



Daily variation in behavioural lateralization is linked to predation stress in a coral reef fish



Maud C. O. Ferrari^{a,*}, Mark I. McCormick^{b,c}, Matthew D. Mitchell^a, Bridie J. M. Allan^{b,c}, Emanuel J. Gonçalves^d, Douglas P. Chivers^e

^a Department of Biomedical Sciences, WCVN, University of Saskatchewan, Saskatoon, SK, Canada

^b ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia

^c College of Marine & Environmental Sciences, James Cook University, Townsville, QLD, Australia

^d MARE – Marine and Environmental Sciences Centre, ISPA – Instituto Universitário, Lisboa, Portugal

^e Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada

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Behavioural lateralization, the preferential use of one side of the body or one of the limbs, is a trait common in vertebrates, and is often expressed as a turning bias in fishes. Recent studies have demonstrated considerable plasticity in lateralization, inferring the role of predation pressure as a key driver of this plasticity over short periods (i.e. days). Such plasticity may be expected if predator pressure is highly variable through space and time and can provide prey with a distinct advantage. We know that increased turning bias is linked with better escape performance, but we do not know the extent to which prey can adjust this trait to match temporal variation in risk. Here we trained juvenile Ambon damselfish to recognize different temporal patterns of risk throughout the day and asked whether their degree of lateralization changed according to this pattern. Damselfish that were taught that midday was risky showed a stronger turning bias at midday than in the evening, whereas damselfish that were taught that evening was risky showed a stronger turning bias in the evening than at midday. Subsequently, we found that fish exposed to cortisol expressed a greater degree of turning bias. Our results suggest that predation stress may be a key factor determining the degree of behavioural lateralization in vertebrates.

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Behavioural lateralization, the asymmetrical use of paired limbs or organs, has been documented in a wide variety of taxa (Csermely, 2013; Vallortigara, Rogers, & Bisazza, 1999) and is especially well studied in vertebrates (Vallortigara & Rogers, 2005). This asymmetry has been described in a number of ecological contexts. For instance, during exploratory or migratory behaviours, the eyes are often used asymmetrically, with general environmental cues being processed preferentially by the left eye (Vallortigara & Rogers, 2005; Wiltschko, Traudt, Güntürkün, Prior, & Wiltschko, 2002). Similar asymmetries in sensory inputs have been reported during agonistic interactions (Hews & Worthington, 2002), predator detection (Franklin & Lima, 2001; Rogers & Kaplan, 2006) or during conspecific recognition tasks (Basile et al., 2009). The asymmetry can also be displayed through ‘handedness’ or turning biases. The preferential handling of tools and food items by

one hand/paw/foot is relatively common in birds and mammals (Rogers, 2009; Rogers & Workman, 1993). Many fishes and amphibians show a consistent rotational turning bias. For many gregarious species, such turning biases even manifest as population-level biases (Dadda, Zandonà, Agrillo, & Bisazza, 2009; Vallortigara et al., 1999).

Despite two decades of research, the origin, evolution and maintenance of cerebral lateralization in animals remain largely unknown. The main issue behind lateralization is that biologically relevant stimuli, such as food patches, competitors or predator attacks can be located randomly on either side of an animal. As such, sensory asymmetries are expected to cause a disadvantage and, consequently, negative selection on cerebral lateralization (Dadda et al., 2009; Rogers, 2002; Rogers, Zucca, & Vallortigara, 2004; Vallortigara & Rogers, 2005). Of course, a number of studies have shown benefits associated with lateralization. For instance, individuals with more intense lateralization show better performance in complex motor activities (Magat & Brown, 2009), multitasking (Dadda & Bisazza, 2006; Rogers et al., 2004), spatial learning (Sovrano, Dadda, & Bisazza, 2005) and predator

* Correspondence: M. C. O. Ferrari, Department of Biomedical Sciences, WCVN, University of Saskatchewan, Saskatoon, SK S7N5B4, Canada.

E-mail address: maud.ferrari@usask.ca (M. C. O. Ferrari).

recognition learning (Chivers et al., 2017). Moreover, increased lateralization is positively correlated with escape performance (Chivers et al., 2016; Dadda, Koolhaas, & Domenici, 2010). However, higher lateralization tendencies are associated with poorer competitive abilities in a coral reef fish (Chivers et al., 2017). Hence, the resulting expression of this trait likely represents a fine balance between the cost and benefits it provides.

One context for which costs appear particularly high is predation. Prey often have a side bias in response to threatening stimuli. Birds and reptiles show an eye preference to look at predators (Koboroff, Kaplan, & Rogers, 2008; Martín, López, Bonati, & Csermely, 2010). For example, some prey have greater detection and escape performance when predators are detected in their left visual field (Austin & Rogers, 2007; Shibasaki, Nagumo, & Koda, 2014). Many show a turning bias in their escape response (Bonati, Csermely, López, & Martín, 2010; Lippolis, Bisazza, Rogers, & Vallortigara, 2002; Yamashita, Naitoh, & Wassersug, 2000). Given that predators are just as likely to appear and attack from either side, one would expect that the trait would be at a selective disadvantage in high-risk environments. However, evidence suggest that under high predation risk conditions, prey tend to display stronger lateralization (Brown, Gardner, & Braithwaite, 2004; Ferrari, McCormick, Allan, Choi, Ramasamy, Johansen et al., 2015). Perhaps faster escape responses associated with increased lateralization explain this paradox. Lateralization is a trait that appears to be highly plastic, as prey exposed to high predation risk show stronger lateralization tendencies than those exposed to low or no risk (Broder & Angeloni, 2014; Ferrari, McCormick, Allan, Choi, Ramasamy, & Chivers, 2015; Jozet-Alves & Hébert, 2013). Moreover, such an increase in laterality appears to be linked to increased survival during predator–prey encounters (Ferrari, McCormick, Allan, Choi, Ramasamy, & Chivers, 2015), although the covariance of multiple traits in response to risk makes it difficult to credit the survival benefits to increased lateralization only (Ferrari, McCormick, Allan, Choi, Ramasamy, Johansen et al., 2015). In concert, these studies suggest that the benefit from lateralization in a predation context must outweigh the cost of sensorial asymmetry.

