



## Paternal programming in sticklebacks



Laura R. Stein<sup>\*</sup>, Alison M. Bell

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

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In a wide range of organisms, including humans, mothers can influence offspring via the care they provide. Comparatively little is known about the effects of fathering on offspring. Here, we test the hypothesis that fathers are capable of programming their offspring for the type of environment they are likely to encounter. Male threespine sticklebacks, *Gasterosteus aculeatus*, were either exposed to predation risk while fathering or not. Fathers altered their paternal behaviour when exposed to predation risk, and consequently produced adult offspring with phenotypes associated with strong predation pressure (smaller size, reduced body condition, reduced behavioural activity). Moreover, more attentive fathers produced offspring that showed stronger antipredator responses. These results are consistent with behaviourally mediated paternal programming: fathers can alter offspring phenotypes to match their future environment and influence offspring traits well into adulthood.

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In a wide range of organisms, including humans, mothers' experiences can affect offspring (Mousseau & Fox, 1998; Uller, 2008). For example, maternal exposure to predation risk alters offspring morphology (Agrawal, Laforsch, & Tollrian, 1999; Weisser, Braendle, & Minoretti, 1999), physiology (Sheriff, Krebs, & Boonstra, 2010) and behaviour (Storm & Lima, 2010). There is also an emerging literature showing that the way mothers behave towards their offspring can have a long-lasting influence on their offspring (Champagne, 2008).

Comparatively less is known about the significance of fathers' experiences and behaviour for offspring. At first glance it might appear that there is little opportunity for fathers' experiences to become embedded in offspring because there is rarely intimate contact between fathers and developing embryos. However, a growing number of studies is showing that fathers' experiences prior to fertilization can influence offspring via, for example, changes in sperm morphology or seminal fluid (beetles: Sirota, Lapointe, Shatters, & Bausher, 2006), the sperm epigenome (mammals: Curley, Mashoodh, & Champagne, 2011) and sperm microRNAs (rats: Rodgers, Morgan, Bronson, Rovello, & Bale, 2013).

A relatively unexplored possibility is that fathers adjust their parenting in response to stressors, and adjustments in care have long-term consequences for offspring, as has been shown for mothers (McLeod, Sinal, & Perrot-Sinal, 2007).

Predation is a strong selective pressure that shapes many traits (Abrams & Rowe, 1996; Endler, 1995). In a predator-rich environment, antipredator defences are key for reproductive success and offspring survival, and predation risk often alters phenotypes in predictable ways. For example, prey in high-predation environments tend to be smaller, less active and have faster life history trajectories than prey from low-predation environments (guppies: Endler, 1995; tadpoles: Relyea, 2004; lizards: Vervust, Grbac, & Van Dame, 2007). If parents can respond to cues that future predation risk is likely to be high, and if they can prepare offspring for living in a predator-rich environment, then this transgenerational plasticity could be adaptive.

Here, we investigate the effects of paternal experience with predation risk on offspring morphological, behavioural and physiological traits in threespine sticklebacks, *Gasterosteus aculeatus*. Sticklebacks are teleost fish in which the father is the sole provider of parental care that is necessary for offspring survival. Therefore, there is no opportunity for differential allocation or compensation by the mother (Curley et al., 2011). During the approximately 5-day incubation period, male sticklebacks 'fan' the eggs with pectoral fins, providing oxygen and clearing carbon dioxide, and remove rotten

<sup>\*</sup> Correspondence: L. R. Stein, School of Integrative Biology, University of Illinois at Urbana-Champaign, 515 Morrill Hall, 505 S. Goodwin Avenue, Urbana, IL 61801, U.S.A.

E-mail address: [stein12@illinois.edu](mailto:stein12@illinois.edu) (L. R. Stein).

eggs and debris (Wootton, 1984). Once the eggs hatch, fathers continue to defend their offspring and retrieve young fry that stray too far from the nest. Previous studies suggested that offspring learn appropriate antipredator behaviour from their father after hatching (Feuth-De Bruijn & Sevenster, 1983; Tulley & Huntingford, 1987).

We used a within-subjects breeding design to test the hypothesis that paternal exposure to predation risk during parenting influences offspring traits. Specifically, males experienced predation risk during one parenting episode ('predator-exposed') and were not exposed to predation risk during the other parenting episode ('unexposed'). We evaluated the effect of paternal predator exposure on the morphology, behaviour and physiology of reproductively mature adult offspring. We further examined correlations between paternal behaviour and offspring behaviour to test the hypothesis that paternal effects on offspring are mediated by paternal behaviour.

## METHODS

### *Study Population and Breeding*

Adult threespine sticklebacks were collected from Putah Creek, a dammed, regulated freshwater stream in northern California, in April 2010. Sculpin (*Cottus* spp.), a fish predator known to prey on stickleback eggs, fry and adults (Moodie, 1972; Pressley, 1981) are present at this site. Fish were shipped to the University of Illinois at Urbana-Champaign, and males were introduced into separate 9.5-litre (36 × 21 × 18 cm) tanks with a refuge (plastic 'plant'), an open plastic box (13 × 13 × 3 cm) filled with fine sand, and filamentous algae for nest building. Following nest completion, males were presented with a gravid female and allowed to spawn. Each male spawned with a unique female. After spawning, the female was removed. Fish were kept at 20 °C on a summer (16:8 h light:dark) photoperiod. Water was cleaned via a recirculating flow-through system that consisted of a series of particulate, biological and UV filters (Aquaneering, San Diego, CA, U.S.A.). Ten per cent of the water volume in the tanks was replaced each day. Fish were fed a mixed diet consisting of frozen bloodworm, brine shrimp and *Mysis* shrimp in excess each day.

