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Laterality is Linked to Personality in the Black-Lined Rainbowfish, *Melanotaenia nigrans*

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KEYWORDS

predation, laterality, personality, Boldness, shyness

ABSTRACT

*Emotions such as fear in vertebrates are often strongly lateralised, that is, a single cerebral hemisphere tends to be dominant when processing emotive stimuli. Boldness is a measure of an individual's propensity to take risks and it has obvious connections with fear responses. Given the emotive nature of this well-studied personality trait, there is good reason to suspect that it is also likely to be expressed in a single hemisphere. Here, we examined the link between laterality and boldness in wild and captive-reared rainbowfish, *Melanotaenia nigrans*. We found that fish from the wild were bolder than those from captivity, which might be a reflection of the differences in the level of predation pressure experienced by the two populations. Secondly, we found that nonlateralised fish were bolder than strongly lateralised fish. In addition, differences in boldness scores between left- and right-biased fish were revealed. We suggest that variation in cerebral lateralisation contributes to the persistence of individual differences in boldness scores in animal populations.*

Introduction

Cerebral lateralisation refers to the preferential analysis of particular types of information and processes such as motor control in a specific brain hemisphere and is a widespread phenomenon among vertebrates. Cerebral lateralisation is often overtly expressed as side biases during the everyday lives of animals, and such biases are referred to as laterality. Classic examples of laterality include the preferential use of one hand over the other as in humans and parrots (Brown and Magat 2011) or more subtle differences such as turn biases when animals are faced with an object which they must detour around (Bisazza et al. 1997). The widespread nature of laterality among vertebrate taxa suggests that it is an ancient evolutionary innovation and likely leads to the most efficient use of expensive neural tissue for maximal processing power (Magat and Brown 2009).

There is some suggestion that fearful and aggressive responses show a consistent pattern of laterality across many vertebrates often processed by the right hemisphere (Rogers 2002; Leliveld et al. 2013). Subordinate baboons, *Theropithecus gelada*, are more likely to be attacked if they approach a dominant male from the left-hand side (Casperd and Dunbar 1996), and lizards are more likely to show aggressive displays towards competitors in the left visual hemifield (Hews and Worthington 2001). In fish, while some species do show population levels of laterality, the pattern of laterality is certainly not conserved across taxa (see Bisazza and Brown 2011 for a review). Variation exists between species (Bisazza et al. 2000a),

between populations within species and at the individual level. For example, populations of fish from high- and low-predation areas vary in the eye they use to fixate on fear-inducing stimuli such as predators (Brown et al. 2004). It could be argued that fish derived from low-predation environments are predator naïve and thus may not process information about predators in the same hemisphere as fish from high-predation areas simply because predators are not pre-associated with fear or negative experiences. Such suggestions have been put forward to explain individual variation in predator inspection behaviour in magpies, *Cracticus tibicen*, where individuals that inspected the predator using their left eye tended to withdraw (fear), whereas those that inspected with the right eye tended to mob (aggression) (Koboroff et al. 2008). Similarly, fish tend to view familiar conspecifics using one eye, but view unknown, potentially threatening conspecifics using the other (Sovrano 2004). Convict cichlids, *Amatitlania nigrofasciata*, prefer to conduct their lateral displays using their right side (Arnott et al. 2011).

One of the outstanding questions in the laterality literature is why we see so many non-lateralised individuals in animal populations. There are numerous examples of advantages of having a lateralised brain (Rogers et al. 2004); thus, one wonders why non-lateralised individuals persist. For example, strongly lateralised parrots are better at solving cognitive tasks compared to non-lateralised parrots (Magat and Brown 2009) and strongly lateralised fish show more rapid anti-predator responses (Dadda et al. 2010). There is also emerging evidence, however, that having a strongly lateralised brain may actually be disadvantageous in some contexts (Vallortigara and Rogers 2005; Dadda et al. 2009). For example, strongly lateralised fish have great difficulty heading directly to a rewarded arm in a radial maze (Brown and Braithwaite 2005). Thus, the distribution of lateralised phenotypes within a population may be a reflection of the relative costs and benefits of laterality at the individual level.

