Dental microwear foraging ecology of a large browsing ruminant in Northern Hemisphere: The European moose (Alces alces)

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Abstract:

Years of studies have already highlighted the complex combination, in moose feeding ecology, of a marked selectivity coupled with a significant dietary adaptability towards changes in the local resource availability. Dental textures resulting from masticatory movements and the properties of ingested food items constitute a link between the animal, its ecology and the environment it occupies. This approach is efficient to decipher subtle variations in diet, at the interspecific but also intra-populational scales. In this study, we explore inter and intra population dietary variations among six Northern European moose populations using DMTA. We show that moose feeding ecology spans a continuum between a diet dominated by tender leaves and a diet consisting of lignified tissues. The structure of habitats is the main driver of these dietary differences between populations. The absence of significant variation between males and females or between seasons is interpreted as a reflection of the food selectivity of this deer on a finer scale. The moose has a long common history with humans, constituting at certain times and in certain places the main food resource of these populations, adapting in other contexts and at other times to the repercussions of increasing anthropization and global climate change. We aim here at characterizing the dental microwear texture diversity hidden within the “browsing” dietary category. This work is also intended to be used as a reference for future paleontological or archeological investigations. We believe that it will contribute to a better understanding of the(paleo)ecology of the species and of the variations in its feeding ecology through time.

Keywords: cervid, diet, tooth wear, foraging behavior, European elk

1. Introduction

After the Last Glacial Maximum (26.5-19 cal kyr B.P.; Peltier and Fairbanks, 2006; Clark et al., 2009), the moose (*Alces alces)* expended across Europe until it occupied most of the continent (Schmölcke and Zachos, 2005; Niedziałkowska et al., 2014). *A. alces* is reported in numerous archeological sites in and outside Europe (see for example: Bridault, 1992; Leduc, 2012; Hofman-Kamińska et al., 2019). The decline of European moose populations started in Europe at the beginning of the Holocene after the Preboreal chronozone (11.5-10 cal kyr B.P. ; Schmölcke and Zachos, 2005). Several causes are put forward (Hundertmark et al., 2002; Schmölcke and Zachos, 2005; Niedziałkowska et al., 2014; Crees et al., 2016; Hofman-Kamińska et al., 2018; 2019), among which habitat changes and human pressure may have played a crucial role (Cardillo et al., 2005). More recently, *Alces alces* has gradually had to face the double challenge imposed by the increasing anthropization of its home range and the recent global climate change (Apollonio et al., 2017; Jones et al., 2019; Linnell et al., 2020).

Temperate and boreal biomes provide favorable environments for the present-day European moose, which has affinities for habitats with cold seasonal climates (Garel, 2005). This cervid occupies in Europe a large range of forested habitats as well as tundra and marshlands (Gębczyńska and Raczyński, 1989; Homolka, 1998; Jędrzejewska and Jędrzejewski, 1998; Henttonen et al., 2011). Among herbivores, while grazers mainly consume herbaceous monocotyledons, growing close to the ground (60 to 100% of the diet; Gagnon and Chew, 2000), browsers, including moose, prefer dicotyledonous plants (trees or forbs; more than 70% of their diet according to Gagnon and Chew, 2000). If moose is generally described as a selective browser (Hofmann, 1989), the availability of vegetal resources in the habitat is known to influence the feeding behavior of the species (Franzmann, 1981; Garel, 2005; Shipley, 2010; Wam and Hjeljord, 2010). Very typical for moose are seasonal migrations and changes of habitat used (Andersen, 1991; Ball et al., 2001; Singh et al., 2012; Borowik et al., 2020). In summer, *A. alces* prefers habitats in close proximity to water, where it often feeds on aquatic plants (Goss, 1983; Henttonen et al., 2011; Kuijper et al., 2016).

63 An important proportion of the diet of the European moose is composed of ligneous material
64 (Morow, 1976; Shipley et al., 1998; Garel, 2005; Spitzer et al., 2020). Browse, including lignified plants,
65 contain larger amounts of proteins and pectins compared to graze. While fibers are abundant and rich
66 in cellulose in graze, the smaller amount of fibers in browse can be strongly lignified, which reduces
67 their digestibility. Secondary compounds are also especially present in browse. They are deterrent for
68 most species and require special adaptations to limit their negative effects (Hagerman and Robbins,
69 1993; Clauss et al., 2008).

70 Dental microwear texture analysis (DMTA) is the analysis of tooth wear that results from a
71 combination of masticatory movements, physical properties and inner composition of masticated food
72 items (with a nutritional value, ingested intentionally or accidently: i. e. insects) that make-up the diet,
73 as well as the accidental ingestion of soil and mineral particles (dust; Ungar, 2015; Calandra and
74 Merceron, 2016; DeSantis, 2016). By combining dental microwear texture analysis with controlled-
75 food trials simulating natural conditions, Merceron et al. (2016b) have moved forward the long-
76 standing debate regarding the relative influence of diet (dietary signal) and soil and mineral particles
77 (environmental signal) on dental microwear (see Appendix S2 in Calandra and Merceron, 2016 for a
78 review).These authors showed that while dust contributes to the formation of dental microwear, diet
79 is the primary cause. More recently, Schulz-Kornas et al. (2020) confirmed the important role of diet
80 but emphasized the multifactorial nature of dental microwear textures.

81 Dental microwear textures mirror what an animal has ingested during the last few days or
82 weeks of its life (Teaford and Glander, 1991; Merceron et al., 2010; Winkler et al., 2020). The diet of
83 herbivores constitutes a window over the vegetal structure of the habitat. The correspondence
84 between resource availability, diet and vegetal structure is more accurate when considering a non-
85 selective herbivore, such as red deer (*Cervus elaphus*, Gebert and Verheyden-Tixier, 2001).
86 Consequently, paleontologists have promoted this method to fulfill their need of a proxy for
87 paleoecological and paleoenvironmental reconstructions. However, this approach is also a

discriminant tool for revealing subtle differences in the diet not only for extinct but also for extant species, at interspecific to intra-populational scales (Teaford and Oyen, 1989; Teaford and Robinson, 1989; Teaford and Glander, 1991; Merceron et al., 2010; Scott, 2012; Calandra et al., 2016a; Berlioz et al., 2017; Bignon-Lau et al., 2017; Percher et al., 2018; Merceron et al., 2020). Recent studies including experimental data have shown that dental microwear textures may significantly vary within each dietary category (namely obligate grazer, variable grazer, browser-grazer intermediate, browser, generalist and frugivore; Gagnon and Chew, 2000) depending on the maturity stage and water content of grasses (Francisco et al., 2018; Winkler et al., 2019), or on the fruit/seed abundances and the nature of the browsing diet (Ramdarshan et al., 2016; Merceron et al., 2018; Louail et al., 2021).

Our study is the first to explore the versatility of moose diet through dental microwear texture analyses. In this study, we have a twofold objective: (1) Methodological: to go further into the characterization of the dental microwear texture diversity hidden within the wide spectrum of the browse diet. To achieve this objective, moose is a species of choice as its feeding preferences, surveyed for decades, attest that it consumes only few herbaceous monocots and dicots (Shipley, 2010 and references therein). (2) (Paleo)ecological: we aimed at exploring and documenting the feeding behavior of extant moose populations with well-known habitats and ecology, using an approach applicable to both present-day and fossil moose populations. In future investigations, this key-reference could allow us to place into perspective past, present and future variations in the feeding ecology of moose.

To this end, we explored inter- and intra-population variations in diet among six populations of European *Alces alces* from northern Europe sampled in different habitats. Bearing in mind that moose feeding ecology is a combination of selectivity and adaptability (Franzmann, 1981; Hofmann, 1989; Garel, 2005; Shipley, 2010; Wam and Hjeljord, 2010), we expected dental microwear texture analysis to reveal inter-population dietary variations resulting from differences in resource availability between contrasted habitats. We also expected seasonal (Biebrza populations) and sexual (Gausdal

and Målselv populations) intra-population variations in diet. For the Biebrza population, for which this hypothesis could be tested, we also expected dietary variations resulting from seasonal changes of the vegetal phenology and seasonal migrations.

2. Material and Methods

2.1. Moose specimens studied

A total of 193 individuals, belonging to six European populations of interest of *Alces alces*, were included in the present study (Table S1, Figure 1). The specimens come from the Białowieża Primeval Forest (n=10), from the region of Polesie (n=9) and Biebrza Marshes (n=43) in eastern Poland, the region of Gausdal (n=62) and Målselv (n=59) in Norway and from the region of Småland (n=10) in Sweden. The Polish samples are stored at the Zoological collection of the Mammal Research Institute, Polish Academy of Sciences in Białowieża, Poland; the ones from Norway at the PALEVOPRIM lab, University of Poitiers, France and the Swedish specimens at the University of Copenhagen Zoological Museum, Denmark.

For most specimens, sex and date of death were provided (Table S1). The majority of the individuals were adults, culled in the framework of cynegetic regulation or found dead. Most moose from the study areas of Białowieża, Gausdal, Målselv and Småland were sampled between September and November while the Polish specimens from Biebrza marshes were culled in summer and fall. No date of death has been recorded for Polesie moose but most specimens must have been culled during the hunting season, between September and December.

2.2. Reference populations

Four additional ungulate populations have been used as reference. Three of them are ruminant browsing species with well-described and contrasting diets. *Cephalophus sylvicultor* (n=27) is an African bovid inhabiting forested habitats from Guinea Conakry to Kenya. Fruits and seeds constitute more than 70% of its diet (Estes, 1991). *Giraffa camelopardalis* (n=16) mostly browses on the highest tree foliage (Leuthold and Leuthold, 1978; Estes, 1991; Parker et al., 2003; O'Connor et al., 2015; Merceron et al., 2018). *Capreolus capreolus* (n=18) is a small-bodied European cervid, selectively

browsing dicot foliage and the most energetic semi-ligneous plants. Fruits and seeds are fallback foods in fall and winter (Tixier and Duncan, 1996; Tixier et al., 1997; 1998). For the population from the Bauges Natural Regional Park, used here as a reference, fruits represent a small proportion of its diet (Redjadj et al., 2014; see also Merceron et al., 2020 in this volume). A fourth sample of reference of grazing red deer (*Cervus elaphus;* n=19) from southern Spain (Azorit et al., 2012; Berlioz et al., 2017) has been added as an out-group. Grasses are the predominant part of their diet (>50%) almost all year round and constitute more than 90% during some months.

2.3. Study areas

The Białowieża Primeval Forest, located at the eastern border of Poland with Belarus (635 km², 23°87'E, 52°77'N; Figure 1), constitutes one of the best-preserved lowland forests in Europe (Jędrzejewska et al., 1994; Borowik et al., 2016). The Polish part of the forest covers 63,000 ha. The forest consists of an important tree cover composed of both deciduous tree species and evergreen coniferous trees: *Pinus sylvestris*, *Picea abies*, *Betula pendula*, *Alnus glutinosa*, *Quercus robur* and *Carpinus betulus* being the most abundant tree species (Borowik et al., 2016; Modzelewska et al., 2021). The primeval forest is peculiar in the sense that no less than three deer species (*Cervus elaphus*, *Capreolus capreolus* and *Alces alces;* respectively 6, 2 and 0.08 individuals per km²) occur in sympatry with *Bison bonasus* (0.75 individuals per km²) and *Sus scrofa* (5.4 individuals per km²) (Gębczyńska, 1980; Jędrzejewski et al., 2002; Borowik et al., 2013; Merceron et al., 2014; *European Bison Pedigree Book*, 2020).

Polesie (Poland, 23° 8'E, 51° 26' N, Fig. 1) including Polesie National Park and its buffer zone, is characterized by high spatial heterogeneity of habitats with patches of fen habitats interwoven with typical forest habitats dominated by *Pinus sylvestris, Betula* sp. and *Alnus glutinosa* and small water bodies (Borowik et al., 2020). The area is inhabited by four ungulate species: moose, red deer, roe deer, and wild boar. To the best of our knowledge, the relative abundances of ungulates in Polesie are not available.

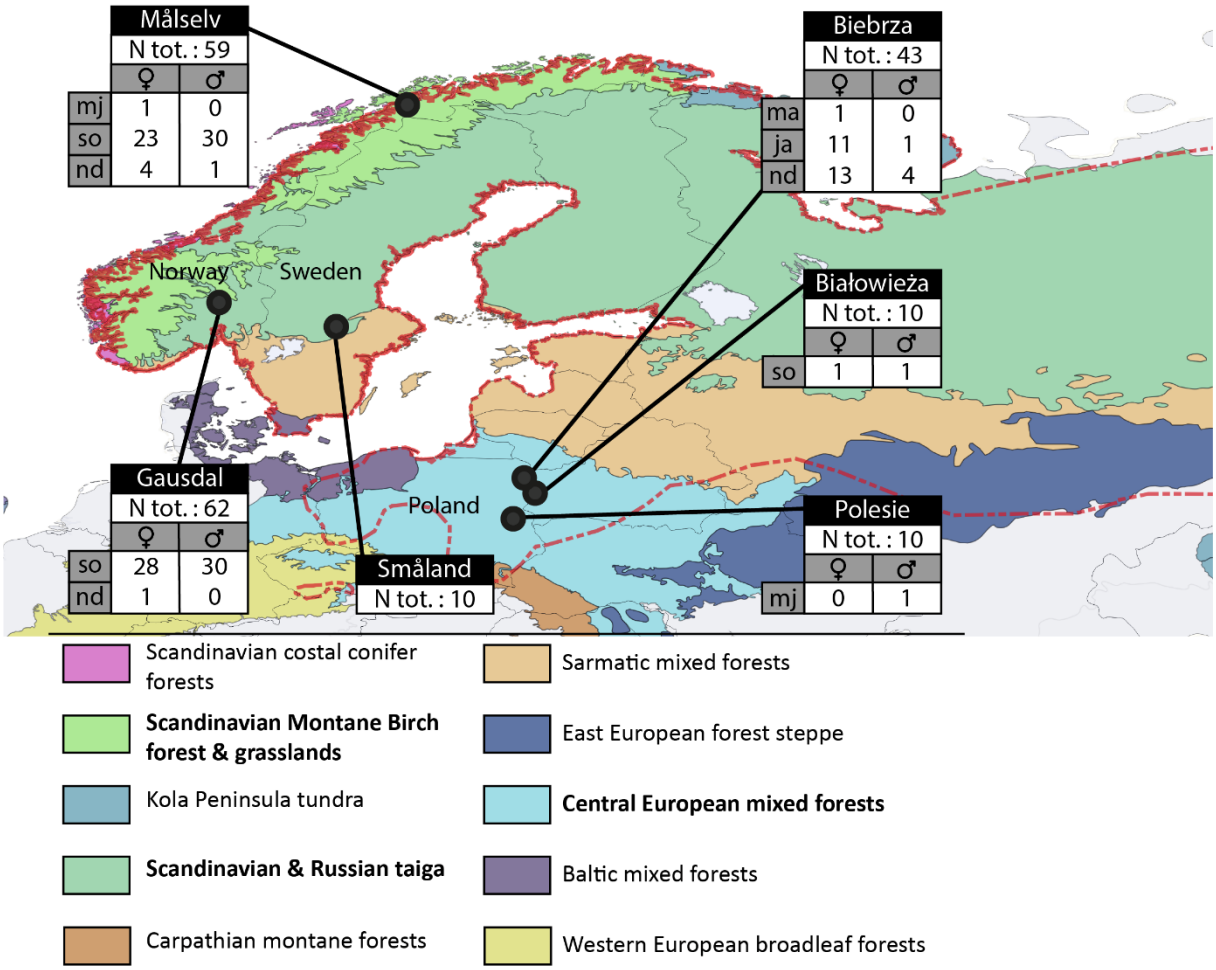


Figure 1: Geographic range of moose in Europe and localization of the 6 populations of interest. Norway: Målselv, Gausdal; Sweden: Småland; Poland: Biebrza, Białowieża, Polesie. Range data for European moose are illustrated by a red dashed line and were downloaded from http://www.iucnredlist.org. Colors represent the ecoregions within A. alces range. In the legend, ecozones including populations of interest are in bold. Ecozone data are from Dinerstein et al. (2017).

