Jennings DJ, Gammell MP.

Lateralisation during lateral display and its relationship with antler size and symmetry in fallow deer (*Dama dama*).

*Laterality* 2017

DOI: [https://doi.org/10.1080/1357650X.2017.1293074](https://doi.org/10.1080/1357650X.2017.1293074)

Copyright:

This is an Accepted Manuscript of an article published by Taylor & Francis in Laterality on 22nd February 2017, available online: [http://www.tandfonline.com/10.1080/1357650X.2017.1293074](http://www.tandfonline.com/10.1080/1357650X.2017.1293074)

DOI link to article:

[https://doi.org/10.1080/1357650X.2017.1293074](https://doi.org/10.1080/1357650X.2017.1293074)

Date deposited:

26/04/2017

Embargo release date:

22 February 2018
Lateralisation during lateral display and its relationship with antler size and symmetry in fallow deer (Dama dama)

Dómhnall J. Jennings ¹ & Martin P. Gammell ²

¹ Institute of Neuroscience, Framlington Place, Newcastle University, Newcastle upon Tyne, NE2 4HH, UK

² Department of Life and Physical Science, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland

Correspondence: domhnall.jennings@ncl.ac.uk

Acknowledgments:
Abstract

Individuals often display a preference for one side of their body during aggressive encounters. This may be a laterised preference for using one structure of a bilateral trait during display or physical attack, or for keeping the opponent in one visual field. Alternatively, it may be the case that behavioural lateralisation and the degree of symmetry expressed by bilateral structures are correlated forms of developmental instability. We examined whether there was an association between lateralisation during a lateral display and different measurements of antler size and symmetry (beam length, beam circumference, brow tine length and coronet circumference). Three models addressed different structural measures: the right antler, the larger antler and antler symmetry. Results showed that beam length was negatively associated with behavioural lateralisation irrespective of structural measure. A second analysis using a composite score of the four antler measurements, one for each structural measure, showed that only antler symmetry was negatively associated with lateralisation during lateral display. Therefore, our second predication was supported. We discuss these findings in relation to predator detection capability and stress reduction in prey species such as the fallow deer.

Key words.

Aggression, antlers, developmental instability, fluctuating asymmetry, behavioural lateralisation
Introduction

During contests, competing individuals often engage in a simultaneous lateral presentation of their body profiles (e.g. Clutton-Brock & Albon 1979; di Marco & Hanlon 1997; Neat et al. 1998a; Jennings et al. 2003). One interpretation of this behaviour is that it is a ritualised act, permitting both contestants visually estimate the competitive quality of their opponent at close quarters. Thus, lateral display behaviour may permit the weaker individual to withdraw before engaging in fighting (Parker 1974; Enquist & Leimar 1983; Payne & Pagel 1997). This is important because fighting imposes a range of costs such as time and energy on the contestants, whilst also increasing the potential of incurring serious injuries (e.g. Wilkinson & Shank 1976; Drews 1996; Neat et al. 1998b; Briffa & Elwood 2001). Avoiding or minimising these costs should prove beneficial to both contestants; thus, lateral display of the body and weapons may permit individuals to coordinate their actions thereby lowering the cost of aggression – an idea that has been incorporated into game theory models of contest behaviour (e.g. Enquist & Leimar 1983).

Consistent with the idea that individuals seek to coordinate the behaviour during contests, there is evidence that individuals display lateralised eye preferences during aggressive encounters (e.g. Hews & Worthington 2001; Hews et al. 2004; Reddon & Hurd 2008, Arnott et al. 2011; Jennings 2012; Austin & Rogers 2012, 2014). This lateralised eye preference reflects hemispheric specialisation in the brain that is known to influence behaviour in a range of tasks (Rogers et al. 2013). For example, lateralised domestic chicks perform better on simultaneously presented tasks processed by the different brain hemispheres – grain pecking and predator avoidance - than non-lateralised chicks (Rogers et al. 2004, see also Dadda & Bisazza 2006 for an example in fish). With respect to animal contests, there is a population level preference for one visual field during lateral display (Arnott et al. 2011; Jennings 2012). Moreover, male fallow deer that exhibit this lateralised eye preference are less likely to be targeted following third-party intervention of fights than less lateralised individuals (Jennings 2014). Being targeted following intervention in the fallow deer is
highly likely to result in defeat, with a consequent loss in dominance rank likely to negatively impact mating success (Jennings et al. 2009, 2014).