An alternative but not mutually exclusive explanation suggests that laterality and personality might have co-evolved because the optimal level of behaviour might vary between lateralised vs. non-lateralised individuals (Reddon and Hurd 2008). Several researchers have addressed this hypothesis, but to date, the results remain equivocal. Irving and Brown (2013), for example, found evidence of behavioural syndromes comprising correlated suites of behaviour in male guppies. However, none of the individual behaviours examined in either males or females were correlated with laterality. Similarly, both Dadda et al. (2007) and Clotfelter and Kuperberg (2007) found no link between laterality and coping style in captive-reared poeciliids and aggression in anabantoid fish, respectively. In contrast, bolder cichlids tended to be more lateralised when exploring a novel environment than shyer ones (Reddon and Hurd 2009). Finally, bishops, *Brachyraphis episcopi*, from high-predation areas tend to be both bolder and strongly lateralised than those from low-predation areas (Brown et al. 2004, 2005, 2007b).

Personality traits, consistent individual differences across time and/or contexts, are now widely studied in animals and have a myriad of ecological and evolutionary consequences (Dall et al. 2012). Boldness is one of the most commonly examined personality traits in animals, particularly in fish (see review by Budaev and Brown 2011). Broadly speaking, boldness describes an individual's propensity to take risks, particularly in novel or potentially threatening situations. Threatening situations inherently induce fear in subjects and fear responses are typically lateralised in vertebrates. Thus, there is good reason to suspect that boldness might be a strongly lateralised trait given its apparent association between fear and risk-taking. For example, it has been argued that bolder animals may prioritise foraging over fear of predation (pace of life syndrome; Réale et al. 2010). Boldness scores have also been linked to underlying stress responses in fearful contexts (Raoult et al. 2012). Thus, we would expect to find correlations between measures of individual laterality and boldness scores.

Here, we examined the relationship between boldness and laterality using the black-lined rainbowfish, *Melanotaenia nigrans*, from high- and low-predation populations. We used rainbowfish as a model because we have previously shown that boldness is correlated with male dominance hierarchies (Colléter

and Brown 2011). In addition, rainbowfish laterality is influenced by both rearing environment and sex (Bibost et al. 2013) and influences schooling behaviour (Bibost and Brown 2013b) and learning performance (Bibost and Brown 2013a). We hypothesised that fish that vary in their pattern of laterality (left, right or non-lateralised) based on their eye preferences while viewing their mirror image would differ in their level of boldness using the standard emergence test (Brown et al. 2005). We could not predict a priori what the relationship between laterality and boldness might look like, simply because (a) we lack information about which hemisphere this species analyses fearful stimuli and (b) rainbowfish tend to show individual variation in laterality (Bibost et al. 2013). Consequently, this study might be viewed as a hypotheses-generating exercise informing future research on this topic.

Methods

Subjects

Rainbowfish were sourced from two separate populations in an attempt to maximise diversity in both laterality and personality. Previous experiments suggest that fish from high-predation environments are bolder and more strongly lateralised than those from low-predation environments (Brown et al. 2007a, b). Wild fish were collected from Rapid Creek (12° 23' 18.70" S, 130° 52' 0.40" E) adjacent to Darwin airport, while captive-reared fish were obtained from a commercial supplier (Aquagreen, Northern Territory). Captive fish were maintained in large outdoor ponds and thus have not experienced predation for multiple generations. In contrast, wild fish occupied a high-predation risk environment characterised by both avian and Piscean predators. Both populations were airfreighted to the laboratory and established in mixed sex groups in four large aquaria (92 × 39 and 36 cm deep) furnished with river gravel and an internal filter. Room temperature was maintained at 26 °C and aquaria were lit by overhead fluorescent lights. Fish were gradually weaned onto commercial flake food by mixing it with live blood worm, *Chironomus* spp. We endeavoured to test 20 males and females from each population of a similar size (ca 50mm); however, after size selection criteria were applied, we retained 21 captive males, 16 captive females, 17 wild males and 19 wild females. All subjects were individually marked using polymer-elastomer tags (North-West Technology). Tagging had no obvious effects on behaviour, and all fish recovered from the light aesthetic (MS222 buffered with NaHCO₃) within minutes.

