



# Do Reindeer Have Front-Limb Biases?

– Forelimb Preferences in *Rangifer tarandus tarandus*

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Degree project/Independent project • (15 hp)  
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Bachelor in Biology  
Uppsala 2020





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**Credits:** 15 hp

**Level:** First cycle, G2E

**Course title:** Independent Project in Biology

**Course code:** EX0894

**Programme/education:** Bachelor in Biology

**Course coordinating dept:** The Department of Soil and Environment

**Place of publication:** Uppsala

**Year of publication:** 2020

**Cover picture:** Heidi Rautiainen

**Keywords:** Reindeer, *Rangifer tarandus*, footedness, handedness, laterality, ambidextrous, behaviour

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## Abstract

Laterality refers to the dominance of the brain's left or right hemisphere over particular functions, such as certain behaviours. One common example is handedness in humans, where right- or left hand preference tends to be regulated by the dominance of one side of the brain.

The purpose of this study is to examine if reindeer (*Rangifer tarandus tarandus*) have front-limb preferences and evaluate if a correlation between lateralization and agonistic behaviour can be found. To do so, twenty reindeer were observed through video analysis when interacting and digging in the snow to reach food, to determine if the reindeer preferred to use one front leg more than the other.

The results from the study suggest that some reindeer do have front-limb preferences, but not in a way that showed statistical significance over the entire population. A positive correlation between stronger laterality and agonistic behaviour was also observed, but further studies are needed to verify these results.

Modern handling and transportation of reindeer during migration between pastures is often necessary due to human infrastructure, but can cause stress-related symptoms in the reindeer. Developments in the understanding of lateralization in animals, along with new ways of measuring lateralization, could potentially be used to improve animal handling. For example, by understanding how a certain reindeer is likely to react to sudden changes or which side it prefers in social interactions, we might be able to reduce induced stress and improve animal welfare.

*Keywords:* Reindeer, *Rangifer tarandus*, footedness, handedness, left/right dominance, laterality, ambidextrous, behaviour

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# 1. Introduction

## 1.1. Lateralization and its Correlation to Behaviour

Laterality is defined as difference in functional specialization between the left and right side of the nervous system (Frasnelli & Vallortigara 2018). In other words, laterality is when either one of the brain's hemispheres specializes in some functional behaviours (The Editors of Encyclopaedia Britannica 2006). The left hemisphere is often optimized to process routine behaviours, such as foraging behaviour, while the right is often specialized to evaluate novel stimuli (MacNeilage *et al.* 2009). One distinct example of specialized functionality is handedness, where a person prefers to use either her right or left hand (Laterality 2006). This example shows that lateralization can be expressed through asymmetrical behaviour, such as asymmetrical use of limbs to perform motor activities (behavioural laterality), but laterality can also be expressed asymmetrical use of sensory pair organs (sensory laterality) (Frasnelli & Vallortigara 2018). Measuring laterality in species, especially wild living species can be difficult, but in a diversity of species, the strength of laterality can be suggested by observing asymmetrical (lateralized) behaviours (Rogers 2002). Many recent studies have shown asymmetrical biases in behaviour for different species and that preferential use of the left or the right side of the body is a widespread phenomenon among different species of animals (MacNeilage *et al.* 2009; Wells & Millsopp 2009; Siniscalchi *et al.* 2017; Frasnelli & Vallortigara 2018).

Lateralization as a phenomenon could be almost as old as the bilaterally structured brain itself (Rogers 1989), but still, the lateralization process is not completely understood. Genetics and ontogenetic processes are important parts to describe laterality, but laterality can also vary with age, experience, and situation (Rogers 1989; Rogers & Andrew 2002). For this reason, the ability to make structural changes of the brain during life is believed to be related to lateralization (Vallortigara *et al.* 2011). This ability of the brain is called neural plasticity (Cech & Martin 2011), and can also allow more flexible behaviour, for example, the adaption to changing environments (Vallortigara *et al.* 2011). Such an adaptive

ability is commonly called behavioural plasticity. Since laterality and behavioural plasticity are both related to neural plasticity, lateralized behaviour can be used to indicate and predict different expressions of behaviour (Found & St. Clair 2017).

Laterality can be associated with qualities such as reactivity and temperament, but also hormone and immune responses (Rogers & Andrew 2002). Hence, fitness benefits can arise from both strong and weak laterality (Vallortigara *et al.* 2011). Laterality can give at least two types of advantages, either on the individual level or the populational level (Rogers & Andrew 2002). For the individual, lateralization can give advantages in the form of faster reaction times and enhanced skills compared to other less lateralized individuals. For example, strong laterality has been correlated with quick responses to stimuli such as predators if one eye is specialized for this task (Vallortigara *et al.* 2011). Individuals with strong laterality do also have an improved ability to multitask (Vallortigara & Bisazza 2002). Populational laterality can give a social advantage when most of a group is lateralized in the same direction (Rogers & Andrew 2002) and the presence (or absence) of laterality has been shown to alter the stability of social hierarchies (Rogers 1989). Behaviours involving interaction among others of the same species, such as agonistic interactions and courting, may have advantages for species-specific direction lateralization (Vallortigara & Bisazza 2002). There are also disadvantages with lateralization; a less lateralized individual may for example have a faster response time to a predator, compared to more lateralized individuals that are approached from their non-dominant side (*ibid.*). A predator could also learn that its prey tends to turn and try to escape in a certain direction, due to behavioural lateralization. Altogether, lateralization may give an advantage due to the specialization it provides, while lack of lateralization instead gives a greater flexibility and possibility to adapt.