Theoretical consideration of lateralised behaviour has sought to discriminate between the evolution of lateralisation at the individual level and at the population level. Whilst lateralisation might evolve at an individual level because it confers advantages in terms of processing efficiency by avoiding duplication across hemispheres (e.g. Rogers et al. 2004), it is less clear why directional asymmetries would evolve at the population level (Vallortigara 2006). Nevertheless, one argument holds that population-level biases may have evolved because it permits asymmetric individuals to coordinate their behaviour with other asymmetric group members (Ghirlanda & Vallortigara 2004; Ghirlanda et al. 2009; Abrams & Panaggio 2012). In support of this approach, turning preferences in response to a predator were compared in solitary and social fish species (Vallortigara & Bisazza 2002): solitary species showed only individual level lateralisation whereas social species showed lateralisation at the population level. Based on these findings it is clear that lateralisation at the individual level differs from that at the population level (Vallortigara 2006). In terms of the present study, where we address the association between lateralisation during lateral display at the individual level and antler structure at both the individual and population level, this distinction is important.

The question as to why individuals vary in the degree to which they are lateralised remains to be answered (Rogers & Andrew 2002; Dadda & Bisazza 2016). Nevertheless, one theory has suggested that lateralisation in brain and behaviour represents a form of developmental instability (DI, Yeo et al. 1993). Importantly, this theory argues that lateralisation is associated with other forms of DI such as fluctuating asymmetry (FA, Yeo et al. 1997). FA is the non-significant, random difference in size observed between bilateral structures (Møller & Swaddle 1997). It is considered a form of DI because each side of a bilateral trait represents an independent replicate of the same developmental event under genetic or environmental stress during development (Møller & Swaddle
Further, FA occurs to a greater degree in secondary sexual traits as the production of such traits is costlier and, therefore, more condition dependent than that of other traits (Møller & Pomiankowski, 1993; Swaddle, 1996; but see Bjorksten et al., 2000). The antlers of deer are such a trait because they are costly to produce (Jennings & Gammell 2013), and have dual functions as weapons and as organs of display (Lincoln, 1992; Berglund et al., 1996, but see Jennings et al. 2002). Nevertheless, while there is some evidence that lateralised cognitive tasks in human subjects are associated with FA (e.g. Yeo et al. 1997, see also Furlow et al. 1997), we are unaware of any studies that investigate the relationship between behavioural lateralisation and FA. Therefore, one aim of this study is to explore this question with respect to lateralisation during lateral display and asymmetry in the antlers of the European fallow deer.

While there have been numerous arguments surrounding the role that FA plays in the study of behaviour (e.g. Møller & Swaddle 1997; Rohde et al. 1997; Simmons et al. 1999), many species fail to show a preference for displaying their symmetry in aggressive or reproductive signalling (e.g. Jennings et al. 2002; Polak & Stillabower 2004). On the contrary, individuals often display a side preference when signalling their quality; for example, male poeciliid fish show a preference for their more colourful body side during courtship (Gross et al. 2007), while male swordtails show a preference to display their less damaged side to females (Amcoff et al. 2009). In theoretical terms, a population level side-bias can be stable (Ghirlanda et al. 2009); with respect to fallow deer, a right-sided bias in antler size and structure has been reported (e.g. Alvarez 1995, Pélabon & Joly 2000, but see Putman et al. 2000, Pélabon & van Breukelen 1998). The directional nature of this bias appears to manifest itself in a form of structural or side-biased lateralisation where there is a preference for the use of the more developed or larger right antler during fighting (Alvarez 1995). Moreover, despite limited study of the question, lateralised eye-use is associated with morphological characters in agonistic encounters between male fighting fish (Takeuchi et al. 2010). Given that there is a population level right-eye bias during lateral display in the fallow deer (Jennings 2012), it may be
that there is a relationship between lateralisation and antler side or size at the individual level. A second objective of this study was to investigate this possibility.