Laterality assay

We used a modified version of the mirror test (Sovrano 2004) to establish lateralised eye preferences as detailed in Bibost and Brown (2013b). We chose the mirror test simply because rainbowfish are a very strongly schooling species, and we modified the Sovrano (2004) setup by introducing a strong flow in the test tank. In the wild, rainbowfish are frequently found schooling in strong currents in fast-flowing streams. Briefly, fish were introduced to a flume (110 long × 30 wide × 30 cm deep) with mirrors on the left and right-hand side. The location of the subject relative to the mirrors was monitored every 10 s for 5 min. Fish that were within four body lengths (ca 10 cm) of the left or right mirrors were scored as being left or right lateralized, respectively. Four body lengths is a common measure of schooling behaviour in fish (Pitcher 1983; Brown and Warburton 1997). The number of occasions the fish was observed on the left or right side was summed over the 30 observations to provide an estimate of the amount of time spent next to each mirror. Fish that spent over 80% time viewing their mirror image with the right eye were considered to have a right preference (R), fish that spent less than 20% of their time viewing their mirror image were considered left preference (L) and all other fish were considered nonlateralised (NL). Note that the distribution was highly bimodal (see "Results"), and there were very few NL fish ($N=30$, 26 and 17 for L, R and NL fish, respectively). Owing to this lack of non-lateralised fish, we chose to include laterality as a categorical rather than a continuous variable in our analyses.

Boldness assay

Boldness was tested using the standard emergence test (Brown and Braithwaite 2004; Brown et al. 2005, 2007a) on three separate occasions (day 1, day 4 and day 7) in a large aquarium (91 × 51 cm; water was 15 cm deep) furnished with river gravel. Briefly, fish were placed in a small darkened hide (9.5 w × 7.5 l × 14.5 h cm) for 2 min before a trapdoor was opened by a remote pulley allowing the subject to emerge from the hide into a novel environment. In order to explore the environment, the subject had to first cross over a high-contrast semicircle of white plastic. Subjects were observed by a web camera mounted overhead, and we simply recorded the time to emerge from the hide as our boldness assay. The time to emerge was taken when the entire body of the fish was out of the hide. Fish that emerge quickly are bolder than those that emerge slowly. On each occasion, the environment was rendered slightly different by placing different coloured blocks of Duplo™ around the arena exterior to ensure the arena remained relatively novel between trials. Room temperature was maintained at 26 °C, and the test arena was lit by fluorescent globes mounted on the ceiling of the room overhead.

Statistical analysis

We then used mixed models to calculate an adjusted global repeatability score over the three repeated trials, where boldness was the dependent variable, sex and population were fixed effect factors and individual identity was a random effect (Nakagawa and Schielzeth 2010). The 95 % credibility intervals were calculated based on Dingemans and Dochtermann (2013). Boldness scores were square root transformed in order to meet the assumptions of normality. Laterality score was then added to this model as a categorical, independent, fixed variable (L, NL and R). This approach enabled us to estimate the proportion of the variation in boldness scores that can be attributed to laterality.

We also used ANOVA to determine if there were differences between the sexes or populations in the laterality scores. Despite the unusual distribution of the data (negative kurtosis), we used ANOVA as an alternative to multiple nonparametric tests which could not directly assess a possible two-way interaction between these factors. Although laterality testing is repeatable both within contexts (Irving and Brown 2013) and between contexts (Bisazza et al. 2001), we did not test it in this instance.

Results

The mixed model found a global adjusted repeatability score (r) for boldness across all three trials of 0.34 ± 0.15 (95 % credibility intervals). Thus, boldness is clearly a robust personality trait in rainbowfish which is consistent with previous studies (Colléter and Brown 2011).

The mixed model examining time to emerge from cover only revealed a population difference ($F_{1, 196} = 12.465$, $P = 0.001$). Wild fish were bolder than captive-reared fish. No effect of sex or an interaction between sex and population was observed ($P > 0.05$ in both cases). When laterality was added to the model, we found a significant effect of laterality ($F_{2, 129} = 4.267$, $P = 0.016$, Fig. 1) and a significant effect of population ($F_{1, 153} = 7.690$, $P = 0.006$, Fig. 2). No other factors or interactions were significant ($P > 0.05$ in all cases). Moreover, when laterality was added to the model, between-individual variance decreased by 26 %. Thus, a good deal of the variation in boldness scores was explained by laterality.

Post hoc tests using the median boldness score for each fish revealed that NL fish were significantly bolder than L fish ($P = 0.044$), which were in turn bolder than R fish ($P = 0.049$). NL fish were far bolder than R fish ($P < 0.001$).

