



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

Emilie Berlioz, Charlotte Leduc, Emilia Hofman-Kamińska, Olivier Bignon-Lau, Rafal Kowalczyk, Gildas Merceron

► To cite this version:

Emilie Berlioz, Charlotte Leduc, Emilia Hofman-Kamińska, Olivier Bignon-Lau, Rafal Kowalczyk, et al.. Dental microwear foraging ecology of a large browsing ruminant in Northern Hemisphere: The European moose (*Alces alces*). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2022, 586, pp.110754. 10.1016/j.palaeo.2021.110754 . hal-03435143

HAL Id: hal-03435143

<https://hal.science/hal-03435143>

Submitted on 30 Nov 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Authors: Emilie Berlioz (1,2)*, Charlotte Leduc (3,4), Emilia Hofman-Kamińska (5), Olivier Bignon-Lau (6), Rafał Kowalczyk (5), Gildas Merceron (2)

1: UMR5608 TRACES, team SMP3C; F-31058 Toulouse cedex 9, France

2: UMR7262 PALEVOPRIM ; 86073 Poitiers Cedex 9, France

3: INRAP Grand-Est; F-57063 Metz, France

4: UMR 8215 Trajectoires; F-92023 Nanterre Cedex, France

5: Mammal Research Institute, Polish Academy of Sciences; 17-230 Białowieża, Poland

6: UMR7041 ArScAn, team Ethnologie préhistorique, F-92023 Nanterre Cedex, France

* Corresponding author: Emilie Berlioz (emilie.berlioz@univ-tlse2.fr)

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-population 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).