Recent evidence on the inducible aspect of these traits (Broder & Angeloni, 2014; Ferrari, McCormick, Allan, Choi, Ramasamy, & Chivers, 2015; Jozet-Alves & Hébert, 2013) implies a cost that is avoided under low-risk conditions. How plastic should the trait be in order to be beneficial? Juvenile whitetail damsel, *Pomacentrus chrysurus*, exposed to injured conspecific cues for only 4 days showed increased behavioural lateralization tendencies over their low-risk counterparts (Ferrari, McCormick, Allan, Choi, Ramasamy, & Chivers, 2015). Data on wild-caught yellow-and-blueback fusiliers, *Caesio teres*, a schooling fish common on coral reefs, indicate that lateralization may in fact change from day to day, as fish showed a gradual decrease in strength of lateralization over the 4 days they were held in the absence of risk (Chivers et al., 2016). In the present study, we investigated the possibility that behavioural lateralization could change in response to diel patterns of predation risk. Several species of prey adjust the intensity of their behavioural response to predators based on the time of day that the predator is actively foraging. For example, woodfrog tadpoles, *Lythobates sylvaticus*, taught to avoid salamanders, *Ambystoma tigrinum*, in the morning show much stronger responses to salamanders in the morning than in the evening, whereas tadpoles that were taught that salamanders were a high risk in the evening responded more to salamander cues in the evening than in the morning (Ferrari, Messier, & Chivers, 2008). Similar temporal patterns of behavioural responses to predators are known in lemon damselfish, *Pomacentrus moluccensis*, that learn foraging patterns of rockcod (*Cephalopholis cyanostigma*) predators (Bosiger, Lonnstedt, McCormick, & Ferrari, 2012).

Using a well-established protocol (Bosiger et al., 2012; Ferrari et al., 2008), we exposed juvenile Ambon damselfish, *Pomacentrus amboinensis*, to one of two predictable patterns of risk for 9 days, with risk peaking either at noon or in the evening. The fish from both groups were then tested both at noon and in the evening. We hypothesized that, if behavioural lateralization is an inducible trait expressed in response to risk, then the expression of lateralization should follow the risk pattern the fish were exposed to, with stronger turning bias tendencies observed at the time of day that is perceived as the most risky. To further investigate a potential mechanism responsible for this plasticity, we exposed fish to waterborne cortisol, a stress hormone, or to a sham control, and compared their lateralization.

METHODS

Ethical Note

All work carried herein followed animal care ethics and was approved by James Cook University protocols A2080, A2005. All fish were released at their capture site at the end of the experiment.

Test Species

The Ambon damselfish is a common planktivorous reef species found throughout the Indo-Pacific. As juveniles, they are prey for a variety of predators, including wrasses, lizardfishes and dottybacks. We collected juvenile Ambon damselfish from reefs surrounding the Lizard Island Research Station (14°40'S, 145°28'E), Great Barrier Reef, Australia in March 2015. Fish were captured on SCUBA using clove oil and hand-nets. The fish were transported back to the laboratory and held in 30-litre flow-through tanks, where they were fed brine shrimp and pellets three times per day.

Experiment 1: Temporal Variation in Behavioural Lateralization

The goal of the first experiment was to test whether fish exhibit temporal variation in their degree of behavioural lateralization in response to variation in diel predation risk.

Risk pattern

We used a well-established technique to create predictable variation in predation risk (Ferrari & Chivers, 2009; Ferrari, Manek, & Chivers, 2010), exposing fish to injured conspecific cues (i.e. alarm cues) at the time of day that was risky, and exposing them to water (low-risk disturbance) at the time of day that was less risky. We created two opposite risk patterns to control for natural diel variation in antipredator responses in fish.

Alarm cues are chemicals located in the skin of many aquatic species and are known to elicit dramatic antipredator responses when detected by nearby conspecifics. Given that these cues can only be released in the water column via mechanical damage to the skin, as would occur during a predator attack, they represent a highly reliable indicator of risk (reviewed in Ferrari, Wisenden, & Chivers, 2010). A wide variety of taxa are known to possess and respond to these alarm cues, including our test species (Ferrari et al., 2011). Alarm cues were prepared by sacrificing five fish (via cold shock followed by pithing) and making eight superficial vertical cuts on either side of the body using a scalpel. The fish were then rinsed in 40 ml of sea water. Each risk exposure consisted of injecting 5 ml of this solution in the tank, for a final concentration of two cuts per litre, a concentration known to elicit overt antipredator response in our test species (Chivers, McCormick, Mitchell, Ramasamy, & Ferrari, 2014). A 5 ml injection of water served as a low-risk exposure.

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