Asymmetry in antlers of barren-ground caribou, Northwest Territories, Canada

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Abstract: Pairs of antlers were obtained from 287 barren-ground caribou (*Rangifer tarandus groenlandicus*) of the Kaminuriak herd in the Northwest Territories, Canada. The morphological dominance of the brow tines by antler pair was determined: 15.7% were enlarged on the left; 14.6% on the right; 14.6% on both sides; and 55.1% on neither side. No evidence for a greater rate of occurrence of left or right dominance of the brow tine was obtained when considered by sex or age class ($P > 0.05$). Antler pairs with both brow and bez tines present varied from 84.4% for males with their 5th to 10th set of antlers; 39.3% for males with their 2nd to 4th set; 21.2% for females with their 5th to 16th set; and 6.3% for females with their 1st to 4th set. Both brow and bez tines were present proportionately more often than expected on antler pairs from males compared to females regardless of age ($P < 0.005$). Both brow and bez tines also were present proportionately more often than expected on antler pairs from males ($P < 0.005$), females ($P < 0.01$), or both sexes combined ($P < 0.01$) with their 5th or later set than compared to when they had their 4th or earlier set.

Key words: barren-ground caribou, antlers, asymmetry, Northwest Territories, Canada.

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Introduction

Pairs of antlers from cervids tend to exhibit bilateral symmetry, with the exception of those from *Rangifer*. Therefore, the consistent lack of bilateral symmetry due to pronounced asymmetry of various opposing tines especially the enlarged brow tine creates interest and speculation about the probable causes and functions of this, seemingly, variant phenomonon in rangiferine antler sets. Particular interest is shown for possible left- or right-sided dominance in asymmetry of rangiferine antler pairs because it could be linked to the more general phenomonon of basically symmetrical organisms occasionally exhibiting functional or morphological one-sided dominance (for related references see: Davis, 1973; Goss, 1980, 1983). To date, however, investigations of the expressions of left- or right-sided dominance in the asymmetry of rangiferine antler pairs have been restricted to the examination of only brow tines (e.g., Banfield, 1954; Skoog, 1968; Davis, 1973; Goss, 1980).

Antler asymmetry in caribou or reindeer (*Rangifer tarandus* spp.) involving the brow tines only has been reported on by Banfield (1954), Skoog (1968), Davis (1973, 1974), and Goss (1980, 1983). All of those researchers but Skoog (1968) concluded that enlarged left brow tines predominated over right ones in *Rangifer*. However, Goss (1980) reached his conclusion by combining his sample with samples from Murie (1935), Banfield (1954), and Davis (1973, 1974).

Motivated by the apparent discrepancies among samples used by Goss (1980), I analyzed the tine configuration of the lower main beam of 287 pairs of antlers from barren-ground caribou (*R. t. groenlandicus*) of one population - the Kaminuriak herd. The following are my findings for the brow tine only analysis and a more detailed combined brow tine and bez tine analysis of those antlers.

Materials and methods

Barren-ground caribou (n = 999) were collected from the Kaminuriak herd, Northwest Territories, Canada, from March 1966 to July 1968 (Miller, 1974b; Dauphine, 1976). The age of each caribou was determined by histological examination of the annulations in the dental cementum of the mandibular teeth (Miller, 1974a, 1974b) and the eruption and wear patterns of the mandibular teeth (Miller, 1972, 1974b).

I obtained 287 pairs of hard antlers (hereafter referred to simply as «antler pairs») from those caribou shot between April and November 1966 (n = 41 pairs), April and December 1967 (n = 181 pairs), and April and July 1968 (n = 65 pairs). The 574 antlers were photographed in lateral view so that the left and right antlers would be facing each other (brow tines directed inwardly), when the left antler is on the left and the right one is on the right (Fig. 1). I placed antler pairs in antler «year» classes: the 1st year class being the set of antlers grown and carried in the 1st year of life; the 2nd year class, those in the 2nd year; *et cetera* to the 16th year. I have followed the classification used by Pocock (1933) for the first two tines of the main beam: (1) first tine equals «brow tine»; and second tine equals «bez tine». Bubenik (1975b:53-55) has, however, argued that the second tine in rangiferine antlers is homologous with the trez tine in *Cervus*.