Male fallow deer cast and re-grow their antlers annually; some weeks prior to the onset of the rut, males shed the antler velvet – an indication that antler growth has ended. Once shed, incidences of agonistic behaviour gradually increase, and peak during the rut as males compete for reproductive opportunities (Clutton-Brock et al. 1988; Moore et al. 1995). The agonistic repertoire of ungulates incorporates a number of different forms of behavioural acts consisting of non-contact displacements including parallel walking to fighting (Jennings & Gammell 2013). During parallel walks, males align head-to-head and walk in a highly stereotyped manner side-by-side often adopting a stiff legged gait (Clutton-Brock & Albon 1979; Alvarez 1993; Jennings et al. 2003; Bartoš et al. 2007) and a population level preference for the right-eye is shown (Jennings 2012). Although lateralisation during lateral display (e.g. Arnott et al. 2011) also facilitates a display of the individual’s weaponry (e.g. Alvarez 1993) the relationship between the two has not been investigated: the present study seeks to redress this omission.
Methods

Population and study site: The study was conducted on a herd of free-ranging European fallow deer in Phoenix Park, Dublin (Ireland). Fawns are tagged shortly after birth during June-July with unique coloured and numbered ear tags. There were approximately 394 and 349 females aged over one year of age during the study period. Mature males, aged four years and older, were identified by a combination of coat colour, antler conformation and ear tag.

Antler collection and measurement: Antlers were collected in Spring during two antler casting seasons. Each morning a search of the males’ night-time range was carried out, and then various bachelor groups were kept under observation until dusk. All collected antlers could be identified as belonging to a particular animal based on (i) unique antler shape (ii) daily records of each animal’s casting date for both antlers and (iii) video recordings and photographs of males taken prior to casting.

We took a number of measurements from pairs of antlers to the nearest millimetre using a soft measuring tape (1996: N = 23; 1997: N = 33; 1998: N = 35): brow tine length, beam length, beam circumference, total antler length, coronet circumference (see Figure 1). In order to examine any changes in antler size or symmetry over years, we initially compared the antlers of the same mature individuals (i.e. four years of age or older) from successive casting seasons (N = 20). Because antlers are functional weapons, we often encountered a breakage that prevented us from making an accurate measurement; when this occurred the individual was excluded from the statistical analyses for that measurement (accounting for differences in the df reported). Following these analyses, we investigated lateralised behaviour during parallel walks and antler size/symmetry to test the objectives of this study (see below for further details).

Figure 1 about here
Parallel walking and laterisation: The protocol for estimating lateralised behaviour during lateral displays are reported in detail elsewhere (Jennings 2012). Briefly, fights (N = 170) between mature males were recorded on video during two consecutive ruts and analysed using the Observer software (Noldus Information Technology, Wageningen, The Netherlands). From these fights, the following data were extracted: the identity of the contestants, whether a parallel walk occurred, the flank presented during parallel walk, and the identity of the individual that terminated the parallel walk. Once the data were extracted a laterality index (LI) was calculated for the number of parallel walks terminated (LI: right-left / right + left, Jennings 2012).

Dominance rank. From the time that males shed the velvet from their antlers in late August, we recorded competitive interactions in the population using all-event methods (Altmann 1974). The dominance rank of each male was determined on the basis of the outcome of all decisively resolved contests recorded prior to matings being observed (i.e. a pre-rut rank, see Jennings et al. 2006). We estimated the dominance rank using David's score (DS, David 1987), a ranking methodology that takes the relative strengths of encountered opponents into account, and that has been shown to be well suited to the system in Phoenix Park (Gammell et al. 2003).

