

Effect of maternal predator exposure on the ability of stickleback offspring to generalize a learned colour–reward association



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Maternal stress can have long-term negative consequences for offspring learning performance. However, it is unknown whether these maternal effects extend to the ability of offspring to apply previously learned information to new situations. In this study, we first demonstrate that juvenile threespine sticklebacks, *Gasterosteus aculeatus*, are indeed capable of generalizing an association between a colour and a food reward learned in one foraging context to a new foraging context (i.e. they can apply previously learned knowledge to a new situation). Next, we examined whether this ability to generalize was affected by maternal predator stress. We manipulated whether mothers were repeatedly chased by a model predator while yolkng eggs (i.e. before spawning) and then assessed the learning performance of their juvenile offspring in groups and pairs using a colour discrimination task that associated a colour with a food reward. We found that maternal predator exposure affected the tendency of offspring to use social cues: offspring of predator-exposed mothers were faster at copying a leader's behaviour towards the rewarded colour than offspring of unexposed mothers. However, once the colour–reward association had been learned, offspring of predator-exposed and unexposed mothers were equally able to generalize their learned association to a new foraging task. These results suggest that offspring of predator-exposed mothers might be able to overcome learning deficits caused by maternal stress by relying more on social cues.

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Maternal effects can occur when a mother's experiences and her reaction to these experiences influence her offspring (Bernardo, 1996; Mousseau & Fox, 1998). For example, in a diversity of taxa, mothers exposed to predation risk produce offspring with altered phenotypes compared to offspring of unexposed mothers (e.g. birds: Coslovsky & Richner, 2011; daphnia: Agrawal, Laforsch, & Tollrian, 1999; fish: McGhee, Pintor, Suhr, & Bell, 2012; mammals: Sheriff, Krebs, & Boonstra, 2009; insects: Storm & Lima, 2010; reptiles: Bestion, Teyssier, Aubret, Clobert, & Cote, 2014). There is growing appreciation of the ecological and evolutionary significance of such nongenetic transgenerational effects (reviewed in: Badyaev & Uller, 2009; Monaghan, 2008; Sheriff & Love, 2013).

Maternal stress can influence a variety of offspring behaviours, including those associated with behavioural plasticity and learning

performance (reviewed in: Maccari, Krugers, Morley-Fletcher, Szyf, & Brunton, 2014; Schoech, Rensel, & Heiss, 2011; Weinstock, 2008). For example, in threespine stickleback, *Gasterosteus aculeatus*, adult offspring of predator-exposed mothers were slower at learning a colour discrimination task compared to offspring of unexposed mothers (Roche, McGhee, & Bell, 2012). Similar detrimental effects of maternal stress on offspring learning have also been documented in mammals and birds (reviewed in: Maccari et al., 2014; Schoech et al., 2011; Weinstock, 2008). However, it is unknown whether the consequences of maternal stress on offspring learning extend to performance in other contexts, such as the ability of offspring to apply previously learned knowledge to new situations.

If a learned association can be generalized across contexts, individuals can potentially reap even greater benefits from learning by behaving appropriately in a novel context without having to discover additional information. For example, learning about one predator can improve antipredator behaviour and survival when exposed to a different predator (Brown et al., 2011; Ferrari, Brown, Messier, & Chivers, 2009; Ferrari, Gonzalo, Messier, & Chivers, 2007; Griffin, Evans, & Blumstein, 2001; Mitchell, McCormick,

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Chivers, & Ferrari, 2013). Similarly, learning about particular prey items can improve foraging performance (or avoidance) when exposed to novel items (Ihalainen, Rowland, Speed, Ruxton, & Mappes, 2012; Marples, Quinlan, Thomas, & Kelly, 2007; Svádová et al., 2009). Thus, the ability to generalize learned associations could be advantageous, particularly in a seasonal and changing environment. If maternal stress affects the overall learning ability of offspring, including their ability to generalize learned associations, this could have important consequences in many contexts.

In this study, we explored how maternal stress affects offspring learning performance and their ability to generalize a learned association in threespine stickleback. Before we could explore the consequences of maternal stress on offspring learning however, we had to determine whether threespine sticklebacks are in fact capable of generalizing information they have learned in one context to a novel context. Thus, our study consisted of two separate experiments. In the first experiment, we determined whether learning a colour–reward association in a group under one set of conditions improved learning performance under a different set of conditions. In the second experiment, we examined whether a mother's experience with predators affected their offspring's ability to generalize a group-learned colour–reward association to a new foraging context. If maternal stress has negative consequences for overall offspring learning performance across a variety of tasks, then we would predict that offspring of predator-exposed mothers would be less able to generalize a colour–reward association compared to offspring of unexposed mothers. In both parts of the study, we interpreted a preference for the rewarded stimulus over the unrewarded stimulus as evidence for a learned colour–reward association.

