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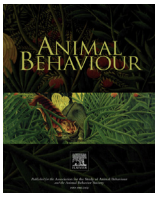

Episodic correlations in behavioural lateralization differ between a poison frog and its mimic

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Sensory and behavioural lateralization is thought to increase neural efficiency and facilitate coordinated behaviour across much of the animal kingdom. Complementary laterality, when tasks are lateralized to opposite sides, can increase the efficiency of multitasking, but predictable behaviour may increase predation risk. Laterality is, however, variable in its scale, existing at both the population and individual level. Population level lateralization is thought to facilitate coordination of social behaviours whereas individual level biases may promote behavioural efficiency. We studied behavioural lateralization in sympatric wild populations of two terrestrial frog species: the Ecuador poison frog, *Ameerega bilinguis*, and its Batesian mimic the sanguine poison frog, *Allobates zaparo*. We used a multivariate approach to study lateralization across four different behaviours: two social behaviours (interactions with conspecifics and heterospecifics) and two nonsocial behaviours (interactions with prey and a simulated predator). We investigated three questions: (1) at what scale is behaviour lateralized, (2) are behaviours lateralized in a complementary manner, and (3) are social and nonsocial behaviours lateralized at different scales? We found no evidence of population level lateralization nor complementary laterality, and limited evidence for individual level lateralization in *Al. zaparo* but not *Am. bilinguis.* We found only weak evidence for differences in lateralization between social and nonsocial behaviour and only in *Al. zaparo*, although counter to our prediction, social behaviour was not lateralized but nonsocial behaviour was weakly lateralized at the individual level. However, we did detect robust, species- and task-specific within-individual correlations. Specifically, *Am. bilinguis* showed shared side use in individuals for certain tasks between consecutive trials, while *Al. zaparo* showed alternating side use in individuals for certain tasks between consecutive trials. Our results suggest that lateralization may be more variable than previously thought and manifest in an episodic fashion under certain conditions.

Asymmetric hand use, or ‘handedness’, has existed in humans since early in our evolution and has shaped the creation of art, tools and even cultural practices (Steele & Uomini, 2005). Although the term ‘handedness’ refers specifically to asymmetric hand use, hand preference is associated with a wider range of asymmetries. These include asymmetric neural organization and processing in the brain (Knecht et al., 2000), asymmetric sensory biases (Shaw, Hämäläinen, & Gutschalk, 2013) and asymmetric motor activities (Sadeghi, Allard, Prince, & Labelle, 2000). All such asymmetries, associated with handedness or otherwise, fall under the term ‘laterality’. Lateralization was once thought to be an exclusively human trait, but it is now recognized to be widespread throughout the animal kingdom (Rogers, Vallortigara, & Andrew, 2013), including, for example, lizards (*Podarcis muralis*; Bonati, Csermely, & Romani, 2008), cuttlefish (*Sepia officinalis*; Jozet-Alves et al., 2012), birds (*Gallus gallus domesticus*; Rogers & Deng, 1999), fish (*Gambusia holbrooki*; Bisazza, Pignatti, & Vallortigara, 1997) and monkeys (*Rhinopithecus bieti*; Pan, Xiao, & Zhao, 2011).

Despite its prevalence, lateralization has clear costs. A lateralized sensory bias can lead to delayed reaction times and limited recognition of stimuli on the off-hand side of the sensory field. Wall lizards, *Podarcis muralis*, for instance, preferentially view predator stimuli with their left eye and attempt to do so even when the left eye is covered (Bonati, Csermely, & Sovrano, 2013). Such biases may

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lead to a delay in recognizing potential predators that appear on the right side of the individual. Similarly, multiple species of toads have been shown to react more strongly to predator stimuli that appear in the left field of vision (Lippolis, Bisazza, Rogers, & Vallortigara, 2002). These data suggest that predators appearing on the right side of the animal will induce weaker escape attempts than those appearing on the left. Wild predators are even recorded to have differential prey capture success when prey items are detected on one side of their body versus the other (Ventolini et al., 2005).

In lateralized species, the cost of delayed reaction times is thought to be counteracted by laterality's ability to increase cognitive performance (Güntürkün et al., 2000; Magat & Brown, 2009) and allowance for dual processing of stimuli by the two hemispheres of the brain (Dadda & Bisazza, 2006a). Dual processing can lead to complementary laterality, a form of multitasking where two tasks are lateralized to opposite sides of the body, allowing them to be performed simultaneously. A common example is using one eye to forage while the other scans for predators (Beauchamp, 2013; Dharmaretnam & Rogers, 2005; Rogers, Zucca, & Vallortigara, 2004) or competitors (Vallortigara, Rogers, Bisazza, Lippolis, & Robins, 1998). This kind of task specialization reduces the need for task switching when foraging in dangerous areas and improves overall foraging efficiency (Dharmaretnam & Rogers, 2005). Overall, evidence for complementary laterality is limited. Most studies have been conducted on long-term captive (Andrew & Rogers, 2002; Robins & Rogers, 2006a; Yamazaki, Aust, Huber, Hausmann, & Güntürkün, 2007) or semicaptive (Lippolis, Joss, & Rogers, 2009) populations (but see Beauchamp, 2013), or domesticated animals (Anderson & Murray, 2013; Dharmaretnam & Rogers, 2005; Shivley, Grandin, & Deesing, 2016; Tomkins, McGreevy, & Branson, 2010). Captive animals like these experience minimal predation pressure or resource stress compared to their free-living counterparts. Research comparing the patterns of lateralization between captive and free-living animals are both limited and conflicting, making it difficult to determine when studies on captive animals are relevant to wild behaviour. Hoffman, Robakiewicz, Tuttle, and Rogers (2006), for instance, found that a population of wild Australian magpies, *Gymnorhina tibicen*, showed similar antipredator and alarm calling lateralization to laboratory animals like the domestic chicken, *Gallus gallus domesticus*. In contrast, Austin and Rogers (2012) found that while feral and domestic horses, *Equus caballus*, show similar leftward biases for aggressive and vigilance behaviours, they differ in their limb preference while grazing. Furthermore, a lack of studies on free-living animals limits our understanding of the prevalence of complementary laterality in the wild, which is where it must have evolved and where it may well still be under selection.

