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Footedness in foraging muskoxen *Ovibos moschatus*

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We investigated the propensity for wild muskoxen *Ovibos moschatus* (Zimmerman, 1780) to exhibit right or left bias in foreleg use while foraging during winter. We found little evidence of such lateralisation, either on the individual or population level. Only 3 of 40 animals exhibited significant right- or left-footedness, and the distribution across the population for use of either limb was near 50%. Time-series analysis revealed that lateralisation of paw use was sequentially dependent. Muskoxen tended to use the same paw for one ensuring bout, but were also inclined to switch sides over durations of 4 bouts. The lack of lateral bias, at least for this behaviour, contrasts with the general, emerging pattern for the Mammalia.

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Introduction

The study of lateralised animal structure and function is central to the understanding of evolutionary relationships. For example, asymmetry of limb preference is well-documented for humans, but the exent of homologous lateralisation amongst the Mammalia remains unclear. In a comprehensive review, Bradshaw and Rogers (1993) concluded that lateralised behavioural biases were not uncommon for vertebrates (eg, Rogers and Workman 1993, Bisazza *et al.* 1996) including mammals (eg, Hook-Costigan and Rogers 1995, Anderson *et al.* 1996). For mammals, however, they noted the fragmentary nature of the evidence, exclusive of Rodentia and Primates. For ungulates, with a few exceptions (Jarman 1972, Thing 1977, Grant *et al.* 1990, Ganskopp 1995), there is a paucity of data on lateral biases.

The burgeoning evidence on lateralisation has been amassed largely through laboratory experiments. Nevertheless, its validity rests on a critical assumption, viz, that artificial trials provide symmetrical sensory input to the animal (Davies and Green 1991). There is a particular need, therefore, for observations under

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natural conditions. For example, Thing (1977) reported that wild caribou preferentially used their right forelegs to crater through snow cover while foraging.

Here, we examined lateralisation of foreleg movements by wild muskoxen *Ovibos moschatus* (Zimmerman, 1780) in the High Arctic. Like caribou, muskoxen regularly use their forelegs to uncover subnivean forages during winter. We examined lateralisation of foreleg use at both the individual and population levels. Furthermore, by applying time-series analysis to our observations, we investigated the degree to which lateralised paw use by foraging muskoxen exhibited temporal dependence.

Methods

We observed muskoxen in the vicinity of Wellington Bay (69°25'N, 106°15'W) in the Canadian Arctic during periods of snow cover, ie November 1992 and early April to late May, 1992 and 1993. Focal animals were observed for approximately 30 min each using 30× spotting scopes, 200–1500 m away. For each animal, we noted each pawing movement with the left or right foreleg and recorded events on audio tape. The data were transcribed using ANSCAN ver. 1.4, a computerised event recorder.

Pawing acts by muskoxen, while cratering, are strongly clustering into bouts (Schaefer and Messier 1995). We used the pawing bout – with a minimum separation interval of 2.3 s between pawing acts, determined by the log-frequency procedure (Schaefer and Messier 1995) – as the unit for further analysis. Each bout was classified as left or right, regardless of the number of pawing acts that it comprised. Bouts involving the use of both legs were rare (2.0% of 1515 bouts) and were discarded. For population-level analysis, we avoided the common error (eg Davies and Green 1991) of pooling the data (Machlis *et al.* 1985) and instead used each animal as the experimental unit. In total, we observed 40 animals, each displaying at least 12 pawing bouts during the observation period.

Data were analysed for lateral bias using non-parametric methods (Siegel and Castellan 1988). To examine the temporal organisation of the behaviour, we used time-series analysis (SPSS Inc. 1993). For each animal, we estimated the autocorrelation function (ACF) from left (0) and right (1) scores, then plotted the average ACF for lags up to 5 bouts.

Results and discussion

We found little evidence of footedness, either on individual or population levels. On the level of the individual, we searched for possible lateral biases by applying a binomial test to the numbers of left and right bouts for each animal. We found that only 3 of 40 animals displayed any significant lateral bias (binomial tests, $p < 0.05$, $12 \leq n \leq 78$). Similarly, the population exhibited a symmetrical, unimodal distribution of footedness, close to being centred on 50% use of either limb (Fig. 1).

