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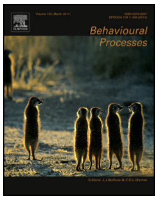

Information gathering during contests: The relationship between lateralisation and contestant behaviour during fallow deer fights

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ABSTRACT

One class of model relating to animal contest behaviour assumes that individuals gather information concerning their opponents' competitive ability; these models argue that such a process allows contestants to avoid engaging in dangerous fighting behaviour with a superior opponent. The brain hemispheres of vertebrates are lateralised in that they are specialised for processing different type of information. Within the context of the current study, we might expect that lateralisation would play a role in facilitating the assessment of opponent quality; nevertheless, the degree of lateralisation shown by individuals can vary suggesting that contest behaviour might also vary based on the ability to process information about competitor quality. The current study tests this hypothesis by predicting that the duration that individuals engage in fighting and the rate of aggressive contest actions should decrease as lateralisation increases. There was a positive relationship between two laterality indices and the duration spent in antler contact; thus lateralised individuals experienced greater time costs. Further, lateralised individuals also experienced a greater disparity in contest actions: there was a negative relationship between lateralisation and the difference in the mean number of backward pushes achieved during fights. When only opponent signal rate was considered there was no effect of lateralisation, therefore, there is support for a mutual assessment process. These results suggest that information gathering via lateral displays may be disadvantageous to lateralised individuals during escalated fighting.

1. Introduction

Fighting is widely considered to be a costly behaviour for individuals in terms of time and energy expenditure (Briffa and Hardy, 2013); investments that might be used pursuing alternative fitness enhancing activities (Payne and Pagel, 1996). Therefore, individuals are expected to adopt strategies that will mitigate these costs; for example, deciding to yield the contest at an early point in the interaction, relates to how efficiently information concerning the quality of an opponent is gathered and processed. In game theoretic terms this strategy is formalised within models of mutual assessment (e.g. the sequential assessment model, SAM: Enquist and Leimar, 1983, see also Briffa and Hardy, 2013). During contests opponents are expected to signal their quality using actions that are presumed to be honest indicators of fighting ability; therefore, these signals are expected to incur some cost (Maynard Smith and Harper, 2003). Under mutual assessment a comparison of the difference in signal rates is expected to permit both contestants determine their quality relative to each other. However, mutual assessment is not the only model under which contestants gather information about opponent quality. There is increasing evidence for an alternative, opponent-only, form of assessment (Arnott and Elwood, 2009) under which contestants attend only to the rate of signalling of their opponent without comparing the difference in signal rates (e.g. Jennings et al., 2012). Nevertheless, under both forms of assessment contestants are expected to benefit by conserving resources that would otherwise be expended on fighting.

One mechanism thought to facilitate information transfer during contests is via a simultaneous lateral display of the body profile. During these displays both contestants align their bodies parallel to each other and walk or swim together for a temporally extended, albeit variable duration (e.g. Enquist et al., 1990; Clutton-Brock and Albon, 1979; Jennings et al., 2003). The assumption is that these ritualised displays serve to communicate the size, and therefore the competitive ability, of each competitor, i.e. their resource holding potential (RHP, Parker, 1974). One novel suggestion relating to the parallel display is that it provides a mechanism by which individuals can efficiently gather and process information concerning opponent RHP through lateralisation (Arnott et al., 2011). Lateralisation is a characteristic of the vertebrate brain whereby the

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two brain hemispheres specialise in processing different types of information (Rogers and Andrew, 2002) and has been shown to mediate aggressive interactions in a range of species (e.g. Hews and Worthington, 2001; Austin and Rogers, 2012). More specifically, during lateral displays cichlid fish orient their right visual field towards their opponent (Arnott et al., 2011) while fallow deer display a similar visual bias in their decision to terminate parallel walks (Jennings, 2012).

The idea that lateralisation might provide a mechanism by which competitors differ in the efficiency by which they can process information about their opponents falls outside the explanatory power of game theoretic models of competition (Arnott and Elwood, 2009). These models assume that the decision to continue or yield will be made at some point during a fight based on the relative difference in competitive ability of the contestants (Payne, 1998). Critically, the ability to acquire and process such information is not expected to differ because it is assumed that optimal decision rules have evolved within the population. However, at a proximate level, differences in the ability of individuals to process such information might exist. This latter view holds that the ability to assess opponent quality might vary with degree of lateralisation expressed by individual group members (Arnott et al., 2011; Jennings, 2012). Lateralisation is associated with enhanced cognitive ability in vertebrates (Magat and Brown, 2009); therefore, where individuals signal their quality through behavioural actions we might expect an association between this feature of contest behaviour and lateralisation. Specifically, I predicted that if lateralisation facilitates assessment of opponent quality it should be associated with shorter contests. Furthermore, if a mutual assessment process is evident then lateralisation should be related to a difference in contestant signal rate; however, if an opponent-only process was evident then there should be an association between lateralisation and opponent signal rate.