Lateralization can also impose costs by increasing an individual's predictability. Population level laterality occurs when all or most of a population shares the direction of their asymmetry. Theoretically, population level laterality should lead to predators taking advantage of the consistent lateralization by approaching prey on their weaker side and prey staying alert on the side most often attacked by predators (Hori, 1993). These costs are predicted to lead to frequency-dependent selection and to cause a roughly even distribution of right- and left-biased individuals in a population (Hori, 1993), otherwise known as individual level laterality. Any individual encountered from a population lateralized at the individual level would therefore have an equal chance of being left- or right-lateralized. Paradoxically, most species studied for laterality remain lateralized at the population level (Ghirlanda, Frasnelli, & Vallortigara, 2009; Vallortigara & Rogers, 2005). The observed predominance of population level lateralization may be partially, although not entirely, explained by investigative bias in the field. Lateralization researchers often look for population level laterality without statistically addressing the possibility of individual level laterality (Anderson & Murray, 2013; Austin & Rogers, 2007; Beauchamp, 2013; Bisazza, De Santi, & Vallortigara, 1999; Hews, Castellano, & Hara, 2004). In addition, Roche et al. (2020) claimed that a combination of failure to account for repeatability in the statistics and the frequently low sample sizes found in lateralization research may have inflated the number of published studies showing population level lateralization.

Vallortigara and Rogers (2005) argued that population level lateralization arises as a result of social coordination. For instance, when fleeing from a predator, schooling fish should coordinate the direction they turn to escape in order to avoid being an odd one out and thus targeted by the predator (Vallortigara & Rogers, 2005). Indeed, in a study comparing the population level lateralization of gregarious versus nongregarious fish, a greater proportion of the social species shared a population level lateralization for turning direction compared to their less social counterparts (Bisazza, Cantalupo, Capocchiano, & Vallortigara, 2000). However, population level lateralization need not be true for only social species, or even all behaviours within a species, but instead should only be relevant for evolutionarily coordinated behaviours (Frasnelli & Vallortigara, 2018). In asocial mason bees, for instance, aggressive interactions were found to be lateralized while nonsocial behaviours such as antennal wiping were not (Rogers, Frasnelli, & Versace, 2016). Expressing population level lateralization of coordinated behaviours but individual level lateralization of noncoordinated behaviours therefore maximizes coordination benefits while minimizing the predictability costs of lateralization. Research on this pattern of laterality is, however, relatively minimal (Frasnelli & Vallortigara, 2018), although some research suggests the division between behavioural types occurs in nonsocial but not highly social species (Rogers et al., 2016).

Laterality studies traditionally either address the neurological underpinnings of asymmetry or catalogue behaviours that demonstrate lateralization. Here we focus on the phenotypic structure of laterality in wild terrestrial frogs living in a complex natural habitat. We explored not only the extent and scale (population versus individual) of lateralization between behaviours, but also their relationships in an ecologically relevant framework. Specifically, we tested three hypotheses. (1) Behaviours will be lateralized, either at the individual or population level. (2) Behaviours will show complementary laterality such that different tasks will be allocated to different sides of the animal. (3) The scale of lateralization will differ between social and nonsocial behaviours such that social behaviours will be lateralized at the population level while nonsocial behaviours will be lateralized only at the individual level.

METHODS

Study Species

We studied sympatric Ecuadorian populations of the Ecuador poison frog, *Ameerega bilinguis* (Dendrobatidae), and the sanguine poison frog, *Allobates zaparo* (Aromobatidae). The two species are brightly coloured but whereas *Am. bilinguis* is chemically defended, *Al. zaparo* acts as a Batesian mimic of *Am. bilinguis* (Darst & Cummings, 2006; Darst, Menéndez-Guerrero, Coloma, & Cannatella, 2005). These two species share many features of their natural history, being similar in size and in conspicuous colouring (Darst & Cummings, 2006), occupying the same myrmecophagous niche in the rainforest leaf litter (Darst et al., 2005; Santos, Coloma, & Cannatella, 2003) and exhibiting parental care (Poelman, Verkade, van Wijngaarden, & Félix-Novoa, 2010; Summers &

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McKeon, 2004). No previous research has been conducted on the territoriality of *Al. zaparo* or the interactions between *Am. bilinguis* and *Al. zaparo*. Members of *Am. bilinguis* are, however, known to be highly territorial with others of their own species (Santos, 2008), and we observed individuals attempting to attack both reflections and conspecifics/heterospecifics contained in deli cups. Typical interactions involved the focal frog orienting towards the mirror/individual and then leaping towards the stimulus with great force (Supplementary Video S1).

