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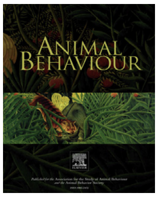

Do reproduction and parenting influence personality traits? Insights from threespine stickleback

Laura R. Stein [a,*], Rebecca M. Trapp [b], Alison M. Bell [b]

[a] Department of Biology, Colorado State University, Fort Collins, CO, U.S.A.
[b] School of Integrative Biology, University of Illinois, Urbana, IL, U.S.A.

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Although one of the hallmarks of personality traits is their consistency over time, we might expect personality traits to change during life history shifts. Becoming a parent is a major life history event, when individuals undergo dramatic behavioural and physiological changes. Here we employ a longitudinal experiment to ask whether personality changes in response to the experience of parenting in male threespine sticklebacks, *Gasterosteus aculeatus*. Life history theory predicts that males should be less risk averse after successfully parenting, and the neuroendocrinology of parenting suggests that parenting could reorganize the hormonal landscape and behaviour of fathers. We randomly assigned males to either an experimental group (reproduced and parented) or a control group (did not reproduce and parent), and repeatedly measured a personality trait ('boldness') and 11-ketotestosterone levels (11-kT, the major androgen in fishes) in individual males. In the control group, males became bolder over time. However, in the experimental group, boldness did not change. Furthermore, 11-kT changed dramatically in the experimental group, and changes in 11-kT in parents were associated with boldness after parenting ceased. Our study is one of the first to assess proximate and ultimate explanations for changes in personality as a function of reproduction and parenting.

The experience of reproducing and becoming a parent is one of the most important life history events for most organisms. Although there is a rich literature documenting physiological and behavioural changes that organisms undergo as they become parents, there are few data in either humans or nonhuman animals that test the intuitive hypothesis that becoming a parent influences personality traits (behaviours that are variable among individuals and consistent within individuals over time; Stamps & Groothuis, 2010). Understanding the robustness of personality traits across critical lifetime events can shed light on their plasticity, causation and evolution (Duckworth, 2015).

It is reasonable to suppose that personality traits might change as a function of reproduction and parenting because we know that parenting can have long-term effects on behaviour. For example, the experience of being a parent influences parenting behaviour during subsequent breeding attempts (Reichert, Cattau, Fletcher, Kendall, & Kitchens, 2012; Royle, Smiseth, & Kolliker, 2012). What has not been explored, however, is whether the experience of becoming a parent influences 'personality traits' (i.e. behaviours that are variable among individuals and consistent within individuals over time).

Here, we investigate the effects of reproduction and parenting on personality (boldness) in threespine sticklebacks, *Gasterosteus aculeatus*. In this species, all of the parental care necessary for offspring survival is provided by the father, and parenting is an energetically costly (Smith & Wootton, 1999) yet critical experience for males that strongly influences fitness (Wootton, 1984). Most freshwater sticklebacks live for 1 year and are seasonal breeders. Boldness is an important source of behavioural variation in this species: some individual sticklebacks are consistently relatively timid while others are bolder (Huntingford, 1976), and this variation influences fitness (Bell & Sih, 2007). Here, we measure boldness as willingness to forage under predation risk.

There are at least two nonmutually exclusive hypotheses to explain how and why boldness might change as a function of reproduction and parenting. First, according to life history theory, investment in current reproduction often comes at a cost to future reproduction; therefore, as the probability of future reproduction decreases, we might expect boldness to increase (Clark, 1994; Montgomerie & Weatherhead, 1988). Indeed, on average, risk-taking behaviour is higher at the end of the breeding season than

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* Correspondence: L. R. Stein, Department of Biology, Colorado State University, E209A Anatomy-Zoology, 200 W Lake Street, Fort Collins, CO 80523, U.S.A.
E-mail address: lrstein@colostate.edu (L. R. Stein).

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at the beginning (fish: Candolin & Voigt, 2003; Magnhagen & Vestergaard, 1991; birds: Pugesek, 1983; insects: Rosenheim, Jepsen, Matthews, Smith, & Rosenheim, 2008; mammals: Dammhahn, 2012; but see Ukegbu & Huntingford, 1988). However, cross-sectional studies that do not repeatedly measure the same individuals cannot tell us whether individuals change their behaviour as a function of experience, or if changes reflect factors such as selection or dispersal, for example. Moreover, work to date has been observational (rather than manipulative); therefore, we do not know the causal factors driving changes in boldness (e.g. experience, age, seasonality).

Another hypothesis (the ‘physiological remodelling hypothesis’) supposes that the dramatic neural (Franssen et al., 2011; Russell, Douglas, & Ingram, 2001) and endocrine (Saltzman & Ziegler, 2014; Wingfield, Hegner, Dufty, & Ball, 1990) changes that accompany reproduction and parenting have long-lasting effects on subsequent behaviour (see also Cost, Lobell, Williams-Yee, Henderson, & Dohanich, 2014; Logan, Hill, Jones, Holt-Lunstad, & Larson, 2014; Macbeth & Luine, 2010). For example, physiological changes associated with parenting might influence personality traits if individuals do not return to a preparenting hormonal state. This hypothesis assumes that changes in physiology are more dramatic in individuals that parent versus those that do not, and it predicts that hormonal changes occurring over the course of parenting are associated with personality traits after parenting has ceased. Importantly, the life history and physiological hypotheses are not mutually exclusive; while the former offers an ultimate explanation, the latter offers a proximate one.