As a result, some individual variation in the degree of laterality can be maintained (Vallortigara *et al.* 2011). Such variations can therefore be used to provide insight into differences in expressions of behavioural plasticity (Found & St. Clair 2017). For example, Found and St. Clair (2017) recorded front-limb biases in wild elk (*Cervus canadensis*) and found that lateralized elks were three times more likely to migrate, while less lateralized elk were more likely to remain near humans year around. In the study, weak laterality was also correlated to bolder personalities. Less lateralized elk responded more to aversive conditioning but were also quicker to reduce their flight response (*ibid.*). This is one indication of what was mentioned above, that less lateralized individuals have more flexible behaviours and therefore are faster to adapt to new situations, something that can be an evolutionary advantage in a changing environment.

Laterality can also be a significant factor to consider when improving animal handling. For example, if the animals have a preferred side for social interaction, this could also be an indication of a preferred side of handling (Farmer *et al.* 2018). Furthermore, Found and St. Clair (2017) suggested that lateralization could play an important role in describing animal responses to human-caused changes. The study of lateralized behaviour, and its connection to other behaviours, could therefore possibly be used in conservation biology as well as in the improvement of handling and understanding of animals (Found & St. Clair 2017). For these reasons, in this study, front-limb preferences in Eurasian tundra reindeer (*Rangifer tarandus tarandus*) were investigated.

Limb preferences can essentially be divided into three categories: 1. Absence of asymmetry, where all the members of a population lack a preference and instead prefer to use both their left and right limbs with equal probability (Ströckens *et al.* 2013). 2. Individual-level asymmetry, where some member of a population prefers to use their left limb and some prefer to use their right, but there is not a general bias for the entire population and 3. population-level asymmetry, where most of the entire population prefer to use either their right or their left limb (*ibid.*). Multiple studies in vertebrates have been performed through the years, and Ströcken *et al.* (2013) analysed 119 studies on different species' limb preferences and found that 51% of the studies showed evidence for population-level asymmetries, 17% for individual level asymmetries and 32% showed no evidence for asymmetry. In the same study they also noted that there is a larger number of individuals without a preference in most non-human vertebrates compared to humans, where 90% were right-handed (Corballis 2009; Ströckens *et al.* 2013).

Reindeer (*Rangifer tarandus*) is an inhabitant of both boreal and arctic parts of the northern hemisphere. Reindeer have physiological and behavioural adaptations to survive in habitats where snow is covering the vegetation during the colder parts of the year (Thing 1977). During winter, the reindeer can utilize lichens under the snow cover as an energy source (Storeheier *et al.* 2002), which the reindeer uncover by digging with their front hooves in the snow (Nationalencyklopedin 2020). While some studies have been performed (Thing 1977; Espmark & Kinderås 2002), little is still known about the lateralization of reindeer. As stated earlier, future knowledge on laterality might be applicable in reindeer husbandry, to improve the reindeer's handling and wellbeing.

## 1.2. Reindeer Husbandry

The Eurasian tundra reindeer is a domesticated species living in herds (Skarin & Åhman 2014). They belong to the ungulate family deer (*Cervidae*)

(Nationalencyklopedin 2020). The reindeer make annual movements to different grazing areas during the winter and summer that can cover more than 400 km (ibid.). Reindeer husbandry is an old tradition, but reindeer have breeding-wise not had such a big development as other livestock, due to the limited ability of controlled breeding (ibid.).

In recent times, the reindeer's big yearly movements are often disturbed (Tryland 2012). Obstructions caused by human activity affects the reindeer's choice of path during seasonal migration (Skarin & Åhman 2014). The need for animal transport in reindeer herding is increasing because of fragmented pasture areas, disturbed migration routes, longer distances to slaughter facilities, increased heard sizes and new pastures (ibid.). The transport efficiency is also increasing with the use of motorized vehicles (ibid.).

Today, parts of the transfer are often done using help from snowmobiles, car-transport and helicopters (Nationalencyklopedin 2020). The handling of reindeer, gathering, corralling and long-distance transport, can be stressful for the reindeer (Tryland 2012). Stress increases the release of certain hormones, which also have an immunosuppressive effect (ibid.). The handling of the reindeer can therefore make the reindeer more susceptible to diseases and, in the long run, lead to financial losses for the reindeer herder (ibid.).

## 2. Purpose of Study

The purpose of this study was to examine reindeer's (*Rangifer tarandus tarandus*) front-limb biases, to determine if they are lateralized, and whether these front-limb biases seem to be related with expression of agonistic behaviour. To investigate this, the study will attempt to answer the following questions:

1. Do individual reindeer tend to use one forelimb significantly more than the other when digging craters in the snow to gain access to food?
2. Can a difference in agonistic behaviour be noted and correlated to front-limb preferences in the reindeer?

Initially, a wider range of behaviours were examined, but the material and time available made it necessary to restrict the study to only evaluate the agonistic behaviour. Only the obtained results relating to agonistic behaviour will therefore be presented, but a short analysis on how to improve the study with an examination of more general behaviours can be found in the discussion section.