164

165 The lowland Biebrza river valley (Poland; 22˚35'E, 53˚26'N, Fig. 1) includes Biebrza National
166 Park (592 km^2; Borowik et al., 2013) and the surrounding forest districts. It is the largest marshland in
167 Central Europe, covering over 100,000 ha of floodplains, marshes, fens, coniferous and bog forests
168 (Borowik et al., 2018). Vegetation is distributed along an altitudinal and flooding range. While *Carex*
169 and *Phragmites australis* (both being herbaceous monocots) constitute the main vegetation close to
170 rivers and in floodplains, *Betula pubescens*, *Salix cinerea*, *Salix pentandra*, *Alnus glutinosa*, *Frangula*
171 *alnus* are the most represented tree species in peatlands. *Pinus sylvestris* and *Picea abies* are more
172 abundant in dryer, more elevated areas (Gębczyńska and Raczyński, 1989; Wassen et al., 2006; Kuijper
173 et al., 2016). In addition to the dominant ungulate population of moose (1-2 ind./km^2), the area is

174 inhabited by a rare but increasing population of *Cervus elaphus* and lower densities of *Capreolus*
175 *capreolus* (Kuijper et al., 2016).

176 The three Polish populations occupy the "Central European mixed forests" ecoregion as
177 defined by Dinerstein et al. (2017; https://ecoregions2017.appspot.com/) and are characterized by a
178 continental climate with Atlantic influences and clearly marked seasons (Jędrzejewska and
179 Jędrzejewski, 1998; Borowik et al., 2020).

180 Gausdal (Norway, 40 km², 9° 48'E, 61° 10'N, Fig. 1) is a boreal forest of medium altitude,
181 characterized by a sub-alpine continental climate. *Betula pubescens* is the most represented tree
182 species, while *Picea abies* is only present at lower altitudes. *Alces alces* is the main large mammal of
183 this locality (0.121 ind./km^2 in 1985-1987; Andersen, 1991; Andersen and Saether, 1992). Gausdal
184 population occupies the "Scandinavian & Russian taiga" ecoregion (Dinerstein et al., 2017).

185 Målselv (Norway), corresponding to the National Park of Øvre Dividalen (750 km^2, 19° 57' E,
186 68° 44' N; Fig. 1) is a boreal forest under a sub-continental climate, with oceanic influences (Davids et
187 al., 2006). The park is situated along the Swedish border. Open forests and swamps with *Pinus, Betula*
188 *nana* and *B. pubescens* are present in valleys under 700 m. Heathers, ferns and mosses constitute the
189 undergrowth. Between 700-1100 m, dwarf birches, ferns and *Epetrium nigrium* are abundant. At
190 higher elevations (1100-1700 m), the vegetation is mainly composed of mountain meadows with
191 grasses and sedges (Karlsson et al., 2005; Davids et al., 2006). In this area, *A. alces* is sympatric with
192 *Rangifer tarandus* (Karlsson et al., 2005; Davids et al., 2006). No information is given regarding the
193 relative densities of these two deer populations at the period of death. Målselv occupies the
194 "Scandinavian Montane birch forest & grasslands" ecoregion (Dinerstein et al., 2017).

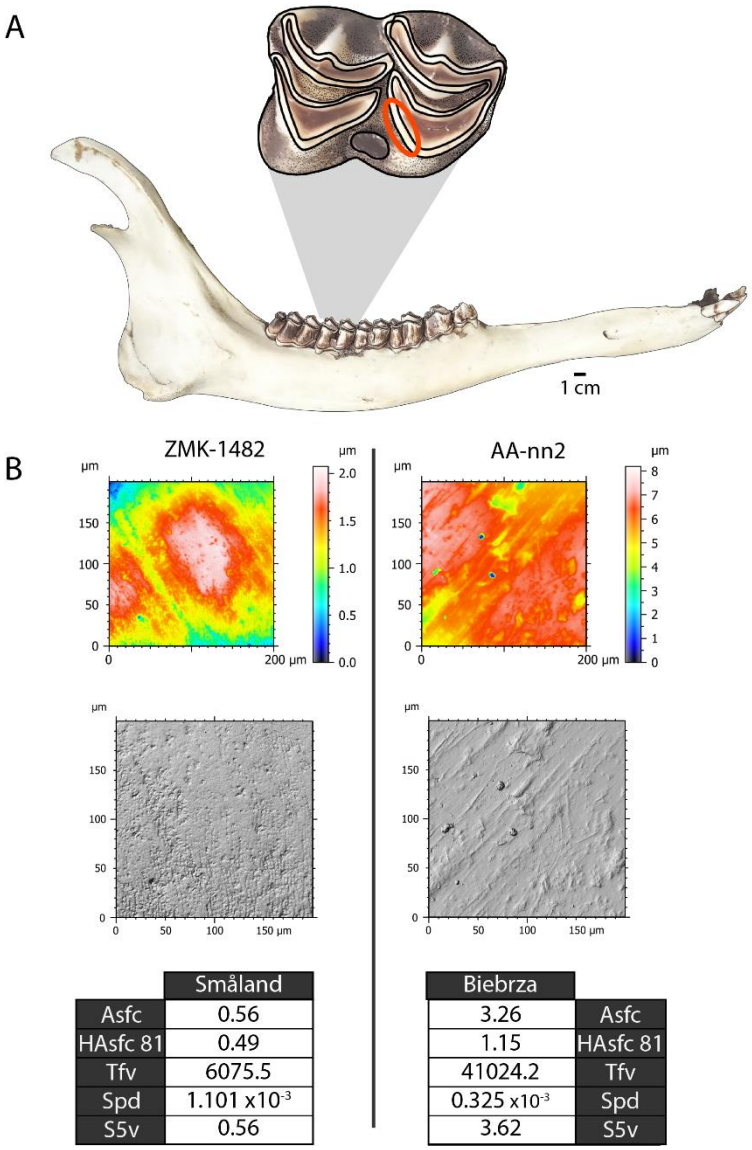
195 Moose from Småland were sampled in southern Sweden (14° 40' E, 59° 49' N, Fig. 1) in the
196 Scandinavian taiga (Dinerstein et al., 2017). The density of moose in Småland is unknown. The area is
197 characterized by a boreal forest dominated by scots pine (*Pinus sylvestris*) and Norway spruce (*Picea*

198 *abies*). *Quercus* spp., typical of the bordering "Sarmatic mixed forest" ecoregion, is also abundant in
199 the area.

200 ## 2.4. Dental microwear texture analysis

201 After molding mostly lower second molars (Figure 2A, Table S1) following standard procedures
202 (Merceron et al., 2016b) using high-resolution polyvinylsiloxane, disto-lingual facets of the protoconid
203 were scanned directly on the mold using "TRIDENT", the white light confocal surface profilometer Leica
204 DCM8, with a 100x objective (working distance: 0.9 mm; numerical aperture: 0.90) at PALEVOPRIM lab
205 (UMR7262, CNRS & University of Poitiers). From a 251 × 333 µm surface (2584 × 1945 point cloud with
206 lateral x and y intervals of 0.129 µm and vertical sampling of 0.001 nm), pre-treatment was done
207 (Figure 2B; see Supplementary Information in Merceron et al., 2016b). A 200x200 µm subsurface was
208 extracted following Merceron et al. (2016b) on which Scale Sensitive Fractal Analyses (SSFA; with SFrax
209 and ToothFrax software, http://www.surfract. com) was applied following procedures shown in Scott
210 et al. (2006). We also computed Surface Texture Analysis (STA; with Leica Map v 8.0) parameters
211 following well-established procedures (Schulz et al., 2013a; Kaiser et al., 2016), as the combination of
212 both SSFA and ISO 25178-2 textural parameters allow for a comprehensive representation of the
213 surface textural information (Calandra et al., 2012). All acquired surfaces are visible in the Annexes 1-
214 1 to 1-6 and MNT files are available upon request to the corresponding author.

215 Complexity (Area-scale fractal complexity, hereafter *Asfc*) quantifies surface roughness (Scott
216 et al., 2009; Scott, 2012; DeSantis, 2016). Anisotropy (exact proportion Length-scale anisotropy of the
217 relief; *epLsar*) is used to quantify the preferential orientation of scars, mostly striations, on enamel
218 surfaces (Scott et al., 2006; Scott, 2012; DeSantis, 2016). The heterogeneity of the complexity
219 (Heterogeneity of the Area-scale fractal complexity, *HAsfc 81*, calculated on each surface divided into
220 9x9 sub-surfaces) describes variations of the complexity over a surface (Scott et al., 2006; 2009;
221 DeSantis, 2016). Textural fill volume (*Tfv*) characterizes the depth and width of scar features. The
222 textures of browsers, which consume tougher lignified plants, less rich in abrasive silica and generally
223 more brittle, are characterized by lower anisotropy than grazers, coupled with medium to high



	Småland
Asfc	0.56
HAsfc 81	0.49
Tfv	6075.5
Spd	1.101 x10^{-3}
S5v	0.56

Biebrza	
3.26	Asfc
1.15	HAsfc 81
41024.2	Tfv
0.325 x10^{-3}	Spd
3.62	S5v

Figure 2: Acquisition of dental textures for Dental Microwear Texture Analysis (DMTA). A: molding of the disto-lingual facet of the protoconid of second lower molars, circled in orange. B: Two contrasted moose dental textures, respectively specimen ZMK-1482 from Småland, Sweden and AA-nn2 from Biebrza marshes, Poland. Texture parameters responsible for significant differences are given in tables below each specimen.

224 complexity (Scott et al., 2005; Scott, 2012; Schulz et al., 2013a; DeSantis, 2016). The complexity of the
225 heterogeneity, reflecting the diversity of ingested food items, is also higher for browsers (Schulz et al.,
226 2013a). *Tfv* is high when the scars on dental facets are deep and/or wide (Scott et al., 2006; 2009;
227 Scott, 2012).

228 For STA we focused on height (*Sa*, *Sp*, *Sq*, *S5v*), surface (*Sha*, *Sda*), feature (*Spd*) and volume
229 (*Vm*, *Vmc*, *Vvc*) parameters. Schulz et al.(2013b) have shown that the textures of browsers are less

anisotropic, with lower volumes and heights, shallower furrows and fewer peaks compared to grazers. In previous STA studies, these 10 parameters have been identified as they are the most discriminating (Calandra et al., 2012; Schulz et al., 2013a; 2013b; Kaiser et al., 2016). All parameters are presented in Table 1. A detailed description of STA parameters is available in Calandra et al. (2012).

Table 1 : Description of the ISO 25178-2 and SSFA parameters included in the study, based on Schulz et al. (2013) and Scott et al. (2006).

Parameter	**Parameter description**	**Unit**
Sa	arithmetic mean of the absolute of the heights	µm
Sp	Maximum peak height	µm
Sq	Standard deviation of the height distribution	µm
S5v	Five point valley height	µm
Sha	close hill area	µm²
Sda	close dale area	µm²
Spd	density of peaks	n/µm²
Vm	material volume at a given material ratio (p=10%)	µm³/µm²
Vmc	material volume of the core at a given material ratio (p=10%, q=80%)	µm³/µm²
Vvc	void volume of the core (p=10%, q=80%)	µm³/µm²
Asfc	Area-scale fractal complexity	
epLsar	exact proportion Length-scale anisotropy of the relief	
HAsfc 81	Heterogeneity of the Area-scale fractal complexity (81 cells)	
Tfv	Textural fill volume	µm³

The analyses were performed with R software (R version 4.0.3, The R Foundation for Statistical Computing; Annex 2). The data exploration was performed following Zuur et al. (2010). Gaussian Generalized Linear Models (G-GLM) were first performed on the global dataset (6 populations, all seasons and both sexes) in order to identify if the differences in the vegetal structure in the habitats of the six moose populations could explain variations in dental microwear textures. At this step, sex and season were not taken into consideration as this information was not available for all specimens. Models, for variables that required it, were transformed (Box-Cox, Log, cubic root; this information is given for each parameter in Annex 3) before analyses to get closer to a gaussian distribution (Zuur et al., 2010; Smith and Warren, 2019). Transformed variables were tested again in order to check if the distribution was improved by the transformation. We then specifically focused on each of the two Norwegian moose populations (Gausdal, n=58; Målselv, n=53), by running a multivariate analysis of

248 variance (manova) followed by analyses of variance (anovas; F-tests) to test whether the sex drives
249 differences in diet among each population at the end of summer (specimens sampled in September-
250 October). Finally, we conducted a manova followed by anovas on Biebrza females (n=24) to explore
251 seasonal variations in diet between summer and fall (specimens sampled in July-August and
252 November-December). For differences between populations, Post-Hoc Tukey's Honestly Significant
253 Difference tests (HSD) were performed on texture parameters responsible for significant differences.
254 Only significant differences supported by HSD were discussed (Table 3, Annex 3). The R script for data
255 exploration and analyses and the raw results from the analyses are respectively available in Annexes 2
256 and 3.