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

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

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

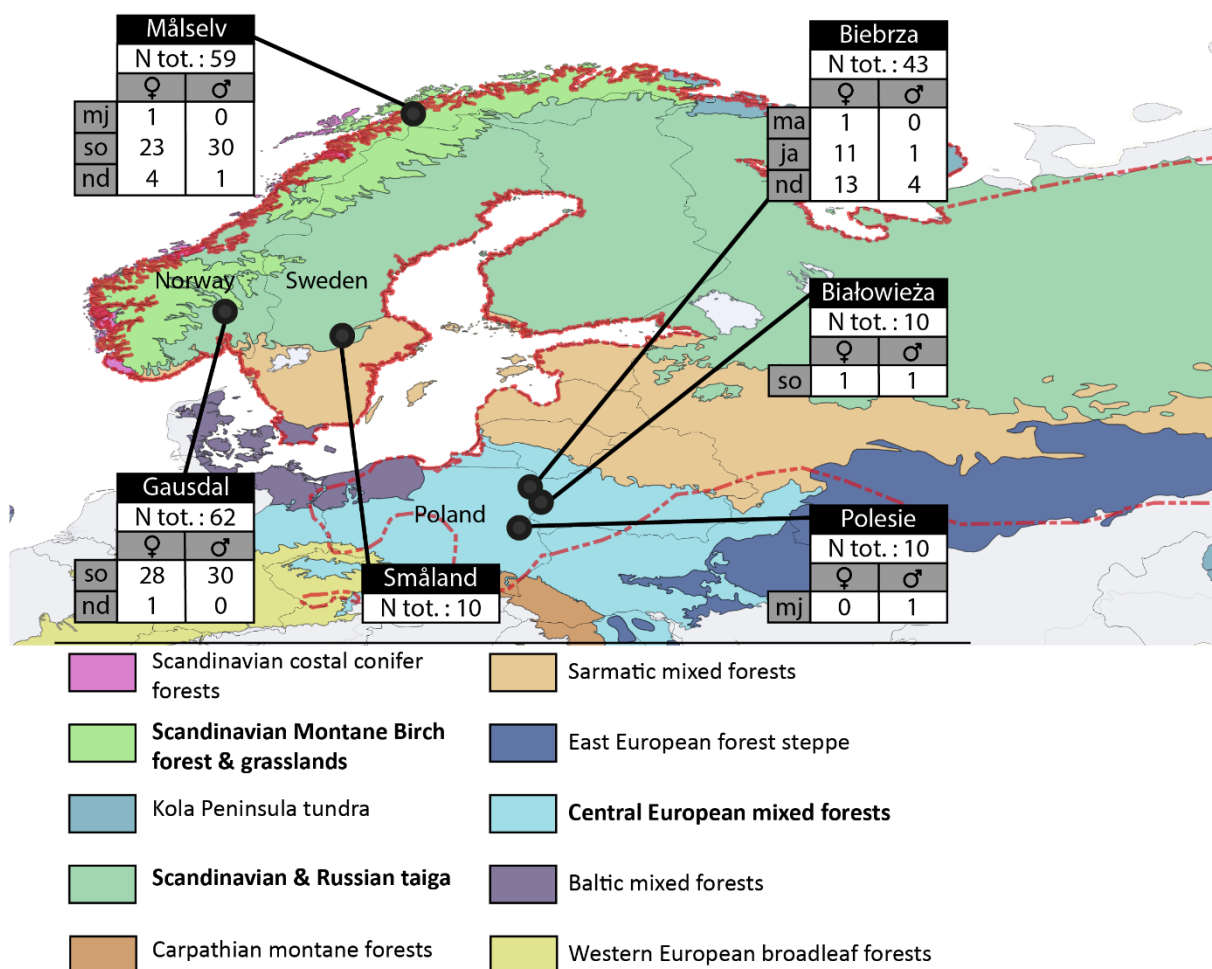


Figure 1: Geographic range of moose in Europe and localization of the 6 populations of interest. Norway: Målselv, Gausdal; Sweden: Småland; Poland: Biebrza, Białowieża, Polesie. Range data for European moose are illustrated by a red dashed line and were downloaded from <http://www.iucnredlist.org>. Colors 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 km²; 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./km²), 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./km² 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 km², 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 nigrum* 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*