Brow tine analysis

A branched or palmated brow tine was designated by an upper case letter: (L) left-sided dominance; (R) right-sided dominance; and (LR) both-sided («double» of Goss, 1980) dominance, regardless of relative size differences (Fig. 1). When the brow tine was a simple single-pointed tine («reduced» of Goss, 1980) it was designated by a lower case letter: (l) left; (r) right; and (lr) no dominance on either side, relative size was not considered (Fig. 1). The same procedure applied when one or both of the brow tines were absent (lr). If a single-pointed brow tine had a flattened cross-section it was still considered simple, if it lacked pronounced terminal bottons and the maximum width of the

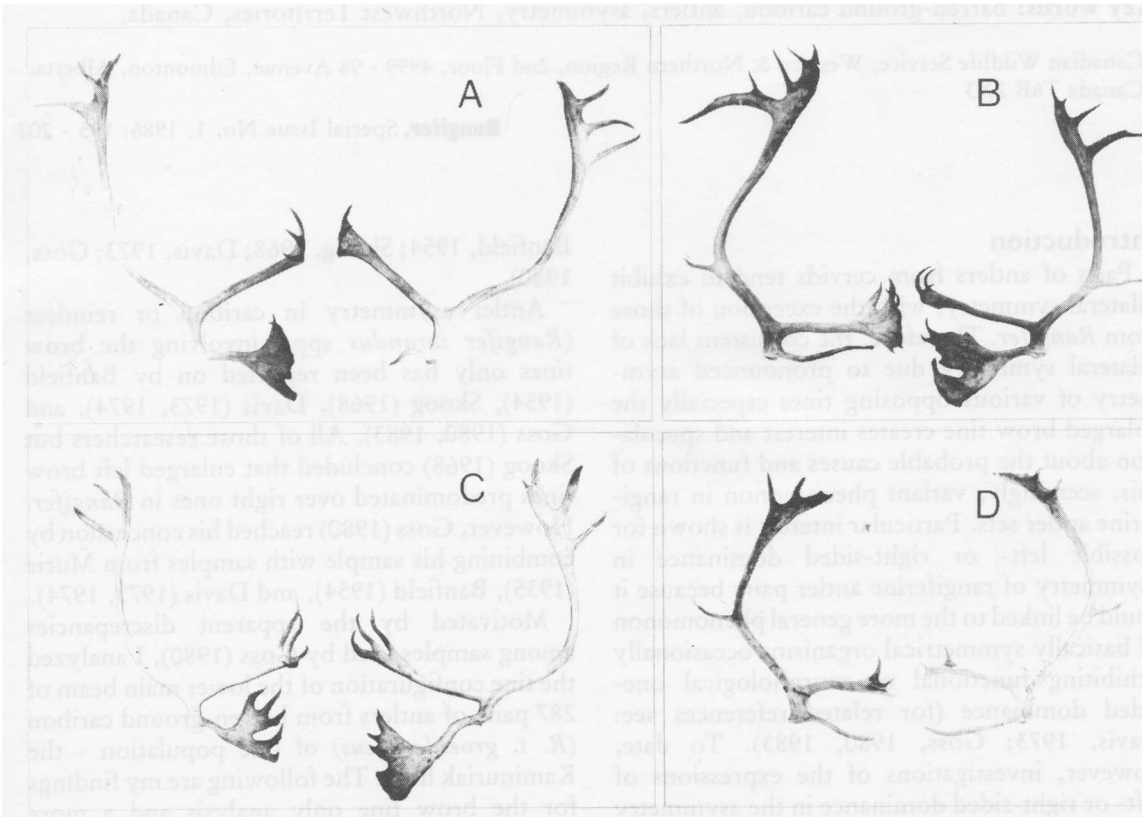

Fig. 1. Illustration of the four types of dominance expressed in the brow tines of rangiferine antler pairs: (A), left sided, (B) right-sided, (C) both sides, and (D) neither side.

flattened surfaces was less than twice the maximum width of the compressed surfaces.

Initially, I recognized a tine as a brow tine from its form, position or origin on the main beam, and generally its orientation to the main beam. However, the form of the tine and its orientation on or to the main beam («descending» of Banfield, 1954) did not appear to be consistent diagnostic characteristics of the brow tine, especially in antlers from females (regardless of age) and from young males. Therefore, when only one tine was present on an antler, it was classed as a brow tine when it originated at the burr on the main beam or within its diameter distance. That is, if a tine was 3 cm in diameter at its origin on the main beam and it originated within 3 cm of the burr, it was classed as a brow tine. If that tine originated beyond 3 cm up that main beam from the burr, it was classed as a bez tine.

