningful effect on these behaviours in *L. goodei*.

Despite the social treatment ceasing 5 months prior to behavioural testing, it influenced how males reacted to females as adults. Males were more aggressive towards females when they had been reared with no adult compared to those that had been reared with either an adult male or female (Table 3). This could be due to social inhibition resulting from interactions with aggressive adults (Hsu et al. 2006). This pattern is also consistent with the possibility that the most aggressive juveniles were killed by the adult male or female in those particular social treatments, resulting in fewer aggressive individuals in those treatments. However, that individuals from the 'no adult' social treatment should show increased aggression towards females, but not males, is inconsistent with this hypothesis.

Because mortality was not equal across treatments, it is possible that the effects we observed were due to selective mortality (i.e. death of particular behavioural types in the rearing tanks) rather than behavioural plasticity. Although we are unable to completely rule out the possibility of selective mortality without behavioural

observations of known individuals through ontogeny, we argue that the patterns we observed are most consistent with behavioural plasticity for two reasons. First, part of the reason that the high-food male treatment had such high average mortality (Fig. 2) was due to two rearing tanks having 100% juvenile mortality. As a result, these tanks contributed zero individuals to the behavioural assays. Second, when we excluded all dyads where one of the males came from a rearing tank that experienced any mortality, individuals showed similar means for the behavioural traits to those of the entire data set (Appendix, Table A4). When we reran our statistical analyses on this reduced data set, we found essentially the same results, at least in terms of the largest *F* values and statistically significant terms (results not shown), although with such a reduced sample size, we could not look for interactions, and thus, our results should be treated cautiously. These results suggest that behavioural plasticity might have a more influential role than selective mortality; however, this is clearly an issue that should be addressed directly and may be more complicated than it first appears. For example, Bell & Sih (2007) found that selective mortality caused by predators can interact with behavioural plasticity to shape correlations among behaviours.

Interestingly, studies examining the effect of early social environment on behavioural plasticity often find inconsistent results. For example, in guppies (*Poecilia reticulata*), Price & Rodd (2006) found that male aggression and courtship tended to increase with the number of males and adults present in rearing tanks. Similarly, Arnold & Taborsky (2010) found that fry of the cooperatively breeding cichlid *Neolamprologus pulcher* that had been reared with adults were more aggressive than those that had been reared without adults and that they were able to adjust their behaviour more appropriately to the social context. In contrast, Magellan & Magurran (2009) found no behavioural consequences for guppies of being reared with an adult, with siblings or in isolation. It is important to keep in mind that social milieu can be manipulated in many ways (e.g. sex ratio, density, frequency of behavioural types, species composition, etc.), resulting in vastly different effects on behaviour and perhaps preventing general conclusions about the importance of the early social environment. However, our results suggest that even crude manipulations of the social environment, such as in this study, can have long-lasting consequences in terms of mating behaviours.

An important assumption we have made throughout this study is that a male's behavioural type and its components are repeatable. Because we did not measure the individuals more than once in this study we do not know how behavioural consistency is affected by food and social manipulations. Although this itself would be an interesting aspect to pursue, our goal in this study was to examine how the early environment might influence the components of a behavioural type that, in field-collected males, is stable across interactions with different males and over several weeks during the breeding season (McGhee & Travis 2010).

When an individual's behavioural type influences the outcome of social interactions and predicts reproductive success, as it does in bluefin killifish (McGhee et al. 2007), it could potentially act as a signal of male quality (Zahavi 1975). For example, if males that experience low stress during development (e.g. high food and low aggression) develop more aggressive behavioural types, then their behavioural type accurately reflects the amount of stress for which they had to compensate to reach adulthood. Our results present a mixed picture of this hypothesis in that some of the behaviours that contribute to a male's behavioural type within the mating context, such as aggression towards females and courtship, are sensitive to early experiences, whereas other behaviours, such as aggression towards males, are not sensitive to early experiences. Whether this reflects a male's ability to adequately compensate for

early stress in aggressive interactions but not in other mating behaviours, or whether aggression displayed in male–male interactions is not an honest signal of previous experiences remains unclear. In addition, whether sensitivity to the early environment is itself a personality trait that differs among individuals is unknown. This study represents a first step in examining these questions and suggests that particular aspects of an individual's early rearing environment can potentially influence the development of personality and play a role in generating the extensive consistent behavioural variation we see among individuals. Taking a developmental reaction norm perspective to further examine these patterns might be particularly interesting (Stamps & Groothuis 2010a, b).