Despite their similarities, however, *Am. bilinguis* and *Al. zaparo* are only distantly related and both are highly diverged from their most recent common ancestor (Grant et al., 2006; Vences et al., 2003). Sympatry and similarity across both morphological and behavioural traits allow us to investigate laterality across shared behavioural trade-offs including ecologically relevant inter- and intraspecific social interactions, prey capture and predator avoidance.

To our knowledge, this is the first study exploring lateralization between a chemically defended and a mimetic species, or aposematic species more generally. Lateralization trade-offs may differ between chemically defended and mimetic species due to their different levels of defence: lateralization has been shown to increase with risk of predation (Brown, Gardner, & Braithwaite, 2004; Ferrari et al., 2015; Ferrari, McCormick, et al., 2015). Furthermore, research on *Am. bilinguis* and *Al. zaparo*, particularly behavioural research, is extremely limited. Lateralization has, however, been found in a wide variety of other frog species (Blackiston & Levin, 2013; Bolis et al., 2020; Lippolis et al., 2002; Liu et al., 2020; Lucon-Xiccato, Chivers, Mitchell, & Ferrari, 2017; Robins & Rogers, 2006b), including laterality of predatory (Robins & Rogers, 2006b) and agonistic responses (Robins, Lippolis, Bisazza, Vallortigara, & Rogers, 1998; Robins & Rogers, 2006b) in naturalistic settings. Given evidence found in other species, we expected similar results in our study species, but that individual level lateralization would be more prevalent in the less defended species.

We conducted all experiments within the Iyarina Forest Reserve at the Andes and Amazon Field School field station (Provincia de Napo, Ecuador). We used 18 adult *Am. bilinguis* (snout−vent length, SVL: mean ± SEM = 22.50 ± 0.38 mm) and 20 adult *Al. zaparo* (SVL: mean ± SEM = 26.59 ± 0.50 mm). Frogs were not identified to sex as these species show limited sexual dimorphism but were most likely to be males due to survey methods. We located frogs by following their advertisement calls, manually disturbing the leaf litter, or by chance while walking transects through the rainforest or disturbed scrubland. We then captured the frogs using 50 ml plastic deli cups to minimize handling. All frogs were also photographed and filmed as part of a series of studies on amphibian visual ecology (McEwen, Anderson, Yeager, Pruitt, & Barnett, 2019). Experiments were approved by the McMaster Animal Research Ethics Board, Ontario, Canada (AREB no.: 18-05-20) and the Ministerio del Ambiente, Ecuador (014-2019-IC-FLO-DNB/MA).

Each frog was initially housed individually in an opaque-sided, cylindrical plastic container (~10 cm diameter by ~10 cm height). Twelve hours before trials began, each focal frog was transferred into a larger opaque, rectangular plastic experimental enclosure (~40 × 25 × 25 cm; later referred to as the 'home' enclosure). After the trials were complete, focal frogs were returned to the smaller enclosures and acted as social stimuli in the subsequent set of trials (see below for treatment designs). All enclosures contained a ~3 cm deep layer of moist soil and a large dead leaf that acted as a shelter, both of which were collected from the same location as the frogs. Frogs were maintained at the local ambient temperature and photoperiod and were fed termites to satiation once per day (Darst et al., 2005). All frogs were held for a maximum of 7 days and then released at their site of initial capture. To minimize welfare impacts on subjects, a maximum of 20 individuals were tested per species, and any frog that showed signs of poor health (e.g. lethargy, not eating) was released.

Behavioural Assays

We assayed frogs for four behaviours: two 'social' behaviours, where the frog responded to a conspecific and a heterospecific (*Am. bilinguis* or *Al. zaparo*), and two 'nonsocial' behaviours, where the frog was presented with prey (~20 live termites) and a simulated predator encounter (the human observer). Although the responses to the social stimuli were primarily aggressive, we interpreted aggression as a social interaction because coordination of behaviour could facilitate ritualized threat assessment of both parties. We organized the experiment into six blocks, within which each behavioural assay was performed once. The first two behavioural assays in each block were the social conspecific and heterospecific stimuli. We independently randomized the sequence (random.org; Haahr, 1998) to eliminate bias from order effects. We then recorded the frog's response to the nonsocial prey and the simulated predator stimuli. We standardized the order of the nonsocial behavioural assays to avoid stress-related carryover effects. We conducted two blocks of assays each day: a morning block, beginning at 0900 hours local time, and an afternoon block, beginning at 1330 hours local time. We therefore assayed each frog a total of 24 times, six times for each behaviour.

We performed the conspecific, heterospecific and prey behavioural assays in the focal frog's home enclosure. During these trials, we positioned the home enclosure under a vertically mounted Canon VIXIA HF r-series camcorder (Canon Inc., Tokyo, Japan). To allow for filming, we removed the shelter leaf, and we replaced the enclosure lid with a single sheet of transparent cling film. We presented the conspecific, heterospecific and prey stimuli in identical clear, cylindrical plastic containers (~4 cm diameter by ~5 cm height). An experimenter placed each stimulus in the centre of the enclosure and moved out of sight of the focal frog. Behavioural recordings proceeded for 10 mins after the experimenter left the frame and was no longer visible to the frog. Following each of these trials, we removed the stimulus, returned the leaf and permitted the frogs a rest period of approximately 2 min. All videos were scored by the same observer (H.M.A.) using Behavioral Observation Research Interactive Software (BORIS; Friard & Gamba, 2016). We recorded the number of times the focal frog attended to a stimulus and the visual hemifield used to observe the stimulus (left, right, or both, if looking straight forward) and recorded these counts as our measure of each behaviour. 'Looks' were considered to be straight forward if the stimulus occupied an approximately 40° angle directly in front of the frog. 'Looks' were considered right or left if the frog was clearly attending to the stimulus but the stimulus was located outside of this range on either the right or left, respectively.