Antlers and antler pairs were further classified as: (1) antler pairs with both brow and bez tines present; (2) single antlers with both the brow and the bez tines present; (3) single antlers with the brow tine missing; (4) single antlers with the bez tine missing; (5) antler pairs with no brow or bez tines present; and (6) antler pairs with no tines, just a main beam present, the simplest form being «spikes».

Brow and bez tine analysis

I decided to make a more detailed analysis of the expression of dominance or the complexity of pattern of caribou antler pairs by considering both the brow and the bez tines of each antler in each pair. The analysis was essentially the same as that for only the brow tine but instead of four possible combinations, when only the brow tine was used, there were now 16 possible combinations (L, R. l and r).

Statistical analyses

In all cases the Pearson Chi-square or goodness-of-fit tests were used (with «Yate's correction» where applicable) to statistically evaluate the assumption that each possible expression of dominance (left-sided, right-sided, both sides, or neither side) of the brow tine or the brow and bez tines together had an equal opportunity to occur in the sample of antler pairs. Therefore, all expected proportions tested with the goodness-of-fit test were equal percentages in all cells. The working hypothesis based on Goss' (1980) results was that, «left-sided dominance of the brow tine of caribou antler pairs in the northern hemisphere predominates over right-sided, both sides, or neither side expressions of dominance in the brow tine». The probability $P < 0.05$ was the level of acceptance for significant relationships.

Results

Brow tine only

Brow tines (or their absence) on the 574 antlers of the 287 antler pairs from barren-ground caribou of the Kaminuriak herd exhibited

Table 1. Frequency of occurrence of brow tines or brow and bez tines together (brow/bez) as expressions of dominance in antler pairs from barren-ground caribou, Northwest Territories, 1966-68.

Antler year class[a] by sex	Antlers N	% dominance[b]							
		Left-sided		Right-sided		Both sides		Neither side	
Male									
2nd-4th	61	19.7	(24.5)	18.0	(18.0)	29.5	(37.7)	32.8	(19.8)
5th-10th	45	35.6	(40.0)	37.8	(26.7)	22.2	(33.3)	4.4	
2nd-10th	106	26.4	(31.1)	26.4	(21.7)	26.4	(35.9)	20.8	(11.3)
Female									
1st-4th	63	3.2	(9.5)	3.2	(8.0)	3.2	(11.1)	90.4	(71.4)
5th-16th	118	12.7	(18.6)	10.2	(12.7)	10.2	(28.0)	66.9	(40.7)
1st-16th	181	9.4	(15.4)	7.7	(11.1)	7.7	(22.1)	75.2	(51.4)

[a] Antler year class is based only on age: 1st year class, 5-12 months, 2nd year class, 17-24 months, *et cetera*.

[b] Expressions of dominance: brow tines, left-sided (Lr), right-sided (IR), both sides (LR), and neither side (lr); brow and bez tines together (brow/bez), left-sided (LLrr, LLrR, LLRr, Llrr, lLrr), right-sided (RRll, RRlL, RRLl, Rrll, rRll), both sides (LLRR, LlRr, lLrR, LlrR, lLRr), and neither side (llrr).

Table 2. Percentage distribution of 574 antlers from barren-ground caribou by presence of the brow and bez tines and absence of the brow or the bez tine, Northwest Territories, 1966-68.

Antler year class	Antlers N	% antler pairs with both brow & bez tines present	% single antlers with brow & bez tines present	% antlers with tines absent					
				Brow absent[a]		Bez absent[a]		Brow & bez absent	
				Left	Right	Left	Right	Left	Right
Males									
2nd-4th	122	39.3	49.2	4.9	3.3	19.7	21.3	0.8	0.8
5th-10th	90	84.4	92.2	4.4	2.2		1.1		
2nd-10th	212	58.5	67.5	4.7	2.8	11.3	12.7	0.5	0.5
Females									
1st-4th	126	6.3	11.1	19.0	19.0	8.7	6.4	16.7	19.0
5th-16th	236	21.2	30.5	14.8	15.3	7.6	11.0	11.0	9.8
1st-16th	362	16.0	23.7	16.3	16.6	8.0	9.4	13.0	13.0

[a] Best guess, based on criteria in methods section.

left-sided dominance 15.7% of the time; right-sided dominance, 14.6%; both sides dominant, 14.6%; and no dominance on either side, 55.1% (Table 1). No predominance of left-sided over right-sided dominance of the brow tine was found ($P > 0.05$).