257 Moreover, we also calculated the relative frequency of specimens with highly complex (high
258 complexity: *Asfc* >2.0) and highly anisotropic (high anisotropy: *epLsar* >5.0 $x10^{-3}$) microwear within
259 each sample of specimens, following Scott et al. (2012; see also Scott et al., 2012; Merceron et al.,
260 2016a). Although these thresholds were initially determined for primates, within the herbivore
261 ecospace, they are effective in identifying grazers, with highly anisotropic textures and browsers and
262 frugivores, with highly complex textures (Scott, 2012; Berlioz, 2017). They are useful when attempting
263 to identify ungulate populations characterized by homogeneously high anisotropy or complexity. Intra-
264 population homogeneity or heterogeneity of *Asfc* and *epLsar* is informative and easily interpreted in
265 terms of availability and choice of ingested food items (Table S2, Figure 3). Moose results were
266 compared to the frequencies of the four samples of reference. SSFA and STA parameters for these four
267 reference populations are given in Table 2. The frequency of specimens with high complexity (*Asfc*
268 >2.0) and high anisotropy (*epLsar* >5.0 $x10^{-3}$) highlighted inter-population and inter-specific differences
269 (Figure 3). No more than 5% of *C. elaphus* are characterized by highly complex textures while 90% of
270 the textures of this grazing deer are highly anisotropic. Among browsers, *C. capreolus* is characterized
271 by a high frequency of individuals with high *epLsar*. Among *G. camelopardalis* and *C. sylvicultor,* fewer
272 specimens present a high *epLsar*. The duiker differs from the giraffe in having more specimens with

high *Asfc*. The moose samples share a low frequency of individuals with high *epLsar*, far away from the red and roe deer samples but next to the values met in the giraffes and duikers (Figure 3, Table S2).

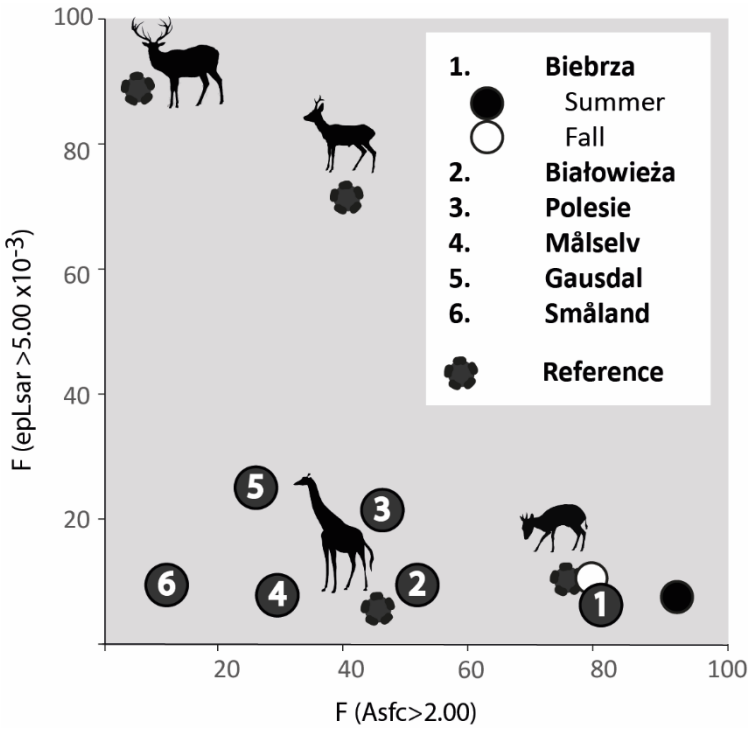
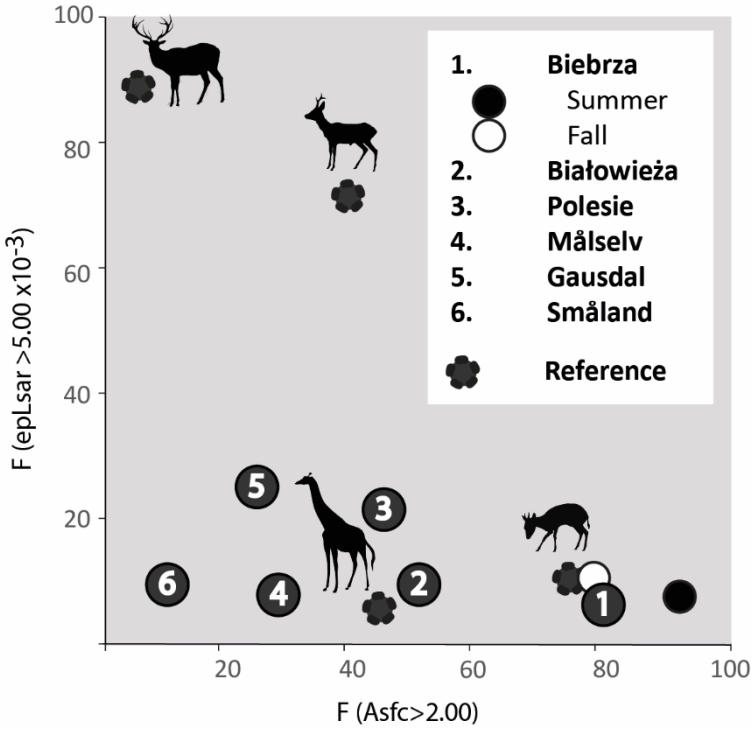


*Figure 3: Frequency of specimens per population with high complexity (Asfc >2.0) and high anisotropy (epLsar >5.00 x 10-3). **Poland**: 1: Biebrza, 2: Białowieża, 3: Polesie; **Norway**: 4: Målselv, 5: Gausdal; **Sweden**: 6: Småland. Four samples of extant ungulate species with well-known diet are used as reference: from upper left to lower right: Cervus elaphus, Capreolus capreolus, Giraffa camelopardalis and Cephalophus sylvicultor.*

3. Results

The frequencies of moose with highly complex (*Asfc* >2.0) dental microwear textures varied from a population to another, with moose from Biebrza marshes having the highest value and Scandinavian samples, notably Småland, characterized by low frequency of specimens with complex enamel textures (Table S2, Figure 3).



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281 Within the herbivore ecospace (explored through the DMTA of African bovids: Scott, 2012; and
282 European cervids: Berlioz, 2017) and in comparison with reference populations (Table 2, Figures 4 and
283 S2), the six moose populations are characterized by low to intermediate values of *epLsar* (Table 2,
284 Figure 4A) low to high *Asfc* (Table 2, Figure 4B) and high *HAsfc 81* (Table 2, Figure 4D). *Tfv* are
285 intermediate to high (Table 2; Figure 4C). For height ISO parameters (Table 2, Figure 4, Table S1) we
286 obtained a large range of values for *Sa*, *Sp* and *Sq* (respectively Figures 4G, 4H and 4I). The same kind
287 of variation is observed for *S5v* (Figure 4F). Surface parameters *Sha* and *Sda* are generally low (Figure
288 S2-D and S2-E). The feature ISO parameter *Spd* (Figure 4E) varies between low and intermediate values.
289 Finally, concerning the volume parameters, *Vm* mean values are low (Figure S2-A). *Vmc* and *Vvc* are
290 high for the six populations (respectively Figure S2-A and Figure S2-C).

291 Inter-population differences based on Gaussian GLM performed on the global dataset followed
292 by manovas, anovas and supported by HSD Post-Hoc tests (Figure 4, see also Annex 3 for AIC and p-
293 values) are presented in Table 3.

Through the intra-population anovas, we were not able to identify any significant difference of texture, neither between females from Biebrza culled in July-August and November-December nor between both sexes in September-October among Norwegian populations (p-values >0.05 in all cases).

4. Discussion

Moose is a selective browser whose nose anatomy limits its access to the herbaceous layer (Shipley, 2010) therefore limiting the ingestion of soil particles close to the ground (Sanson et al., 2007). In addition, moose populations studied in this article occupy relatively humid northern European habitats. Diet has been shown to be one of the main drivers of dental wear (Merceron et al., 2016b; Ramdarshan et al., 2016; Winkler et al., 2019; Ackermans et al., 2020; Schulz-Kornas et al., 2020). These three arguments justify the interpretation of these results in terms of feeding ecology.

4.1. *Alces alces*: a browsing diet

Differences between *Cervus elaphus*, *Capreolus capreolus*, *Giraffa camelopardalis* and *Cephalophus sylvicultor* in the frequencies of individuals with highly complex and highly anisotropic enamel textures (Figure 3) depict variations in grass, fruit/seed components, tough foliage, and lignified tissues in the diet of these ruminants. Among browsers, due to its small body mass, roe deer targets the most nutritive and digestible foliage from semi-ligneous bushes and forbs avoiding as much as possible lignified foliage (Tixier and Duncan, 1996; Tixier et al., 1997; 1998). Some foliage is tough and therefore requires prevailing shearing forces (forces applied parallel to the planes of contact between upper and lower teeth; Kay and Hiiemae, 1974) to extract cell content (Hua et al., 2015 and references therein), explaining the high *epLsar* for roe deer. The duiker consumes high amount of large and small fruits that require more crushing (forces applied perpendicularly to the upper and lower dental facets during mastication; Kay and Hiiemae, 1974) before and during rumination, explaining the high *Asfc* (Lumpkin and Kranz, 1984; Gagnon and Chew, 2000; Hua et al., 2015). The giraffe ingests large quantities of foliage from the upper parts of trees, incorporating lignified small branches, which require more crushing than shearing to extract cell content (Leuthold and Leuthold, 1978; Estes, 1991; Parker et al., 2003; O'Connor et al., 2015; Merceron et al., 2018). Lignified small branches require less

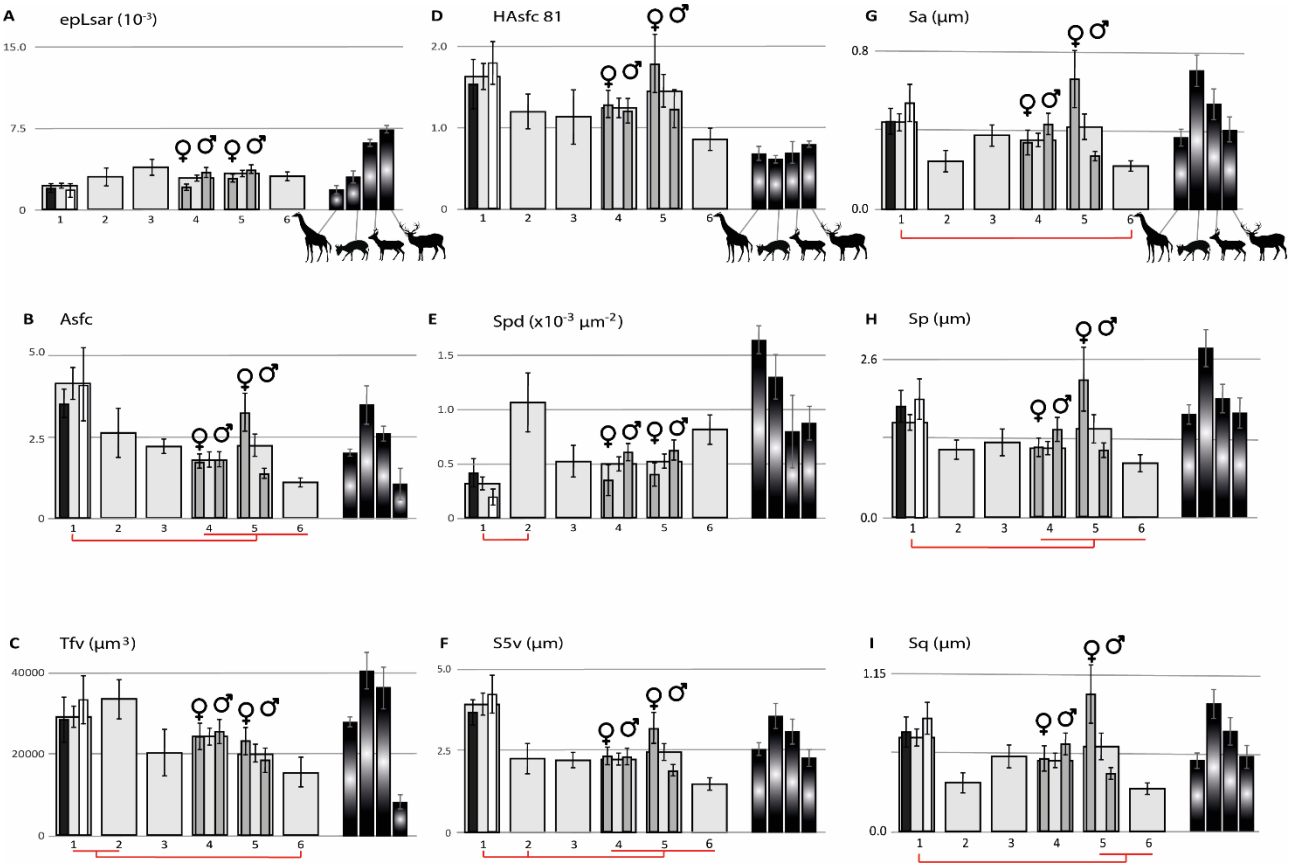

Figure 4: Barplots representing mean and standard error of mean for textural parameters that are mentioned in the discussion of the article. Parameters are illustrated for the six moose populations. Poland: 1: Biebrza, 2: Białowieża, 3: Polesie; Norway: 4: Målselv, 5: Gausdal; Sweden: 6: Småland. In addition, for Biebrza, females culled in July-August are represented by a black bar while females sampled in November-December are in white. Males and females slaughtered in September-October in Målselv and Gausdal are in grey. Sexes are identified by symbols. On the right side of each barplot, mean and standard error of mean for the four samples of extant ungulate species used as reference are illustrated (from left to right: Giraffa camelopardalis, Cephalophus sylvicultor, Capreolus capreolus, Cervus elaphus).

320 crushing than fruits to be processed, which explains that the giraffe presents lower *Asfc* than the
321 duiker. The red deer population consuming large amounts of abrasive grasses, requiring substantial
322 shearing forces, accounts for the particularly high *epLsar* for this grazing population.

323 For all moose populations, frequencies strongly differ from the ones observed for the grazing
324 red deer reference population. With a low frequency of individuals with highly anisotropic dental
325 microwear texture (Figure 3), the diet composition of moose appears in general different from that of
326 the roe deer, suggesting a lower amount of tough foliage requiring mainly shearing action. The
327 variations of frequencies of individuals with complex surfaces (Figure 3) reflect variations in the
328 abundance of hard tissues in the diet depending on local food resources and season. Significant

variations in *Asfc* indicates a diet richer in hard tissues for Biebrza population than for Scandinavian populations (Figure 4B).