### 3. Method

The project consisted of a behavioural study performed through video analysis of reindeer in two different enclosures during February and March 2020. The reindeer studied were marked with numbers painted in red on their sides to make it possible to keep track of them individually. The reindeer were between 8 and 9 months old when the video recordings took place. The video material used was part of the material from a project called Reinfed (Skarin 2020). A total of 20 reindeer were observed.

#### 3.1. Study Area 1 – Porjus

Study area 1 was located in Porjus (Y: 709182 X: 7435997.9) and the group consisted of 10 reindeer from the Sirges reindeer herding district.

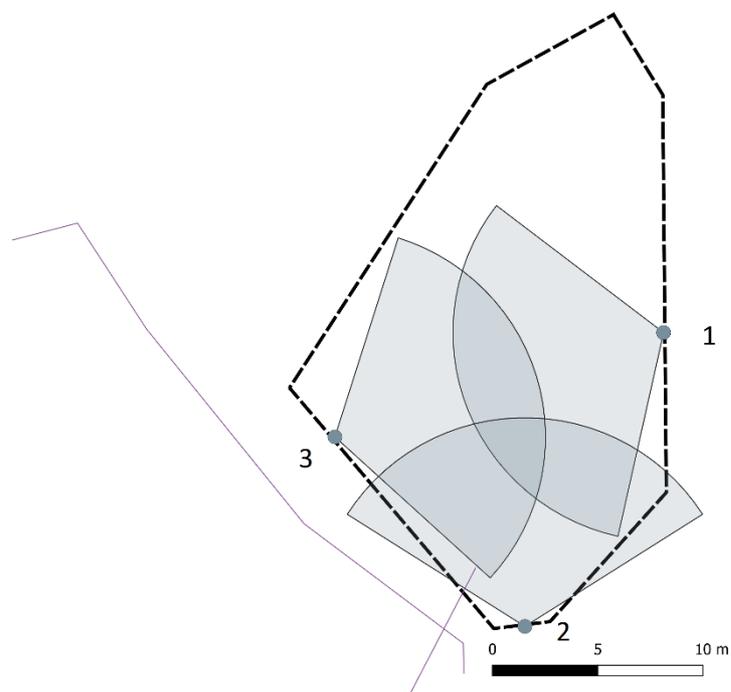


Figure 1. Illustration of enclosure in study area 1 and the placement of camera 1 to 3 in Porjus.

In the enclosure, cavities were dug in the snow and filled with reindeer lichen (*Cladonia rangifera*) and pellets. Smaller trees with pail-footed horsehair lichen (*Bryoria fuscescens*) were chopped down and put up standing in the enclosure to resemble natural lichen grazing. The enclosure also had some full-grown spruce and pines, but neither had reachable branches for the reindeer. Replenishment of resources was done during the forenoon. The enclosure had three cameras recording from different angles. The cameras recorded 12 hours a day from around 6:00 in the morning to 18:00 in the evening.

### 3.2. Study Area 2 – Voulda

Study area 2 was located in Voulda (Y: 629218.95 X: 7344848.98). The study group consisted of 10 reindeer from the Ståkke reindeer herding district.

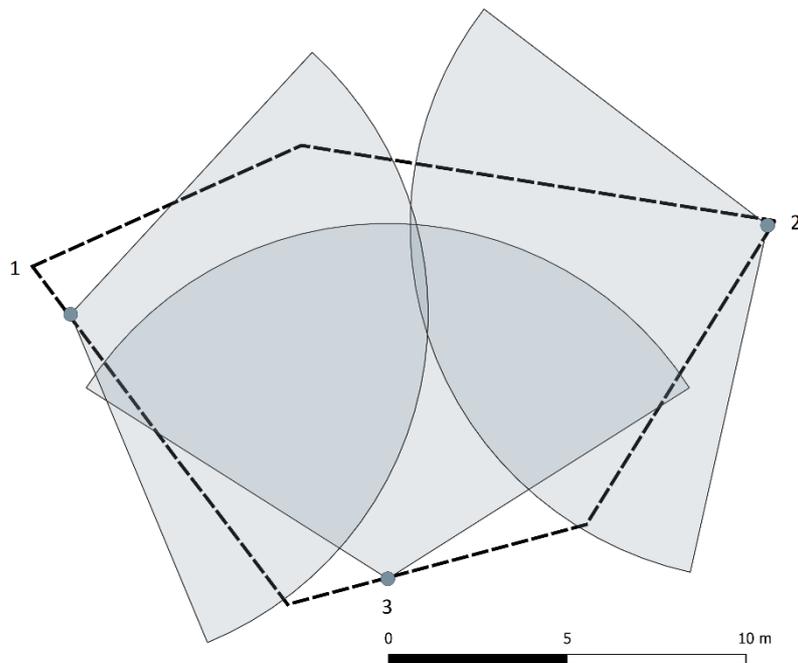


Figure 2. Illustration of enclosure in study area 2 and the placement of camera 1 to 3 in Voulda.

Pellets were always available in a feed trough in the enclosure. Cavities were dug in the snow and filled with reindeer lichen (*Cladonia rangifera*) and pellets. In Voulda, there were no small trees with pail-footed horsehair lichen (*Bryoria fuscescens*) and instead twigs and branches were placed in the enclosure and manlay were draped over them. Replenishment of resources was done during the forenoon.