Statistical Analyses

In order to determine whether there was a change in antler size and symmetry between field seasons we used a repeated measures GLM in SPSS (version 23). There were 20 pairs of antlers available for this analysis; however, damage to some of the structures meant that not all 20 replicates could be used. We then investigated whether there was a meaningful association between lateralisation during lateral display and antler structure. There was a sample size of 37 males where a lateralisation score and antler measurements were available; six males were present in the sample in both years (N = 32 individuals). We initially analysed the four measurements of antler size and
symmetry independently in order to determine which (if any) individual measurement was
associated with lateralisation. We computed a composite measure for the right antler size, the larger
antler size, and antler symmetry by summing the individual measurements of the three antler
variables following Yeo et al. (1997), and ran a model that included each of the three composite
measures in order to determine which structural variable was best associated with lateralisation.

The analyses were conducted with multiple regression models using Bayesian methods
with Markov Chain Monte Carlo (MCMC) sampling. We controlled for any effects of individual by
incorporating identity into the model as a random effect; moreover, because age and dominance
rank can be related to antler structure we included these variables both as main effects and as
interaction terms with identity (Jennings & Gammell 2013). Prior to analysis we log transformed the
individual antler measurements in order to improve the distribution of the data where necessary,
and then standardised all the model parameters including age and dominance rank (Kruschke 2015,
see also Yeo et al. 1997).

We sampled the posterior distribution of each models’ parameters using the freely
available JAGS software (version 4.2, Plummer 2003) controlled from within the RunJags package
(version 2.0.4-2, Denwood 2015) in R (version 3.3.1). The models were run with an adaptive phase
(including burnin) of 11,000 iterations across three independent chains running in parallel that used
dispersed initial values. Following the model setup, a posterior phase consisting of 100,000 iterations
was sampled by taking every 40th iterate in order to reduce autocorrelation. We tested convergence
in the model chains using the Gelman-Rubin statistic (Gelman & Rubin 1992) – a convergence level of
<1.1 for each parameter in the model indicated that the adaptive phase of the model was sufficient
(Kruschke 2015). The model parameters were given a weakly informative prior with a half-t model in
order to reduce influence on the posterior distribution (Gelman et al. 2008). Inferences regarding
the importance of each model parameter were made based on the posterior mean and 95% credible
confidence intervals. We estimated the proportion of each parameters posterior distribution that
crossed zero; if less/more than 5% crossed zero (i.e. <5% or >95%) we considered that the parameter
was meaningfully (positively or negatively) associated with individual lateralis-

tion. Where a parameter’s posterior mean was below 0.02 we considered there to be no biologically meaningful
effect regardless of the distribution of the posterior chain (Jennings et al. 2016).
Results

A repeated measures GLM compared the four antler measurements based on side (left/right) and year. Coronet circumference was significantly larger for the right antler (Mean ± SE: Right = 188.55 ± 2.1; Left = 186.47 ± 1.95); none of the other measurements showed a significant main effect of side (see Table 1). Two of the four measurements showed that as the males aged there was a significant increase in antler size (Beam circumference: Mean ± SE = 105.72 ± 1.9; 111.22 ± 1.7; Coronet circumference: Mean ± SE = 184.18 ± 2.3; 190.84 ± 1.8 for years 1 and 2 respectively). There was no interaction between antler side and year.

A comparison of the level of symmetry displayed by the antler measurements showed that there was no difference across years (Table 2); therefore, antlers retained similar levels of symmetry despite showing a significant increase in size over casting seasons.

Lateralisation and antler structure

**The size of the right antler.** In general, the posterior distributions of the parameters were weakly correlated (largest r = -.42 between beam circumference and coronet circumference). An examination of the distribution of the posterior chains for the four measurements indicated that greater than 5% of posterior chain crossed zero in three parameters (Brow tine length = 64.7 %, Beam circumference = 24.3 %, Coronet circumference = 24.9 %); however, the measurement for beam length indicated a meaningful negative association with lateralisation (97.3 % of the chain...
crossed zero, see Figure 2). There was no meaningful association between age (34.3 %) and dominance rank (65.2 %).