Table 2: Inter- and intra-population values for DMTA-SSFA and DMTA-STA parameters. m: mean; s: standard error of mean; n= sample size. Populations: 1: Biebrza; 2: Białowieża; 3: Polesie; 4: Målselv; 5: Gausdal; 6: Småland. STA parameters: height parameters: Sa, Sp, Sq, S5v, surface parameters: Sha, Sda, feature parameters: Spd and volume parameters: Vm, Vmc, Vvc. SSFA parameters: Asfc: complexity; epLsar: anisotropy; HAsfc 81: heterogeneity of the complexity (9x9 cells), Tfv: Textural fill volume. Mean and standard error of mean for SSFA and STA parameters are also given for the four reference populations: C. s.: Cephalophus silvicultor, G. c.: Giraffa camelopardalis, C. e.: Cervus elaphus, C. c.: Capreolus capreolus.

loc	season	sex	n	Sa		Sp		Sq		S5v		Sha		Sda		Spd (10^{-3})		Vm		Vmc		Vvc		Asfc		epLsar (10^{-3})		HAsfc81		Tfv	
				m	s	m	s	m	s	m	s	m	s	m	s	m	s	m	s	m	s	m	s	m	s	m	s	m	s	m	s	m	s
1	all	all	43	0.44	0.04	1.59	0.13	0.69	0.06	3.92	0.34	743.0	130.8	395.8	28.6	0.32	0.06	0.018	0.002	0.41	0.04	0.49	0.05	4.17	0.49	2.15	0.23	1.63	0.16	29179.7	2619.8
	jul. aug.	all	12	0.39	0.06	1.64	0.23	0.62	0.11	3.45	0.43	793.9	140.5	402.2	46.8	0.46	0.13	0.021	0.004	0.36	0.06	0.46	0.08	3.27	0.43	2.40	0.49	1.53	0.21	28269.3	4649.4
		f	11	0.42	0.06	1.70	0.24	0.67	0.10	3.68	0.39	810.6	158.2	396.4	50.9	0.42	0.14	0.022	0.004	0.39	0.06	0.49	0.08	3.55	0.36	2.08	0.41	1.54	0.23	28543.2	5084.3
		m	1	0.07	/	1.01	/	0.10	/	0.83	/	659.8	/	466.6	/	0.95	/	0.004	/	0.08	/	0.10	/	0.26	/	5.90	/	1.37	/	25256.0	/
	mar. apr.	all	1	0.33	/	1.52	/	0.46	/	3.06	/	389.3	/	362.7	/	1.50	/	0.018	/	0.34	/	0.45	/	3.28	/	3.02	/	0.62	/	30910.7	/
		f	1	0.33	/	1.52	/	0.46	/	3.06	/	389.3	/	362.7	/	1.50	/	0.018	/	0.34	/	0.45	/	3.28	/	3.02	/	0.62	/	30910.7	/
	nov. dec.	all	18	0.53	0.09	1.73	0.25	0.79	0.12	4.16	0.44	749.3	188.4	443.2	59.2	0.22	0.06	0.020	0.004	0.51	0.09	0.60	0.11	4.57	0.87	2.13	0.40	1.63	0.23	32545.2	4782.1
		f	13	0.51	0.09	1.81	0.31	0.76	0.11	4.23	0.57	693.3	232.8	501.2	74.1	0.19	0.07	0.022	0.005	0.47	0.10	0.59	0.13	4.12	0.71	1.93	0.53	1.80	0.30	33436.9	5654.8
		m	4	0.38	0.13	1.30	0.53	0.57	0.21	3.39	0.37	910.9	623.8	243.9	32.1	0.32	0.14	0.018	0.010	0.36	0.10	0.47	0.17	3.07	0.48	2.38	0.33	1.25	0.27	25604.1	11345.9
2	all	all	9	0.24	0.05	1.14	0.16	0.36	0.07	2.25	0.48	539.2	136.5	394.9	75.5	1.07	0.28	0.012	0.002	0.25	0.06	0.32	0.07	2.65	0.77	2.99	0.82	1.20	0.22	33501.1	4876.6
	sep. oct.	all	2	0.15	0.07	0.82	0.39	0.19	0.10	0.73	0.02	282.7	16.7	297.4	66.6	1.86	0.31	0.009	0.006	0.17	0.08	0.22	0.12	0.94	0.68	6.35	2.97	0.91	0.60	46186.3	10372.6
		f	1	0.22	/	1.21	/	0.29	/	0.75	/	299.4	/	230.8	/	2.18	/	0.015	/	0.24	/	0.34	/	1.62	/	9.32	/	0.31	/	56558.9	/
		m	1	0.08	/	0.43	/	0.09	/	0.72	/	266.1	/	364.0	/	1.55	/	0.003	/	0.09	/	0.10	/	0.25	/	3.38	/	1.50	/	35813.7	/
3	all	all	10	0.37	0.05	1.26	0.22	0.55	0.09	2.21	0.24	334.5	137.5	385.7	61.4	0.53	0.15	0.016	0.004	0.36	0.05	0.43	0.08	2.22	0.23	3.88	0.75	1.13	0.34	20344.3	5714.7
	may june	all	1	0.25	/	0.97	/	0.34	/	1.87	/	499.1	/	284.5	/	1.13	/	0.010	/	0.26	/	0.29	/	1.67	/	4.68	/	0.51	/	29951.4	/
		m	1	0.25	/	0.97	/	0.34	/	1.87	/	499.1	/	284.5	/	1.13	/	0.010	/	0.26	/	0.29	/	1.67	/	4.68	/	0.51	/	29951.4	/
4	all	all	59	0.35	0.03	1.16	0.11	0.52	0.05	2.24	0.17	790.7	132.1	434.0	41.9	0.50	0.07	0.014	0.002	0.34	0.03	0.39	0.04	1.79	0.16	2.87	0.28	1.25	0.12	24376.5	2096.1
	may june	all	1	0.37	/	1.36	/	0.51	/	1.30	/	763.3	/	426.6	/	0.65	/	0.014	/	0.38	/	0.49	/	1.36	/	5.03	/	0.45	/	32380.0	/
		f	1	0.37	/	1.36	/	0.51	/	1.30	/	763.3	/	426.6	/	0.65	/	0.014	/	0.38	/	0.49	/	1.36	/	5.03	/	0.45	/	32380.0	/
	nov. dec.	all	5	0.21	0.03	0.71	0.07	0.30	0.04	1.53	0.18	220.8	70.1	179.8	41.5	0.54	0.13	0.009	0.001	0.21	0.02	0.24	0.02	1.87	0.62	1.76	0.34	1.27	0.52	15370.1	6614.1
		f	4	0.19	0.03	0.69	0.09	0.27	0.04	1.41	0.17	185.0	77.8	191.2	51.6	0.54	0.16	0.008	0.002	0.19	0.02	0.23	0.03	1.36	0.45	1.93	0.39	1.40	0.65	17960.2	7856.8
		m	1	0.28	/	0.78	/	0.42	/	2.02	/	364.2	/	134.5	/	0.53	/	0.009	/	0.27	/	0.28	/	3.93	/	1.08	/	0.76	/	5009.7	/
	sep. oct.	all	53	0.36	0.04	1.20	0.12	0.54	0.06	2.33	0.19	854.7	146.6	458.1	45.1	0.50	0.07	0.014	0.002	0.35	0.04	0.40	0.04	1.79	0.17	2.94	0.30	1.26	0.13	25075.2	2226.7
		f	23	0.32	0.06	1.05	0.14	0.48	0.09	2.33	0.29	677.3	103.9	424.4	74.7	0.35	0.06	0.012	0.002	0.29	0.05	0.32	0.05	1.75	0.25	2.19	0.26	1.30	0.22	24394.0	3397.9
		m	30	0.40	0.05	1.32	0.18	0.58	0.07	2.32	0.26	984.3	241.3	483.9	56.2	0.61	0.12	0.016	0.003	0.39	0.05	0.46	0.06	1.82	0.23	3.51	0.47	1.23	0.16	25597.5	2994.9
5	all	all	62	0.42	0.07	1.48	0.24	0.62	0.10	2.47	0.26	542.3	67.2	431.5	42.9	0.53	0.07	0.018	0.004	0.39	0.06	0.47	0.07	2.25	0.36	3.30	0.30	1.45	0.20	20262.1	2210.2
	nov. dec.	all	1	0.31	/	1.05	/	0.44	/	2.17	/	656.1	/	242.0	/	0.50	/	0.011	/	0.30	/	0.34	/	1.70	/	1.92	/	0.70	/	6288.7	/
		f	1	0.31	/	1.05	/	0.44	/	2.17	/	656.1	/	242.0	/	0.50	/	0.011	/	0.30	/	0.34	/	1.70	/	1.92	/	0.70	/	6288.7	/
	sep. oct.	all	59	0.42	0.07	1.51	0.25	0.64	0.10	2.50	0.27	555.3	70.5	443.1	44.6	0.53	0.07	0.019	0.004	0.40	0.07	0.48	0.08	2.28	0.37	3.36	0.31	1.49	0.21	20604.1	2291.8
		f	28	0.62	0.14	2.09	0.49	0.92	0.20	3.20	0.52	406.2	58.0	532.7	79.7	0.40	0.07	0.027	0.008	0.57	0.13	0.67	0.15	3.27	0.73	3.00	0.37	1.79	0.36	23368.9	3445.7
		m	30	0.26	0.02	1.01	0.11	0.39	0.04	1.90	0.19	681.0	118.8	368.9	39.4	0.63	0.12	0.011	0.002	0.25	0.02	0.32	0.03	1.39	0.16	3.76	0.49	1.24	0.24	18710.5	3079.7
6	all	all	10	0.22	0.03	0.92	0.15	0.32	0.04	1.48	0.19	439.7	84.3	354.6	58.4	0.82	0.14	0.010	0.002	0.22	0.03	0.28	0.04	1.12	0.14	3.03	0.41	0.86	0.14	15592.5	3608.4
	G. c.		16	0.37	0.04	1.69	0.16	0.51	0.06	2.55	0.20	897.2	112.8	313.9	83.3	1.66	0.13	0.023	0.003	0.38	0.10	0.47	0.07	1.97	0.23	2.17	0.44	0.68	0.12	27251.7	4762.5
	C. s.		27	0.71	0.08	2.79	0.30	0.93	0.11	3.57	0.38	778.9	194.1	627.4	51.9	1.32	0.21	0.035	0.004	0.78	0.07	0.99	0.11	3.50	0.50	3.04	0.33	0.61	0.04	40349.2	1744.8
	C. e.		19	0.41	0.07	1.71	0.25	0.54	0.08	2.27	0.26	728.0	88.7	664.0	72.7	0.89	0.16	0.021	0.004	0.45	0.09	0.56	0.09	1.06	0.10	7.26	3.78	0.80	0.08	8183.5	1251.2
	C. c.		18	0.54	0.08	1.96	0.23	0.73	0.10	3.08	0.39	993.9	458.2	430.8	45.4	0.81	0.34	0.024	0.004	0.58	0.05	0.71	0.09	2.61	0.59	6.05	0.55	0.70	0.05	36152.8	4490.7

These interpretations based on dental microwear analysis are in line with previous studies based on other proxies exploring the feeding ecology of this cervid that underlined the importance of ligneous elements in its diet (rumen content analysis: Morow, 1976; measured bites: Shipley, 2010; feces analysis: Kuijper et al., 2016). *Alces alces* has specific physiological adaptations, including the ability to produce tannin-binding proteins which counteract the negative effects of tannins (toxicity, astringency and limiting for digestibility and absorption) of the woody species that make up its

preferred diet (Hagerman and Robbins, 1993; Clauss et al., 2008; Moreira et al., 2013; Spitzer et al., 2020). Among ingested elements are buds, twigs, stems, foliage and berries. Bark and leaf-litter can also constitute large amounts of moose diet. For instance, bark represents up to 39% of moose spring-diet before the spring green-up and leaf litter accounts for 55-65% of early winter diet in Central Alberta (Renecker and Hudson, 1988). The specialized long muscular prehensile nose of moose, however, prevents it from consuming the herbaceous layer, so grass and forbs never make up a large part of its diet (Shipley, 2010; Spitzer et al., 2020). However, the amount of grasses and forbs in diet varies seasonally and from one habitat to another. While many studies report a small amount of herbaceous monocots (<1.5% sedges, rushes, and grasses; e.g. in Morow, 1976), others populations may incorporate more of them, especially in summer (up to 25% for one Norwegian population in Wam and Hjeljord, 2010; 10-17% of sedges, rushes and grasses in Biebrza moose diet in Kuijper et al., 2016).

Table 3: Significant inter-population differences supported by HSD tests. Populations: 1: Biebrza; 2: Białowieża; 3: Polesie; 4: Målselv; 5: Gausdal; 6: Småland.

	1	2	3	4	5	6
1		*S5v, Spd*		*Sp, S5v, Asfc*	*Sp, Sq, S5v, Asfc*	*Sa, Sp, Sq, S5v, Asfc, Tfv*
2						*Tfv*
3						
4						
5						
6						

4.2. Different ways to browse: inter-population variations

Shipley (2010) defines the feeding ecology of moose as being "a continuum between the facultative specialist and the facultative generalist". In many habitats across Europe, *Alces alces* is indeed focusing mainly on only one genus of plant, if not one species only. For example, *Salix* spp. account for 50 to 60 % of the diet in certain regions and seasons, as is the case with Biebrza moose summer diet (Sæther and Andersen, 1990; Kuijper et al., 2016), and *Pinus sylvestris* represents more than 60% of moose winter diet in Sweden (Shipley et al., 1998). Browse resource in particular can be

366 based on one species only, as is the case for *Betula pubescens* in the winter diet of Gausdal moose
367 (Sæther and Andersen, 1990). However, moose is also able to broaden or even change the spectrum
368 of foods it consumes whenever this is necessary, following seasonal variation in vegetal phenology or
369 environmental changes (Franzmann, 1981; Garel, 2005; Hofman-Kamińska et al., 2019) and important
370 inter-regional dietary differences exist (Morow, 1976; Shipley, 2010). Further exploring the inter-
371 population feeding ecology of *A. alces* through DMTA (Figure 4) has allowed us to identify inter-
372 population differences in diet, that reflect a wider disparity hidden behind Scott's "browser" and
373 "frugivore" dietary categories (Scott, 2012).

