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Vegetation cover induces developmental plasticity of lateralization in tadpoles

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Abstract

Lateralization of cognitive functions influences a large number of fitness-related behaviors and shows, in most species, substantial variation in strength and direction. Laboratory works and field data have suggested that this variation is often due to adaptive phenotypic plasticity. Strong lateralization should be favored in some ecological conditions, for example, under high risk of predation. For anuran tadpoles, the presence of cover affects predation risk, with tadpoles being more exposed to predators in environments with reduced cover. We tested the hypothesis that the amount of cover experienced early in life affects lateralization in the edible frog, *Pelophylax esculentus*, tadpoles. We exposed embryos and larvae to high or low vegetation cover environments. For half of the subjects, the treatment was constant whereas the remaining subjects were switched to the opposite treatment after hatching. In agreement with the theoretical expectation, tadpoles exposed to low vegetation cover for the entire development were more lateralized and showed a stronger alignment in directionality of lateralization compared with tadpoles exposed to high vegetation cover. This indicates a possible role of natural variation in vegetation abundance and developmental plasticity as determinants of between-population and between-individual differences in lateralization. We also found that shifting from high to low vegetation cover treatments and vice versa disrupted lateralization alignment, suggesting that developmental trajectories for this trait are determined at the embryonic stage and need environmental stability to be fully expressed.

Key words: lateralization, light exposure, *Pelophylax esculentus*, phenotypic plasticity

In many animals, specific cognitive functions such as individual recognition, acoustic communication, prey catching, or predator recognition are preferentially performed by one brain hemisphere, either the left or the right (Bisazza and Brown 2011; Vallortigara et al. 2011; Rogers and Vallortigara 2017). This causes left–right differences in the perception and elaboration of stimuli associated with these functions, and asymmetries in the resulting motor responses (e.g., Deckel 1995; Bisazza et al. 1996; Vallortigara et al. 1998).

One aspect of lateralization often reported in humans and other species is the presence of consistent variation in both strength and direction; individuals might differ in the preferential use of either their left or right cerebral hemisphere and with regard to how strongly a specific function is linked to one hemisphere (Knecht et al. 2000; Reddon and Hurd 2008). The pattern of cerebral lateralization can have important effects on fitness. For example, in the goldbelly topminnow *Girardinus falcatus*, strongly lateralized individuals were better at schooling and were more efficient in performing 2 simultaneous cognitive tasks such as foraging while avoiding unsolicited males' mating attempts (Bisazza and Dadda 2005; Dadda and Bisazza 2006a). On the contrary, strong lateralization can cause pseudoneglect, that is, the failure to properly respond to a significant stimulus when it appears on the side of the body that transfers information to the hemisphere not specialized for its processing (Chiandetti 2011). Prey-catching behavior, for example, is

highly lateralized in amphibians: toads are much more likely to strike at prey moving on their right than on their left visual hemifield (Vallortigara et al. 1998). Conversely, anole lizards, *Anolis* spp., and gelada baboons, *Theropithecus gelada*, direct fewer agonistic responses to rivals seen on their right side (Deckel 1995; Casperd and Dunbar 1996).

Because the advantages and disadvantages of lateralization often vary in time and space, a possible explanation for lateralization variability is differential selection (Levins 1968). Laboratory studies have revealed that strongly lateralized fish and birds exhibit faster predator detection and higher escape reactivity (Rogers et al. 2004; Dadda et al. 2010). In addition, in some circumstances, alignment of lateralization at the population level (i.e., individuals showing similar directionality of lateralization) enhances coordination during collective antipredator behavior such as schooling in fish (Bisazza and Dadda 2005; Bibost and Brown 2013). In other cases, having a specific direction of lateralization might confer advantages, such as improved escape performance (Chivers et al. 2016) and greater predator recognition ability (Lucon-Xiccato et al. 2017). Along with these direct advantages of lateralization in dealing with predators, other studies indicate the presence of indirect advantages: lateralized individuals were more efficient in capturing live prey while monitoring for a predator compared with nonlateralized individuals (Rogers et al. 2004; Dadda and Bisazza 2006b). Collectively, these findings suggest that strong lateralization, and in some cases, a specific alignment of lateralization should be selected for in high-predation environments. On the contrary, evidence of costs of lateralization (e.g., pseudoneglect: Dadda et al. 2009; Chiandetti 2011) indirectly suggests that weakly lateralized individuals should be favored in low-predation risk environments. Support for this hypothesis is provided by field data on the distribution of lateralized individuals in wild-caught fish from high and low predation sites (Brown et al. 2007). A limit of this hypothesis is that, despite lateralization being affected by genes in some species (mouse: Collins 1985; *Pan troglodytes*, chimpanzee: Hopkins et al. 1994; goldbelly topminnow: Bisazza et al. 2000; *Brachyrhaphis episcopi*: Brown et al. 2007), genetic factors account for only a fraction of the observed variation.