Expressions of dominance or the lack thereof by the brow tines on antler pairs from young males (Table 1:2nd-4th sets) varied non-significantly ($P > 0.05$). Among bulls (Table 1:5th-10th sets) expressions of left-sided and right-sided dominance of the brow tine in antler pairs were proportionately overrepresented while dominance on both sides and, more so, no expression of dominance were underrepresented ($P < 0.01$). The frequency of occurrence among left-sided, right-sided, and both sides expressions of dominance in the overall sample, by age, or by sex were not significant ($P > 0.05$). Antler pairs with both brow tines simple or absent (lr) were proportionately overrepresented among females regardless of age (Table 1:$P < 0.005$) and were proportionately underrepresented among bulls (Table 1:$P < 0.01$).

Many of the antlers (43.4%) were lacking a brow or a bez tine, especially on antlers from females (regardless of age) and young males (Table 2). Only 39.9% of all antlers had both the brow tine and the bez tine present (Table 2). The brow tine was apparently missing more often than the bez tine on antlers from mature bulls and females (regardless of age); while on antlers from young males it was the bez tine (Table 2). Both brow and bez tines were missing from 16.8% of all antlers. The brow tine only was missing from 23.5% of the antlers: 12.0%, left side; and 11.5%, right side. The bez tine only was missing from 19.8% of the antlers: 9.2%, left side, and 10.6%, right side.

Only 6.8% (39) of the antlers were spikes (26 individuals) with no tines or palmation of the main beam. All but two of the spike antlers were from females (Table 3). Nine (45.0%) of the 20 antlers from female long yearlings (2nd year class) and two (7.1%) of the 28 antlers from male long yearlings were spikes ($P < 0.005$). Some

Table 3. Percentage distribution of 37 spike antlers from female barren-ground caribou by antler year class, Northwest Territories, 1966-68.

Antler year class	Antlers N	% paired spikes	% additonal spike antlers		% total spikes in year class
			Left	Right	
1st	6	100.0			100.0
2nd	20	30.0		15.0	45.0
3rd	60	13.3		8.3	21.7
4th	40			2.5	2.5
6th	26			3.8	3.8
7th	66	3.0			3.0
8th	30		3.3		3.3
9th	42	2.4			2.4
10th	24	8.3			8.3

females up to the 10th year class carried spike antlers (Table 3), while no males beyond the 2nd year class did. An additional nine of the females (3rd-16th sets) with no brow or bez tines present had relatively small antlers with short terminal tines (bifurcations) or slight palmations of the main beam compared to others in their antler year classes (based on this sample, field workers should note that small size and simplistic form, even spikes, does not necessarialy identify an animal as a long yearling).

I subsequently isolated all those antler pairs with both the brow and the bez tines present, as I was not always confident of my classification of a tine as a brow tine, when only one tine was present on the lower portion of the antler. Consequently the sample was reduced from 287 to 91 antler pairs: 68.1% from males and 31.9% from females. Seventy (76.9%) of these 91 pairs exhibited dominant brow tines: most (54.3%) were contributed by mature bulls (5th-10th sets); then 24.3% by young males (2nd-4th sets); and 21.4% by cows (5th-16th sets). The observed distribution of the expression of dominance of the brow tines in the 91 pairs was: left-sided, 29.6%; right-sided, 26.4%; both sides, 20.9%; and no dominance, 23.1%. There was no significant difference ($P > 0.05$) in the distribution of the 91 pairs by the four possible combinations of the brow tines or among the 70 pairs by side of dominance exhibited by the brow tines.

Brow and bez tine together

In all cases the frequency of occurence of left-sided dominance of the brow and bez tines together are non-significantly ($P > 0.05$) higher than the rate for brow tines only (Table 1.) This condition also was apparently true for the occurence of both sides dominant (Table 1:$P > 0.05$) Thus, those antler pairs exhibiting either right-sided dominance or no expression of dominance for both brow and bez tines together were seemingly lower proportionately ($P > 0.05$) than for the brow tine only (Table 1).