374 With especially high *Asfc* and *HAsfc 81* coupled with low *epLsar* for most specimens (Figure 3,
375 4A, 4B, 4D, Table S1, Figure S1), dental microwear textures of Biebrza moose place this population
376 among browsers, at one of the extremes of the herbivore ecospace. Such results reflect a browsing
377 diet dominated by hard tissues (Figure 3, Table 2). High mean values for height ISO parameters (*S5v*,
378 *Sa*, *Sp*, *Sq*; Figure 4 F, G, H, I) complete the characterization of the food ingested by these moose. *S5v*
379 is an estimate of the depth of the valleys composing the dental texture. A high S5v typically is the result
380 of chewing large hard items that produce deep pits on the dental facet (i.e. fruits, seeds or bark:
381 Calandra et al., 2012; Leach, 2013). High *Sa*, *Sp* and *Sq* also reflect the consumption of hard items
382 (Calandra et al., 2012; Kaiser et al., 2016). Feces analysis of Biebrza moose in summer supports our
383 results, demonstrating that up to 80% of the diet of moose was composed of lignified species of shrubs
384 and trees, including almost 60% of *Salix cinerea* (Kuijper et al., 2016). When browsing, moose takes
385 large, non-selective bites, including not only stripped leaves but also harder lignified elements like
386 twigs (Vivås et al., 1991; Kossak, 1992; Shipley et al., 1998). In Biebrza, moose consume a particularly
387 high proportion of these large lignified elements compared to other populations. Peculiarities of the
388 vegetal availability in this relatively open habitat could explain this diet consisting of more lignified
389 plants (Kuijper et al., 2016). As a result, their DMTA differs significantly from that of Scandinavian
390 moose. The populations of Målselv, Gausdal and Småland are indeed characterized by particularly low

391 values of *Asfc* (Figure 4B) and *S5v* (Figure 4F). *Sp* values are also lower for Scandinavian moose (Figure
392 4H) as will be further discussed below.

393 The populations of Polesie and Białowieża reflected comparable values for texture parameters.
394 This may result from utilization of similar mosaic habitats including wet forests, marshlands and river
395 valleys (Kossak, 1992; Jędrzejewska and Jędrzejewski, 1998). Strong habitat heterogeneity of both
396 areas make moose dependent on a more diversified diet (Borowik et al., 2020). These two populations
397 are characterized by medium *epLsar* and *HAsfc 81* and high *Asfc* (Table 2, Figure 4) that, coupled with
398 frequencies (Figure 3) of specimens with highly anisotropic (*epLsar*) and highly complex (*Asfc*) textures,
399 reflect a browsing diet dominated by leaves. Differences of SSFA parameters between Polesie and
400 Biebrza moose are not significant (Figure 4). However, the *S5v* values (Tables 2, 3 and Figure 4F) and
401 the frequency plot (Figure 3) suggest less lignified elements in the diet of Białowieża moose compared
402 to Biebrza moose. Such results are coherent with previous studies of the feeding ecology of Białowieża
403 moose. In Białowieża, moose diet is indeed most of the year composed of almost 60% leaves and twigs
404 from shrubs and trees including semi-ligneous brambles (*Rubus* sp.) and ligneous trees and bushes
405 (*Salix* sp., *Betula pubescens*, *Populus tremula*, *Frangula alnus*, *Sorbus aucuparia*). Less-lignified dwarf
406 shrubs compose 35% of moose diet notably including *Vaccinium vitis-idaea* and *Vaccinium myrtillus* in
407 spring. Diet also includes dicots from the herbaceous layer (*Lysiamachia vulgaris*, *Vicia* sp., *Juncus*
408 *effusus),* 7% grasses and sedges, and some water plants (Kossak, 1992 and references therein). The
409 ISO feature parameter *Spd* is also significantly different between Białowieża and Biebrza (Figure 4E).
410 *Spd* represents the density of peaks on the dental texture and is therefore influenced by the contacts
411 of the tooth with the dietary bolus and by attrition (Kaiser and Brinkmann, 2006; Leach, 2013). If we
412 refer to Kaiser et al. (2016, based on three datasets : ungulates, rabbits and primates), higher *Spd*,
413 rather than directly reflecting peculiarities of the ingesta properties, is negatively correlated with the
414 occlusal degree of freedom (see also Calandra et al., 2016b). As we consider dietary variations between
415 populations belonging to the same species, a higher *Spd* for Białowieża moose may result from
416 processing a dietary bolus that induce higher masticatory constraints.

417 Compared to Biebrza, Scandinavian moose sampled from Norwegian (Gausdal and Målselv)
418 and Swedish (Småland) boreal forests constitute a group characterized by markedly lower *Asfc*. *EpLsar*
419 is low to intermediate and *HAsfc 81* presents intermediate values (Table 2 and Figure 4). *S5v* (Figure
420 4F) and *Sp* are also significantly lower than for Biebrza. Such results for Scandinavian moose may
421 therefore reflect the ingestion of fewer large hard elements. These results are compatible with a leaf-
422 dominated diet and may be explained by the fact that dental textures reflect moose summer diet (most
423 specimens were culled in September-October). Indeed, while twigs are the most consumed items in
424 winter, Scandinavian moose summer diet consists of a high proportion of young leaves (Wam and
425 Hjeljord, 2010). Two extensive studies (Norway: Hörnberg, 2001; Sweden: Wam and Hjeljord, 2010)
426 have shown that *Betula* spp., *Salix* spp., *Pinus silvestris*, *Juniperus communis*, *Sorbus aucuparia* and
427 *Populus tremula* were the six main browse species consumed by *Alces alces* in Scandinavia. *Betula* spp.
428 are preferentially selected in summer, while *Sorbus aucuparia* are eaten preferentially in winter.
429 *Vaccinium myrtillus* is one of the few species dominating moose diet all year round. Mean percentage
430 of herbaceous monocots and dicots account for less than 9% and 2.5% of the diet, respectively (means
431 calculated on the basis of the results of the fecal analysis of 12 Norwegian moose populations, taken
432 from Figure 4 in Wam and Hjeljord, 2010). The asynchronous melting of the Scandinavian snow cover
433 compared to Poland results in a delayed growing season (Karlsen et al., 2009), that in turn may result
434 in the availability of less mature, therefore less lignified vegetation at the same period. This could also
435 contribute to DMTA differences with Biebrza moose and the tendency toward lower *Asfc* (Figure 4B)
436 and *HAsfc 81* (Figure 4D) than observed for Polesie and Białowieża moose.

437 In Gausdal, plant diversity is low, dominated by *Betula pubescens* and *Pinus sylvestris*, resulting
438 for moose to almost exclusively forage on deciduous *B. pubescens* (Sæther and Andersen, 1990; Davids
439 et al., 2006). In Målselv however, moose focus on a taxonomically more diversified diet composed of
440 *Salix* spp., *Sorbus aucuparia*, *Populus tremula*, *Prunus padus* (Sæther and Andersen, 1990). The
441 difference in diet between the two Norwegian populations is not reflected by the dental microwear
442 textures here as the main browsing resources of these two populations likely share similar physical

and mechanical properties (Figure 4, Table 2). DMTA inter-population similarities may be increased for these two populations as their dental textures reflect the summer diet, characterized by the abundance of deciduous leafy resources in many habitats in both temperate and boreal biomes. The dental microwear textures of Småland moose are comparable to those of other Scandinavian ones. Similarly, they are interpreted as reflecting a diet dominated by soft and non-tough leaves. *Tfv* (Figure 4C) measures the volume of surface roughness, taking into account the whole surface. As *S5v* (which focuses on the 5 deepest valleys of the surface only), it is classically higher when deep and/or large marks are present on the dental facets, a situation that is typical of a diet dominated by hard elements (Scott et al., 2006; Scott, 2012; DeSantis, 2016). Therefore, the significant *Tfv* differences between Småland moose and Biebrza and Białowieża moose reflect the fact that the Polish and Swedish populations are at both ends of a continuum between a diet dominated by tender leaves and a diet dominated by lignified plants.

Exploring sexual dietary differences among Gausdal and Målselv populations showed that the summer diets of moose cows and bulls are similar in terms of physical and mechanical properties. During this season, males and females focus mainly on young leaves. In the same way, the exploration of seasonal dietary variation of Biebrza moose cows showed that there were no differences between summer and fall (see below).

4.3. An edifying example of selective browsing: Biebrza moose

Moose from Biebrza marshes constitute an interesting illustration of the selective behavior of this deer, which is reflected by its dental microwear textures. In this locality, moose occupy valleys, characterized by swamps and marshes, and by extensive open sedge-dominated communities in spring and summer. In fall and winter, due to the flooding of the floodplain, moose migrate to the edges of the valleys, at a higher elevation and in more forested areas (pine forests) (Borowik et al., 2020). Kuijper (2016) performed a microscopic analysis of epidermal fragments occurring in moose fecal material sampled during the vegetation growing season (June-August) and showed that during this period woody material represents 80% of moose diet, including 60% of willow (*Salix cinerea*). While

the herbaceous vegetation constitutes the main resource available in this summer habitat, herbaceous monocotyledons, including sedges and rushes, represent only 20% of their diet during this season (Wassen et al., 2006). DNA-based analysis of moose diet in Biebrza in winter also showed dominance of woody species in their diet with *Pinus sylvestris*, *Alnus* spp., *Ribes* spp., *Corylus avellana* and *Carpinus betulus* most often browsed (Czernik et al., 2013). As mentioned earlier, dental microwear textures, notably the high *Asfc*, indicate a diet mainly composed of lignified tissues for both summer and winter (Table 2; Figures 3,4A-D, F and S1). While seasonal variations in the vegetal phenology coupled with moose annual migration between contrasted habitats at Biebrza result in important seasonal changes in vegetal resource availability (Borowik et al., 2020), dental microwear textures does not reflect these changes, as diet for both seasons reflects similar physical and mechanical properties of the food resources. Based on feces analyses, Czernik et al. (2013; DNA analysis; sampling from March to December) and Kuijper et al. (2016; microscopic analysis; sampling from June to August) came to the same conclusions. Bearing in mind that microwear is well known for its ability to emphasize seasonal and/or sexual differences in diet corresponding to fluctuations in needs and resource availability (Teaford and Oyen, 1989; Teaford and Robinson, 1989; Teaford and Glander, 1991; Merceron et al., 2010; Berlioz et al., 2017; Percher et al., 2018), the absence of significant seasonal differences in dental microwear textures between Biebrza females culled in summer and winter supports the selective behavior of this population. A relatively large size of home-ranges for moose, as well as migratory strategies (up to 25 km^2, depending on habitat, season, sex and age of the individuals; Franzmann, 1981; Cederlund and Sand, 1994; Borowik et al., 2021) may facilitate the search for the preferred resources. Biebrza moose focus all year long on preferred food resources rather than considering most abundant food items, a feeding behavior that contrasts with e.g. the red deer, this species being characterized by a high trophic plasticity (Goffin and De Crombrugghe, 1976; Gebert and Verheyden-Tixier, 2001; Berlioz, 2017).

5. Conclusions

The feeding ecology of moose is a complex combination of marked selectivity and significant dietary adaptability toward changes in local resource availability, that dental microwear texture analyses (DMTA) witness. We explored and perceived this variability at the inter- and intra-population scales, through the investigation of six moose populations from northern Europe occupying three contrasting types of habitats. The diversity of physical and mechanical properties of the ingested food items and the masticatory dynamics required to comminute them have allowed us to highlight different ways to browse, demonstrating once again the capacity of DMTA to decipher even subtle dietary differences. The use of both SSFA and STA parameters led us to describe and discuss different aspects of these dietary variations. DMTA reveal that the diet of these present-day European moose varies along a continuum between soft-leaf browsing and a browsing diet dominated by lignified tissues. By studying the intra-specific scale of dietary variation and by highlighting such a continuum rather than considering separate dietary categories among browsers, we pursue the work initiated on African bovids, getting a step closer to ecological diversity and contributing to a now growing DMTA corpus of reference for European large ungulates. Our results are in good agreement with previous studies of the habitat and feeding ecology of the same populations. The availability of resources in each type of habitat, from Scandinavian boreal forests to Polish marshes, seems to be the strongest driver of the dental microwear texture variations for moose at the inter-population scale. At the intra-populational scale, no significant dietary differences between males and females or between seasons were identified. In Biebrza marshes in particular, we have shown that there is no difference in diet between females in summer and fall, even though summer and fall habitats are very contrasted in terms of resources availability. Our findings underline the strong selectivity in feeding behavior of this cervid and complete our knowledge of the ecology of this population.

The present study has obvious potential to contribute to future paleontological and archeological investigations through the analysis of dental microwear textures. Such studies would

provide a better understanding of past adaptative answers of moose facing paleoenvironmental changes.

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Data Availability

Research data are available upon request to the corresponding author.

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Supplementary Informations

Table S1: information and texture parameters for all specimens. Populations: 1: Biebrza; 2: Białowieża; 3: Polesie; 4: Målselv; 5: Gausdal; 6: Småland. Tooth: lm: lower molar; UM: upper molar; dP4: decidual 4th premolar. Seasons: jf: January-February; ma: Mars-April; mj: May-June; ja: July-August; so: September-October; nd: November-December. Sex: f is for female, m is for male. / is used when data is missing.

Table S2: Sample sizes (n) and frequencies (%) of specimens with high complexity (*Asfc* >2.0) and high anisotropy (*epLsar* >5x10^{-3}), for the six moose populations and the four reference populations. Data were used for Figure 2.

Figure S1: Complexity (*Asfc*) and Heterogeneity of the complexity (*HAsfc 81*) for the six moose populations and for reference populations. Mean and standard error of mean are represented for: **Poland:** 1: Biebrza, 2: Białowieża, 3: Polesie; **Norway:** 4: Målselv, 5: Gausdal; **Sweden:** 6: Småland. Reference populations with well-known diet, from left to right: *Cervus elaphus*, *Giraffa Camelopardalis,Capreolus capreolus* and *Cephalophus sylvicultor*.

Figure S2: mean and standard error of mean for textural parameters that are not illustrated in Figure 4. A: *Vm*; B: *Vmc*; C: *Vvc*; D: *Sha*; E: *Sa*. **Upper line:** parameters are illustrated for the six moose populations. **Poland:** 1: Biebrza, 2: Białowieża, 3: Polesie; **Norway:** 4: Målselv, 5: Gausdal; **Sweden:** 6: Småland. **Second line**: for Biebrza, females culled in July-August are identified by a sun symbol while females sampled in November-December are illustrated by a dead leaf. Sexes are identified by symbols. **Bottom line**: values for the four samples of extant species used as reference (from left to right: *Giraffa camelopardalis, Cephalophus sylvicultor, Cervus elaphus, Capreolus capreolus*) are given.