We evaluate evidence for the life history and physiological remodelling hypotheses by repeatedly measuring boldness before and after reproduction and parenting in male sticklebacks. A control group was also repeatedly measured for boldness but did not rear offspring. By comparing individuals that reproduced and parented (experimental) with the control group, we could ask whether changes experienced by males in the experimental group were specifically due to reproduction and parenting, or whether they reflect confounding effects such as time, age or seasonality. We first confirmed that our measures of boldness were personality traits, then asked how the experience of becoming a parent influences boldness by comparing the average risk-taking behaviour between males in the experimental and control groups. To test the physiological remodelling hypothesis, we repeatedly measured excreted 11-ketotestosterone (11-kT), the main androgen in fishes associated with courtship and parenting (Pradhan, Solomon-Lane, Willis, & Grober, 2014) and examined how changes in 11-kT levels were related to boldness. We chose to measure 11-kT as opposed to other steroids (e.g. cortisol) as it has been previously established in stickleback that while 11-kT changes over the nesting cycle and is important in reproduction and parenting (Pall, Mayer, & Borg, 2002), nonandrogen steroids remain at similar levels (Sebire, Katsiadaki, & Scott, 2007).

METHODS

Adult threespine stickleback were collected from Putah Creek, California, U.S.A. in April 2013. At this time, adults in this population begin showing nuptial coloration but have not yet begun breeding. Therefore, it is unlikely the males in this study had previous parenting experience. Fish were shipped to the University of Illinois at Urbana-Champaign (Champaign, IL, U.S.A.). On days when risk-taking behaviour was measured, males were not fed except during the trials. All assays were conducted from May to July 2013. None of the males in this experiment were infected with *Schistocephalus solidus*, a tapeworm known to influence risk-taking behaviour (Barber & Dingemanse, 2010; Giles, 1987).

Fish were kept at 20° C on a summer photoperiod (16:8 h light:dark cycle). 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 (*Chironomus* spp.), brine shrimp (Artemia spp.) and *Mysis* shrimp in excess each day.

Boldness Assay

Males were introduced into separate housing tanks. One week later, individuals were phenotyped for boldness (the ‘Before’ trials) in an observation tank ($53 \times 33 \times 24$ cm) with a 5×2 grid drawn on the front, a gravel bottom and plastic plants for refuge. A model great egret, *Casmerodius albus*, skull was attached over the observation tank. The egret skull was situated so that when it was released via a lever from behind a blind, the tip of the egret's bill splashed the water surface (Fig. 1). This stimulus simulated the sudden overhead attack of an egret searching for prey (Giles & Huntingford, 1984).

To phenotype boldness for each fish, we transferred a single male into the observation tank, and 30 s later, we added 10 live bloodworms directly under the egret skull. If the male did not approach the bloodworms within 5 min ($N = 35$ of 169 trials), he was given a score of one greater than the maximum ‘latency to eat’ (301 s), and these trials were not used in analysis of ‘number of pecks at food’ and ‘number of squares moved’ (see below).

When the male approached within one body length of the bloodworms, we released the egret skull to splash the water twice in quick succession, and then affixed the skull so that it remained above the water (Alvarez & Bell, 2007; Bell, 2005). Following the simulated attack, we recorded three behaviours: time to resume eating following the predator attack (‘latency to eat’), number of pecks at the bloodworms (foraging under risk, ‘pecks at food’) and total number of times that the individual's head passed into a new square (activity under risk, ‘squares moved’) for 5 min from behind a blind.

We observed each male three times, with 24 h between trials, and measured males for standard length and body mass after the third trial.

Experimental and Control Groups

Following all three ‘Before’ boldness trials, we randomly assigned males to either the experimental or the control group. Males in the experimental group were randomly assigned to be ‘paired’ with a male from the control group (Fig. 1). While males were kept individually, males in paired groups were measured for all behaviours and 11-kT at the same time. This experimental design allowed us to control for variation among experimental males in time to spawn and time to complete a clutch. Males from both control and experimental groups were kept in individual 9.5-litre tanks containing a refuge, an open plastic box filled with fine sand and gravel, and filamentous algae for nest building.

Once both the control and experimental males within a pair had built nests, we selected a gravid female at random and weighed her, then placed the female in a long-necked flask inside the paired control male's tank for 5 min. This allowed the male to interact with and court the female but not spawn. We then placed the same female directly into the tank of the experimental male. We subtracted female body mass after spawning from female body mass prior to spawning to estimate egg mass. We acknowledge that the experience of reproduction and parenting were confounded in this experiment. However, if we had