DIRECTIONAL ASYMMETRY IN MOOSE

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ABSTRACT: The structural asymmetry of 1,772 European moose (*Alces alces alces*) and of 5 Shiras moose (*Alces alces shirasi*) skulls was studied by checking the deviation of rostral bones from the midline of the skull roof. A significant directional asymmetry was found. The lingual cusp height of corresponding teeth on the left and right cheek tooth rows differed significantly in the skulls with different rostral orientation. The antlers of the 689 best Finnish trophies on record and antlers of all of the bulls ($n = 239$) shot in the Kuhmo Game Management Unit of Finland during the 1995 hunting season (ages 1.5-14.5 years) were tested for left/right differences. No significant differences were found. The fluctuating asymmetry of left/right-differences decreased from young to old age classes in antler base circumference, palm/beam length, and tine number. Tine length and circumference did not show significant changes. Obstacle avoidance and feeding laterality was studied along 433.27 km of moose tracks in winter by counting all the trees and bushes on the right and left side of the tracks within reach of the animal. A selection of forest road lane was studied with 769 observed sections of moose tracks in summer. Functional right side preference was observed in both cases.

ALCES VOL. 36: 147-154 (2000)

Key words: antlers, directional laterality, functional laterality, moose, skull

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Since Louis Pasteur presented his opinion on the asymmetry of the universe to the French Academy of Sciences in 1886, many examples of asymmetry in nature have been published. Not only molecules studied by Pasteur (1886) but seemingly everything in nature is structurally asymmetric. Despite their many mirror-symmetrical structures, living organisms also show left/right differences in most of their organs. Morphological asymmetry may be antisymmetrical, directional, or fluctuating (Van Valen 1962). It is often connected with functional asymmetry. In many cases the causal relationships between the asymmetric structure of an organ complex and its asymmetric functions are not apparent. Structural asymmetries may or may not be correlated with each other (Glassman and Bass 1986, Brown and Wolpert 1990). In vertebrates, directional asymmetry expressed as differences in bilateral structural characters or behavior seems to be quite consistent, suggesting genetic control (Annett 1985). It is also assumed to be the result of a laterally biased brain development due to naturally occurring axon loss, learning, or brain injury (Witelson and Nowakowski 1991). The evolutionary background of laterality is in most cases unknown.

The relationship between fluctuating asymmetry and genetic variability has been studied in several species and populations (Van Valen 1962, Smith *et al.* 1982, Vrijenhoek and Lerman 1982, Leary *et al.* 1985, Palmer and Strobeck 1986). The distribution of left/right- differences in a population has been used as a measure of developmental stability. This was criticized by Novak *et al.* (1993) because the long intrauterine period of some homeotherms would decrease the impact of environmental conditions. Asymmetry has been studied in humans (Salive *et al.* 1993), primates (Schultz 1926, 1937; Annett and Annett 1991), and horses (Deuel and Lawrence

1986). In cheek tooth rows, horses often show sharp edges on buccal or lingual margins due to uneven wear. This is thought to be caused by unilateral mastication movements (S. Paatsama, Veterinary College, Helsinki, Finland, *pers. comm.*). If moose, and other ruminants, preferentially masticate in a clockwise or counter-clockwise direction, the direction of jaw rotation may be reflected by asymmetry in skull bone structure. In this paper, I present some observations on asymmetry in skull bones and laterality in feeding behavior and obstacle avoidance of moose.

METHODS

Moose skull asymmetry was studied by aligning a string through the nasion and akrochranial notch. The orientation of rostral parts of incisival bone to the right or to the left of this line was determined in 1,772 dry skulls (1,581 males, 191 females, 1-24 years-of-age) of *Alces alces alces,* studied in Finland, Sweden, Norway, Republics of Karelia and Komi in the Russian Federation, Estonia, Lithuania, Latvia, Byelorussia, and Poland. Five adult skulls of *A. a. shirasi* were incidentally measured to check whether or not the observed rostral orientation is also seen in American moose. Five Finnish moose fetuses, aged 4 - 8 months were studied radiologically for skull bone laterality. The lingual cusp heights were measured on both cheek tooth rows in 84 Finnish adult moose skulls previously checked for rostral orientation. The precise site of measurement varied among individuals due to the different wear of the teeth, but the height of corresponding teeth of the same skull were always measured from the corresponding points of the lingual crest to the surface of the palate. For each skull, a height index was calculated, where the sum of heights of the right tooth row was divided by the sum of heights of the left tooth row. The height indices of right and left-oriented skulls were compared with an unpaired *t*-test. To compare the left and right halves of mature bull antlers, measurements of the 689 best Finnish medal-class trophies according to CIC rules were used (Trense 1980). All trophies were measured and recorded by or under the supervision of the author. The dimensions of right and left antler halves were compared with a paired *t*-test.