Lesley Rogers theorized an alternative explanation for lateralization variability. Matching of individual lateralization to actual environmental conditions can also be the consequence of adaptive phenotypic plasticity. In the early 80s, she discovered that light that passes through the eggshell influences the development of laterality in domestic chicks: chicks hatching from light incubated eggs are more strongly lateralized than dark incubated chicks (Rogers 1982). She suggested that this may be part of an adaptive mechanism that allows the mother to adjust the phenotype of chicks to the current ecological conditions by spending more or less time at the nest or by choosing a particular nest site (Adret and Rogers 1989). For example, weakly-lateralized chicks hatching from dark-incubated eggs outcompete conspecifics during foraging (Wichman et al. 2009), suggesting that this phenotype should be favored in environments with high levels of intraspecific competition.

In recent years, evidence of developmental plasticity of lateralization has continued to accumulate. For example, exposure to predation risk during development increased the occurrence of lateralized individuals in juvenile fish and anuran larvae (guppy, *Poecilia reticulata*: Broder and Angeloni 2014; whitetail damselfish, *Pomacentrus chrysurus*: Ferrari et al. 2015; wood frog, *Lithobates sylvaticus*: Lucon-Xiccato et al. 2017). Early social environment affects lateralization in Rainbowfish *Melanotaenia duboulayi* (Bibost et al. 2013) and altered water conditions reduce

lateralization in several fishes (Domenici et al. 2012; Domenici et al. 2014; Lucon-Xiccato et al. 2014). In addition to domestic chicks, early lighting conditions influence development of lateralization in goldbelly topminnows and in zebrafish *Danio rerio* (Andrew et al. 2009; Dadda and Bisazza 2012; Sovrano et al. 2016). Environmental light intensity may correlate with other important ecological factors. In guppies, for example, the light intensity has a strong effect on vulnerability to predators and indirectly influences schooling and mating behavior (Endler 1987).

In this study, we tested whether an environmental factor that is a predictor of predation risk affects lateralization in tadpoles via developmental plasticity. Predation is a major source of mortality for many anuran species (Calef 1973; Heyer et al. 1975) and habitat complexity, that is, the amount of vegetation cover, greatly affects the survival of larvae to predation from both vertebrates and invertebrates (Figiel and Semlitsch 1991; Babbitt and Tanner 1997; Babbitt and Tanner 1998; Tarr and Babbitt 2002; Baber and Babbitt 2004; Kopp et al. 2006; Hartel et al. 2007). The edible frogs, *Pelophylax esculentus*, lay eggs in habitats that vary considerably in the amount of vegetation cover (Ildos and Ancona 1994; Warren and Büttner 2008). We reasoned that this factor might affect the lateralization of edible frogs and we tested our hypothesis by comparing the behavioral lateralization of tadpoles raised from eggs with high and low vegetation cover. Since the amount of cover affects predation, we expected that tadpoles raised with reduced vegetation cover—hence under potentially greater predation risk—will be more lateralized and more aligned compared with tadpoles raised with high vegetation cover. In other anurans, lateralization plasticity may differ according to the developmental stage (embryonic or larval) in which the stimulation occurs (Tyrone Lucon-Xiccato, unpublished data). Soon after hatching, we reversed the condition in half of the subjects of each treatment, allowing us to measure the effects of cover amount on embryonic and larval stages separately.

