Lateralization of lateral displays in convict cichlids

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We examine lateralization of lateral displays in convict cichlids, Amatitlania nigrofasciata, and show a population level preference for showing the right side. This enables contesting pairs of fish to align in a head-to-tail posture, facilitating other activities. We found individuals spent a shorter mean time in each left compared with each right lateral display. This lateralization could lead to contesting pairs using a convention to align in a predictable head-to-tail arrangement to facilitate the assessment of fighting ability. It has major implications for the common use of mirror images to study fish aggression, because the ‘opponent’ would never cooperate and would consistently show the incorrect side when the real fish shows the correct side. With the mirror, the ‘normal’ head-to-tail orientation cannot be achieved.

Keywords: aggressive displays; Amatitlania nigrofasciata; animal contests; cooperation; convict cichlids; lateralization

1. INTRODUCTION

Agonistic interactions often include displays involving a lateral aspect of the body, which may provide information about size and fighting ability [1]. If both contestants provide information, the weaker may quit and avoid the costs of continuing when likely to lose and the winner also avoids those costs [1,2]. Thus both benefit by predictable [3], cooperative information exchange [4], with a shared interest in limiting fight costs [1,2]. This mutual benefit [5] may be an important factor in the evolution of cooperative ritualized aggressive displays, which up until now has been relatively overlooked.

Lateral displays occur during red deer (Cervus elaphus) contests whereby the contestants walk in the same direction, in parallel, such that the two align head to head [6], and in cichlid fish, when contestants each present one side to the opponent while extending unpaired fins [7]. Like deer, cichlid displays are mutual, but the fish typically align head to tail (figure 1) and often circle each other [2]. If each fish selected a side to display at random they would enter head to tail as often as head to head. However, lateralization of behaviour would result in more consistent head-to-tail orientation.

Lateralization involves the selective processing of information in one hemisphere [8]. It occurs in all vertebrate classes [9] and affects various activities [8] including agonistic behaviour [10,11]. There is a left-eye–right-hemisphere dominance in eliciting aggressive responses in tetrapods [8]; however, teleost fish show right-eye dominance in agonistic situations [12,13]. Further, males are frequently more strongly lateralized than females [14] and convict cichlids (Amatitlania nigrofasciata) show differences in individual lateralization dependent on sex and aggressiveness [15]. Moreover, contest behaviour has been well examined in convict cichlids [16] and there are sex differences in the use of specific displays, with females using more frontal activities but less lateral displays than males [17].

First, we examine whether population-level lateralization of lateral displays occurs in convict cichlids in terms of number and total duration of use. Second, we predict that each use of the ‘correct’ side will last longer than each of the ‘incorrect’ side. Third, we investigate whether there are sex differences in the degree of lateralization of lateral display.

2. MATERIAL AND METHODS

We re-analysed video footage of dyadic encounters between convict cichlids, A. nigrofasciata, from a previous study (details of methods and ethical considerations in Arnott & Elwood [17]). Subjects (36 males, 24 females) were housed per 12 l tank, and visually isolated for 48 h. Random same sex pairs were selected and placed in an observation chamber with a one-way mirror (human observer can view fish undetected) over two adjacent tanks and an opaque divider between the tanks (see [17]). After 30 min, the divider was removed and interactions began with the approach of both fish to the ‘display’ window and a focal fish observed for 12 min. Recordings were analysed with a Psion Workabout hand-held computer using Observer v. 3.0 software (Noldus Technology, Wageningen, The Netherlands). The opaque dividers were replaced and 24 h later the original pairs were rested in the same manner, but with the other fish being designated the focal fish.

We focused on lateral displays, defined as a contestant presenting its side to an opponent while extending its unpaired fins and lowering its gill covers [7]. We recorded frequency and duration of lateral displays, together with the side presented by the focal individual. For example, a ‘right lateral display’ was recorded when the longitudinal axis was less than 45° to the glass, with the right side to the opponent.