Annex 1: Photosimulations and false color elevation maps of molar facets of the six moose populations, scanned at the PALEVOPRIM Lab by E. Berlioz, PhD, with "TRIDENT" white light confocal microscope Leica DCM8. **Poland:** Annex 1_1: Biebrza, Annex 1_2: Białowieża, Annex 1_3: Polesie; **Norway:** Annex 1_4: Målselv, Annex 1_5: Gausdal; **Sweden:** Annex 1_6: Småland.

Annex 2: R script used to explore and analyze the dataset of the present study.

Annex 3: Raw results for GLM, manovas and anovas performed on the datasets (at the inter-population and intra-population scales).

853 Table S1 :

reference	pop.	tooth	sex	season	*Sa*	*Sp*	*Sq*	*S5v*	*Sha*	*Sda*	*Spd* (10^{-3})	*Vm* (10^{-3})	*Vmc*	*Vvc*	*Asfc*	*epLsar* (10^{-3})	*H81*	*Tfv*
aa201091	5	lm2	f	so	0.27	1.44	0.39	1.89	363.13	310.29	0.13	14.11	0.28	0.36	1.40	1.86	1.12	50416.4
aa219275	5	lm2	f	so	0.16	0.79	0.24	1.32	603.55	200.65	0.48	8.50	0.16	0.19	0.84	2.06	0.80	37218.6
aa235258	5	lm2	/	/	0.12	0.63	0.15	0.71	296.93	115.46	0.90	4.51	0.13	0.17	0.49	3.06	0.62	5329.4
aa237228	5	lm2	m	so	0.28	0.67	0.44	2.98	38.34	373.26	0.25	5.59	0.23	0.24	1.90	1.68	2.31	2664.7
aa237299	5	lm2	m	so	0.26	1.38	0.51	2.13	/	284.08	0.05	13.79	0.24	0.40	1.42	1.93	2.79	19533.6
aa237309	5	lm2	m	so	0.08	0.41	0.10	0.66	360.34	242.24	0.63	3.02	0.08	0.11	0.14	2.47	0.95	0.0
aa254284	5	lm2	f	so	0.19	0.76	0.27	1.57	466.69	129.29	1.33	5.73	0.19	0.20	2.18	0.80	0.88	1812.0
aa263104	5	lm2	f	so	2.17	5.07	2.80	9.43	156.84	465.91	0.28	42.31	2.48	2.60	15.66	1.67	0.80	35693.8
aa263122	5	lm2	m	so	0.19	0.87	0.24	0.77	325.18	288.05	2.75	8.49	0.22	0.27	0.78	7.00	0.33	959.3
aa263154	5	lm2	f	so	0.13	0.40	0.19	0.98	497.60	151.19	0.55	2.95	0.13	0.13	0.53	4.66	0.94	639.5
aa263155	5	lm2	m	so	0.11	0.60	0.14	0.59	114.51	349.45	0.60	5.25	0.12	0.15	0.22	5.71	1.02	0.0
aa263159	5	lm2	m	so	0.21	0.68	0.27	2.30	615.03	374.38	1.10	8.81	0.23	0.30	1.24	6.92	0.83	1492.2
aa263162	5	lm2	f	so	0.20	0.99	0.26	1.05	410.37	302.47	1.08	9.82	0.21	0.26	0.79	7.40	0.48	20145.2
aa263163	5	lm2	f	so	0.71	1.44	1.09	3.91	133.90	263.62	0.23	16.69	0.64	0.71	6.57	2.37	1.19	48632.2
aa263172	5	lm2	f	so	0.12	0.65	0.19	1.26	265.22	121.87	0.43	9.43	0.11	0.15	1.03	3.62	0.73	426.4
aa263173	5	lm2	f	so	0.17	0.72	0.25	1.10	1146.56	135.57	0.68	10.17	0.16	0.20	0.84	3.21	0.61	39755.7
aa263177	5	lm2	f	so	0.14	0.52	0.23	1.72	452.04	272.39	0.35	3.80	0.13	0.15	0.80	0.98	0.99	106.6
aa263178	5	lm2	m	so	0.15	0.74	0.22	1.68	211.55	350.38	0.28	7.10	0.15	0.18	1.16	2.76	0.97	42247.5
aa263183	5	lm2	m	so	0.48	1.52	0.71	3.77	1651.00	439.36	0.23	14.20	0.43	0.49	3.32	0.57	1.26	29067.1
aa263184	5	lm2	f	so	0.43	1.77	0.76	2.71	/	1179.18	0.08	16.07	0.38	0.57	1.68	4.86	1.77	13010.7
aa263186	5	lm2	f	so	2.16	7.57	3.35	4.71	/	1701.35	0.00	126.91	1.94	2.72	5.72	4.29	5.37	32880.8
aa263187	5	lm2	m	so	0.25	1.67	0.35	1.52	248.43	959.96	0.13	14.61	0.26	0.39	0.56	3.40	1.15	60047.7
aa263190	5	lm2	m	so	0.11	0.51	0.14	0.56	344.50	142.10	0.90	7.84	0.13	0.16	0.32	6.92	0.57	426.4
aa263191	5	lm2	f	so	1.81	4.08	2.46	7.41	264.81	763.77	0.10	41.22	1.88	1.64	11.50	2.99	1.56	35643.5
aa263197	5	lm2	f	so	1.36	2.79	2.10	6.34	/	669.31	0.00	37.75	0.98	0.88	6.80	3.48	3.23	49807.4
aa263202	5	lm2	m	so	0.26	0.89	0.36	2.01	524.60	200.02	0.75	8.81	0.27	0.31	2.14	2.69	0.52	20465.0
aa263214	5	lm2	f	nd	0.31	1.05	0.44	2.17	656.10	241.98	0.50	11.45	0.30	0.34	1.70	1.92	0.70	6288.7
aa263216	5	lm2	f	so	0.18	0.61	0.31	2.54	760.19	431.08	0.25	5.45	0.14	0.16	1.83	2.18	1.03	746.1
aa263218	5	lm2	m	so	0.35	1.15	0.46	2.06	402.92	591.80	0.58	11.67	0.37	0.44	0.89	8.58	0.91	8100.7
aa263221	5	lm2	m	so	0.22	0.57	0.29	1.43	792.17	164.36	0.88	7.39	0.24	0.22	1.35	5.25	0.79	21211.1
aa263222	5	lm2	f	so	0.07	0.45	0.10	0.48	463.87	140.54	1.23	3.68	0.07	0.10	0.28	3.84	0.51	0.0
aa263227	5	lm2	f	so	0.89	2.45	1.32	4.84	32.02	826.84	0.18	50.42	0.79	0.74	5.36	4.20	2.30	31565.7
aa263230	5	lm2	f	so	0.11	0.55	0.17	1.38	508.49	133.09	0.58	3.11	0.11	0.11	1.09	1.00	0.58	17693.7
aa263232	5	lm2	f	so	1.73	7.23	2.63	7.11	/	1267.92	0.03	108.54	1.60	2.17	6.77	0.71	3.13	42193.4
aa263233	5	lm2	m	so	0.17	0.66	0.23	1.91	1616.61	222.05	0.40	6.77	0.18	0.20	1.49	1.87	0.60	34641.3
aa263235	5	lm2	m	so	0.25	0.65	0.39	1.35	761.13	222.36	0.35	6.92	0.24	0.28	1.75	2.04	0.93	29844.8
aa263244	5	lm2	m	so	0.48	2.16	0.74	2.59	2531.59	337.74	0.15	23.71	0.45	0.48	3.35	2.38	1.00	28497.6
aa263248	5	lm2	m	so	0.33	1.29	0.43	1.73	487.73	898.16	0.73	17.28	0.36	0.46	1.33	6.55	0.66	10735.7
aa263250	5	lm2	m	so	0.10	0.51	0.14	1.01	486.00	220.41	1.33	4.85	0.10	0.13	0.59	1.50	0.62	11831.3

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reference	pop.	tooth	sex	season	Sa	Sp	Sq	S5v	Sha	Sda	Spd (10-3)	Vm (10-3)	Vmc	Vvc	Asfc	epLsar (10-3)	H81	Tfv
aa263251	5	lm2	f	so	0.20	0.70	0.31	2.61	779.69	678.50	0.23	8.79	0.19	0.25	1.22	1.81	1.93	30550.6
aa263259	5	lm2	m	so	0.18	1.36	0.24	1.08	172.92	224.12	0.50	8.99	0.19	0.22	1.14	0.66	0.64	24835.1
aa263266	5	lm2	f	so	0.57	2.18	0.90	3.48	/	655.43	0.10	23.01	0.49	0.60	3.05	2.28	1.24	28969.2
aa263273	5	lm2	m	so	0.22	0.61	0.36	2.88	1550.25	125.67	0.23	6.45	0.19	0.20	3.63	0.57	0.51	3943.8
aa263281	5	lm2	m	so	0.33	1.18	0.41	1.31	350.86	356.71	2.68	14.59	0.38	0.50	1.71	8.49	0.37	17054.2
aa263285	5	lm2	m	so	0.07	0.50	0.11	1.04	858.08	90.51	0.70	2.30	0.07	0.09	0.70	2.04	0.59	0.0
aa263286	5	lm2	m	so	0.29	0.69	0.44	0.90	827.21	439.36	0.75	6.34	0.28	0.26	0.90	8.47	0.70	20271.0
aa263289	5	lm2	m	so	0.43	1.17	0.64	2.66	876.11	451.41	0.35	16.41	0.38	0.46	1.76	0.70	1.78	37653.6
aa263290	5	lm2	f	so	0.13	0.49	0.23	1.30	61.95	401.97	0.25	7.72	0.11	0.15	0.52	5.31	0.82	2558.1
aa263291	5	lm2	f	so	2.11	10.84	3.34	10.71	/	1133.31	0.03	167.86	1.70	2.31	9.45	1.29	6.69	48305.8
aa263295	5	lm2	f	so	0.35	0.98	0.43	1.21	264.37	661.50	0.53	8.48	0.39	0.44	0.29	7.32	0.96	1172.5
aa263296	5	lm2	/	/	0.35	0.80	0.49	2.51	61.25	260.59	0.20	5.98	0.36	0.34	3.16	1.47	0.89	28992.1
aa263299	5	lm2	m	so	0.24	0.96	0.31	0.87	765.65	314.93	0.78	9.04	0.26	0.34	0.51	6.18	0.70	54859.7
aa263312	5	lm2	/	so	0.11	0.57	0.17	1.13	546.19	90.09	1.08	3.98	0.11	0.13	0.93	1.28	0.57	0.0
aa263315	5	lm2	m	so	0.53	3.39	1.09	4.79	/	/	0.00	56.30	0.37	0.82	2.01	5.56	7.25	23040.5
aa263323	5	lm2	f	so	0.22	0.85	0.27	0.82	444.36	361.37	1.18	11.07	0.26	0.32	0.64	6.50	0.41	17373.9
aa263336	5	lm2	m	so	0.44	1.34	0.59	1.98	/	580.21	0.23	20.73	0.47	0.54	1.10	5.60	0.80	35788.0
aa263339	5	lm2	m	so	0.19	0.56	0.31	2.06	112.25	249.00	0.40	4.61	0.18	0.21	1.45	1.49	0.91	639.5
aa263361	5	lm2	f	so	0.20	0.61	0.30	1.72	162.08	206.66	0.50	6.41	0.17	0.21	1.45	0.38	1.26	31294.9
aa263362	5	lm2	m	so	0.22	0.62	0.37	3.56	/	515.45	0.05	5.60	0.23	0.28	1.29	2.35	3.51	0.0
aa49641	5	lm2	m	so	0.27	0.93	0.53	2.72	/	689.95	0.08	14.48	0.23	0.33	1.58	0.65	1.14	21462.7
aa56851	5	lm2	f	so	0.41	1.10	0.74	4.15	/	1122.97	0.05	14.85	0.27	0.28	2.32	1.62	8.14	34969.7
aa56853	5	lm2	f	so	0.10	0.51	0.16	1.82	291.89	226.26	0.53	2.85	0.08	0.10	0.99	1.38	0.77	746.1
aa257373	4	lm2	f	so	0.18	0.58	0.24	1.17	481.71	366.48	1.13	4.57	0.19	0.21	0.52	2.99	0.65	33341.1
aa257381	4	lm2	f	so	0.18	0.79	0.28	2.05	651.27	425.28	0.70	8.60	0.17	0.21	1.08	2.64	0.95	38052.1
aa257396	4	lm2	m	so	0.65	1.50	0.83	2.02	527.48	703.73	0.58	16.86	0.75	0.83	2.19	9.26	0.70	22159.9
aa257398	4	lm2	f	so	0.12	0.53	0.19	1.84	675.60	116.79	0.45	6.08	0.11	0.13	1.51	0.43	0.80	52121.8
aa257400	4	lm2	m	so	0.45	1.12	0.63	2.98	2437.06	538.35	0.15	11.45	0.47	0.51	1.71	3.13	1.65	45866.0
aa257403	4	lm2	m	so	0.29	0.88	0.42	1.98	383.64	341.92	1.25	12.87	0.30	0.34	2.13	4.80	0.69	29205.2
aa257404	4	lm2	m	so	0.19	0.81	0.27	1.48	601.05	189.70	1.25	8.83	0.19	0.24	1.53	2.24	0.56	29418.4
aa257405	4	lm2	m	so	0.16	0.48	0.23	1.73	220.00	155.91	3.28	5.54	0.17	0.20	1.99	2.20	0.58	18546.4
aa257411	4	lm2	m	so	0.19	0.51	0.34	2.27	19.14	379.73	0.20	6.01	0.15	0.17	1.25	1.18	1.48	746.1
aa257416	4	lm2	f	so	0.25	1.17	0.35	2.42	1192.10	229.91	0.33	10.59	0.26	0.32	1.72	0.62	1.12	37964.7
aa257419	4	lm2	f	so	0.29	1.36	0.55	3.18	700.18	1073.77	0.18	15.03	0.20	0.29	1.81	3.61	4.58	16674.9
aa257420	4	lm2	m	so	0.34	1.13	0.53	2.14	911.96	630.73	0.28	20.09	0.29	0.43	1.72	3.24	1.31	42516.4
aa257421	4	lm2	m	so	0.19	0.65	0.35	1.93	/	315.19	0.08	7.93	0.17	0.19	0.60	4.02	0.86	37139.9
aa257439	4	lm2	m	so	0.48	1.77	0.60	1.18	833.88	590.27	0.78	27.24	0.60	0.71	0.88	10.29	0.41	41113.4
aa257441	4	lm2	f	so	1.19	2.52	1.71	4.18	/	911.45	0.08	24.47	1.18	1.05	4.46	1.31	1.69	19255.4
aa257444	4	lm2	m	so	0.22	0.71	0.28	0.75	489.67	327.32	1.65	8.75	0.27	0.28	0.81	5.49	0.43	49474.4

