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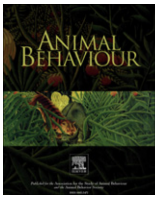

Early food and social environment affect certain behaviours but not female choice or male dominance in bluefin killifish

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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.

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 × width × height: 50 × 25 × 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; H0 = high food, no adult; LM = low food, adult male; LF = low food, adult female; L0 = 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; H0 = 9; LM = 10; LF = 11; L0 = 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