We calculated the lateralization index (LI) (right – left)/(right + left). We used the index for number and mean duration in a series of one between (gender) and one-within (order of testing) two factor ANOVAs. If the order of testing had no effect, population-level laterality was tested for each measure using a one-sample t-test against zero. Non-normality meant a non-parametric equivalent approach for total duration of each display direction. Alpha was set using Holm’s sequential Bonferroni method. Data were lost for two focal individuals (frequency and total duration n = 58) and two used no left-sided displays, so for the mean duration of displays n = 56.

3. RESULTS

The sexes did not differ in the LI for number (F1,27 = 0.08, p = 0.78) or mean duration of displays (F1,25 = 0.07, p = 0.77), or for the order of testing on the number (F1,27 = 0.02, p = 0.89) or the mean duration (F1,25 = 0.97, p = 0.33) of displays, and there was no significant interaction effect for number (F1,27 = 0.12, p = 0.73) or mean duration (F1,25 = 1.06, p = 0.31). The mean LI for number was +0.252 (s.e. ± 0.038; ¼ 6.61, p < 0.0001) and for mean duration was +0.404 (s.e. ± 0.047; ¼ 8.59, p < 0.0001) indicating a strong preference for showing the right side. For total duration, there was a negatively skewed index (+0.539, s.e. ± 0.047; one-sample sign, p < 0.0001), but there was no effect of gender on the index (Mann–Whitney, p = 0.69) or order of test (Wilcoxon paired test, p = 0.84). The fish spent 78.5 per cent of their total lateral display showing the right side and only 21.5 per cent the left.

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Population-level lateralization in behaviour is commonly observed [8]. However, while there are obvious advantages of individual-level lateralization [22,23], the reason(s) for the evolution of population-level biases are less clear. Recently, a game theoretical approach [24] demonstrated that the need to coordinate behaviour during intraspecific encounters could result in the evolution of population-level lateralization, while still maintaining non-trivial use of the minority direction. Our results predict that coordination of aggressive activities would be enhanced by population-level lateralization in display behaviour. However, the need for cooperation may not necessarily be the selective force for lateralization [24] and cooperation might simply be a consequence of lateralization. We suggest that lateralization provides a simple mechanism [25] that allows contestants to cooperate in minimizing fight costs.

Previous studies speculated that there is an underlying sex difference in the strength of lateralization [15,17] and recent evidence suggests a role of testosterone in mediating sex differences in laterality [26]. However, no sex difference was found with the present data, but might be seen in real contests rather than displays across a glass barrier. Nonetheless, other workers [27] have also failed to detect any overall sex differences in lateralization when convict cichlids were navigating novel or familiar environments. Both sexes are highly aggressive and territorial (e.g. [28]), engaging in numerous contests that include intersexual encounters [7], and likely benefit equally from performing lateral display in a coordinated and predictable way [4]. Thus, while they may differ in the frequency with which particular displays (lateral or frontal) are used [17] they may not differ in lateralization of lateral display.

To conclude, our findings show a strong right-side bias in displays that should result in coordination of social behaviour. Moreover, consistent with our second prediction, we found that each of the more frequent right-side displays lasted longer than the less frequent side. Future studies on agonistic interactions would benefit from recording the orientation pattern of both fish simultaneously.

Our findings have important implications for the very common use of mirrors in fish aggression studies. With a mirror, each time the fish turns to show the preferred right side, the image will show the left and apparently align head to head. This apparent failure to cooperate may markedly affect behaviour. Indeed, a recent study [29] found that fish showed different brain gene expression when ‘fighting’ a mirror image rather than a real opponent, suggesting the mirror evokes a strong fear response. Mirror displays also fail to evoke the normal production of testosterone seen in real contests [30]. Further work on mirror images and real opponents may determine if the head-to-tail configuration is an essential component that allows cooperation in fights.

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