EXPERIMENT 1

Can Sticklebacks Generalize a Learned Colour–Reward Association?

Methods

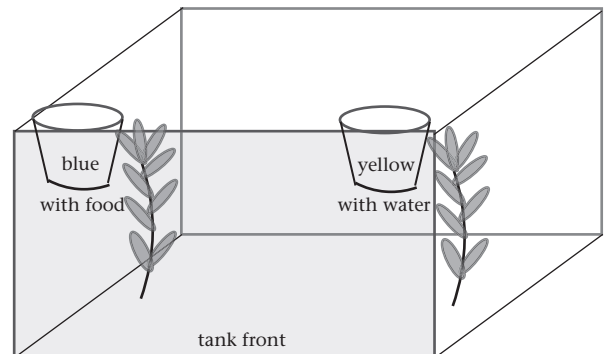
Juvenile collection and housing. Sixty threespine stickleback juveniles (average standard length \pm SE = 20.5 \pm 2.0 mm) were collected from the Navarro River, CA, U.S.A. in summer 2013. Piscivorous predators such as sculpin are present in this population and are primarily a threat to eggs and juvenile stickleback, although small adults are also vulnerable (Maccoll & Chapman, 2011; Pressley, 1981). Juveniles were transported by air to the University of Illinois and housed in groups of six in 26.5-litre tanks ($N = 10$ tanks, 36 \times 33 \times 24 cm, length \times width \times height) with gravel on the bottom of the tank and two plastic plants on opposite sides of the tank. These tanks are referred to as 'initial group tanks'. The fronts of the tanks were covered with opaque plastic to minimize disturbance due to human movements in the fish room. When fish were not being trained or tested, the sides of the tanks were left uncovered and fish could see neighbours. Fish were maintained at 20.6 °C on a summer photoperiod schedule (16:8 h light:dark cycle) and water was cleaned in all tanks via a recirculating flow-through system with particulate, biological and UV filters (Aquaeneering, San Diego, CA, U.S.A.). Using a clear pipette, we fed juveniles a slurry of frozen adult *Artemia*, mysis shrimp, bloodworms and cyclopeez once a day. The juveniles were acclimated in the laboratory for 2.5 weeks prior to any training.

Training trials. The juveniles were randomly assigned to either a colour–reward association training or a no-training treatment. The training treatment consisted of colour–reward association training in groups and subsequently in pairs, and the no-training treatment consisted of neither group nor pair training ($N = 10$ groups with six individuals per group; $N = 30$ pairs). We elected to train and test

sticklebacks with other individuals rather than by themselves because pilot studies showed that juvenile sticklebacks from this population were unlikely to explore the tank when alone. Note that both treatments were handled in the same way, with the only difference being the presence or absence of coloured cups during the group and pair training periods.

Groups in the training treatment were trained to associate a coloured cup with a food reward for 7 days. We trained fish twice a day at random times to prevent individuals from associating feeding with particular times of day. Opaque screens were placed in between tanks during feeding. During a training trial, two Solo® brand coloured cups (one blue and one yellow) were submerged 1 cm into the surface of the water at the front on opposite sides of the tank (Fig. 1a). The bottom of both cups had a small opening for the release of food or water from a pipette within. The blue cup was always rewarded and the pipette within it contained chopped bloodworms, whereas the yellow cup was never rewarded and the pipette within it contained tank water. After an individual in the group oriented to the blue cup, a food reward was pipetted into the water. The individual then moved towards the blue cup to obtain the food. In contrast, when an individual in the group oriented to the yellow cup, tank water was pipetted into the water. The trial ended when three different individuals were rewarded following orientation to the rewarded cup. During 7 days of group training, we recorded how quickly the first (the leader), second and third individuals oriented to the rewarded blue cup. The total time it took three fish to orient to the rewarded cup decreased as the training

(a) Training set-up:



(b) Testing set-up:

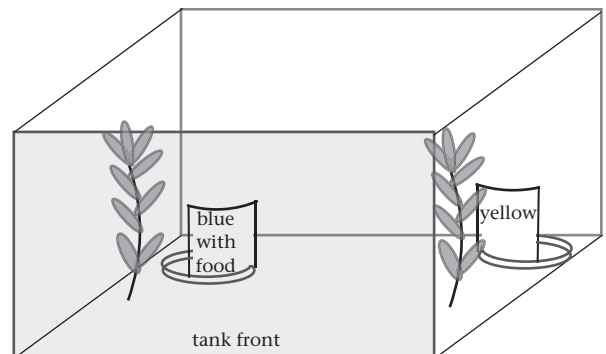


Figure 1. Experimental set-up during (a) training and (b) testing of threespine stickleback in a novel context. Note that the side with the rewarded blue cup was randomly determined. The sides and back of the tanks were covered with opaque plastic during the training and testing assays.

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