**The larger of the two antlers.** Examination of the correlation between the posterior chains indicated that they were weak (largest $r = -0.47$ between beam circumference and coronet circumference). An inspection of the posterior chains revealed that only beam length was meaningfully associated with antler length (95.5 % of the posterior chain crossed zero, see Figure 3); the remaining parameters did not show a meaningful relationship with laterisation (Brow tine length = 16.2 %; Beam circumference = 21.3 %; Coronet circumference = 48.1 %). Moreover, there was no association between age (40 %) or dominance rank (53.1 %) and laterisation.

**Antler symmetry.** The relationship between the posterior chains of the covariates was in general weak (largest $r = -0.32$ between coronet circumference and dominance rank). Investigation of the association between the parameters revealed that three of the four antler parameters posterior distributions crossed zero by more than five percent (Brow tine length = 22.2 %; beam circumference = 70 %; Coronet circumference = 75.1 %). However, the measurement for beam length indicated that there was a meaningful negative association between asymmetry and laterisation (99.03 % of the posterior distribution was negative, see Figure 4). The regressors for individual age (36.76 %) and dominance rank (46.8 %) were not meaningful.
Composite measures of size and symmetry

We ran an initial model containing the compound scores for the three covariates for the right antler, the largest antler and symmetry; however, an examination of the posterior chains revealed a very strong correlation between the compound scores for the right antler and the largest antler ($r = -0.80$) suggesting redundancy in these two parameters. Therefore, we removed the covariate for antler size from the model because the association between antler beam length and lateralisation showed the weakest association, and re-ran the analysis (Figure 5). The reduced model showed that the posterior chains of the remaining four model covariates were weakly correlated (largest $r = -0.34$) between the right antler and age); moreover, there was a meaningful association between antler symmetry and lateralisation – 98.8% of the posterior chain crossed zero indicating a strong negative effect (see Figure 5). The covariate for the right antler displayed a weaker association with lateralisation: 90.8% of the posterior chain crossed zero. The covariates for both age (12.3%) and dominance rank (60%) were not meaningfully associated with lateralisation.

1 A second composite model addressing the role of the larger antler (omitting the composite covariate for the right antler) and antler symmetry in relation to lateralisation revealed a similar pattern of findings. Therefore, we have omitted reporting this model in further detail.
Discussion

The present study investigated two hypotheses concerning the relationship between behavioural lateralisation and antler size and symmetry. The first hypothesis stated that antlers function as badges of quality (Berglund et al. 1996); therefore, a lateralised bias at the individual level during lateral display might represent a preference for the use of the larger structure in display and during combat (Alvarez 1995; Jennings & Gammell 2013). Secondly, we tested the hypothesis that individual variation in lateralisation during lateral display and antler fluctuating asymmetry are measures of developmental instability (Yeo et al. 1997).

A general issue in the study of animal aggression is the attempt to gain an understanding of the interaction between weapons borne by individuals, and the fitness benefits that accrue from their use in intraspecific contests (e.g. Clutton-Brock 1982; Parker 1983). In this respect, individuals that possess larger weapons often tend to be more successful in competitive encounters (e.g. Sneddon et al. 1997; Hoem et al. 2007; Rudin & Briffa 2011; Umbers et al. 2012). Moreover, the experimental removal of these structures leads to a rapid decline in fighting ability and dominance rank (Lincoln 1972; Clutton-Brock et al. 1982). We show that antler size increased with age for three of the four measurements taken, and that a single measurement indicated that the right antler was larger than the left. Critically, there was no interaction between antler size and year suggesting that growth was uniform. There is some evidence for lateralised use of antlers during contests; for example, there is a directional bias and that the larger structure is favoured during combat (Alvarez 1995; Pélabon & Joly 2000; Jennings & Gammell 2013). In theoretical terms, it has been shown that populations showing left or right lateralisation can be stable (e.g. Ghirlanda et al. 2009). Therefore, we examined the possibility that there may be an association between antler size and behavioural lateralisation during lateral display. Our results were consistent: there was a negative association between antler beam length irrespective of whether we investigated the right or larger structure,
and lateralisation. Therefore, as beam length increased there was a decrease in lateralised behaviour during parallel walks.