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APPENDIX

Table A1

Mortality data for those rearing tanks of bluefin killifish that had fry mortality

Tank no.	Treatment		Number of fry dead at			Final number of fry alive (out of 4)
	Food	Social	4 months	5 months	6 months	
2	Low	No adult	1	0	1	2
17	High	Male	2	2	X	0
5	High	No adult	0	1	0	3
7	High	Male	0	2	0	2
9	High	Female	0	1	0	3
40	High	Male	0	4	X	0
42	High	Female	0	1	0	3
45	Low	Male	0	2	1	1
46	High	Male	0	1	0	3
1	High	Male	0	0	1	3
13	High	Male	0	0	1	3
21	High	No adult	0	0	1	3
29	High	Male	0	0	3	1
35	Low	Female	0	0	2	2
36	High	Female	0	0	1	3
48	High	Female	0	0	2	2
54	High	No adult	0	0	2	2

Each tank initially had four fry, and no tanks experienced mortality at 3 months. Note that at the 5-month census, the ‘treatment adults’ were removed.

Table A2

Repeated measures mixed model results on mass of bluefin killifish over time (months 4 to 10)

Effect	ndf, ddf	F	P
Food treatment (F)	1, 59	96.3	<0.0001
Social treatment (S)	2, 59.7	0.5	0.606
Time (T)	3, 683	382.36	<0.0001
F×S	2, 60.4	4.32	0.018
F×T	3, 682	0.15	0.931
T×S	6, 682	1.32	0.244
F×S×T	6, 682	1.54	0.162

Rearing tank was the repeating subject.

Table A3

Repeated measures mixed model results on body condition of bluefin killifish over time (months 4 to 10)

Effect	ndf, ddf	F	P
Food treatment (F)	1, 59.3	5.07	0.028
Social treatment (S)	2, 60	0.80	0.454
Time (T)	3, 683	23.40	<0.0001
F×S	2, 60.7	1.82	0.171
F×T	3, 683	14.30	<0.0001
S×T	6, 683	0.64	0.695
F×S×T	6, 683	2.73	0.013

Body condition was calculated as the residuals from a regression of mass on standard length. Rearing tank was the repeating subject.

Table A4

Means (\pm SE) for each treatment group of bluefin killifish from the entire data set and the reduced data set (excluding dyads in which one member was from a rearing tank that experienced mortality)

	Food treatment		Social treatment		
	High food	Low food	No adult	Male	Female
Entire data set					
<i>Choice trials</i>	<i>N</i> =25	<i>N</i> =25	<i>N</i> =16	<i>N</i> =20	<i>N</i> =14
Female preference time (s)	279.9 (53.5)	213.7 (48.6)	242.9 (58.7)	266.0 (68.2)	223.8 (56.3)
Male up–down activity	28.4 (5.4)	40.0 (7.0)	33.7 (8.1)	28.1 (6.5)	43.4 (9.1)
<i>Dominance trials</i>	<i>N</i> =27	<i>N</i> =27	<i>N</i> =16	<i>N</i> =20	<i>N</i> =18
No. of aggressive behaviours to male	7.3 (2.0)	9.1 (2.9)	11.8 (3.7)	4.6 (1.1)	8.9 (3.8)
No. of aggressive behaviours to female	2.2 (1.2)	3.8 (1.5)	6.1 (2.6)	1.6 (0.7)	1.8 (1.3)
No. of courtship behaviours	1.2 (0.5)	3.2 (1.0)	3.0 (1.3)	1.3 (0.5)	2.6 (1.2)
Reduced data set (excluding tanks with mortality)					
<i>Choice trials</i>	<i>N</i> =13	<i>N</i> =13	<i>N</i> =8	<i>N</i> =8	<i>N</i> =10
Female preference time (s)	288.0 (68.7)	225.0 (68.7)	248.9 (76.9)	287.8 (114.5)	237.6 (76.6)
Male up–down activity	22.8 (6.1)	39.8 (10.6)	30.2 (9.9)	29.6 (13.1)	33.4 (10.6)
<i>Dominance trials</i>	<i>N</i> =14	<i>N</i> =14	<i>N</i> =8	<i>N</i> =8	<i>N</i> =12
No. of aggressive behaviours to male	6.6 (1.9)	9.4 (3.4)	13.5 (4.7)	5.5 (1.9)	6.0 (2.9)
No. of aggressive behaviours to female	1.0 (0.4)	6.3 (2.6)	6.6 (3.6)	2.5 (1.7)	2.4 (2.0)
No. of courtship behaviours	1.3 (0.8)	3.4 (1.4)	2.9 (1.3)	1.2 (0.7)	2.7 (1.7)