Materials and Methods

Subjects

We collected edible frogs as freshly laid eggs from a stream close to Padova, Italy (45°32′30″ N, 11°53′40″ E). Eggs were raised in 20 20-L plastic pails. Each pail contained ∼50 eggs and was randomly assigned to the experimental treatments (see Experimental treatment). Embryos and larvae were kept outdoors, in semi-natural conditions, exposed to normal temperature and precipitation. After hatching, we fed rabbit pellets *ad libitum* to the larvae, to supplement the algae already present in the pails and to ensure no differences in nutrient availability across the treatments. Water used during the procedures derived from a pond filled with well water 6 weeks before the beginning of the experiments and enriched with the algae and plants from the sampling site. Each day, 80% of the pail water was substituted with new water from the pond. Tadpoles were returned to their natal stream after the experiments, in the same area where sampling occurred.

Experimental treatments

We followed prior studies that manipulated exposure to vegetation to investigate behavioral plasticity in this species (Lucon-Xiccato 2019a, 2019b). Ten pails were kept under high vegetation cover conditions for the entire embryonic stage: water surface was completely covered by duckweed, *Leman minor*, collected from the near pond. The remaining 10 pails were kept under low vegetation cover conditions: <20% of water surface was covered by duckweed. One

day after hatching, we split each group of pails in 2. Half of the pails were kept under high vegetation cover conditions, whereas the remaining pails were kept under low vegetation cover conditions. This resulted in a 2×2 experimental design, having 5 pails with embryonic and larval high vegetation cover conditions (HH); 5 pails with embryonic and larval low vegetation cover conditions (LL); 5 pails with embryonic high vegetation cover condition and larval low vegetation cover condition (HL); and 5 pails with embryonic low vegetation cover condition and larval high vegetation cover condition (LH). The amount of vegetation used in the treatments mirrored the variation in vegetation observed at the sampling site.

Lateralization test

Fifteen days after hatching, we tested 8 tadpoles matched for size from each pail in the rotational preference test to assess lateralization (overall $N = 160$; N per treatment $= 40$). The rotational preference is used to assess lateralization in tadpoles of different species and allows to measure preferential swimming direction (Blackiston and Levin 2013; Lucon-Xiccato et al. 2017). We placed the subject in a 0.5-L white cup filled with pond water. We started the assessment after a 15-min acclimation period. We noted the spontaneous swimming direction of the subject (clockwise or anticlockwise) 10 times, using scan sampling with a 2-min interval between observations. If the subject did not swim during one observation, we repeated the observation later. If the subject did not swim in 3 consecutive observations, we removed it from the experiment ($\sim$25% of subjects). Because of the discarded subjects, the final dataset consisted of 29 HH tadpoles, 29 LL tadpoles, 27 HL tadpoles, and 30 LH tadpoles.

Statistical analysis

To analyze the data, we computed 2 commonly used lateralization scores for each subject, the absolute lateralization index and the relative lateralization index (Bisazza et al. 1997; Lucon-Xiccato et al. 2017). The absolute lateralization index considered strength (intensity) of lateralization irrespective of directionality and was computed as |relative lateralization index|. The absolute lateralization index ranged from 0 (tadpoles that swam in equal proportion clockwise and anticlockwise) to 100 (tadpoles that swam constantly in a clockwise or anticlockwise direction). The absolute lateralization index showed non-normal distribution. We, therefore, conducted the analysis following the permutation procedure described by Manly (2018). The relative lateralization index accounted for directionality and strength of lateralization: (n. of clockwise observations − n. of anticlockwise observations) $\times$ 100/n. of observations. On the basis of the relative lateralization index, individuals were classified between the extreme values of "100" (tadpoles that always swam clockwise) and "−100" (tadpoles that always swam anticlockwise). The distribution of the relative lateralization index did not depart from a normal distribution (Kolmogorov–Smirnov test).