Although neither individual nor population biases were evident, we found that the temporal sequence of limb use was non-random. This pattern was not evident at the individual level, perhaps due to the low statistical power at small sample sizes. We found just 2 of 40 individual cases of temporal non-randomness (one-sample runs tests, $p < 0.05$), implying sequential independence between left and right bouts. Temporal structure of forelimb use, however, was revealed by

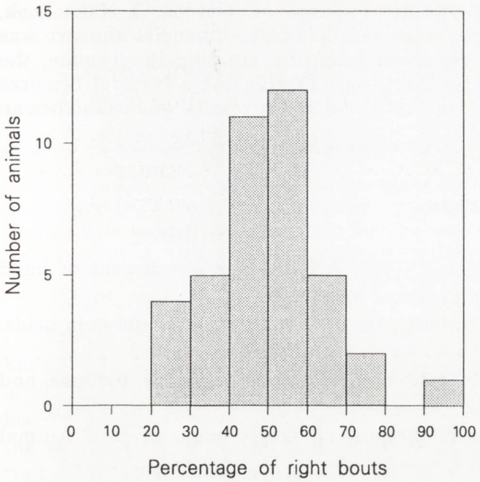

Fig. 1. Distribution of left/right paw preference by foraging muskoxen.

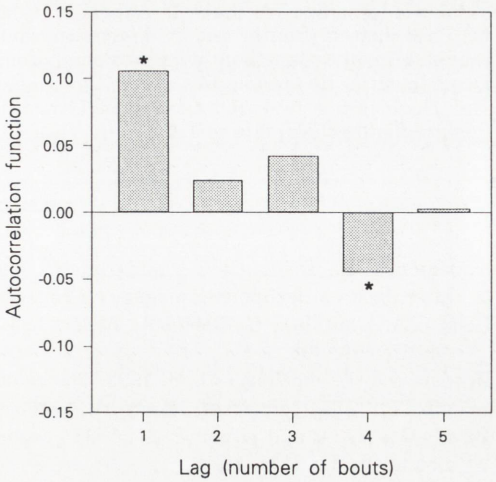

Fig. 2. Temporal autocorrelation of left/right pawing bouts by muskoxen. Values significantly different from zero ($p < 0.10$) are indicated by *.

time-series analysis. ACF was positive ($p < 0.05$) for the first ensuing bout, but decayed and became marginally negative ($0.05 \leq p \leq 0.10$) when the lag increased to 4 bouts (Fig. 2). This indicated that muskoxen generally used the same limb for one successive bout, but tended to switch between forelimbs over longer periods.

On a population level, the lack of lateral bias by muskoxen – at least with respect to this behaviour – generally contrasts with the emerging pattern for non-rodent, non-primate mammals (Walker 1980, Bradshaw and Rogers 1993). Amongst bovids, Jarman (1972) noted a right-sided tendency for injuries from aggressive encounters in impala and Grant *et al.* (1990) reported on a left-side selection in cows while lying and ruminating. Hosoi *et al.* (1995a, b) also remarked on individual lateral preferences in T- and Y-mazes for goats, sheep, and cows, but they further suggested that such biases might have been artefacts of the artificial environment. Indeed, Ganskopp (1995) documented an absence of turning bias, for both individuals and the population, in free-ranging angora goats while foraging. Nevertheless, we cannot dismiss the possibility that muskoxen may exhibit forelimb bias under varying nival conditions, for example.

Our results contrast with Things (1977) observations on caribou, who documented a slight bias (ie, 53.16% of all pawing acts) toward right-pawedness. Nonetheless, we hypothesise that, with respect to large herbivore foraging – where favourable food patches are liable to appear irrespective of side – lateral asymmetry is unlikely to be favoured. Overall, we concur with Bradshaw and Rogers (1993) that more evidence will be required before the patterns of lateral asymmetries in non-primate and non-rodent Mammalia can be widely generalised.

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