We also tested the hypothesis that behavioural lateralisation and fluctuating asymmetry are correlated forms of developmental instability. Antler symmetry is considered to be a genetic or environmental representation of an individual’s ability to withstand stress, and may thus be a reliable indicator of individual quality (Leary & Allendorf, 1989; Møller & Pomiankowski, 1993; Clarke, 1993). In this latter respect the evidence is mixed, some studies have found a relationship between asymmetry and measures of individual quality whilst others have not (e.g. Malyon & Healy, 1994; Putman et al., 2000; Mateos et al., 2007 but see Pelabon & Joly, 2000; Kruuk et al., 2003). We show that FA did not differ between years suggesting environmental conditions and individual quality - assuming they are related to symmetry - were relatively uniform during antler growth. We make no claim here as to whether genetic or environmental influences are responsible for the individual expression of lateralisation or FA in this population; however, our results show that asymmetry in beam length was negatively associated with behavioural lateralisation. Thus, as individual males showed an increasing bias towards lateralisation during lateral display, their antlers also showed greater symmetry.

Taken together, our analysis of different measurements failed to distinguish between the three measures of antler size and symmetry for beam length. Therefore, using individual measures of antler structure to distinguish between the two alternative hypotheses was not successful. In an attempt to disentangle the issue, we collapsed the four individual antler measurements into a single regressor (see Yeo et al. 1997); consequently, the right antler, the larger antler and asymmetry measurements were entered into a single model. But although we found it necessary to selectively remove antler size due to concerns over redundancy in the model, our results were unambiguous: there was sufficient evidence to conclude that antler symmetry is associated with behavioural lateralisation. Thus, we find some support for the DI hypothesis forwarded by Yeo et al. (1997).
However, an alternative explanation of our findings is possible. Lateralised eye-use during lateral display is expected to be beneficial during escalated contests (e.g. Arnott et al. 2011); there is an association between individual lateralisation during lateral display and suffering an attack following intervention of an ongoing fight (Jennings et al. 2014). This highlights a more general issue in the ecology of deer; specifically, that individuals that show lateralised eye-use may also avoid being attacked – a not insignificant ability for prey species (see also Lippolis et al. 2002). This is in general agreement with studies on other species where It has been shown lateralised individuals are better at detecting danger whilst engaged in other tasks (e.g. feeding) than non-lateralised individuals (e.g. Rogers et al. 2004; Dadda & Bisazza 2006). Therefore, deer that show behavioural lateralisation may also suffer less stress; consequently, they also show a reduction in the level of FA expressed (e.g. Clarke 1993; Moller & Swaddle 1997; Putman & Sullivan 2000). We note, however, that in order to test this hypothesis, an experimental approach, beyond the scope of the observational field approach taken here, is needed.

In conclusion, we have investigated the relationship between behavioural lateralisation during fallow deer parallel walks and antler size and symmetry. A body of evidence supports the idea that antler size is an important correlate of success in ungulate contests (Jennings & Gammell 2013), and critically, that use of the more developed right antler is preferred during fights (Alvarez 1995). However, we failed to show that lateralisation during lateral display was positively associated with either the size of the right antler or the size (right or left) of the larger antler when antler symmetry was included in the model. Nevertheless, we have shown that FA is negatively associated with behavioural lateralisation. But although the evidence tends to support the general argument that lateralisation is a form of developmental instability, we suggest that there are other plausible explanations for this finding, and will need to be appropriately tested.
References