2. Materials and methods

2.1. Study site and population

A herd of free-ranging European fallow deer at Phoenix Park (Dublin, Ireland) were observed over two consecutive field seasons. Fawns are tagged in each ear with unique colour/numbered tags shortly after birth. Identification of mature males in the population is facilitated by a combination of coat colour, antler conformation and ID tag.

2.2. Data collection and analysis

Fights were recorded on video tape and analysed using the Observer (Noldus Information Technology); fights involve a range of actions including parallel walking, backward pushing and jump clashing (Jennings et al., 2003, 2005). During parallel walks both contestants present one flank to its opponent; the display ends when one individual either resumes fighting or disengages from the contest by moving away from its opponent. At this point a decision is made to terminate the display presumably because sufficient information has been acquired concerning opponent RHP relative to its own. I calculated a lateralisation index (LI: right − left flank/right + left flank) for the mean number and duration of parallel walks terminated by fifty mature males recorded over two consecutive field seasons (see Jennings, 2012 for further details of this measure of LI). Thus, lateralisation for each individual is shown as their score for LI approaches either 1 (a right-eye preference) or −1 (a left-eye preference) with a score of zero indicating no eye preference. I normalised eye preferences to remove negative scores; therefore, individuals that expressed a left-eye preference (e.g. −1) were given the same signed score as those that expressed a preference for their right-eye (i.e. both individuals were scored as +1).

I investigated whether fighting behaviour was related to LI (number and duration) using Pearson correlations with an alpha level of .05 (SPSS, v 21); therefore, in order to assess evidence for mutual assessment I calculated the difference in the mean number of backward pushes per minute and jump clashes per minute. In order to investigate whether opponent-only assessment was related to lateralisation I estimated the rate of backward pushing and jump clashing per minute for opponents of the focal individuals. A third measure of contest behaviour based on average fighting duration (antler contact) where the focal animal was the loser was also used. Backward pushing is related to dominance rank; competitors force their opponents backwards while their antlers are locked. Jump clashing involves initiation of antler contact by jumping towards the opponent with lowered antlers. The three parameters were chosen because physical contact represents the most intense phase of fighting (e.g. Enquist et al., 1990). The frequency and distribution of backward pushing and jump clashing conform to a mutual assessment process (Jennings et al., 2005); moreover, I wished to remove the effects of parallel walk duration on contest duration by focussing on antler contact duration only (Jennings et al., 2003).

3. Results

3.1. Lateralisation and duration spent fighting

When only fights that were lost were considered there was a positive relationship between the time spent fighting (i.e. antler contact) and lateralisation, LI (number, $r = 0.403$, $N = 30$, $P = .027$, Fig. 1a) and LI (duration, $r = 0.388$, $N = 30$, $P = .034$, Fig. 1b). Thus, highly lateralised individuals took longer to reach the decision to concede a fight than less lateralised individuals.

3.2. Lateralisation and contest action rates

There was no relationship between lateralisation and the number of attacking contest actions conducted by an opponent for LI (number, Backward pushes: $r = 0.081$, $N = 52$, $P = 0.57$; Jump clashes: $r = -0.026$, $N = 52$, $P = 0.85$) or for LI (duration, Backward pushes: $r = 0.092$, $N = 52$, $P = 0.52$; Jump Clashes: $r = 0.082$, $N = 52$, $P = 0.56$). Further, there was no relationship between lateralisation and the difference in the number of jump clashes observed for LI (number, $r = -0.069$, $N = 52$, $P = 0.63$) although the relationship between LI (duration) approached significance ($r = -0.245$, $N = 52$, $P = 0.08$). However, there was a negative relationship between lateralisation and the difference in the number of backward pushes observed for LI (number, $r = -0.285$, $N = 52$, $P = 0.04$ see Fig. 2a) and LI (number, $r = -0.282$, $N = 52$, $P = 0.043$, see Fig. 2b).

4. Discussion

During fights contestants often engage in a lateral display of the body profile; a display that is thought to play a role in gathering information about opponent quality (e.g. Clutton-Brock and Albon, 1979; Enquist et al., 1990). As a consequence, lateral displays between opponents have assumed an important role in game theoretic models that stress mutual assessment as a competitive strategy; specifically, because fighting is inherently risky the ability to accurately assess an opponent's RHP is a critical aspect of contest behaviour (Enquist and Leimar, 1983). Therefore, the ability to acquire information should lead to shorter periods of physical fighting since information is cumulatively gathered over stages increasing the accuracy in assessment. With this in