Statistical tests were performed using R version 3.2.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). We used 2-tailed tests and we set the threshold for significance at $P = 0.05$. We analyzed the 2 indexes with 2-way ANOVAs fitted with larval (high vegetation cover versus low vegetation cover) and embryonic treatment (high vegetation cover versus low vegetation cover). We used post hoc independent sample t-tests to perform pairwise comparisons.

For the relative lateralization index, we conducted an additional analysis that allowed to test the presence of significant lateralization bias at the population level. We used 1-sample t-tests to assess whether tadpoles of the 4 groups swam in anticlockwise direction more often than chance (chance level: relative lateralization index $= 0$). We then used post hoc independent sample t-tests to perform pairwise comparisons between groups of tadpoles that showed significant lateralization.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted (University of Padova Animal Welfare Committee, permit number 51/2016).

Results

Absolute lateralization index

The ANOVA found a significant embryonic $\times$ larval treatment interaction ($F_{1,111} = 4.342$, $P_{perm} = 0.039$; Figure 1). Post hoc t-tests indicated that LL tadpoles were more lateralized than tadpoles from the remaining 4 treatments (versus HH: $P_{perm} = 0.022$; versus HL: $P_{perm} = 0.033$; versus LH: $P_{perm} = 0.041$; remaining comparisons: $P_{perm} > 0.2$). The main effect of embryonic treatment was significant ($F_{1,111} = 7.554$, $P_{perm} = 0.007$). There was no significant main effect of larval treatment ($F_{1,111} = 1.571$, $P_{perm} = 0.247$).

Relative lateralization index

The ANOVA found a significant interaction between the 2 treatments ($F_{1,111} = 14.156$, $P < 0.001$; Figure 2). There was no significant main effect of the 2 treatments (embryonic treatment: $F_{1,111} = 1.173$, $P = 0.281$; larval treatment: $F_{1,111} = 2.708$, $P = 0.103$; Figure 2).
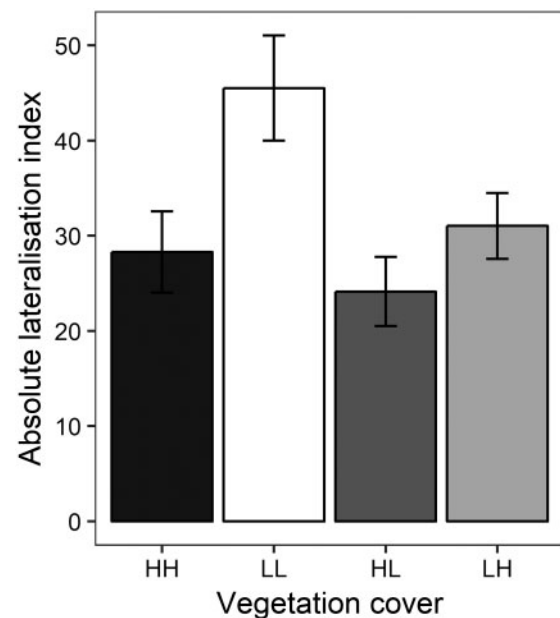

Figure 1. Absolute lateralization index (mean $\pm$ SE) of tadpoles exposed to the 4 treatments assessed with the rotational preference test. Left bars represent tadpoles exposed to constant high (HH) or low (LL) vegetation cover. Right bars represent tadpoles exposed to changing conditions between embryonic and larval stage: from high to low vegetation cover (HL) and from low to high vegetation cover (LH).

Both HH and LL tadpoles swam in anticlockwise direction more often than chance (1-sample *t*-test: HH: $t_{28} = 2.31$, $P = 0.028$; LL: $t_{28} = 4.097$, $P < 0.001$; Figure 3), indicating the presence of lateralization. Conversely, tadpoles that underwent a transition between the different treatments during the development (HL and LH) were

not lateralized (1-sample *t*-test: HL: $t_{26} = 0.122$, $P = 0.904$; LH: $t_{29} = 0.496$, $P = 0.624$; Figure 3). The post hoc test between the groups that showed significant lateralization at population level indicated that that lateralization tended to be greater in LL than in HH tadpoles (independent samples *t*-test: $t_{56} = 1.821$, $P = 0.074$).