# List of tables

## Table 1. A comparison of four different measurements between pairs of antlers over two field seasons.

<table>
<thead>
<tr>
<th>Measurement (mm)</th>
<th>df</th>
<th>Side</th>
<th>Year</th>
<th>Side * Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brow tine length</td>
<td>1,19</td>
<td>F = 0.00, p = .99</td>
<td>F = 2.48, p = .1</td>
<td>F = 0.01, p = .98</td>
</tr>
<tr>
<td>Beam length</td>
<td>1,16</td>
<td>F = 0.33, p = .6</td>
<td>F = 3.20, p = .09</td>
<td>F = 1.27, p = .3</td>
</tr>
<tr>
<td>Beam circumference</td>
<td>1,15</td>
<td>F = 1.24, p = .3</td>
<td><strong>F = 31.16, p &lt; .001</strong></td>
<td>F = 0.02, p = .9</td>
</tr>
<tr>
<td>Coronet circumference</td>
<td>1,18</td>
<td>F = 7.69, p = .01</td>
<td><strong>F = 37.52, p &lt; .001</strong></td>
<td>F = 0.23, p = .6</td>
</tr>
</tbody>
</table>

## Table 2. A comparison of antler symmetry across two field seasons.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Mean difference ± SE</th>
<th>df</th>
<th>t, p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brow tine length</td>
<td>-0.009 ± 0.02</td>
<td>19</td>
<td>t = -0.60, p = .6</td>
</tr>
<tr>
<td>Beam length</td>
<td>-0.007 ± 0.01</td>
<td>16</td>
<td>t = -0.63, p = .5</td>
</tr>
<tr>
<td>Beam circumference</td>
<td>0.011 ± 0.03</td>
<td>15</td>
<td>t = 1.53, p = .2</td>
</tr>
<tr>
<td>Coronet circumference</td>
<td>0.005 ± 0.02</td>
<td>18</td>
<td>t = 1.24, p = .2</td>
</tr>
</tbody>
</table>
List of Figures

Figure 1. Diagram of an antler with four measurements marked (BL = beam length; BC = beam circumference; BTL = brow tine length; CC = coronet circumference: the circumference of the outermost edge of the coronet).

Figure 2. Summary of the parameter posterior distributions indicating the relationship between lateralisation and the regressors (four measurements of antler size for the right antler, age and dominance rank). For each parameter, the mean is denoted by the black square and the 95% credible intervals by the thin line.

Figure 3. Summary of the parameter posterior distributions indicating the relationship between lateralisation and the regressors (four measurements of antler size for the larger antler, age and dominance rank). For each parameter, the mean is denoted by the black square and the 95% credible intervals by the thin line.

Figure 4. Summary of the parameter posterior distributions indicating the relationship between lateralisation and the regressors (four measurements of antler size for antler symmetry, age and dominance rank). For each parameter, the mean is denoted by the black square and the 95% credible intervals by the thin line.

Figure 5. Summary of the parameter posterior distributions indicating the relationship between lateralisation and the regressors (for composite measures of asymmetry and right antler size, age and dominance rank). For each parameter, the mean is denoted by the black square and the 95% credible intervals by the thin line.
Figure 2

- Effect size
  - Intercept
  - Brow tine length
  - Beam length
  - Beam circumference
  - Coronet circumference
  - Age
  - Dominance rank
  - Individual identity
  - Identity * age
  - Identity * rank

Effect size

-1 -0.5 0 0.5 1 1.5
Figure 3

- Intercept
- Brow tine length
- Beam length
- Beam circumference
- Coronet circumference
- Age
- Dominance rank
- Individual identity
- Identity * age
- Identity * rank

Effect size
Figure 4

Effect size
Intercept
Brow tine length
Beam length
Beam circumference
Coronet circumference
Age
Dominance rank
Individual identity
Identity * age
Identity * rank

-1 -0.5 0 0.5 1 1.5
Effect size
Figure 5

-1 -0.5 0 0.5 1
Effect size

Intercept
Asymmetry
Right antler
Age
Dominance rank
Individual identity
Identity * age
Identity * rank