Antler pairs with brow or bez tines that exhibited dominance on both sides or were left-sided dominant were proportionately over-represented and those that were right-sided dominant or lacked any expression of dominance were underrepresented ($P < 0.005$) in the observed sample of male antler pairs. However, no significant difference ($P > 0.05$) could be found among left-sided, right-sided, and both sides dominance expressions of the brow or bez tines in those antler pairs, nor between left-sided and right-sided dominant sets ($P > 0.05$).

Antler pairs with brow and bez tines that were simple or absent (no expressed dominance) were overrepresented ($P < 0.005$) in the observed sample of female antler pairs. Expressions of left-sided, right-sided, and both sides dominance of the brow and bez tines were all less than expected among female antler pairs ($P < 0.005$). No evidence could be obtained for any significant variation among the occurrences of left-sided, right-sided, and both sides dominance ($P > 0.05$) or between antler pairs expressing left-sided versus right-sided dominance ($P > 0.05$).

Discussion

Only tentative acceptance of the apparent predominance of enlarged (dominant) left brow tines over right ones for the entire species (at least, in the northern hemisphere) is currently warranted on the basis of existing data (Table 4). I could not find a disproportionately high occurrence of left-sided dominant brow tines compared to right-sided dominant ones in my sample; nor was there in the samples from Murie, Skoog, or Goss (Table 4), when treated separately. Only two (Table 4: Banfield and Davis) of the six samples reported in Table 4 demonstrate significantly high occurrences of left-sided dominance over right-sided dominance in the brow tines of antler pairs. Thus, most of the contribution to the Chi-square comes from only 32.4% of the antler pairs with left or right dominant brow tines (Table 4: Banfield and Davis). When the other 67.6% of the antler pairs (Table 4: Murie, Skoog, Goss, and this study) are combined, that overall sample yields a non-significant difference in the rates of occurrence of left or right dominant brow tines in antler pairs. All the caribou in Banfield's (1954) sample were adult bulls and on the basis of what can be gleaned from Davis' (1973) report, it is likely that all of his specimens were also only from adult bulls. As essentially all of the significant difference in the occurrence of left versus right dominant brow tines is contributed by these two samples of adult bulls, it seems an exaggeration of fact to suggest that the trait is necessarily common to all members of the species (in the northern hemisphere). If Banfield (1954)

and Davis (1973) actually wanted to investigate this antler growth phenomonon at the species level, one must ask as why they did not examine antler pairs from females and young males as well as those from adult bulls(?). Surely, such material was available to both of them.

I see no objective reason for accepting the sample of 70 antler pairs obtained from reindeer introduced to South Georgia (54°-55°S, Leader-Williams, *in* Goss, 1980) as strong evidence for a predominance of enlarged right brow tines (n = 27) over left ones (n = 19) in the southern hemisphere; and thus, supposedly opposite to *Rangifer* in the northern hemisphere. The supposed disproportionate representation of an expression of dominance in right versus left brow tines (27 vs. 19) is non-significant (P >0.1). Thus, the suggested higher occurrence of right dominance over left dominance in these brow tines likely could be due to chance alone from the small sample size.

If further work is done on this subject, I suggest that standard criteria be used for recognizing the brow tine, when only the brow or the bez tine is present on one or both antlers of a pair. Differing criteria could confound initial findings and subsequent comparative results. Form, orientation to the main beam, or even origin on the main beam may not always be a diagnostic characteristic of the brow tine in *Rangifer*, especially when related to antlers from females or young males. The fixed relationship for the point of origin on the main beam that I used should continue to be used as an objective criterion for designating a tine as the brow tine (see Methods). Also, if a single-pointed brow tine is flattened in cross-section but not broadly palmate, its form should be considered simple (subject to the width restrictions given in the Methods).

I also suggest that each antler pair in future samples be identified by sex and at least approximate age of the donor animal to allow evaluations of antler pairs by sex and age class. Whenever possible antler pairs should be separated by sex and at least two age classes for subsequent evaluation, such as 1-4 years and 4 years or older. Antler pairs from young prime bulls (4-5 yr), prime bulls (6-9 yr), and possible 10 years olds, are undoubtedly the best specimens to describe side of dominance in the brow tines, as prime bulls have the most advanced development in the rangiferine antler, while female antlers apparently represent one of the earliest stage of morphogenesis of antlers in *Rangifer* (Bubenik, 1975a).