The ANOVA examining laterality scores revealed no significant differences between populations or sexes nor was there a significant interaction ($P > 0.26$ in all instances). Laterality scores were strongly bimodal in their distribution (Fig. 3).

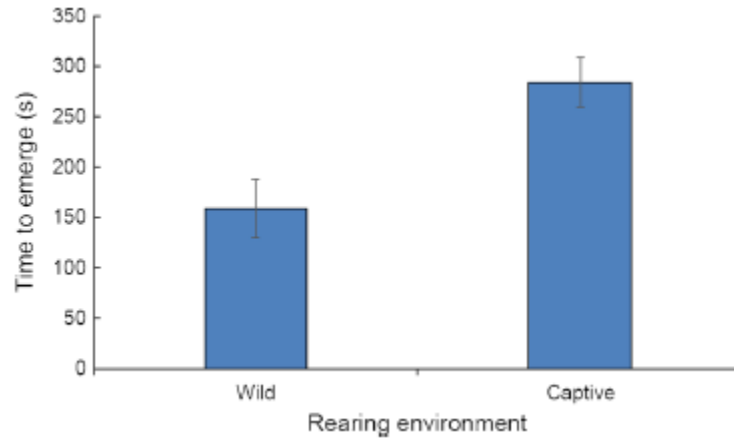


Fig. 1. Mean time (s) to emerge from cover for rainbowfish captured in the wild or reared in captivity. Faster emergence is indicative of greater boldness

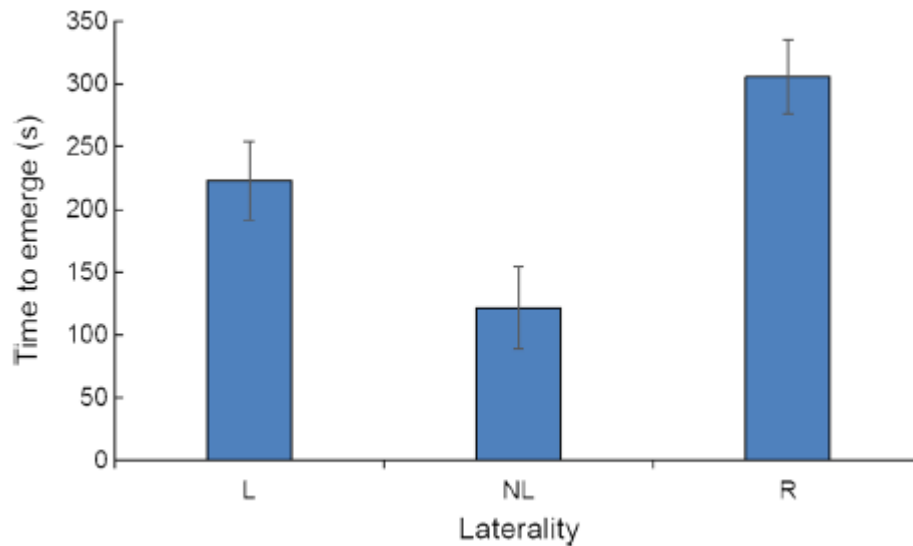


Fig. 2. Mean time (s) to emerge from cover for three classes of lateralized rainbowfish: left, non-lateralised and right. Faster emergence is indicative of greater boldness

Discussion

Our analysis of boldness scores showed clear effects of laterality and rearing environment. Fish from high-predation environments (wild) were significantly bolder than those from low-predation environments (captive-reared), which conforms to previous work on poeciliids (Brown et al. 2005). More importantly,

non-lateralised fish were significantly bolder than both left- and right-lateralised fish, which suggests that when fear is heightened, it is primarily processed by a single hemisphere.

Non-lateralised rainbowfish were significantly bolder than strongly lateralised fish, but differences also exist between left- and right-biased fish. Fish that used their left eye to inspect their reflection in a mirror were bolder than those that used their right eye to inspect their mirror image. There are two possible explanations for this variability. The first explanation relates to variability in how individual fish interpret their mirror image. It is rare in nature for a fish to see its own reflection; thus, a fish seeing its mirror image is much like seeing an unfamiliar individual. Fish often engage the opposite hemisphere when inspecting familiar or unfamiliar conspecifics (Sovrano 2004) likely as a result of heightened fear of unfamiliar fish. Their degree of fear when dealing with strangers may well be linked to their position in the hierarchy and/or their prior social experiences (Hsu and Wolf 1999). Thus, the large individual variation in eye preferences for viewing their reflection we observed may relate to some degree on how threatening they find their own image.