The enclosure had three cameras recording from different angles. The cameras were active around 12 hours a day from 6:00 in the morning to 18:00 in the evening.

### 3.3. Behavioural Observations

The video analysis was performed using the event-logging software Boris (Friard & Gamba 2016). In Boris, a project-based ethogram was defined, see Table 1.

*Table 1. Ethogram constructed with behaviours described in terms of their structure. The division of some behaviours into the subcategory “Specific Behaviour”, was done mainly for grouping behaviour and simplicity when using Boris.*

<b>Movement</b>		Moving forward by alternating moving legs from one point to another.
	<i>Walking</i>	<i>Moving around in a slow pace while alternating moving the legs from one point to another.</i>
	<i>Trotting</i>	<i>Moving around with legs in diagonal pairs, with a pace somewhere between walking and running.</i>
	<i>Running</i>	<i>Moving fast in a two-beat stride were all four legs are off the ground at once.</i>
<b>Shaking</b>		Moving body quickly in sideways patterns while the legs are standing still.
<b>Cafing</b>		Rubbing antlers or head up and down against tree more than twice.
<b>Laying</b>		Laying on ground with legs either folded or extended.
	<i>Down</i>	<i>Laying on the ground with legs folded under the body.</i>
	<i>Side</i>	<i>Laying on the ground with legs extended on the side of the body.</i>
<b>Digging</b>		Using a front hoof to scratch in the snow or ground repetitively while standing.
	<i>Left hoof</i>	<i>Digging with the left front hoof two times or more.</i>
	<i>Right hoof</i>	<i>Digging with the right front hoof two times or more.</i>
<b>Foraging</b>		Searching for or consuming food while standing still or moving around slowly.

	<i>Grazing</i>	<i>Lowering the head towards the ground while standing, sniffing or eating from ground.</i>
	<i>Browsing</i>	<i>Sniffing or eating from trees or bushes.</i>
<b>Standing</b>		Standing up on all four legs without moving in any direction, with head in any position.
<b>Getting up</b>		Using hind- and front legs to get up into a standing position from laying.
<b>Stretching</b>		Standing while stretching out either hind- or front legs in an outstretched position bending the back.
<b>Agonistic behaviour</b>		Charging or pushing away an individual or being charged or pushed away by another individual.
	<i>Charging</i>	<i>Running towards other reindeer with head down getting closer than one and a half meter.</i>
	<i>Butting</i>	<i>Pushing on other reindeer using head or antlers.</i>
	<i>Provoked</i>	<i>Subject for the charging/butting</i>
<b>Scratching</b>		Rubbing head towards own hind leg.
<b>Missing Data</b>		Focal animal either not possible to identify or not present
<b>Other</b>		Other behaviour than already stated.

### 3.4. Recording Methods

The following recording methods were used in the study:

#### 3.4.1. Behavioural Sampling

Behaviour sampling involves observations of the whole group and each occurrence of a particular behaviour gets noted as well as the individuals involved in the behaviour (Martin 2011).

#### 3.4.2. Scan Sampling

During scan sampling, a whole group of individuals are scanned at regular intervals and their behaviour is noted (ibid.). Scan sampling is good for behaviours with longer duration, but there is chance that shorter behaviour are missed (ibid.).

### 3.4.3. Continuous Sampling

During continuous recording, every occurrence of a behaviour is recorded (ibid.) Continuous recording is used to give an exact and faithful record of the behaviour measured and at the times the behaviour pattern stopped and started (ibid.).

### 3.4.4. Time Sampling – Instantaneous Sampling

According to Martin (2011), in time sampling, the behavioural sampling is collected periodically instead of continuously (ibid.). Using this method, less information is preserved, but it is also a good way to densify information (ibid.). In instantaneous sampling, an observation is divided into short sample intervals. At every sample point a recording is then made of what behaviour that occurred at that point in time. Instantaneous recordings do not give true durations and it can be difficult to distinguish between shorter and longer occurring behaviour (Martin 2011), for example walking and standing.

## 3.5. Implementation

All behavioural data were based on one hour of video material from each study area. All of the 10 reindeers in each both enclosures were observed. For both areas, a time window at the fourth day of the Reinefeed project (of 5 and 6 days in total) was chosen for analysis in this study. This choice was made so that the reindeer would have had time to acclimatize to (i.e., get used to) the enclosure. In addition, a daytime hour was required since the reindeer had to be active and the number marking of the reindeer had to be clearly visible. To minimize confounding factors on reindeer behaviour caused by human presence, time was also chosen when no humans were present in the enclosure during or in association with the chosen time interval.

Reindeer in study area 1 (Porjus) were observed from 7:00 am to 8:00 am. This choice was made because the reindeer got a refill of fresh trees around 9:00 am that day, and therefore were less prone to show digging behaviour after that time, when easier obtainable food was available. Reindeer in study area 2 (Voulda) were observed between 9:17 am and 10:17 am. This was right after humans had been in the enclosure to replenish the reindeer lichen hid under the snow. In addition, the reindeer had easily available pellets in a feed trough, and were therefore not very prone to digging before the refill of the lichen.