The function(s) of the brow tine in *Rangifer* has not been analyzed. Suppositions about feeding animals using them to move snow have no bases in fact. Goss (1980) suggested that future considerations of the function of the brow tine should include, «....the possibility that enlarged brow tines could function in the semiannual migration of reindeer and caribou, or might protect the eyes against wind and snow.» These two possibilities seem most unlikely as (1) essentially all animals that would have been carrying large antlers with markedly enlarged

Table 4. Summary of 1168 pairs of antlers from *Rangifer* in the northern hemisphere showing percentages possessing brow tines observed to be left-sided dominant, right-sided dominant, dominant on both sides, and neither side dominant by six different investigators.

	% dominance of brow tine[b]				
Source[a]	Left-sided (n = 395)	Right-sided (n = 287)	Both sides (n = 125)	Neither side (n = 361)	Subsample total
Murie (1935)	7 (ns)	7 (ns)	11		25
Banfield (1954)	24 (**)	8 (**)	3		35
Skoog (1968)	150 (ns)	132 (ns)	26	193	501
Davis (1973)	123 (***)	66 (***)	22		211
Goss (1980)	46 (ns)	32 (ns)	21	10	109
This study	45 (ns)	42 (ns)	42	158	287

[a] Data from Murie (1935), Banfield (1954), Davis (1973), and Goss (1980) also given in Table 1 of Goss (1980).
[b] Left- versus right-sided dominance of the brow tines in antler pairs: ns = non-significant; ** = P <0.01; and *** = P <0.005.

brow tines would be antlerless (if anything, new antler growth would be beginning) during spring migration; (2) autumn migration includes the time of the rut, and migration is not necessarily consistent or always unidirectional and often actually occurs in multidirectional stages; (3) also, essentially only mature bulls have enlarged brow tines of significant size and such males do not normally lead migrations; (4) essentially all adult males, many young males, and some females would be antlerless during the wintery period when antlers would be needed the most, if enlarged brow tines were for the protection of the eyes against wind and snow; and (5) even during the period of the year when antlers were present about half, at least, of the caribou in a herd would be without the benefit of enlarged brow tines.

Pruitt's (1966) suggestion that brow tines serve to protect the eyes of mature males, when thrashing bushes during the rut, might have some truth to it. However, it is difficult to accept that such and elaborate appendage would have evolved for that sole function. Reluctance to accept Pruitt's (1966) reasoning is particularly strong, when one considers that all other North American male cervids are equally vigorous bush or tree thrashers without the benefit of any such elaborate protection, and they apparently are not plagued by eye injuries. Bubenik (1975b) disagrees with Pruitt's (1966) interpretation and argues that it is the function of the second tines, and not the enlarged brow tine, to protect the eyes (and also the whole facial region). Bubenik (1975a:448) suggest that the function of the enlarged brow tine is for offensive use and display.

Goss (1980:364) believed that, «Whatever the true function might be, it must be consistent with the fact that brow tines do not develop fully until sexual maturity, that they are present in both males and females, that antlers are shed in winter by males and barren females but in spring by calving mothers, and that one, both, or neither of the brow tines may be enlarged.» The majority of female caribou likely do not even possess antlers with (enlarged) brow tines present; and those that do, have only primitive, small models compared to the advanced, large models of mature bulls (these conditions also apply to many young males). Therefore I do not think that the function, if any, of the morphologically dominant but relatively small brow tine of females or young developing males is necessarily the same as that of the large, morphologically advanced brow tine of mature bulls.

Future investigation of the possible primary function of the enlarged brow tine in *Rangifer* should be restricted to mature bulls or bulls should be considered separately from females. Thus, the major points to be considered seem to be (1) development is delayed until sexual maturity; (2) most all mature and essentially all prime bulls possess at least one enlarged brow tine; (3) the antlers of most mature and essentially all prime bulls are shed in late autumn and not fully regrown again until pre-rut during the following early autumn. This means that the function of the enlarged brow tine of mature bulls is restricted to, at most, about 3 months of the year which coincides with the pre-rut and rutting periods. This seemingly leads to the likelihood that the probable function of the enlarged brow tine in mature bulls is linked to their courtship behaviour.

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