Discussion

For amphibian larvae, predation risk substantially declines in the presence of vegetation cover (Figiel and Semlitsch 1991; Babbitt and Tanner 1997; Kopp et al. 2006). Because lateralization allows coping with predators (e.g., Rogers et al. 2004; Brown et al. 2007; Dadda et al. 2010; Lucon-Xiccato et al. 2017), tadpoles from environments with different amounts of vegetation are expected to exhibit different lateralization phenotypes via developmental plasticity. Here, we found support for this hypothesis, suggesting adaptive phenotypic plasticity of tadpoles' lateralization according to the perceived level of risk.

Tadpoles constantly raised with low vegetation cover were more lateralized than tadpoles raised with high vegetation cover during the entire development and during only one developmental stage. Frogs likely recognized environmental cues signaling vegetation amount at the embryonic stage and thereafter undertook specific developmental trajectories for lateralization phenotype based on perceived predation risk. Similarly, in fish and other anuran species, exposure to predation risk cues was consistently reported to increase the proportion of lateralized individuals (Broder and Angeloni 2014; Ferrari et al. 2015; Lucon-Xiccato et al. 2017). One may speculate on the selective advantages that promote high lateralization in tadpoles from high-risk environments and low lateralization in tadpoles from low-risk environments. Studies on other taxa suggest that highly lateralized individuals might enjoy an advantage in monitoring predators while simultaneously foraging (Dadda and Bisazza 2006b) and in responsiveness to predators (Rogers et al. 2004; Dadda et al. 2010). Highly lateralized tadpoles that develop
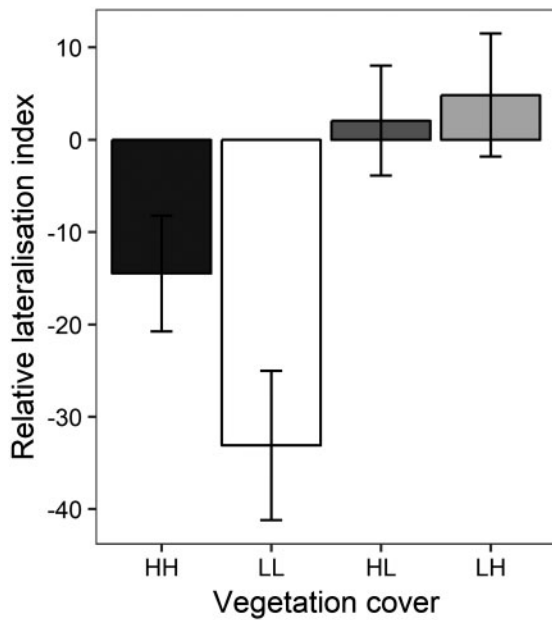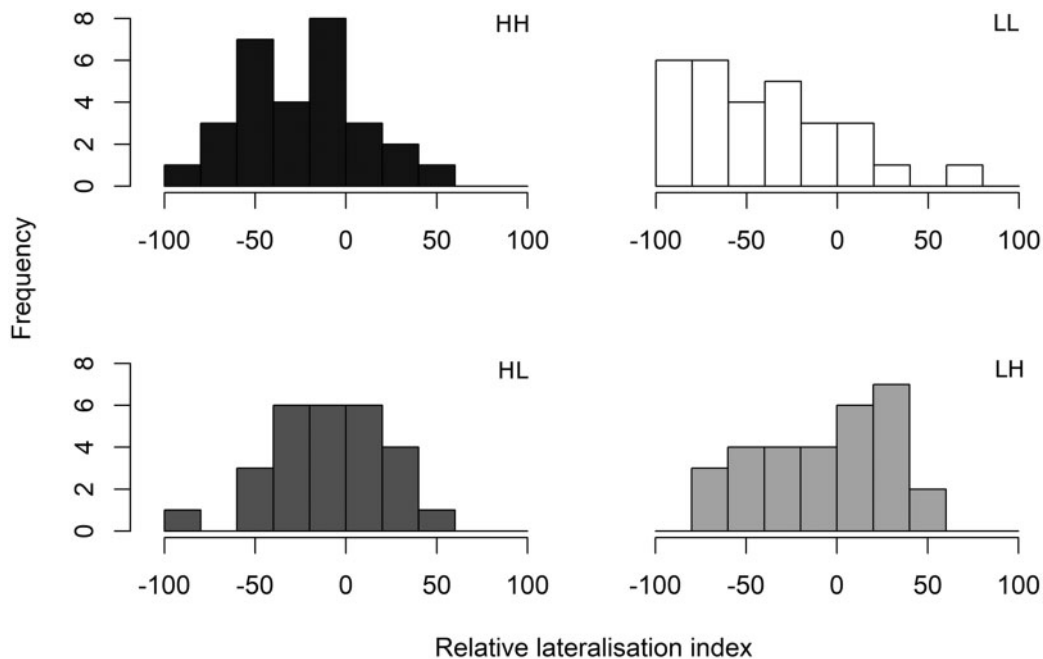