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

2.4. Dental microwear texture analysis

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

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

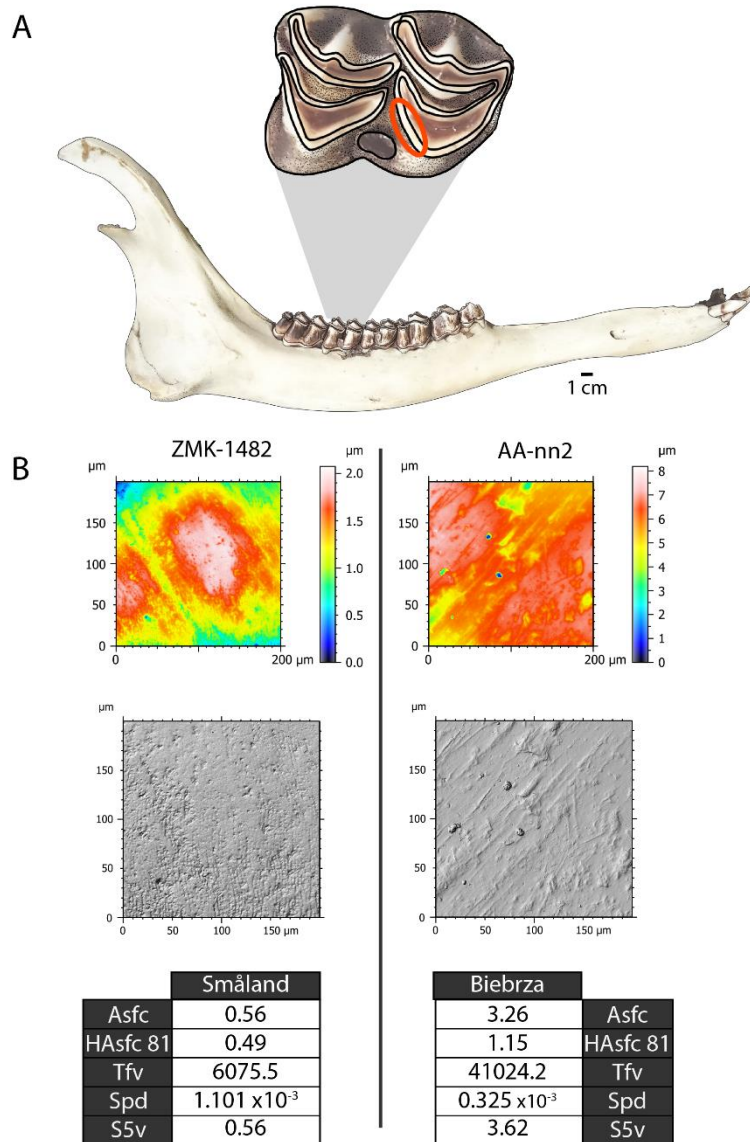


Figure 2: Acquisition of dental textures for Dental Microwear Texture Analysis (DMTA). A: molding of the disto-lingual facet of the protoconid of second lower molars, circled in orange. B: Two contrasted moose dental textures, respectively specimen ZMK-1482 from Småland, Sweden and AA-nn2 from Biebrza 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
<i>Sa</i>	arithmetic mean of the absolute of the heights	μm
<i>Sp</i>	Maximum peak height	μm
<i>Sq</i>	Standard deviation of the height distribution	μm
<i>S5v</i>	Five point valley height	μm
<i>Sha</i>	close hill area	μm^2
<i>Sda</i>	close dale area	μm^2