We suggest that the variation we observe in the flume, however, is most likely a true reflection of individual differences in cerebral lateralisation given that we have found that laterality measured via this means has a number of important fitness correlates in rainbowfish including learning rates (Bibost and Brown 2013a) and the position the fish adopt within a school (Bibost and Brown 2013b). This latter observation is particularly important as it shows that the preference for particular locations in real schools closely matches the eye used in the flume test. If we assume that the flume test is indicative of cerebral lateralisation, then we must conclude that fear can be partitioned in opposite hemispheres in different individuals. Although we cannot determine which hemisphere is responsible based on the present experiment, we suggest that fear is expressed more strongly when it is largely analysed in one hemisphere rather than the other. We can similarly conclude that when boldness is shared between hemispheres, then it is not strongly expressed; thus, bold fish tend to be non-lateralised.

A number of studies present evidence suggesting that when information processing is shared between two hemispheres of the brain, competition and/or interference can reduce efficiency when the animal comes to act on this information (Rogers et al. 2004). For example, strongly lateralised parrots tend to be better at solving complex tasks than non-lateralised parrots (Magat and Brown 2009). Part of the problem fish face, and indeed other non-mammals, is that there is relatively little neural crossover between hemispheres, and thus, each hemisphere acts largely independently of the other. If non-lateralised fish need to act quickly, they must draw information from both hemispheres, compare it, integrate it and then make a decision. Comparison and integration of information from different hemispheres is likely to be greatly impeded in the absence of a corpus callosum or similar structure; however, fish do have numerous inter-hemisphere neural connections. In contrast, strongly lateralised fish need only draw on information from a single hemisphere and can act immediately. However, strongly lateralised fish pay a high performance cost when comparing information from two eyes likely for the same reason (Dadda et al. 2009). While this interference has mostly been discussed in terms of the cognitive advantages of laterality, it equally applies to other forms of data processing.

From a mechanistic perspective, it is likely that the decision to engage with novel objects, enter and explore novel arenas and other behaviours associated with bold behaviour comes down to a trade-off between competing motivators. We suggest that exploration is likely the primary motivating factor; fish search for food and mates by default, but such decisions are moderated by fear. If non-lateralised individuals process fear-related stimuli comparatively slowly or inefficiently, it may be that the moderating effect of fear is somewhat lessened in comparison to strongly lateralised individuals. One could envisage that this may result in a reduced level of fear generally, or perhaps the decision to explore is already

made before the moderating effect of fear comes into play. Either scenario would adequately explain our observation that non-lateralised fish are bolder than lateralised fish.

It is important to note that there is another potential explanation as to why non-lateralised fish tend to be bolder than lateralised fish. Bold fish are potentially less likely to school in the flume because they have reduced fear in novel contexts; thus, they will show no particular preference for their mirror image on either side of the flume. While there is evidence of a sociality-boldness syndrome in some fish species, including guppies (Irving and Brown 2013), previous experiments on a different species of rainbowfish found no such correlation (Colléter and Brown 2011). Similarly, no correlation between schooling and boldness was found in three strains of zebrafish (Moretz et al. 2007). While the relationship between boldness and schooling tendency has yet to be examined in the present species, it remains a possible, indirect explanation for high boldness scores in non-lateralised fish. This explanation, however, has no bearing on the differences in boldness we observed between strongly left- and right-lateralised fish.