Figure 2. Relative lateralization index (mean ± SE) of tadpoles exposed to the 4 treatments assessed with the rotational preference test. Left bars represent tadpoles exposed to constant high (HH) or low (LL) vegetation cover. Right bars represent tadpoles exposed to changing conditions between embryonic and larval stage: from high to low vegetation cover (HL) and from low to high vegetation cover (LH). Positive values indicate clockwise swimming preference in the lateralization test; negative values indicate anticlockwise swimming preference.

Figure 3. Frequency distribution of the relative lateralization index of tadpoles exposed to the 4 treatments. Positive values indicate clockwise swimming preference in the lateralization test; negative values indicate anticlockwise swimming preference.

in environments with low vegetation (and thus high-predation risk) may similarly enjoy cognitive advantages in defense against predators. Indeed, a prior study on wood frogs tadpoles demonstrated that lateralization favors the learning of novel predator olfactory cues (Lucon-Xiccato et al. 2017). On the contrary, disadvantages associated with lateralization might impose unnecessary costs to lateralized tadpoles in low-predation risk areas. Pseudoneglect (i.e., the tendency to shift spatial attention to one side of the body) and reduced competitive abilities have been observed in lateralized individuals in a variety of species (Dadda et al. 2009; Wichman et al. 2009; Chiandetti 2011). If similar disadvantages are present in our species, then they are expected to promote development of nonlateralized phenotypes when predation risk cues are absent during ontogeny. Therefore, studies on fitness consequences of lateralization are required to understand the adaptive value of plasticity in response to predation risk.

In this study, tadpoles exposed to low vegetation during embryonic and larval stage also exhibited alignment of lateralization at the population level causing a significant anticlockwise turning preference in the rotational test. Tadpoles exposed to high vegetation during embryonic and larval stage exhibited evidence of alignment but to a lesser extent. Results on directionality of lateralization in other species varied across studies: whitetail damselfish and guppies did not show an effect of predation risk (Broder and Angeloni 2014; Ferrari et al. 2015), whereas wood frogs showed higher occurrence of phenotypes with a specific directionality but in opposed direction compared with the present study (Lucon-Xiccato et al. 2017). It is currently unclear whether these inconsistencies were due to species differences or to the different assays adopted to measure lateralization. It may be argued that the advantages of being lateralized outlined above should be independent of the directionality of lateralization, and therefore they do not explain the alignment observed in our study. Traditionally, alignment of lateralization direction has been associated with group coordination in behaviors such as escaping from predators (Ghirlanda and Vallortigara 2004; Bisazza and Dadda 2005; Vallortigara and Rogers 2005). One could object that the above reasoning does not apply to our study species because sociality is poorly developed in amphibians and is generally restricted to sexual and aggressive behavior. Yet, though most tadpoles do not show a true shoaling behavior like fish, in several species they do manifest aggregative behavior, which appears to be based on kin or familiarity (Katz et al. 1981; Wassersug et al. 1981; Lum et al. 1982). Wassersug et al. (1981) found that tadpoles of 2 anuran species tend to orient parallel to nearest neighbors in a sort of stationary schooling and Watt et al. (1997) demonstrated that tadpoles suffer less predation in more cohesive aggregations. These nonrandom spatial aggregations possibly have an antipredator function (Wassersug et al. 1981). This does not allow excluding collective behavior as a cause for the lateralization alignment observed in our study. Another possible explanation does not involve collective behavior. In several species, the same hemisphere performs a certain cognitive task in the great majority of individuals. This occurs, among the others, for language in humans (Knecht et al. 2000), for food processing in parrots (Brown and Magat 2011) and for the response to predators in domestic chickens (Rogers 2000). Alike, wood frog tadpoles exposed to predation risk as embryos developed more frequently one direction of lateralization and tadpoles with this directionality learned to recognize the olfactory cues of novel predators much faster (Lucon-Xiccato et al. 2017). Similar biases in learning capacity may be considered a promising factor to explain