<i>Spd</i>	density of peaks	$\text{n}/\mu\text{m}^2$
<i>Vm</i>	material volume at a given material ratio (p=10%)	$\mu\text{m}^3/\mu\text{m}^2$
<i>Vmc</i>	material volume of the core at a given material ratio (p=10%, q=80%)	$\mu\text{m}^3/\mu\text{m}^2$
<i>Vvc</i>	void volume of the core (p=10%, q=80%)	$\mu\text{m}^3/\mu\text{m}^2$
<i>Asfc</i>	Area-scale fractal complexity	
<i>epLsar</i>	exact proportion Length-scale anisotropy of the relief	
<i>HAsfc 81</i>	Heterogeneity of the Area-scale fractal complexity (81 cells)	
<i>Tfv</i>	Textural fill volume	μm^3

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: $epLsar > 5.0 \times 10^{-3}$) 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 ($epLsar > 5.0 \times 10^{-3}$) 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).

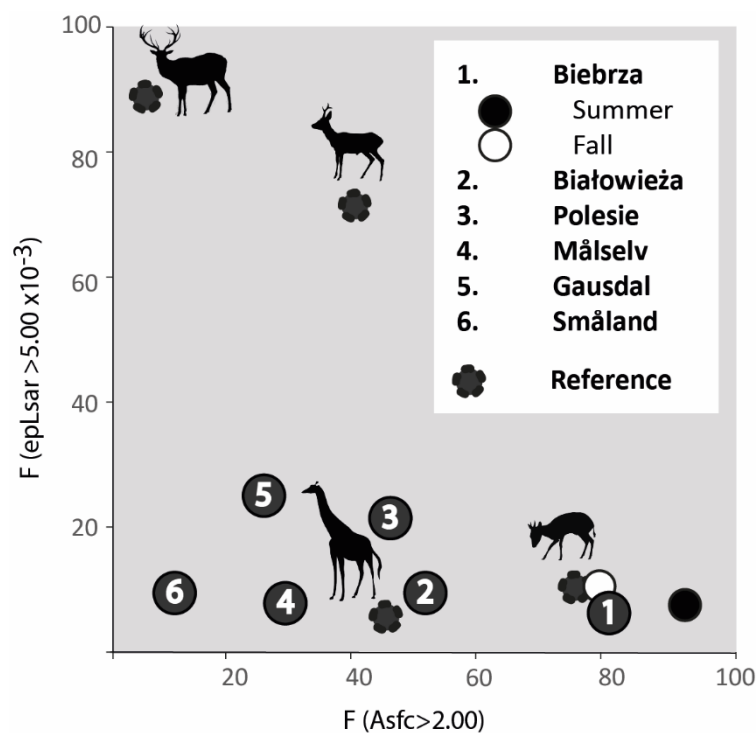
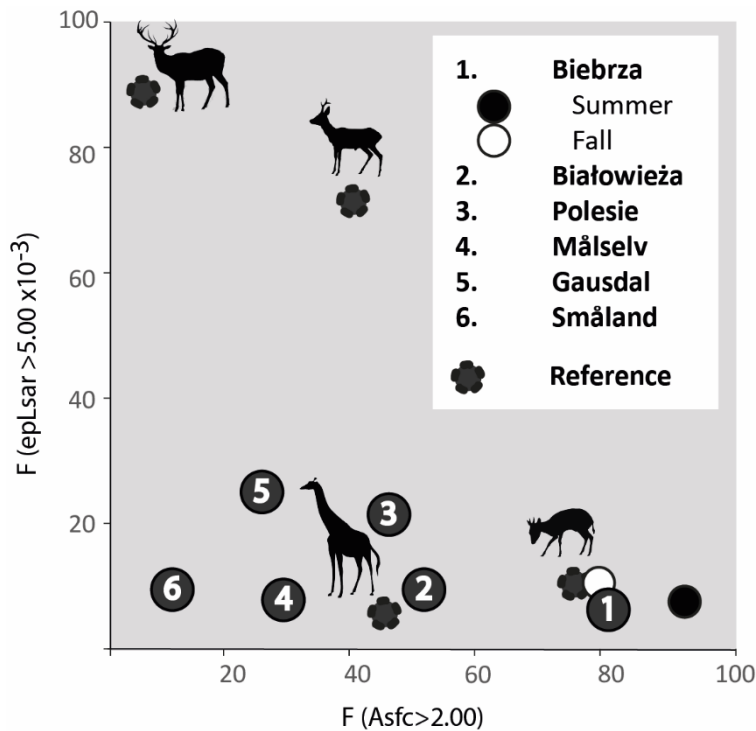