reference	pop.	tooth	sex	season	Sa	Sp	Sq	S5v	Sha	Sda	Spd (10-3)	Vm (10-3)	Vmc	Vvc	Asfc	epLsar (10-3)	H81	Tfv
aa257446	4	lm2	f	so	0.28	0.70	0.46	2.77	19.04	377.04	0.18	7.92	0.25	0.26	1.87	4.13	1.11	18439.8
aa257447	4	lm2	f	so	0.21	0.80	0.33	2.95	/	332.87	0.05	8.36	0.19	0.20	2.47	0.22	1.49	16521.2
aa257448	4	lm2	m	so	0.42	1.70	0.52	2.19	1136.82	357.95	0.48	26.71	0.47	0.65	1.28	4.69	0.54	39709.4
aa257449	4	lm2	m	so	0.36	0.97	0.58	2.32	/	901.35	0.10	7.65	0.29	0.30	1.13	4.14	3.07	36026.9
aa257452	4	lm2	f	so	0.14	0.48	0.22	1.24	632.50	169.06	0.38	7.04	0.13	0.15	0.68	1.80	0.80	852.7
aa257456	4	lm2	m	so	0.26	0.89	0.36	1.67	2221.00	175.08	0.43	9.57	0.27	0.28	2.31	2.07	0.59	19612.3
aa257509	4	lm2	m	so	0.44	0.97	0.68	2.78	180.41	713.51	0.13	10.05	0.39	0.42	0.67	0.72	1.69	15775.1
aa257519	4	lm2	m	so	0.50	1.95	0.68	1.92	1517.55	1084.14	0.48	25.82	0.51	0.63	1.55	8.24	1.09	37796.3
aa257521	4	lm2	f	so	0.14	0.80	0.24	1.16	1086.13	236.59	0.43	2.70	0.12	0.13	1.28	3.76	1.20	532.9
aa257526	4	lm2	f	so	0.11	0.48	0.17	0.74	237.16	148.41	0.90	4.90	0.09	0.13	0.49	1.07	1.01	426.4
aa257528	4	lm2	m	so	0.98	5.20	1.66	6.79	/	1510.74	0.05	67.27	0.80	1.30	3.68	1.95	4.24	50841.7
aa257534	4	lm2	f	so	0.29	0.96	0.45	2.40	211.61	238.31	0.20	12.01	0.25	0.28	2.05	2.68	0.77	34980.2
aa257535	4	lm2	f	so	0.30	0.84	0.54	1.88	938.04	682.99	0.33	7.60	0.25	0.29	1.14	3.00	0.51	7567.8
aa257538	4	lm2	m	so	0.53	1.07	0.91	3.54	34.66	555.82	0.08	11.42	0.41	0.43	3.50	4.15	1.29	25326.0
aa257539	4	lm2	m	so	0.16	0.58	0.24	1.72	379.24	330.64	0.48	6.33	0.15	0.17	0.72	4.64	0.71	0.0
aa257544	4	lm2	f	so	0.60	3.23	0.95	4.97	/	572.03	0.03	36.42	0.51	0.65	4.56	2.67	1.00	41674.3
aa257546	4	lm2	m	so	0.09	0.49	0.13	0.92	565.34	262.61	0.98	3.47	0.09	0.12	0.31	3.19	1.61	4263.5
aa257547	4	lm2	f	so	1.10	1.96	1.71	6.76	/	427.19	0.08	28.17	0.72	0.71	4.17	2.08	3.76	32429.0
aa257557	4	lm2	f	so	0.17	0.61	0.27	1.62	434.35	212.25	0.35	7.65	0.14	0.14	1.46	2.46	1.18	0.0
aa257597	4	lm2	m	nd	0.28	0.78	0.42	2.02	364.16	134.46	0.53	9.07	0.27	0.28	3.93	1.08	0.76	5009.7
aa257602	4	lm2	f	so	0.31	0.87	0.45	2.95	1743.33	238.97	0.28	12.12	0.32	0.39	2.44	0.53	1.05	47538.5
aa257604	4	lm2	f	so	0.23	1.03	0.32	1.47	401.74	189.82	0.33	15.20	0.23	0.27	1.30	3.19	0.47	21850.6
aa257607	4	lm2	m	so	0.72	3.11	1.26	6.61	/	629.97	0.08	42.57	0.53	0.70	4.95	0.94	2.60	47684.8
aa257610	4	lm2	m	so	0.49	0.84	0.67	2.54	895.02	665.37	0.35	6.94	0.51	0.50	1.54	4.77	0.84	8846.8
aa257617	4	lm2	m	so	0.24	0.84	0.33	1.53	573.92	133.45	0.70	9.61	0.24	0.28	2.08	1.98	0.60	6075.5
aa257618	4	lm2	f	so	0.48	1.43	0.61	1.90	1138.98	1639.40	0.55	18.26	0.56	0.60	0.93	3.42	0.54	45051.7
aa257622	4	lm2	f	so	0.22	0.71	0.31	1.40	1152.22	127.72	0.23	6.76	0.23	0.26	1.47	2.22	0.73	17587.1
aa257624	4	lm2	f	nd	0.11	0.49	0.16	1.14	153.76	100.74	0.90	4.14	0.12	0.15	0.93	2.00	0.62	38904.8
aa257626	4	lm2	f	so	0.23	0.66	0.33	1.45	57.29	326.97	0.33	9.32	0.24	0.27	1.00	1.07	3.19	17906.9
aa257627	4	lm2	m	so	0.71	2.08	1.03	3.08	158.09	330.82	0.30	26.85	0.67	0.80	5.00	0.52	1.35	36413.0
aa257632	4	lm2	f	nd	0.23	0.83	0.34	1.88	147.09	156.68	0.38	11.94	0.23	0.25	2.55	1.38	0.65	20571.6
aa257636	4	lm2	f	nd	0.22	0.61	0.32	1.21	403.73	167.77	0.73	8.37	0.21	0.27	1.48	3.00	0.99	3197.7
aa257642	4	lm2	m	so	0.17	0.77	0.24	1.33	347.05	264.31	0.68	6.46	0.17	0.21	1.20	1.19	1.36	7354.6
aa257645	4	lm2	m	so	0.25	1.67	0.32	1.30	5332.98	276.09	0.13	15.31	0.27	0.37	0.73	1.71	1.47	23982.4
aa257680	4	lm2	m	so	0.13	0.65	0.18	1.36	643.83	221.90	1.35	5.49	0.12	0.14	0.77	1.76	0.89	426.4
aa257683	4	lm	m	so	0.07	0.42	0.11	1.19	509.91	224.18	0.75	3.29	0.06	0.09	0.38	1.93	1.38	106.6
aa257704	4	lm2	m	so	0.79	2.77	1.04	3.78	3820.31	669.10	0.30	51.21	0.84	1.05	2.15	7.58	0.49	31373.5
aa257705	4	lm2	f	so	0.10	0.53	0.15	1.43	253.60	376.01	0.15	4.74	0.10	0.11	0.50	0.41	0.91	18653.0
aa257708	4	lm2	m	so	0.36	1.06	0.50	1.58	656.32	310.95	0.93	10.56	0.38	0.40	1.69	0.82	0.62	21104.5

reference	pop.	tooth	sex	season	Sa	Sp	Sq	S5v	Sha	Sda	Spd (10-3)	Vm (10-3)	Vmc	Vvc	Asfc	epLsar (10-3)	H81	Tfv
aa257710	4	lm2	f	so	0.21	1.12	0.31	1.77	862.75	341.51	0.43	15.46	0.22	0.28	1.28	3.95	0.45	41639.0
aa257726	4	lm2	f	nd	0.18	0.85	0.24	1.43	35.40	339.48	0.18	9.45	0.21	0.25	0.47	1.34	3.35	9166.6
aa257729	4	lm2	f	mj	0.37	1.36	0.51	1.30	763.31	426.64	0.65	14.38	0.38	0.49	1.36	5.03	0.45	32380.0
aa257731	4	lm2	m	so	1.14	2.04	1.61	2.97	194.41	727.27	0.13	19.01	1.16	1.05	4.12	2.48	1.78	39018.2
170602	3	UM2	/	/	0.40	1.11	0.52	2.43	535.41	210.62	0.78	11.31	0.46	0.47	3.37	4.05	0.63	31550.2
170603	3	lm2	f	jf	0.63	2.56	0.88	3.61	/	683.08	0.08	49.16	0.63	0.65	1.69	3.11	1.10	24279.3
170604	3	lm2	f	jf	0.30	1.09	0.45	2.55	24.40	374.87	0.13	13.38	0.27	0.38	1.60	3.29	0.86	7994.1
170605	3	UM2	m	/	0.34	1.28	0.44	2.64	1156.82	467.18	0.90	16.51	0.41	0.43	2.16	2.23	0.75	30173.2
170752	3	lm2	m	ja	0.68	2.51	1.06	1.59	/	573.39	0.03	31.84	0.65	1.02	3.04	1.03	0.89	58565.5
170765	3	lm2	f	nd	0.45	0.99	0.81	2.97	24.50	645.11	0.10	13.18	0.29	0.31	3.02	5.32	4.11	12364.3
170766	3	UM2	f	jf	0.22	0.71	0.31	1.76	45.89	245.58	0.40	6.40	0.22	0.27	1.54	0.95	0.94	5969.0
170892	olesi	UM2	/	ja	0.19	0.52	0.28	1.25	170.64	213.86	1.25	2.94	0.17	0.16	1.58	8.92	1.03	1279.1
-a_04-05-18	3	lm2	m	mj	0.25	0.97	0.34	1.87	499.13	284.51	1.13	9.93	0.26	0.29	1.67	4.68	0.51	29951.4
AA-321AC	2	UM	/	/	0.22	0.89	0.42	4.56	137.87	249.56	0.13	11.22	0.21	0.29	2.47	0.49	1.60	46334.4
AA-322AC	2	UM	/	/	0.14	0.78	0.25	1.30	800.08	900.67	0.58	4.94	0.14	0.18	1.39	4.78	0.95	49802.9
AA-324AC	2	UM	/	/	0.17	1.30	0.25	1.05	305.31	109.87	2.05	8.27	0.17	0.21	2.67	3.57	1.08	3943.8
AA-326AC	2	UM	/	/	0.70	2.11	0.94	4.43	567.57	595.22	1.15	28.73	0.76	0.86	9.20	0.58	0.77	35510.4
AA-327AC	2	UM	/	/	0.17	0.75	0.24	2.19	545.63	275.45	0.63	7.83	0.16	0.24	1.55	1.88	0.74	26433.9
AA-A4	2	UM2	m	so	0.08	0.43	0.09	0.72	266.09	363.96	1.55	2.90	0.09	0.10	0.25	3.38	1.50	35813.7
AA-A5	2	lm2	f	/	0.21	1.72	0.28	1.21	435.73	250.02	2.23	14.15	0.24	0.29	2.87	1.79	1.00	32007.6
AA-A6	2	dP4	f	/	0.17	0.86	0.28	2.64	/	618.17	0.05	8.91	0.17	0.24	1.65	2.57	1.27	18228.0
AA-A7	2	lm	f	/	0.33	1.37	0.54	3.70	1495.44	355.75	0.18	18.34	0.30	0.40	2.78	1.55	2.83	30377.7
Zinv_85099	2	lm	f	so	0.22	1.21	0.29	0.75	299.41	230.76	2.18	14.73	0.24	0.34	1.62	9.32	0.31	56558.9
AA_120992	1	lm	f	ja	0.72	3.36	1.44	5.44	/	303.25	0.00	58.55	0.51	0.88	4.62	0.88	2.03	33701.2
AA-04-2010	1	lm2	f	nd	0.21	0.94	0.33	2.54	/	204.89	0.13	10.75	0.19	0.23	1.86	1.74	0.83	55745.8
AA-08-2010	1	lm2	m	nd	0.19	0.62	0.28	3.07	1534.75	223.93	0.55	6.33	0.19	0.22	2.42	2.21	1.01	36879.6
AA-120989	1	UM2	f	ja	0.79	2.52	1.05	2.11	1764.96	611.15	0.38	37.14	0.88	0.80	2.49	0.63	0.80	24392.7
AA-120990	1	lm2	f	ja	0.26	1.01	0.41	2.62	399.58	177.80	1.68	13.60	0.23	0.29	3.80	0.91	0.74	8527.1
AA-120991	1	UM	f	ja	0.29	2.28	0.51	3.31	818.93	485.98	0.68	20.27	0.19	0.30	4.01	3.39	1.77	52179.4
AA-120992	1	lm2	f	ja	0.72	3.36	1.44	5.44	/	303.25	0.00	58.55	0.51	0.88	4.62	0.88	2.03	33701.2
AA-120994	1	UM2	f	ja	0.47	1.14	0.65	5.06	/	621.04	0.23	13.71	0.50	0.52	4.29	3.88	1.71	25513.1
AA-12937	1	lm	f	ja	0.22	1.64	0.43	4.83	497.17	435.39	0.23	21.35	0.18	0.23	2.35	4.27	2.79	39011.4
AA-138864	1	lm2	f	ja	0.20	0.87	0.33	2.68	418.77	265.27	0.30	7.11	0.18	0.22	2.79	2.86	0.95	4583.3
AA-138865	1	lm2	f	ja	0.44	1.58	0.77	4.51	/	234.10	0.18	20.87	0.42	0.59	5.31	1.81	2.83	43136.8
AA-140164	1	lm2	f	ja	0.59	2.11	0.86	2.64	760.43	637.24	0.23	30.48	0.52	0.88	2.08	0.32	0.97	51273.6
AA-15-2010	1	lm2	f	nd	0.90	3.43	1.07	2.48	/	485.71	0.13	48.43	1.10	1.26	1.97	6.04	1.64	37805.0
AA-16-2010	1	UM2	f	nd	0.15	0.52	0.30	3.61	1355.58	355.51	0.10	6.42	0.13	0.18	2.25	0.42	3.67	2470.8
AA-17-2010	1	lm	f	nd	0.54	2.76	0.80	3.75	603.07	623.19	0.28	32.65	0.52	0.58	3.72	1.63	0.94	32913.0
AA-18-2010	1	lm2	f	nd	1.23	4.23	1.60	3.64	/	756.39	0.13	55.80	1.19	1.86	3.04	6.13	0.85	38786.7