The simulated predator encounters took place in a white opaque-sided, rectangular plastic arena (~70 × 24 × 45 cm), in the centre of which we placed a bent cardboard wedge with an angle of 60° and sides of 25 cm. We placed focal frogs ~5 cm from the centre line (fold) of the wedge, facing towards the cardboard. With the experimenter (H.M.A.) positioned behind the frog and visible, the frog was allowed to either freely make an escape attempt or, following 10 s of inactivity, was touched on the midline of its back (slightly posterior to the iliosacral joint) with the eraser of a mechanical pencil. The observer then recorded the direction of the frog's escape (left, right, or straight forward, with straight forward occurring when the frog jumped into the point of the wedge rather than to either side) by hand. We recorded six jumps per block ($N = 36$ jumps per frog). Two frogs (one *Am. bilinguis* and one *Al.*

zaparo) were subsequently found to be missing a single jump, and instead had a total of 35 jumps.

Analysis

We calculated a lateralization index (LI) for each trial using the formula:

$$\mathrm{LI} = \frac{\sum \text{left} - \sum \text{right}}{\sum \text{left} + \sum \text{right} + \sum \text{straight forward}}$$

The LI has a maximum range of -1 to 1, with negative values indicating a rightward bias, positive values indicating a leftward bias, and zero indicating no directional bias. Frogs with an LI close to an absolute value of one are therefore considered to be highly lateralized for the trial in the corresponding direction, while frogs with an LI score close to zero (in the negative or positive range) are considered to have relatively low lateralization for the trial. Trials where a frog failed to interact with the stimulus were assigned a value of NA and not included in the overall analysis (24 total trials). Trials where a frog only interacted with the stimulus once (thereby receiving a perfect maximum LI) were removed from the analysis to avoid artificially skewing the results (91 total trials). All analyses were conducted in R v.3.6.3 (R Core Team, 2020).

We wished to determine (1) the degree of lateralization at the individual and population level for each behaviour, (2) whether the lateralization was complementary and (3) whether social and nonsocial behaviours differ in their degree of lateralization. To do so, we fitted two multivariate mixed-effects models, one for each species, with the four behaviours as response variables. The estimated intercepts for each behaviour indicate whether there is population level lateralization: an intercept below zero denotes the population is right-lateralized and an intercept above zero indicates the population is left-lateralized. Frog identity (ID) was included as a random factor, allowing us to estimate the among- and within-individual variances, which we subsequently used to calculate the repeatability of the LI scores. Repeatability is defined as the proportion of total variance accounted for by differences among individuals and was calculated using the posterior distribution of the among-individual distribution of each model, following methods outlined in Nakagawa and Schielzeth (2010). High repeatability scores signify individuals have different mean values of LI, indicative of individual level lateralization.

Our multivariate models were also used to estimate both the among- and within-individual covariances for each pair of behaviours (Brommer, 2013; Dingemanse & Dochtermann, 2013; Hadfield, 2010). We calculated the among- and within-individual correlations using the following general formula:

$$\mathrm{Corr}_{\mathrm{SaSb}} = \frac{\mathrm{COV}_{\mathrm{SaSb}}}{\sqrt{\mathrm{V}_{\mathrm{Sa}} \times \mathrm{V}_{\mathrm{Sb}}}}$$

$\mathrm{COV}_{\mathrm{SaSb}}$ is the among-individual covariance of behaviour A and behaviour B (for among-individual correlations), or the residual covariance of behaviour A and behaviour B (for within-individual correlations), V_{Sa} is the variance of behaviour A and V_{Sb} is the variance of behaviour B (referring to the among-individual or residual variance, depending on whether the among- or within-individual correlation, respectively, is being calculated; Dingemanse & Dochtermann, 2013).

The among-individual correlation indicates whether individuals that have on average a higher score for one behaviour have on average a higher or lower score for the other behaviour. Negative among-individual correlations between the LI scores for two behaviours are therefore evidence of complementary lateralization since this indicates opposing laterality for the behaviours (i.e. leftward bias for one behaviour and rightward bias for the other behaviour). Positive scores in contrast indicate parallel laterality, where an individual favours the same side for both behaviours. Within-individual correlations show whether LI scores from an individual are correlated within the same block, so if in the third block the individual tended to favour the right side for behaviour A, it favoured the same side for behaviour B (positive within-individual correlation) or the opposite side for behaviour B (negative within-individual correlation) in the same block. Within-individual correlations can be indicative of temporary factors such as motivation, prior sensory activation or energetic costs favouring the use of the same or different sides in a given block (Dosmann, Brooks, & Mateo, 2015).

We fitted models for both frog species in the R package MCMCglmm (Hadfield, 2010). We used noninformative priors and ran the models for 300 000 iterations, with a burn-in of 50 000 and thinning of 100. We provide the modes and 95% credible intervals (CIs) for the repeatability scores, correlations and intercepts. We consider an intercept or a correlation to be different from zero if its upper and lower 95% CIs (UCI and LCI, respectively) did not cross zero.