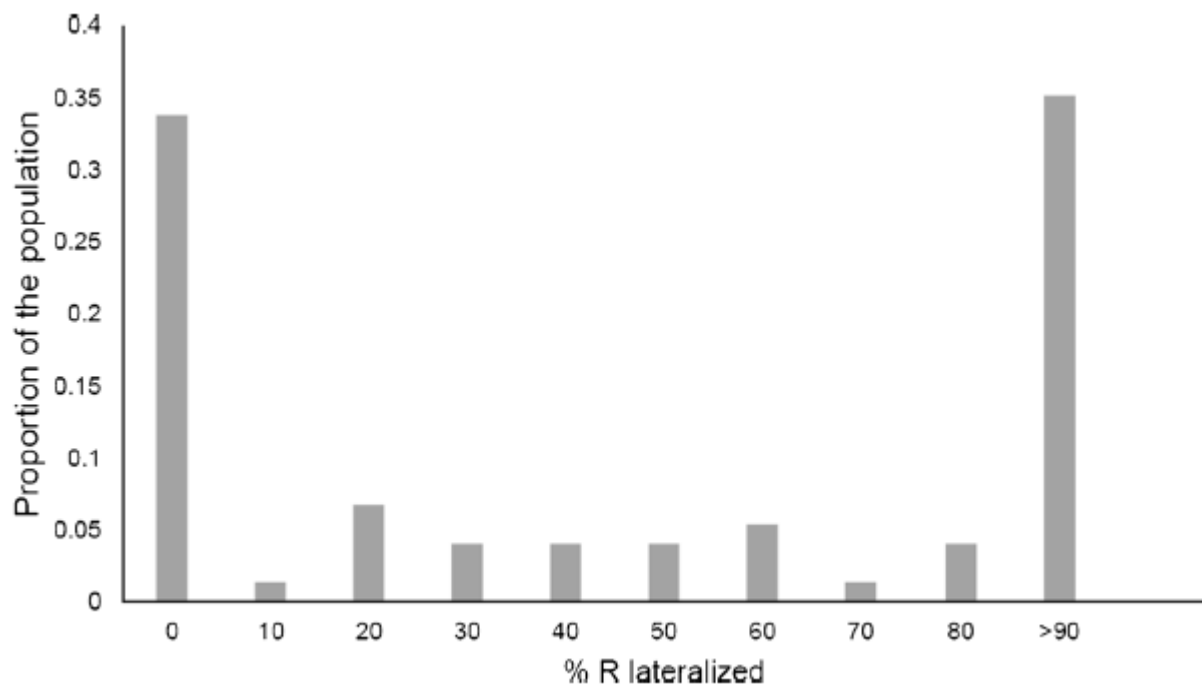


Fig. 3. Frequency distribution of laterality scores in the rainbowfish *Melanotaenia nigrans*

The similarities between personality and laterality are certainly intriguing and hint at a single underlying function or mechanism. Both traits may be shaped via frequency-dependent selection (e.g. Dall et al. 2004; Brown 2005; Vallortigara and Rogers 2005) and key ecological factors such as variation in predation pressure (Brown et al. 2004, 2005). Variation in selective pressure due to different contexts and/or environmental stochasticity often favours the maintenance of trait diversity within populations (Dingemanse et al. 2004). While both traits are heritable in fish (Brown et al. 2007a, b; Bisazza et al. 2000b), there is no evidence for assortative mating (Godin and Dugatkin 1996). Here, we suggest a much more mechanistic explanation for similarities between these traits, that is, aspects of personality traits are actually caused by variation in laterality. While it is interesting that we find correlations between personality and laterality, it is often difficult to determine cause and effect from correlative data. We strongly suspect, however, that because fear and aggression are often strongly lateralised across all

vertebrates (Rogers 2002), processing of fear in one hemisphere or the other is responsible for individual variation in boldness rather than vice versa.

The fact that we found that wild fish were significantly bolder than captive-reared fish is not surprising; indeed, we specifically chose to use these populations because they differ in their exposure to predators. We have previously found that fish from high-predation populations tend to be far bolder than those from low-predation locations in poeciliids (e.g. Brown et al. 2005). The fact that we found no difference in boldness between the sexes, however, is somewhat unusual since it is almost universally the case that males are bolder than females among vertebrate taxa (Brown et al. 2007a). This is symptomatic of the high levels of testosterone in males that make them prone to risk-taking (Vermeersch et al. 2008). Nevertheless, the trend was in the expected direction. Further studies could explicitly examine the link between hormone expression and boldness in rainbowfish (Raoult et al. 2012).

In conclusion, our findings demonstrate clear differences in boldness scores that relate to both the rearing environment and the laterality of test subjects. We suggest that variation in boldness scores within populations is generated by variation in laterality. Nevertheless, explaining how and why variation in laterality persists in natural populations remains a topic of intense research and will most likely benefit from a classic behavioural ecology cost-benefit approach.

Acknowledgments

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Ethical standards

All procedures adhere to the current laws in Australia and were covered by the Macquarie University Animal Ethics Committee ARA # 2010/028.

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