All 239 bulls shot during the 1995 hunting season in the East Finnish game management unit Kuhmo (64°N 30°E; 4,823 km^2) were measured by the same rules. The ages, determined by counting the *cementum annuli* from I_1, varied from 1.5 - 14.5 years (mean±SD = 4.0±2.0 yrs). Antler asymmetry was studied by dividing the right/left difference by the mean of the same measurements of antler base circumference, antler (palm/beam) length, tine circumference, tine length, and number of tines. After log transformation the correlation of age and antler measurements was determined. Due to a heavy local harvest pressure designed to lower the moose population density more than 30%, and because local hunters are traditionally oriented to a meat harvest, the harvest was considered to be a representative sample of moose bulls of Kuhmo.

During the winters of 1991-1996, 433.2 km of individual moose tracks were followed and measured with the aid of a distance (thread) measuring device (Uittokaluste oy, Finland) in 4 areas in central Finland. All trees and bushes were recorded in a strip 1 meter from the midline on both sides of the track. The encountered plants were checked for bite marks and recorded accordingly as "browsed" or "unbrowsed." The total plants encountered and used on both sides of the track were compared by a sign test. The median of the observed left/right comparison was used as a sample median. The hypothesized population median used was 1.000, representing no side preference in obstacle avoidance or feeding.

I also checked 769 observations on moose walking at least 20 meters along a forest road during the summer months in Eastern Finland for right or left lane preference. The presence of browse or obstacles on both sides of the road was recorded in each case. The selection of lane was checked against 95% confidence limits of the material in both alternatives of browse or obstacle presence. For statistical calculations, Systat 7 software (SPSS Inc., Chicago, IL) was used. Results were considered significant when $P = 0.05$.

RESULTS

Skulls. — In the European female and male moose skulls, 1,548 (87%) were right-handed and 211 (12%) were left-handed. In 13 (1%) of the cases I was not able to determine laterality. The 95% approximate confidence limits for the right-deviated skulls were 85 - 89% and 10 - 14% for the left-inclined ones. All 5 bull skulls studied in the USA were directed to the right. In the majority of samples, asymmetry was obvious on the rostral parts of incisival bones and in the nasal and frontal areas of the skull. The results obtained from the cleaned and dried skulls were verified radiologically in 11 fresh skulls. All 5 fetus skulls showed rostral orientation to the right.

Tooth wear. — The mean tooth height index of the right-oriented skulls ($n = 59$) was 1.020 ± 0.042 (mean ± SD) indicating higher lingual cusp edges on the right cheek tooth row. In the left- oriented skulls ($n = 25$), the mean height index was 0.982 ± 0.029 (mean ± SD) indicating greater height on the lingual edge of the left tooth row. The mean height indices differed significantly ($t = 4.08$, 82 df, $P < 0.001$) in the left-oriented and right-oriented skulls.

Antlers. — Of the 689 best trophies measured in Finland, 511 were palmated and 178 were non-palmated. These types differed very significantly ($P < 0.001$) in beam circumference, palm lengths, and tine numbers but not in greatest spread ($P > 0.400$). The dimensions of right and left antler halves of both types were very similar with standard deviations typically under 10% of the sample mean (Table 1). In the total 1995 bull harvest of Kuhmo, no significant right/left differences were found in beam circumferences, length of palm, tine

Table 1. Antler measurements (cm) of 689 best Finnish moose trophies measured according to CIC moose antler evaluation rules (Trense 1980).

Measurement	Palmated type ($n = 511$) Mean ± SD	Palmated type ($n = 511$) Range	Non-palmated type ($n = 178$) Mean ± SD	Non-palmated type ($n = 178$) Range
Overall spread	114.8 ± 10.4	75.3-149.0	111.9 ± 11.5	82.5-139.0
Beam circumference				
Right	19.1 ± 1.8	14.4-26.6	19.4 ± 2.1	15.3-28.0
Left	19.2 ± 1.9	14.8-30.4	19.5 ± 2.2	15.3-28.0
Length of palm/beam				
Right	101.5 ± 8.5	77.8-125.4	103.9 ± 9.2	77.7-123.8
Left	101.0 ± 8.7	75.7-125.7	103.5 ± 9.6	77.5-125.3
Number of tines				
Right	9.0 ± 1.5	5-13	6.1 ± 1.1	3-9
Left	9.0 ± 1.6	6-14	6.2 ± 1.1	3-10

length, tine circumference, or the number of tines of left or right antlers (Table 2). The mean differences in antler base circumference, antler length, and tine numbers decreased with increasing age. Mean tine circumference and mean tine length did not decrease with age (Table 3).