Repeatability scores range from zero to one and, therefore, the CIs never cross zero. In the absence of a clear threshold, we compared our results to the meta-analysis of Bell, Hankison, and Laskowski (2009), which found mean repeatability of behavioural traits to be 0.37. Repeatability scores close to or greater than this average were therefore judged as being relatively high repeatability values, while those much less than this average are considered low repeatability scores. To determine whether there was population-level and/or individual-level lateralization (Question 1), we assessed whether the intercepts were different from zero (population-level lateralization) and assessed the degree of individual-level lateralization based on the magnitude of the repeatability scores, although this metric cannot be boiled down to present or absent. To determine whether there was complementary lateralization (Question 2), we assessed whether there were negative among-individual correlations between behaviours. To determine whether social behaviours were more highly lateralized at the population level than nonsocial behaviours (Question 3), we compared the intercept modes, and whether they were different from zero, between the two social behaviours (response to heterospecific and conspecific) and the two nonsocial behaviours (response to the prey and predator stimuli).

RESULTS

Description of Behavioural Responses

Throughout the experiment the two species interacted with the behavioural trials in a similar manner. We found that the behavioural repertoires of the focal frogs were similar when presented with either a social stimulus (conspecific or heterospecific) or the prey stimulus. We observed that focal frogs of both species would typically approach the stimulus cup, hop away and then return to the cup multiple times throughout a trial. Focal frogs would also occasionally circle the cup, hop on top of the cup or hop directly into and push against the cup. In the simulated predator trials, the focal frogs almost always jumped to either the left or the right of the cardboard wedge and only rarely jumped straight forward. There were no trials in which the frog hopped backwards towards the observer. Most jumps were initiated independently by the frog without the need for physical prodding by the observer.

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Individual and Population Level Lateralization of Behaviour

We found no evidence of population level lateralization. No LI intercept was found to be different from zero for any of the four behaviours in either species (Fig. 1, Appendix, Table A2), suggesting no bias in the statistical distribution of population level asymmetry. We did find limited support for individual level lateralization in *Al. zaparo* but no evidence in *Am. bilinguis*. We also found no LI repeatability greater than 0.37, the average repeatability found in the meta-analysis by Bell et al. (2009). However, *Al. zaparo* displayed the highest repeatability scores, with a predator response repeatability mode of 0.251 (LCI = 0.128, UCI = 0.522) and a prey response repeatability mode of 0.234 (LCI = 0.073, UCI = 0.519; for repeatability estimates, see Fig. 2, Appendix, Table A1). These results are generated through Bayesian statistics, and so repeatability (and therefore individual lateralization) is measured on a continuous scale rather than as a binary report of significant versus nonsignificant. Consequently, we interpret these results as showing limited evidence for individual lateralization in *Al. zaparo* in the predator and prey behavioural assays.

Complementarity of Lateralization

We found no nonzero among-individual correlations for either *Am. bilinguis* or *Al. zaparo* (Fig. 3, Appendix, Table A3). We therefore found no support for either parallel or complementary laterality at the individual level. Note, however, that the CIs of all of the among-individual correlations were particularly wide, suggesting a limited degree of precision in our estimates.

We found two nonzero within-individual correlations: a positive correlation between the heterospecific and predator-avoidance behaviours in *Am. bilinguis* and a negative correlation between the heterospecific and conspecific behaviours in *Al. zaparo* (Fig. 4, Appendix, Table A3). The within-individual correlations suggest that the extent of lateralization within a given block was positively associated in *Am. bilinguis* for heterospecific and predator behaviours and negatively associated in *Al. zaparo* for heterospecific and conspecific behaviours. The CIs of the within-individual correlations were also noticeably narrower than those of the among-individual correlations, indicating a greater degree of precision for our estimates of the within-individual correlations.

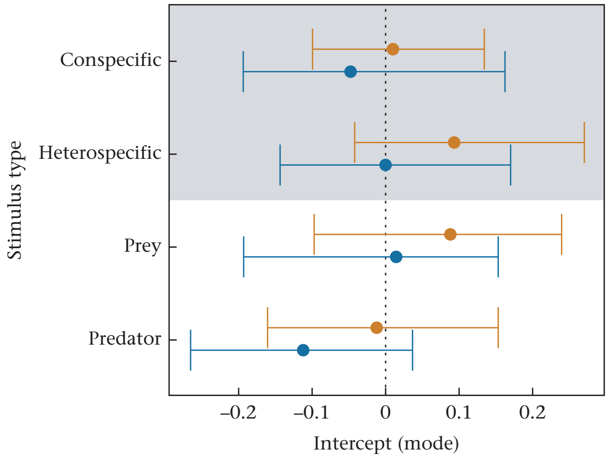

Figure 1. Mode values of LI location effects for *Allobates zaparo* (orange) and *Ameerega bilinguis* (blue) across stimuli (conspecific, heterospecific, prey, predator). Horizontal lines represent the upper and lower 95% credible intervals (CI). Shaded area demarks social stimuli. The CI of all intercepts cross zero, offering no support for population level lateralization in either species.