Digging behaviour was measured, using continuous recording with point measuring. Every time a digging behaviour (with two or more consecutive strokes) took place, the occurrence of behaviour, which limb was used, and starting time

was noted using Boris. Reindeer can only use one hoof at a time when digging craters in the snow to access snow-covered food (Found and St. Clair 2017), so there were no ambiguous digging events. Next, more general behaviour were measured during the same hour, now by using instantaneous sampling. Every five minutes, the behaviour of the reindeer was recorded as point events for every individual. Noted was also if the behaviour involved any other individual. Apart from the instantaneous sampling, continuous recording with point measuring was also used to measure agonistic behaviour during the same hour as the other measurements, to get a better understanding of the reindeer's relations.

### 3.6. Statistical Analysis

Matlab R2019B and Excel 2016 were used for the statistical analyses. The digging behaviour was modelled by the assumption that the number of digs with the right front-limb,  $r_i$ , performed by reindeer  $i$ , can be treated as a binomially distributed random variable with unknown  $p$ -parameter  $p_i$  and  $n$ -parameter ( $n_i$ ) equal to the total amount of digs. The  $p_i$ -parameter is treated as individual for each reindeer and can be interpreted as a representation of the reindeer's front-limb preference.

$$r_i = \text{Bin}(p_i, n_i) \quad (1)$$

From  $p_i$  the laterality  $L_i$  is defined as  $L_i = |2p_i - 1|$ .

The agonistic behaviour was modelled by the assumption that the total number of times agonistic behaviour was performed by an individual during the observed hour,  $a_i$ , can be described by a poisson distributed random variable, with unknown  $\lambda$ -parameter  $\lambda_i$  and also allowed to vary individually for each reindeer.

$$a_i = \text{Po}(\lambda_i) \quad (2)$$

To estimate the unknown parameter  $p_i$ , the estimator  $\hat{p}_i$  was constructed by:

$$\hat{p}_i = \frac{r_i}{n_i} \quad (3)$$

This equation could then be used to estimate  $L_i$  using  $\hat{L}_i$ :

$$\hat{L}_i = |2\hat{p}_i - 1| \quad (4)$$

This value for laterality ( $\hat{L}_i$ ) is equivalently described by the equation:

$$\left| \frac{r_i - (n_i - r_i)}{n_i} \right| \quad (5)$$

where complete ambidexterity corresponds to the value zero and more lateralized reindeer favouring their left or right hoof get a more positive value.

Next, confidence intervals for  $p_i$  and  $\lambda_i$  were determined. A confidence interval is an estimation of the uncertainty associated with estimates of population parameters obtained using sampling data (DePoy & Gitlin 2019). To compute a confidence interval for the  $p_i$ -parameter, a Wilson score interval was used (Wallis 2013). This could then be used to determine a confidence interval for the laterality  $L_i$  by finding the corresponding values given by equation 4.  $\lambda_i$  could be naturally estimated by  $\hat{\lambda}_i = a_i$ . To compute a confidence interval for  $\lambda_i$ , the chi-square method was used (Sahai & Khurshid 1993).

In an attempt to find a relation between laterality and agonistic behaviour, linear regressions were used to examine if a correlation between laterality and behaviour could be found (Reis & Saraiva 2004). This was done with different subsets of the reindeer, by introducing a threshold value  $N$  determining the least amount of digs a reindeer had to have performed in order for the obtained laterality estimate  $\hat{L}_i$  to be considered meaningful. Different values for  $N$  were tested.

To further investigate the presence of laterality, a null hypothesis that “*all reindeer are completely ambidextrous*” was tested. Ambidextrous in this context refers to the assumption that the reindeer completely lack front-limb preference and hence that each dig has equal probability for use of either front-limb. This corresponds to  $L_i = 0$  and  $p_i = 0.5$  for all  $i$ . A P-value for this hypothesis was then computed for each reindeer, as well as for the two study groups as a whole using Fisher’s combined probability test (Fisher’s method 2019). Similarly in this context, the combined P-values for subsets of reindeer determined by the threshold  $N$  were examined.

## 4. Results

Both some reindeer from Voulda and some reindeer from Porjus exhibited front-limb biases, but the direction and magnitude varied. In total 109 digs were registered for 10 of the reindeer from Voulda, and 146 digs for the 10 reindeer from Porjus. Table 2 and Table 3 shows the amounts of digs per hoof,  $\hat{p}_i$ ,  $\hat{L}_i$  and P-values for Voulda and Porjus. Small P-values ( $< 0.05$ ) indicates that the null hypothesis might be discarded, while big P-values can be obtained either from a small amount of digs or because the reindeer is ambidextrous. Reindeer 1 from Voulda was discarded in further analysis due to lack of digs.