Feeding and obstacle avoidance. — During the tracking study in the snow period, 129,536 trees and bushes of 9 genera (*Alnus*, *Betula*, *Salix*, *Picea*, *Pinus*, *Populus*, *Juniperus*, *Sorbus*, and *Rhamnus*) were encountered. The directional response of moose was calculated for 4 of the 19 species, sallow (*Salix caprea*), European aspen (*Populus tremula)*, rowan *(Sorbus aucuparia)*, and common juniper *(Juniperus communis)*. In the majority of cases, moose tended to pass the left side of an encountered stem that could have been passed on either side. In the sign test, the sample median was 1.017, with 160 values above, 126 values below and 8 equal to the hypothesized median ($Z = 0.05$, $P = 0.05$). While feeding, the animals chose items more from the right than from the left side of their tracks. Here, the sample median was 1.029. Of all values, 163 were above, 121 below, and 10 equal to the hypothesized median ($Z = 2.433$, $P = 0.015$). Scots pine (*Pinus silvestris*) and rare contorta pine *(Pinus contorta)* stems were passed on either side ($P = 0.634$) and eaten accordingly ($P = 0.471$). Birch (*Betula verrugosa*, *B. pubescens*) stems were passed on the left ($P = 0.001$) but used from either the right or the left ($P = 0.062$).

Pine and birch represented 77% of all stems counted. Judged from stem utilization rates, pine was eighth and birch was sixth on the preference list. Third on the abundance and second on the preference list were bush-like willows (*Salix cinerea*, *S. lapponum*, *S. myrsinifolia*, *S. myrtilloides*, *S. pentandra*, *S. phylicifolia*, and *S. starkeana*), representing 7% of the stems. Moose did not have a directional response to these willow species ($P \leq 0.51$

Table 2. Antler measurements (cm) of all moose harvested in Kuhmo, Finland, 1995 ($n = 239$). In case of only 1 tine in an antler half, the length = 1. Otherwise, CIC trophy evaluating instructions (Trense 1980) were followed.

Measurement	Mean ± SD	Min	Max
Beam circumference			
Right	12.27±2.90	6.4	19.6
Left	12.20±2.92	5.6	20.4
Length of palm/beam			
Right	47.87±32.4	1	122.0
Left	48.06±31.5	1	115.0
Tine circumference			
Right	8.39±1.38	4.7	11.8
Left	8.29±1.44	4.4	11.8
Tine length			
Right	20.76±6.34	4.6	38.1
Left	20.51±6.38	4.9	44.2
Number of tines			
Right	2.89±1.72	1	9
Left	2.85±1.62	1	8

Table 3: Age-dependent changes of Kuhmo 1995 moose antlers (n = 239), right versus left.

Age vs log mean diff. of;	Pearson correlation	Significant coefficients
Base circumference	-0.287	Yes
Palm/beam length	-0.335	Yes
Tine number	-0.603	Yes
Tine circumference	-0.075	No
Tine length	-0.004	No

for avoidance and 0.452 for usage). *Salix caprea*, the only tree-like willow, was at the top of the preference list. It was passed by on the right ($P \leq 0.01$) and used from the left ($P \leq 0.01$). Rowan (*Sorbus aucuparia*), third in preference and often showing signs of successive feeding, was kept on the left side ($P = 0.013$) and browsed more from the left ($P = 0.003$). European aspen (*Populus tremula*), fourth on the preference list, was kept on the left side ($P = 0.005$), and used by turning the head to the left ($P = 0.003$). Common juniper (*Juniperus communis*) was also kept on the left, ($P = 0.004$), and used from the left ($P = 0.001$). Rowan, aspen, and juniper totaled 8.4% of the stems counted.

Norway spruce (*Picea abies*), grey alder (*Alnus incana*), and European alder *(Alnus glutinosa)*, seldom even tasted by moose, totaled 6.9% of the stems counted. The 3 species were passed either way but when eaten, the stem most frequently was on the left side of the moose (spruce: $P = 0.001$; alders: $P = 0.018$).