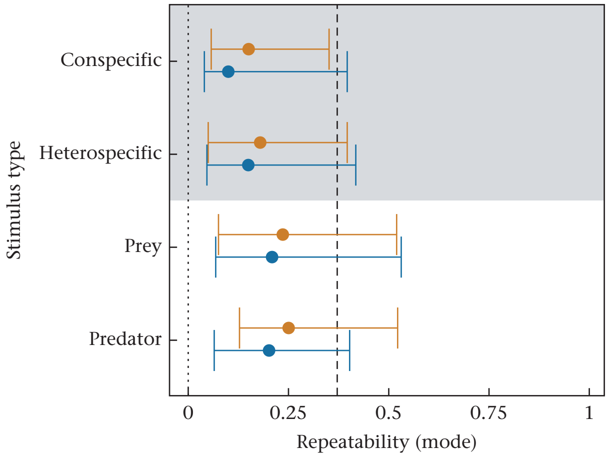

Figure 2. Mode of LI repeatability scores for *Allobates zaparo* (orange) and *Ameerega bilinguis* (blue) across stimuli (conspecific, heterospecific, prey, predator). Horizontal lines represent the upper and lower 95% credible intervals. Shaded area demarks social stimuli. No repeatability mode was observed to be greater than the average found by Bell et al. (2009; represented by dashed grey line), with the greatest values being the predator and prey responses by *Allobates zaparo*.

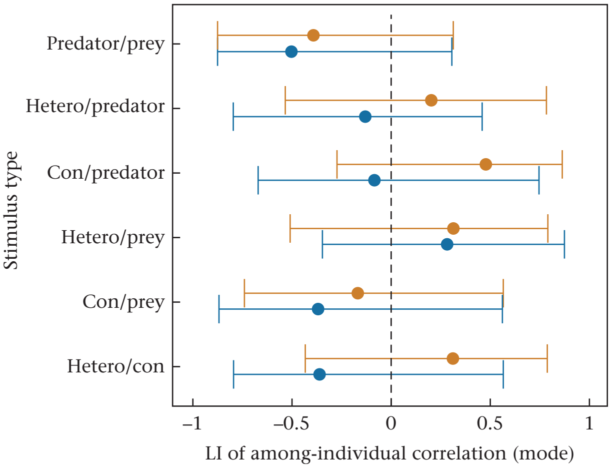

Figure 3. Mode of LI among-individual correlations for *Allobates zaparo* (orange) and *Ameerega bilinguis* (blue) across all stimuli (predator/prey, heterospecific/predator, conspecific/predator, heterospecific/prey, conspecific/prey, heterospecific/conspecific). Horizontal lines represent the upper and lower 95% credible intervals (CI). The CI of all among-individual correlations cross zero, offering no support for among-individual correlations generally or complementary laterality specifically.

Social versus Nonsocial Behaviours

There was no observable difference of LI between social and nonsocial behaviour for *Am. bilinguis* (Appendix, Tables A1, A2). In contrast, in *Al. zaparo*, although social behaviours showed no laterality, as indicated by the repeatability scores, at either the individual or the population level (Appendix, Tables A1, A2), nonsocial behaviour showed weak laterality at the individual level (Appendix, Table A1).

DISCUSSION

Here, we tested three hypotheses regarding the behavioural context of lateralization using wild individuals. We found limited evidence for consistent lateralization at any level and across any of the behaviours (Figs 1, 2, Appendix, Tables A1, A2). We did, however, detect consistent relationships between the transient

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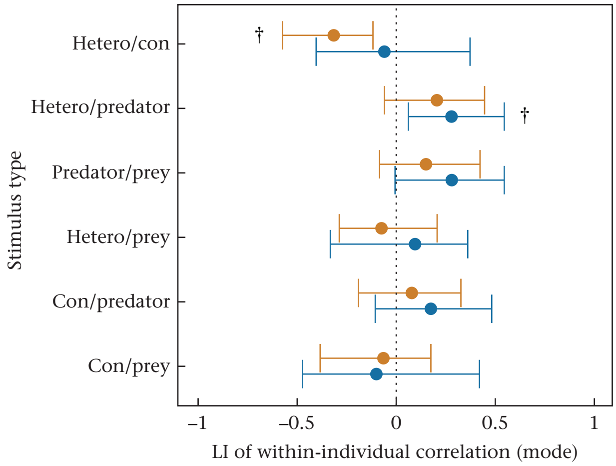

Figure 4. Mode of LI within-individual correlations for *Allobates zaparo* (orange) and *Ameerega bilinguis* (blue) between all stimuli (heterospecific/conspecific, heterospecific/predator, predator/prey, heterospecific/prey, conspecific/predator, conspecific/prey). Horizontal lines represent the upper and lower 95% credible intervals. †Nonzero negative correlation (heterospecific*conspecific stimuli) in *Allobates zaparo*; nonzero positive correlation (heterospecific*predator stimuli) in *Ameerega bilinguis*.

laterality of certain behaviours in both species we studied (Fig. 4, Appendix, Table A4), suggesting episodic associations that may have been hidden within behavioural variation.