*Table 2. Digging events with left and right hoof of 10 individuals at Study Area 2 (Voulda) observed between 9:17 am and 10:17 am. Results showing number of digging events with left hoof, right hoof, right hoof frequency ( $\hat{p}$ ), laterality ( $\hat{L}$ ) and P-values. P-values are relative to the ambidexterity null hypothesis and P-value  $< 0.05$  indicate significant individual lateralization. Reindeer 1 was discarded from analysis due to lack of digs.*

Subjects	Left hoof	Right hoof	$\hat{p}_i$	$\hat{L}_i$	P-value
<b>1 Voulda</b>	0	0	-	-	1.0000
<b>2 Voulda</b>	11	2	15%	0.69	0.0225
<b>3 Voulda</b>	8	22	73%	0.47	0.0161
<b>4 Voulda</b>	0	4	100%	1.00	0.1250
<b>5 Voulda</b>	13	11	46%	0.08	0.8388
<b>6 Voulda</b>	2	0	0%	1.00	0.5000
<b>7 Voulda</b>	1	1	50%	0.00	1.0000
<b>8 Voulda</b>	4	3	43%	0.14	1.0000
<b>9 Voulda</b>	1	2	67%	0.33	1.0000
<b>10 Voulda</b>	12	12	50%	0.00	1.0000

Table 3. Digging events with left and right hoof of 10 individuals at Study Area 1 (Porjus) observed between 7:00 am to 8:00 am. Results showing number of digging events with left hoof, right hoof, right hoof frequency ( $\hat{p}_i$ ), laterality ( $\hat{L}_i$ ) and P-values. P-values are relative to the ambidexterity null hypothesis and P-value <0.05 indicate significant individual lateralization.

Subjects	Left hoof	Right hoof	$\hat{p}_i$	$\hat{L}_i$	P-value
1 Porjus	14	12	46%	0.25	0.8450
2 Porjus	1	0	0%	1.00	1.0000
3 Porjus	3	5	63%	0.40	0.7266
4 Porjus	5	3	38%	0.16	0.7266
5 Porjus	3	7	70%	0.25	0.3438
6 Porjus	4	3	43%	0.25	1.0000
7 Porjus	7	8	53%	0.08	1.0000
8 Porjus	18	30	63%	1.00	0.1114
9 Porjus	0	4	100%	0.14	0.1250
10 Porjus	11	8	42%	0.07	0.6476

Within the reindeer from Voulda 25 agonistic behaviours occurred during the time of observation and 21 agonistic behaviour were performed by the reindeer from Porjus. In Table 4 and Table 5, the agonistic behaviour butting and charging were combined for the reindeer performing the behaviour.

Table 4. Agonistic behaviour at Study Area 1. – Porjus. Showing both the initiator and subject of the agonistic behaviour, with a summary of the total amount of preformed agonistic behaviour per reindeer.

		Initiator of Agonistic behaviour									
Subject of Agonistic Behaviour		1	2	3	4	5	6	7	8	9	10
	Subject: Porjus										
	1		0	0	0	0	0	0	1	0	2
	2	0		0	0	0	0	0	4	1	1
	3	0	0		0	0	0	0	0	0	0
	4	0	0	1		0	0	0	0	0	0
	5	1	1	0	0		0	0	2	0	1
	6	0	0	1	0	0		0	0	0	0
	7	0	0	0	0	0	1		0	0	0
	8	0	0	0	0	0	0	0		0	0
	9	0	0	0	0	0	0	0	0		0
	10	0	0	1	0	0	1	0	0	0	
	Unknown	0	0	0	1	0	0	0	1	0	0
Sum Agonistic Behaviour		1	1	3	1	0	2	0	8	1	4

Table 5. Agonistic Behaviour at Study Area 2. – Voulda. Showing both the initiator and subject of the agonistic behaviour, with a summary of the total amount of preformed agonistic behaviour per reindeer.

		Initiator of Agonistic Behaviour									
Subject: Voulda		1	2	3	4	5	6	7	8	9	10
Subject of Agonistic Behaviour	1		1	1	0	0	0	1	0	1	0
	2	0		2	0	0	0	0	0	0	0
	3	0	0		0	0	0	0	0	1	1
	4	0	0	0		0	0	0	0	0	0
	5	0	0	1	0		0	0	0	0	0
	6	0	0	0	0	1		0	0	0	0
	7	0	2	0	0	0	0		0	0	1
	8	0	2	3	0	0	0	0		0	1
	9	0	2	2	0	0	0	0	0		0
	10	0	0	2	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	0	0	0	0
Sum Agonistic Behaviour		0	7	11	0	1	0	1	0	2	3

When plotting and comparing the reindeer's laterality  $L$  and amount of performed agonistic behaviour  $a$  in Figure 3, no obvious difference can be seen between the result from Voulda and Porjus. The plot also displays the big statistical uncertainties that are present, according to the chosen models.