### *Exposing Fathers to Predation Risk and Recording Paternal Behaviour*

Males were randomly assigned to either the 'unexposed' or 'predator-exposed' treatment for their first clutch. On the third day after males spawned (when the embryos were 3 days old), males in the 'predator-exposed' treatment were chased with a 10 cm rubber model sculpin (Jewel Bait Company, Bakersfield, MO, U.S.A.) for 2 min to simulate a nest predation attempt. A predator of this size is a threat to the eggs and fry, but not to the adult males (Moodie, 1972; Pressley, 1981). Previous research has shown that adult sticklebacks show relevant antipredator behaviours when confronted with a realistically painted model (Grobis, Pearish, & Bell, 2013). It is unlikely that the embryos were exposed to visual cues of the model predator, as during the 'predator-exposed' treatment, the optic cups of the 3-day-old embryos were still developing (Swarup, 1958) and the eggs were covered by nesting material. For males in the 'unexposed' treatment, we removed the top of the tank and gently splashed the water when the eggs were 3 days old to simulate the water disturbance caused when the model predator entered the tank. Males were only exposed to the predator once.

After spawning, we observed paternal behaviour every day for 5 min between 1000 and 1300 hours Central Standard Time (CST) from 1 day after spawning through 5 days after the eggs hatched (when fry from this population naturally disperse in the wild). We measured the total time that the male was within one body length

of the nest (total time at nest) and the total amount of time that the male spent fanning his eggs, a paternal behaviour that oxygenates the eggs (Wootton, 1984), is important for proper offspring development (von Hippel, 2000) and consistently varies among fathers (Stein & Bell, 2012). The simulated predation threat (or water splashing) occurred after the daily observation of paternal behaviour. There were subtle but detectable effects of predator exposure on paternal behaviour. For example, 'predator-exposed' fathers decreased total time fanning relative to control males for 2 days following exposure to the model predator, but afterwards resumed normal activity (Stein & Bell, 2012). More details on parental behaviour are presented in Stein and Bell (2012).

Five days after the eggs hatched, males were placed in new tanks and allowed to construct second nests and the entire process, including daily behavioural observations, was repeated for the second clutch. Males that had been in the 'predator-exposed' treatment in the first clutch were assigned to the 'unexposed' treatment for the second clutch and vice versa.

Ten males completed at least one clutch; of these, eight completed two clutches. Initial treatment did not affect whether males completed a second clutch (of those that completed two clutches, four were 'unexposed' and four were 'predator-exposed' in their first clutch), and parental behaviour in the first clutch did not predict whether a male completed a second clutch (Stein & Bell, 2012). We did not detect a difference in parental behaviour between the first and second clutches or an effect of the order in which a male experienced a model predator (i.e. a male's experience with parenting or with a predator did not influence his behaviour in his second clutch).

### *Offspring Morphology and Antipredator Behaviour*

Once fry were approximately 1 cm in length (~1 month old), each full-sibling family was split across at least two tanks at a density of six fish per tank. Offspring were fed newly hatched *Artemia nauplii* shrimp in excess each day until they reached 3 cm in length, at which time they were fed the adult slurry of frozen food. Offspring were kept this way for 1 year; during this time they experienced a simulated winter (LD 8:16) photoperiod from November 2010 to March 2011.

At 1 year of age, when the offspring were reproductively mature, we measured their morphology, behaviour and cortisol response to predation risk. Specifically, we measured standard length and weight and scored colour (males only) using a ranking method (Boughman, 2007). Throat redness was measured as the sum of throat red area and red intensity scores (range 0–3 for each). Body brightness ranged from 0 to 5, with 5 being very bright. Throat hue and body brightness were measured on the side of the fish.

For behavioural testing of predator responses, fish were transferred individually to an observation tank in an opaque cylinder (10 cm in height, 10 cm diameter) plugged with a cork. The observation tank (53 × 33 × 24 cm) had a 5 × 2 grid drawn on the front, a gravel bottom and two plastic plants for refuge, one on each side of the tank. After a 15 min acclimation period, we removed the cork remotely and, after emerging from the cylinder, the fish acclimated to the observation tank for 1 h.

We recorded behaviour with a high-definition JVC Everio camcorder from behind a blind. Behaviour was recorded (see below for details) for 3 min without a stimulus to obtain a baseline level of behaviour ('before'). After 3 min, we introduced a 15 cm clay sculpin (model predator) painted with natural markings to the tank to measure antipredator behaviour. A predator this size is a threat to adult sticklebacks (Moodie, 1972; Pressley, 1981). The model predator was attached with fishing wire to a rod that could be manipulated from behind the blind. We introduced the model to

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