Tracks on roads. — The 769 moose tracks counted in the summer months on the forest roads were in the right lane 70% of the time. Feeding signs indicated the use of the plants on both sides of the road. The Pearson chi-square test for no dependence between lane selection and browse or obstacle availability was not significant ($P > 0.30$). When there were browse items or obstacles by the roadside, the left lane was selected in 31% and the right lane in 69% of the cases. The 95% confidence limits were 27 - 36% and 64 - 73% respectively. With no browse or obstacles present, the left lane was chosen in 27% and the right lane in 73% of the cases. The confidence limits for the left lane were 21 - 34% and 66 - 79% for the right.

DISCUSSION

Rostral asymmetry to the right is present in European and possibly also in North American moose skulls. Orientation to the right occurred in females and males alike and in all age classes, including intrauteral stages. Tooth wear is correlated with rostral orientation. As in most of the mammals, active breakdown of food occurs unilaterally in the moose mouth cavity, aided by the reasonably close fit of the molar rows (Hiiemae and Crompton 1985). Moose tend to grasp a mouthful of browse by a sidewise movement showing individual left- or right-side preference (K. Nygren, *pers. obs.*). Laterality is also seen in mastication movements: each individual moves its lower jaw either in a clockwise or counter- clockwise direction while chewing. In horses, the fixed jaw movement patterns often result in uneven wear of cheek teeth rows (Deuel and Lawrence 1986). The leading edge wears more than the trailing edge. Nevertheless, the results of the crown height measurement show that the same mechanism affects moose tooth wear. The dominant counter- clockwise lower jaw movement causes a greater wear on the lingual crest of the upper left cheek tooth row leaving the right one higher. The relatively wide mouth of the moose indicates the importance of sidewise head movement in food item grasping instead of using the rostral lips and front teeth (Hofmann and Nygrén 1992).

The mature antlers did not show significant laterality in the characteristics measured according to the CIC rules. In antlers, laterality was not expected due to the static load they cause to the skull structure (Nygrén *et al.*1992). Mirror-symmetrical antler halves of similar weight would be more balanced. The fluctuating asymmetry in antlers decreased with age, as observed by Smith *et al.* (1982) in white-tailed deer.

The deviation of rostral skull bones may be biologically significant. It may be connected with one or several behaviors of moose. While feeding, significant right-side preference was observed. In contrast, moose pass by obstacles on either side. Interesting differences are seen in browse plant species encountered and used. Birch was kept on the right and sallow on the left. Low and bush-like species such as juniper and willow are eaten either way. The 4 most preferred species were eaten significantly more from the left. During the fieldwork, tracks suggested that these species were also actively searched for. After an olfactory location of the target, the visual impression of an edible item may play a role in selecting approach and handling movements needed. The most common species, pine and birch, did not appear to be actively searched for. The least preferred species, such as alder and spruce, were eaten very significantly from the left. The observed differences between tree species may be due to different handling techniques needed in food intake.

When walking along a forest road, moose seemed to prefer the right lane. The narrow open space in the forest, such as a forest road, may affect orientation in an environment providing few optical stimuli of this kind. The right lane preference may reveal a very basic habit of obstacle avoidance, also seen with the tree stems encountered. As an animal of forested environments, the European moose may be responding to and searching for the vertical lines (tree stems) instead of the horizontal ones (open spaces, coastlines) in its "Umwelt" (Von Uexküll 1921, Bubenik 1998). Ever since Pasteur's observations, asymmetry and lateral preferences are usually regarded as a curiosity with no obvious advantage. From the morphological or ecological point of view there are no obvious reasons for a moose to move on the right or the left side of an obstacle, but there are clear reasons for consistently chewing to the left or right with respect to tooth wear.

The true biological importance of laterality may lie in an imprinted pattern of behavior, aided by directional asymmetry and activated automatically without hesitation and time-loss whenever needed. In the feeding situation, automatic approach and handling movements may save energy and result in better cost efficiency in food intake. When avoiding the attack of a predator, or on the road facing an on-coming car, an imprinted left or right movement may influence the probability of survival.

ACKNOWLEDGEMENTS

I wish to thank Professor Petter Portin for valuable comments on the script. Catherine Hestin and Toni Sarapohja helped in fieldwork and statistics. Most of all, I wish I could show my gratitude to my late friend and colleague, Professor Saki Paatsama, who initiated this study with his field observations on several species of big mammals.

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