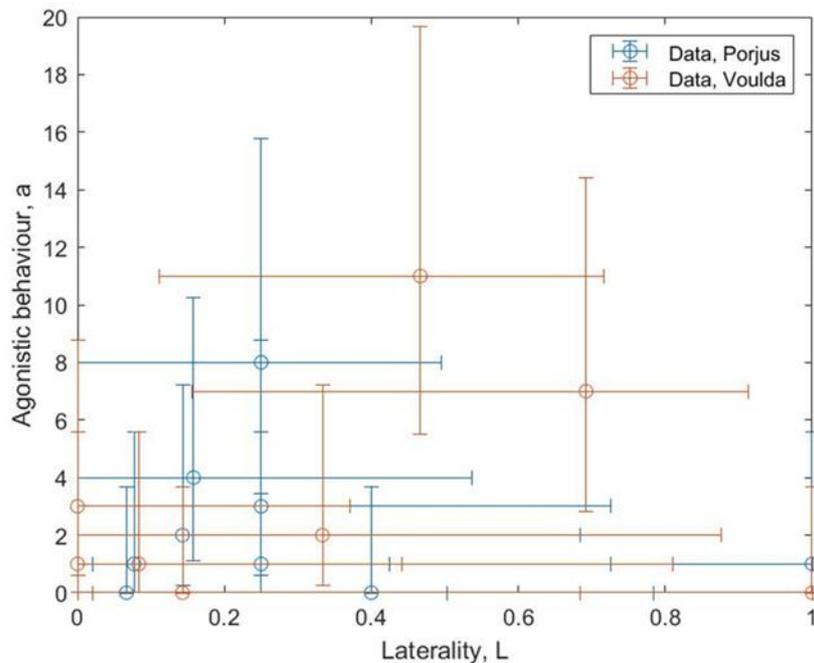


Figure 3. Plot showing laterality,  $L$  and amount of agonistic behaviour,  $a$ , in reindeer. Measurements and uncertainties per reindeer are shown in blue for reindeer's from Porjus and red for reindeer from Voulda.

A very weak negative correlation ( $R = -0.048$ ,  $k = -0.4$ ) can be seen between lateralization and agonistic behaviour when taking all of the reindeer into account, see Figure 4 and Table 6. Although, this correlation is so weak that it might as well be considered non-existent, due to the uncertainty in the data that can be seen in Figure 3. These uncertainties partly arise from the uncertainty in laterality that is due to the few number of digs performed by some of the reindeer. When increasing the threshold for number of digs to a minimum of 6 digs during observation ( $N = 6$ ), a stronger positive correlation can instead be observed between lateralization and agonistic behaviour ( $R = 0.58$ ,  $k = 10.0$ ), see Figure 4 and Table 6, and this apparent correlation is maintained when raising the threshold further ( $N = 8$  and  $10$ ). Although a correlation coefficient value above 0.5 is generally considered indicating at least moderate correlation between the variables, it is hard to determine exactly how the process of N-filtering has affected the validity of this result. On the one hand, the observed lateralization of reindeer with the least number of digs could likely be considered highly random, and reducing the influence of this noise should make the obtained results more trustworthy. On the other hand, a further study with an increased amount of data would have been preferred, to avoid reducing the sample size to just 9-13 reindeer ( $N = 6-10$ ) as well as eliminating the possible bias that originates from the selection of the most active reindeer.

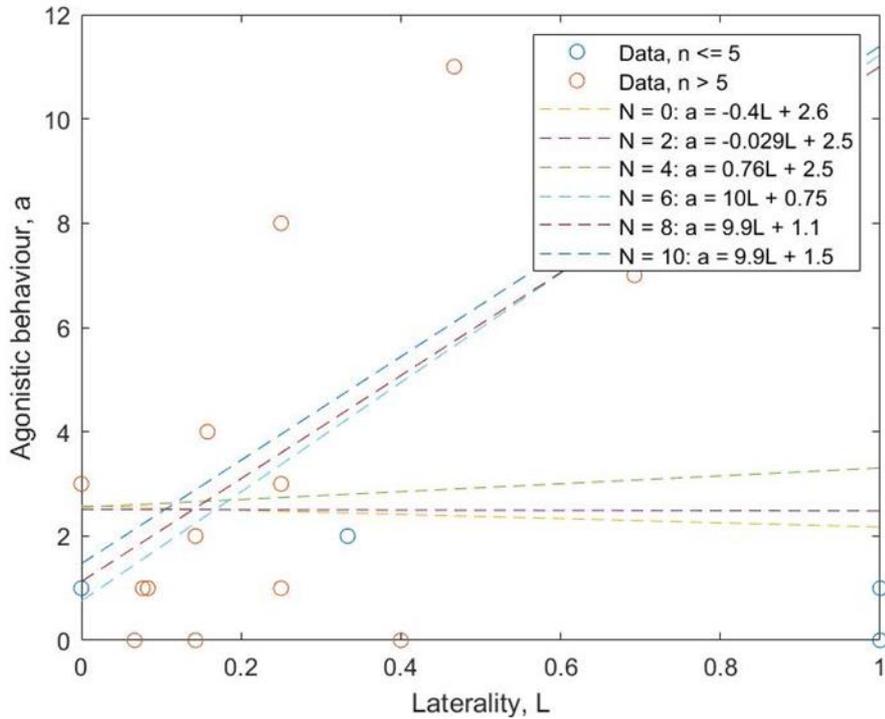


Figure 4. Linear regressions showing correlations between laterality  $L$ , and agonistic behaviour  $a$ , in reindeer. Measurements per reindeer are shown as circles where blue circles represent reindeer that did five or fewer digs while red circles represent those that performed six or more. The different lines show different linear regressions obtained when changing the threshold for digs required,  $N$ . The sign of the slope indicates a positive or negative- correlation between laterality and agonistic behaviour.

There is a big decrease in P-values for bigger  $N$  resulting from the higher level of accuracy achieved by excluding the reindeer with few digs, see Table 6. This indicates that the significantly larger P-values achieved when taking the entire population into account strongly depends on the uncertainties associated with sparsely digging reindeer, and should not be seen as a sign of ambidexterity.

Table 6. Table showing the threshold for number of digs  $N$ , the number of reindeer meeting the requirement of at least  $N$  amount of digs, combined Fisher P-value, slope ( $K$ ), and Pearson's correlation coefficient ( $R$ ).