We found no evidence for population level laterality across both species and all behaviours. We did, however, find limited evidence for individual level laterality in *Al. zaparo* for predation and antipredator behaviour. This contrasts with previous work on captive animals that has often found evidence for lateralization, with population level lateralization being detected particularly often (Anderson & Murray, 2013; Austin & Rogers, 2012; Dadda & Bisazza, 2006b; Koboroff, Kaplan, & Rogers, 2008; Magat & Brown, 2009; Vallortigara & Rogers, 2005; but see Roche et al., 2020), including population level antipredator responses in other species of anuran amphibians (Lippolis et al., 2002). Although *Al. zaparo* showed no population level lateralization, individual lateralization of predation and antipredator behaviours circumstantially support the hypothesis that nonsocial behaviours should be lateralized at the individual level (Frasnelli & Vallortigara, 2018). The overall *Al. zaparo* population should remain unpredictable to predators by exhibiting among-individual variation in lateralization, but individual *Al. zaparo* may still benefit from the hypothesized cognitive benefits of lateralization (Güntürkün et al., 2000; Magat & Brown, 2009). Interestingly, previous research has found that lateralization tends to increase with predation risk, with low-risk populations showing relatively low lateralization (Brown et al., 2004; Ferrari et al., 2015; Ferrari, McCormick, et al., 2015). *Allobates zaparo*'s relatively weak lateralization may then be due to the protection given by its high-fidelity mimicry, whereas *Am. bilinguis*'s absence of lateralization may be due to the increased protection of combining both aposematic coloration and toxic defence (Darst & Cummings, 2006).

We found no evidence for complementary lateralization in either species. While the low degree of certainty in our estimates of the among-individual correlations means we cannot rule out lateralization, among-individual correlations are often found between behaviours using the mixed-model framework (Dingemanse & Dochtermann, 2013). We therefore do not think our statistical approach is the reason that we failed to detect complementary lateralization. Instead, much of the variation in the behaviours we measured was within individuals instead of among individuals.

We detected a small difference in lateralization between social and nonsocial behaviours in *Al. zaparo* but no difference in *Am. bilinguis*. The difference in *Al. zaparo* was, however, weak, and failed to show the hypothesized pattern of population level laterality of social behaviours (conspecific and heterospecific interactions), although individual level lateralization of the nonsocial behaviours (predator and prey interactions) was observed. It may be that the aggressive interactions between *Am. bilinguis* and *Al. zaparo* are too infrequent or too competitive or intense for coordination to be important, or that territorial disputes are predominantly mediated through other sensory modalities such as vocal communication. While population level lateralization of aggressive behaviour has been found in a number of species, aggression is usually low risk, as in cane toads, *Rhinella marina* (formerly *Bufo marinus*), where attacks are nondamaging (Robins et al., 1998) or mediated by a threat display, as in green anoles, *Anolis carolinensis* (Deckel, 1995), convict cichlids, *Amatitlania nigrofasciata* (Arnott, Ashton, & Elwood, 2011), and cuttlefish (*Sepia apamal*; Schnell, Jozet-Alves, Hall, Radday, & Hanlon, 2019). Inter- and intraspecific interactions between *Am. bilinguis* and *Al. zaparo* were, in contrast, highly aggressive and lacked any noticeable visual threat displays. The lack of visual threat displays in particular suggests that aggressive interactions are too swift and unritualized in both inter- and intraspecific contexts to foster high levels of lateralization. It may therefore be that the predictability conferred by lateralization, population level or otherwise, would be especially costly in such encounters. Indirect support for this hypothesis is found in ambon damselfish, *Pomacentrus amboinensis*, where lateralized individuals show reduced success when competing for shelter compared to nonlateralized fish (Chivers et al., 2017).

We found two within-individual correlations. Within-individual correlations indicate that variation for one trait is associated with the variation of another trait within the same individual and within the same temporal block of assays (Dingemanse & Dochtermann, 2013). In terms of behavioural laterality, this means that the strength and direction of lateralization in two behaviours are related within a short period. We found a positive within-individual correlation between the heterospecific and predator stimuli in *Am. bilinguis,* meaning that during a trial when a frog's lateralization for interacting with heterospecifics is either less or greater than its own average, then the frog's lateralization for interacting with predators is correspondingly less or greater than its own average in the same direction and during the same block of assays. For example, during a trial an individual was more left-biased than usual when interacting with a heterospecific. Then, in the same block of trials, the individual was correspondingly also more left-biased than usual when fleeing from the simulated predator. In contrast, in *Al. zaparo*, we found a negative within-individual relationship between heterospecific and conspecific stimuli, meaning that during a trial when a frog's lateralization for interacting with heterospecifics was either less or greater than its own average, then the frog's lateralization for interacting with conspecifics was correspondingly greater or less in the opposite direction during the same block of assays. For example, if during a block of trials, an individual that was more right-biased than usual when interacting with a heterospecific was then also more left-biased than usual when interacting with a conspecific during the same block.

We propose the within-individual correlations observed express underlying biases in stimulus classification. For *Am. bilinguis*, the positive correlation between heterospecific and predator responses may suggest similar classification of both stimuli. Previous work has shown that lateralization tends to increase with perceived risk (Broder & Angeloni, 2014; Brown et al., 2004; Ferrari, McCormick, et al., 2015), even on a short-term basis (Chivers et al., 2016;

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Ferrari et al., 2017). Shared laterality in both the conspecific and predator trials then suggests that both stimuli are classified as similarly risky, possibly due to this species' smaller size relative to heterospecific opponents. In contrast, *Al. zaparo* showed a negative relationship between conspecific and heterospecific stimuli, which suggests that conspecific and heterospecific stimuli may have been categorized differently by *Al. zaparo*. Although there was no threat of predation in either scenario, a territorial threat was present, a risk factor that could reasonably lead to a similar increase in lateralization and behavioural biases. The stimuli being relegated to opposite eyes, then, might suggest opposite cognitive categorization of the stimuli: e.g. own species versus other species. We posit that such within-individual correlations may represent complexes of associated stimuli and behaviours that remain largely undetectable until circumstances that require the use of heightened lateralization.