reference	pop.	tooth	sex	season	Sa	Sp	Sq	S5v	Sha	Sda	Spd (10-3)	Vm (10-3)	Vmc	Vvc	Asfc	epLsar (10-3)	H81	Tfv
AA-22-2010	1	lm2	f	nd	0.18	0.90	0.39	3.82	1921.01	512.12	0.18	5.32	0.12	0.19	2.42	0.67	2.96	4911.8
AA-24-2010	1	lm2	m	nd	0.19	0.72	0.31	3.94	/	337.84	0.08	7.06	0.19	0.28	2.21	1.51	1.89	2451.5
AA-30-2010	1	lm2	m	nd	0.73	2.87	1.18	4.06	/	192.17	0.08	46.97	0.61	0.96	4.31	2.92	1.49	51680.2
AA-32-2010	1	lm2	m	nd	0.40	1.00	0.53	2.49	287.08	221.72	0.58	10.11	0.44	0.44	3.35	2.86	0.64	11405.0
AA-33-2010	1	UM2	f	nd	0.29	1.10	0.39	2.10	639.77	164.11	0.95	8.72	0.30	0.30	2.62	0.61	0.64	30670.9
AA-36-2010	1	lm2	f	nd	0.37	1.55	0.64	5.60	110.87	347.33	0.10	26.67	0.31	0.43	5.90	1.56	1.30	34658.6
AA-37-2010	1	lm2	f	nd	0.65	1.59	0.90	3.33	152.94	303.68	0.23	17.86	0.70	0.66	9.49	0.61	1.46	63564.7
AA-3769	1	lm2	/	/	0.39	1.20	0.57	2.60	29.87	311.04	0.13	13.29	0.37	0.46	1.33	4.73	1.75	54068.3
.A-39370-69	1	UM3	f	ma	0.33	1.52	0.46	3.06	389.25	362.68	1.50	17.66	0.34	0.45	3.28	3.02	0.62	30910.7
.A-39405-70	1	UM2	m	ja	0.07	1.01	0.10	0.83	659.83	466.58	0.95	3.98	0.08	0.10	0.26	5.90	1.37	25256.0
.A-39432-70	1	lm2	f	ja	0.35	1.36	0.51	5.12	759.45	305.12	0.48	15.55	0.37	0.42	5.05	1.79	1.34	22703.3
AA-41-2010	1	lm2	f	nd	0.28	1.01	0.46	2.27	735.95	542.48	0.15	10.15	0.26	0.34	1.50	1.63	1.96	26433.9
AA-42-2010	1	lm2	f	nd	0.54	1.68	0.91	9.13	/	646.92	0.08	12.66	0.50	0.52	8.26	0.58	1.78	53428.7
AA-43-2010	1	lm2	/	nd	1.52	2.52	2.14	6.31	874.30	485.84	0.10	14.21	1.49	1.23	16.42	3.67	0.94	48717.3
AA-45-2010	1	lm	f	nd	0.49	1.19	0.86	6.45	27.12	395.46	0.08	14.22	0.30	0.34	5.90	2.24	1.37	2025.2
AA-48-2010	1	lm2	f	nd	0.72	2.57	1.20	6.31	/	1177.59	0.00	34.47	0.54	0.72	4.63	1.28	4.01	51264.9
AA-nn10	1	lm2	/	/	0.39	1.21	0.55	2.82	439.16	193.28	1.13	13.67	0.37	0.40	4.52	0.76	0.51	13217.0
AA-nn13	1	lm2	/	/	0.44	1.12	0.65	3.33	3643.33	365.23	0.18	13.85	0.42	0.48	4.88	0.26	1.27	22780.2
AA-nn14	1	lm2	/	/	0.18	1.60	0.60	5.59	/	312.00	0.03	4.70	0.12	0.16	5.47	2.52	3.01	30804.1
AA-nn16	1	lm2	/	/	0.43	1.88	0.67	4.13	1544.67	313.99	0.20	14.86	0.40	0.55	5.11	1.60	1.50	19484.6
AA-nn3	1	lm2	/	/	0.12	0.73	0.19	1.42	956.20	178.44	0.53	3.16	0.11	0.13	1.15	0.53	0.71	20465.0
AA-nn4	1	lm2	/	/	0.16	0.61	0.23	2.60	285.07	353.59	0.23	9.22	0.16	0.19	1.21	2.53	2.01	0.0
AA-nn5	1	lm1	/	/	0.43	1.25	0.66	4.06	/	444.87	0.08	9.63	0.42	0.43	4.33	1.46	1.03	6182.1
AA-nn6	1	lm2	/	/	0.39	1.36	0.69	2.11	23.13	249.70	0.10	16.22	0.29	0.35	3.94	3.22	2.01	29872.7
AA-nn7	1	dp4	/	/	0.50	1.20	0.75	4.52	272.36	344.28	0.20	15.44	0.46	0.47	4.24	0.91	1.33	16734.4
AA-nn8	1	lm2	/	/	0.66	2.60	1.60	14.24	9.44	367.25	0.05	22.52	0.48	0.56	16.72	1.11	6.02	32099.5
AA-w2011	1	lm	/	/	0.34	1.35	0.51	2.17	230.63	415.95	0.10	20.72	0.32	0.43	2.58	2.81	1.37	41220.0
ZMK1482	6	lm2	f	so	0.15	0.50	0.19	0.56	233.55	99.48	1.10	5.57	0.18	0.22	0.56	2.21	0.49	6075.5
ZMK1484	6	lm2	f	so	0.14	0.43	0.19	1.48	284.54	166.51	0.75	4.45	0.15	0.21	0.90	2.52	0.75	2984.5
ZMKCN1448	6	lm2	f	so	0.18	0.57	0.26	1.05	858.98	272.27	0.45	6.28	0.18	0.22	0.62	3.09	0.58	2131.8
ZMKCN1481	6	lm2	f	so	0.36	0.89	0.65	1.87	/	595.78	0.15	9.81	0.30	0.32	1.85	2.07	1.72	13933.4
ZMKCN1483	6	lm2	f	so	0.13	0.65	0.19	1.32	322.57	221.49	0.48	11.00	0.13	0.16	0.85	4.43	1.00	426.4
ZMKCN2924	6	lm2	f	/	0.36	1.46	0.60	4.12	210.44	749.37	0.03	14.41	0.35	0.48	2.40	1.08	1.05	15609.0
MK1044	6	lm2	m	so	0.19	0.94	0.25	1.41	372.29	328.30	0.98	6.42	0.21	0.26	0.78	5.25	0.50	20145.2
ZMKK91	6	lm2	f	so	0.09	0.31	0.13	1.14	243.86	119.70	0.55	3.87	0.09	0.11	0.84	3.11	0.52	959.3
ZMKMK939	6	lm2	m	so	0.20	0.69	0.27	1.47	1311.60	606.93	0.65	7.70	0.22	0.29	0.51	4.37	0.62	33573.5
ZMKMK940	6	lm2	f	so	0.13	0.51	0.23	1.35	121.30	595.62	0.13	5.06	0.13	0.16	0.84	1.91	2.59	3197.7

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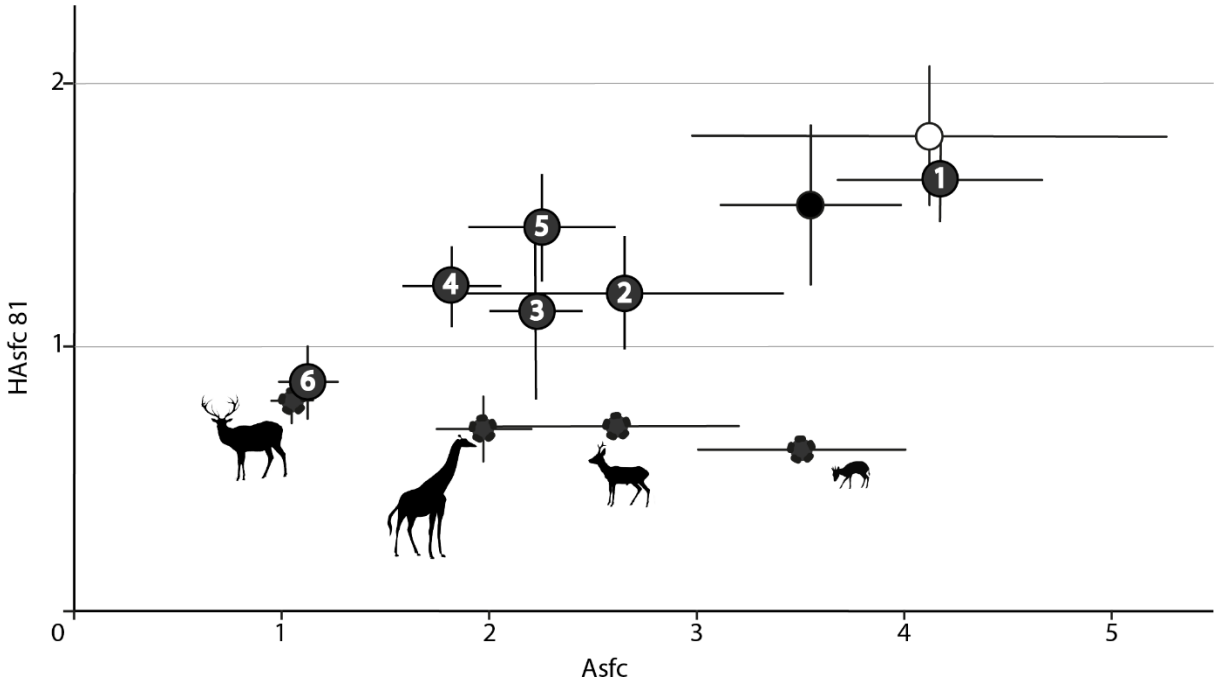
Table S2:

Population	n	n (Asfc>2.0)	n (epLsar>0.005)	% (Asfc>2.0)	% (epLsar>0.005)
1-Biebrza	44	35	3	79.5	6.8
Jul.-Aug.	12	11	1	91.7	8.3
Nov.-Dec.	18	14	2	77.8	11.1
2-Białowieża	10	5	1	50.0	10.0
3-Polesie	9	4	2	44.4	22.2
4-Målselv	59	18	5	27.8	8.5
5-Gausdal	62	15	16	24.2	25.8
6-Småland	10	1	1	10.0	10.0
Giraffa camelopardalis	16	7	1	43.8	6.3
Cephalophus silvicultor	3	20	3	74.1	11.1
Cervus elaphus	19	1	17	5.3	89.5
Capreolus capreolus	18	7	13	38.9	72.2

867 Figure S1:



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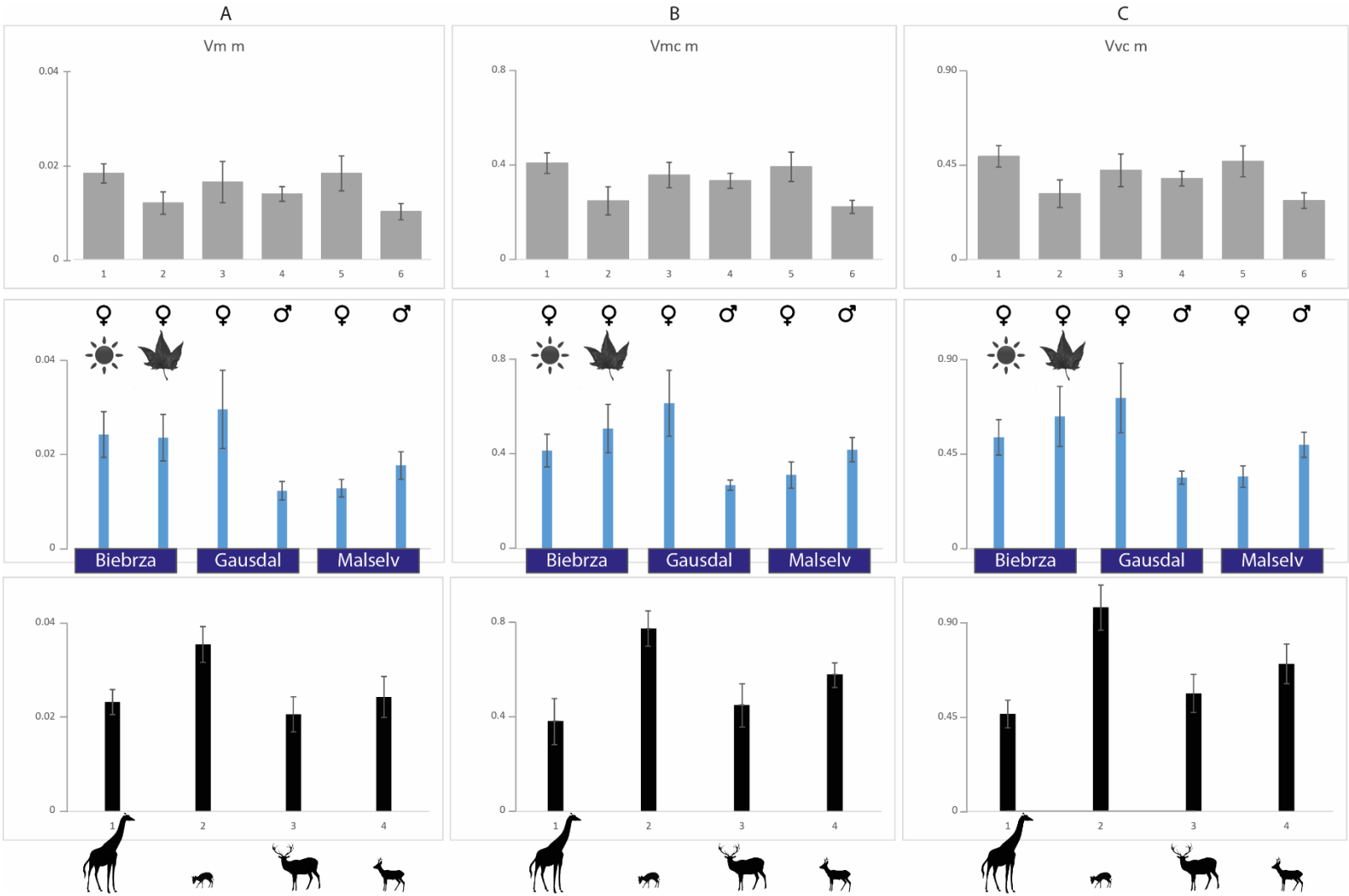
870 Figure S2:



871