$N$	Number of reindeer	P-value <sub>(combined)</sub>	$k$	$R$
0	19	0.61	-0.4	-0.048
2	18	0.52	-0.029	-0.003
4	15	0.3	0.76	0.073
6	13	0.51	10	0.58
8	11	0.29	9.9	0.56
10	9	0.16	9.9	0.58

## 5. Discussion

In this study, the possibility that reindeer could have front-limb biases was investigated. The main results of this study were, first, that some reindeer showed significant signs of laterality, although it could not be interpreted on a populational level. The two reindeer with significant laterality were both from Voulda (see Table 2), where one preferred the right front limb and the other one the left. Second, that a positive correlation between lateralization and agonistic behaviour was observed, but only when the reindeer with least number of digs were disregarded due to the large uncertainties involved.

When studying the reindeer's front-limb preferences for digging craters in the snow, multiple reindeer showed signs of laterality. These results are in accordance with the two previous studies that have examined if reindeer have front-limb biases, which both found indications of lateralization. One study was performed by Thing (1977), and the other by Espmark and Kinderås (2002), but their studies found populational biases of opposite directions. Espmark and Kinderås (2002) reported a significant leftward bias, where 72% (21 out of the 29 monitored reindeer) preferred their left front-leg and only 28% preferred their right front-leg. Thing (1977) on the other hand reported a rightward bias where 56%, (15 of 27 of the caribou (wild reindeer) preferred using their right hoof. However, this study examined lateralization mainly on an individual level, and the results from this study and theirs are therefore not completely comparable. For future studies both populational and individual lateralization would be of interest since the mentioned studies indicates that lateralization can vary between groups.

Comparing the positive correlation between laterality and agonistic behaviour found in this study, with the negative correlation found by St. Clair (2017) observed between laterality and bold behaviour, it must be kept in mind that their definition of "bold" consisted of five different attributes. In their study, "socially and physically dominant" was one of the five attributes for "bold", but other attributes like "shorter flight response distances" and "greater explorations of novel objects" were weighted in as well (ibid.). In this study agonistic behaviour was defined as the reindeer either charging towards the other reindeer with head or antlers or butting at the other reindeer (see Table). The results may therefore not be completely contradicting, and it would be interesting to study more of the reindeer's

general behaviour in correlation to laterality. As an example, Farmer *et al.* (2018) found a significant bias towards the left for affiliative interactions in horses, but also that these closely corresponded to leftward biases in agonistic behaviour. Future studies of agonistic behaviour and affiliative interactions in reindeer may therefore give an idea of whether reindeer have a preferred side of handling.

In this study only two reindeer showed statistically significant lateralization (see Table 2). However, because of the other 17 reindeer without statistically significant signs of lateralization, the presence of front-limb biases in the population in general could not be proven significantly. This can be explained either by uncertainty in the data or very weak laterality. The fact that the combined P-value was drastically reduced when only the reindeer with the most digs were considered (for example,  $N = 10$  yielded a combined P-value of 0.16) seems to indicate that asymmetries are indeed present, and that the inability to show this with statistical significance is mostly due to a lack of data.

For future studies, one way of obtaining more data for common behaviours would be to use focal sampling. Focal sampling is when all behaviours for every individual is being recorded during a determined time period (Martin 2011). This would have given a better general overview of the reindeer's common behaviour and their relations within the group. For example, analyzing affiliative behaviours could be a good way of determining if there is a general preferred side for social interactions.

In this study, scan sampling and instantaneous sampling were used to analyse the reindeer's common behaviour, chosen partly because it was possible to implement due to its time efficiency. The scan sampling, unfortunately, turned out to be too biased towards longer occurring events such as the reindeer's foraging or laying down, which occurred for longer timespans than shorter point events. Hence, instead of increasing the number of sampling points, data collection on agonistic behaviour was performed by continuous recordings. Another improvement for future studies would be to observe the reindeer during a longer timeframe to get larger amounts of data. By studying agonistic behaviour during multiple shorter periods, the uncertainties in agonistic behaviour as well as laterality would be smaller. In order to create a model that better reflects reality, noting how long each digging behaviour occurred would perhaps be of interest, since in this study only the occurrence of the behaviour were noted and the reindeer might have preferred to use one side during longer durations of digging behaviour.

Another aspect that would be interesting to examine is whether the reindeer's low age could have affected the results, since laterality sometimes can depend on age (Rogers & Andrew 2002). Examining if there is a difference in laterality between

different ages, but also sex, could therefore be of interest to better understand lateralization in reindeer.

From the results of the study, it can be concluded that there are reasons to believe that some reindeer tend to use one forelimb significantly more than the other. However, more data is needed to completely rule out that reindeer are ambidextrous and draw any further conclusions. Since a connection between laterality and other behaviours is also suggested in the data gathered, such further studies could highlight important features to consider in the further improvement of reindeer handling.

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## Acknowledgements

I want to give a special thanks my supervisor Heidi Rautiainen who taught me a lot about behavioural studies and really inspired me for what I want to do in the future. I also want to thank my assistant supervisor Anna Skarin for input on my written project along the way. Lastly I want to thank my partner, for supporting me and listening while I only talked about reindeer for the past few months.