Overall, we detected no evidence of population level laterality or complementary laterality in either of our focal species, and only a weak signature of laterality at the individual level. This is in direct contrast to previous work on laterality in both captive (Anderson & Murray, 2013; Bisazza et al., 1997; Dharmaretnam & Rogers, 2005; Lippolis et al., 2002; Magat & Brown, 2009) and wild populations (Austin & Rogers, 2012; Bonati et al., 2013; Hoffman et al., 2006; Koboroff et al., 2008; Reimchen & Spoljaric, 2011; Ventolini et al., 2005) and illustrates the need for more research into lateralization in wild or naturalistic settings. Yet, our analysis suggests a potentially new scale of laterality not yet considered. Specifically, we found evidence for within-individual correlations in laterality that were episodic in nature, and these associations were stimulus and species specific. We hypothesize that such correlations represent consistent relationships that are only revealed when lateralization is high, such as in high-risk settings. Combining the study of lateralization with the use of mixed-effects models could help enable the field of lateralization to consider new forms and interpretations of lateralization and to better classify lateralization at scales already familiar to the behavioural ecology literature. We further hope that expanding lateralization into an analytical framework increasingly becoming the norm for behavioural trait research will facilitate more research combining both fields, allowing for a deeper understanding of both lateralization specifically and behavioural traits more generally.

Data Accessibility

Raw data are available from Mendeley Data (https://doi.org/10.17632/bt33w4h3b9.1).

Author Contributions

All authors contributed to experimental design. H.M.A., B.L.M. and J.B.B. collected the data in the field, H.M.A. ran the lateralization trials, H.M.A. and D.N.F. collated the data and conducted the analyses, J.Y. acquired the permits, and H.M.A. wrote the first draft of the manuscript with subsequent input from all authors.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2021.01.011.

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Appendix

Table A1
Repeatability scores for MCMC GLMMs across both species and all stimuli

Behaviour	*Ameerega bilinguis* Mode (LCI, UCI)	*Allobates zaparo* Mode (LCI, UCI)
Heterospecific	0.147530 (0.045972, 0.415573)	0.181218 (0.047578, 0.396480)
Conspecific	0.099562 (0.039526, 0.394674)	0.151240 (0.057270, 0.348217)
Prey	0.209426 (0.067799, 0.531024)	0.234429 (0.073361, 0.519447)
Predator	0.200398 (0.060158, 0.399680)	0.250837 (0.073361, 0.522188)

LCI, UCI: lower, upper 95% credible interval.

Table A2
Intercepts for MCMC GLMMs across both species and all stimuli

Behaviour	*Ameerega bilinguis* Mode (LCI, UCI)	*Allobates zaparo* Mode (LCI, UCI)
Heterospecific	0.00001 (-0.14301, 0.168297)	0.09392 (-0.04310, 0.27093)
Conspecific	-0.04826 (-0.19498, 0.161267)	0.01001 (-0.09969, 0.13246)
Prey	0.01356 (-0.19409, 0.15139)	0.08666 (-0.09942, 0.23841)
Predator	-0.11365 (-0.26703, 0.03506)	-0.01111 (-0.16090, 0.15398)

LCI, UCI: lower, upper 95% credible interval.

Table A3
Among-individual correlations for MCMC GLMMs across both species and all stimuli

Behaviour	*Ameerega bilinguis* Mode (LCI, UCI)	*Allobates zaparo* Mode (LCI, UCI)
Heterospecific/Conspecific	-0.36014 (-0.78986, 0.56206)	0.31116 (-0.43831, 0.79438)
Heterospecific/Predator	-0.13030 (-0.79514, 0.46153)	0.20275 (-0.53769, 0.78076)
Heterospecific/Prey	0.28282 (-0.34579, 0.86467)	0.31877 (-0.50936, 0.79337)
Conspecific/Predator	-0.07807 (-0.67155, 0.74750)	0.47738 (-0.27499, 0.85934)
Conspecific/Prey	-0.36675 (-0.86140, 0.56237)	-0.16553 (-0.74117, 0.56772)
Predator/Prey	-0.49818 (-0.87132, 0.30831)	-0.38643 (-0.87033, 0.31388)

LCI, UCI: lower, upper 95% credible interval.

Table A4
Within-individual correlations for MCMC GLMMs across both species and all stimuli

Behaviour	*Ameerega bilinguis* Mode (LCI, UCI)	*Allobates zaparo* Mode (LCI, UCI)
Heterospecific/Conspecific	-0.05618 (-0.40078, 0.37247)	-0.30986 (-0.57130, -0.11378)
Heterospecific/Predator	0.28325 (0.06448, 0.53419)	0.20554 (-0.05026, 0.44031)
Heterospecific/Prey	0.09374 (-0.32962, 0.36019)	-0.07041 (-0.27870, 0.20694)
Conspecific/Predator	0.17382 (-0.10838, 0.47336)	0.08158 (-0.18366, 0.32330)
Conspecific/Prey	-0.09258 (-0.46577, 0.41737)	-0.06138 (-0.38689, 0.17598)
Predator/Prey	0.27640 (-0.00578, 0.54041)	0.15467 (-0.08255, 0.41958)

LCI, UCI: lower, upper 95% credible interval.

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