the occurrence of individuals with a specific lateralization direction in our study species.

Other hypotheses besides that of adaptive phenotypic plasticity have been proposed to explain the variability of lateralization, most of them based on differential selection on genotypes in the different environments (Levins 1968; Vallortigara et al. 1999; Ghirlanda and Vallortigara 2004; Vallortigara and Rogers 2005). These hypotheses are supported by the observation of significant hereditability for lateralization (Collins 1985; Hopkins et al. 1994; Bisazza et al. 2000). Our results do not necessarily conflict with the hypotheses of genetic differences. If there is genetic flow between different habitats or if selective factors vary rapidly in time, then an adaptive mechanism based only on genetic variability is likely to cause mismatches between the lateralization phenotype selected in the previous generation and the most advantageous phenotype in the actual ecological situation. In this scenario, phenotypic plasticity might have been positively selected as a secondary mechanism to cope with environmental uncertainty. To confirm this hypothesis, future studies should simultaneously address the role of plasticity and the role of genes in determining lateralization phenotypes in natural environments.

What could be the mechanism underlying the observed lateralization plasticity? Light exposure seems the best candidate because the vegetation cover treatments substantially altered the amount of light in the environment. In line with this hypothesis, our results resemble those obtained by laboratory studies that directly manipulated light exposure on fish (Andrew et al. 2009; Dadda and Bisazza 2012; Sovrano et al. 2016). On the contrary, it is also possible that chemical cues emanating from vegetation induce lateralization plasticity, as do chemical alarm cues emanating from injured tadpoles (Lucon-Xiccato et al. 2017). Certainly, to better understand plasticity of lateralization, future research should pay particular attention to the mechanisms involved.

Interestingly, tadpoles that were crossed between the 2 vegetation treatments after hatching did not develop evident alignment of lateralization. This effect was also apparent compared with the tadpoles exposed to high vegetation cover treatment during embryonic and larval stage, which exhibited only a low level of lateralization. It is possible that animals living in unpredictable environments may benefit from relatively symmetrical processing of information because of linkages to decision-making. Reddon and Hurd (2009) proposed that in weakly lateralized individuals, either hemisphere may be able to override the actions of the other hemisphere. This mechanism may cause delay in decision-making processes and hesitancy or anxiety in behavior, which are expected to confer advantages in highly variable environments. Alternatively, the development of behavioral lateralization at the population level might not be possible without a certain level of habitat stability and might, therefore, be blocked by alteration in cover-abundance. The instantaneous switch between environmental conditions (i.e., reduction or increase of vegetation cover) might resemble a natural phenomenon, for example, in case of large floods. However, in some freshwater environments, including those inhabited by edible frogs, human activities, such as weed cutting or river bed cleaning, cause a quick reduction in vegetation. It will be important to determine whether the disruption of lateralization due to rapid changes in vegetation cover has consequences on tadpoles' fitness in anthropogenic habitats.

Acknowledgments

Conflict of interest

The authors declare that they have no conflict of interest.

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