Figure 3: Frequency of specimens per population with high complexity (*Asfc* > 2.0) and high anisotropy (*epLsar* > 5.00 × 10⁻³). **Poland:** 1: Biebrza, 2: Białowieża, 3: Polesie; **Norway:** 4: Målselv, 5: Gausdal; **Sweden:** 6: Småland. Four samples of extant ungulate species with well-known diet 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).



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

Inter-population differences based on Gaussian GLM performed on the global dataset followed by manovas, anovas and supported by HSD Post-Hoc tests (Figure 4, see also Annex 3 for AIC and p-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

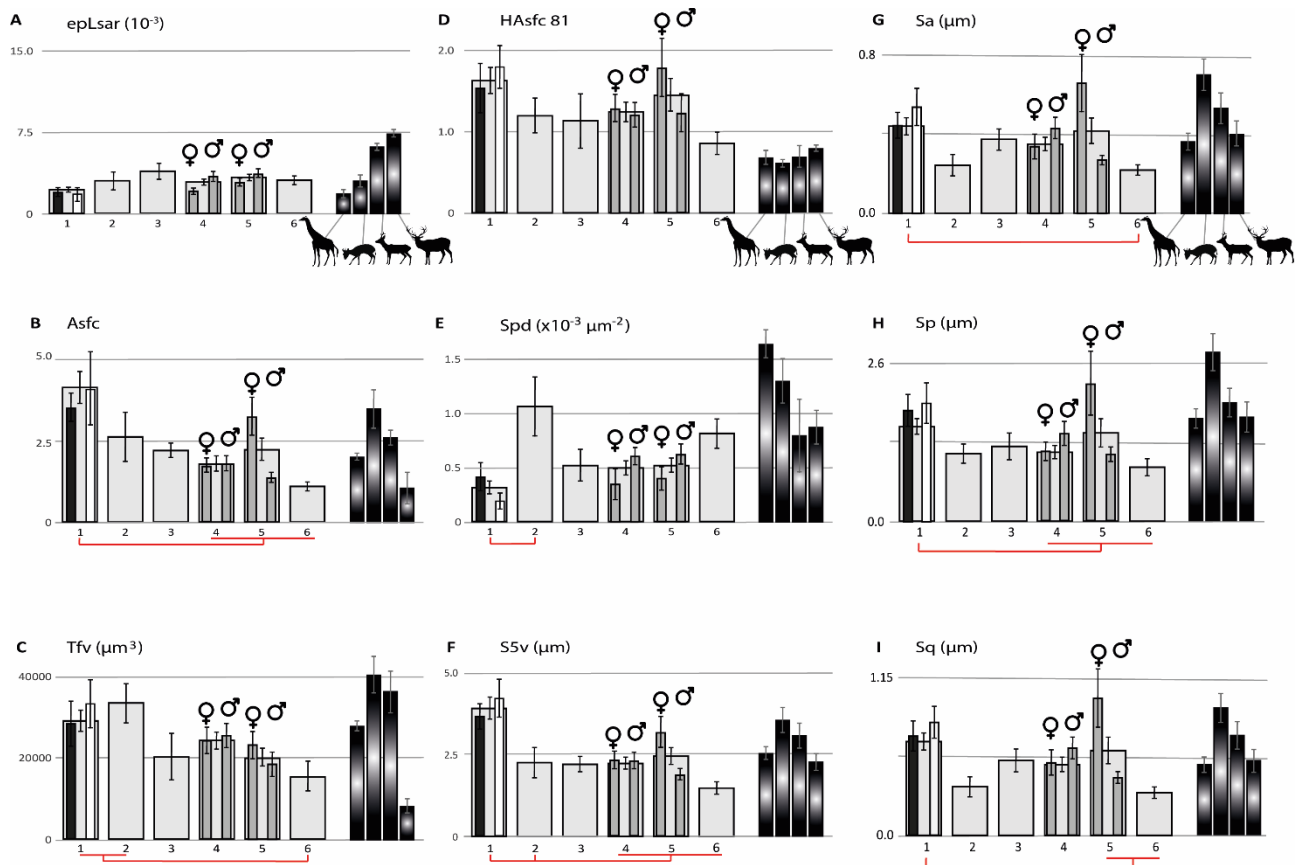


Figure 4: Barplots representing mean and standard error of mean for textural parameters that are mentioned in the discussion of the article. Parameters are illustrated for the six moose populations. Poland: 1: Biebrza, 2: Białowieża, 3: Polesie; Norway: 4: Målselv, 5: Gausdal; Sweden: 6: Småland. In 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 sylvicultr, 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

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

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

loc	season		sex	n	<i>Sa</i>		<i>Sp</i>		<i>Sq</i>		<i>S5v</i>		<i>Sha</i>		<i>Sda</i>		<i>Spd</i> (10 ⁻³)		<i>Vm</i>		<i>Vmc</i>		<i>Vvc</i>		<i>Asfc</i>		<i>epLsar</i> (10 ⁻³)		<i>HAsfc</i> 81		<i>Tfv</i>	
					<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>	<i>m</i>	<i>s</i>
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
	all	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
	all	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
	all	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	/
	all	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	/
	all	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	/
	all	m	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	/
	all	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
	all	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
	all	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
	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
	all	f	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
2	all	all	2		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	/
	all	f	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	/
	all	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	/
	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
	all	f	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	/
	all	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	/
	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
	all	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	/
	all	m	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	/
	all	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
	all	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
	all	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	/
3	all	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
	all	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
	all	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
	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
	all	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	/
	all	m	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	/
	all	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
	all	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
	all	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
	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
	all	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
	all	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
	all	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
	all	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

338 These interpretations based on dental microwear analysis are in line with previous studies
 339 based on other proxies exploring the feeding ecology of this cervid that underlined the importance of
 340 ligneous elements in its diet (rumen content analysis: Morow, 1976; measured bites: Shipley, 2010;
 341 feces analysis: Kuijper et al., 2016). *Alces alces* has specific physiological adaptations, including the
 342 ability to produce tannin-binding

344 preferred diet (Hagerman and Robbins, 1993; Clauss et al., 2008; Moreira et al., 2013; Spitzer et al.,
 345 2020). Among ingested elements are buds, twigs, stems, foliage and berries. Bark and leaf-litter can
 346 also constitute large amounts of moose diet. For instance, bark represents up to 39% of moose spring-
 347 diet before the spring green-up and leaf litter accounts for 55-65% of early winter diet in Central
 348 Alberta (Renecker and Hudson, 1988). The specialized long muscular prehensile nose of moose,
 349 however, prevents it from consuming the herbaceous layer, so grass and forbs never make up a large
 350 part of its diet (Shipley, 2010; Spitzer et al., 2020). However, the amount of grasses and forbs in diet
 351 varies seasonally and from one habitat to another. While many studies report a small amount of
 352 herbaceous monocots (<1.5% sedges, rushes, and grasses; e.g. in Morow, 1976), others populations
 353 may incorporate more of them, especially in summer (up to 25% for one Norwegian population in
 354 Wam and Hjeljord, 2010; 10-17% of sedges, rushes and grasses in Biebrza moose diet in Kuijper et al.,
 355 2016).

356 Table 3: Significant inter-population differences supported by HSD tests. Populations: 1: Biebrza; 2: Białowieża; 3: Polesie; 4:
 357 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						

358

359 4.2. Different ways to browse: inter-population variations

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

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

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

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

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

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

In Gausdal, plant diversity is low, dominated by *Betula pubescens* and *Pinus sylvestris*, resulting for moose to almost exclusively forage on deciduous *B. pubescens* (Sæther and Andersen, 1990; Davids et al., 2006). In Målselv however, moose focus on a taxonomically more diversified diet composed of *Salix* spp., *Sorbus aucuparia*, *Populus tremula*, *Prunus padus* (Sæther and Andersen, 1990). The difference in diet between the two Norwegian populations is not reflected by the dental microwear 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 km², 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-population 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.

Acknowledgements

This study was funded by the French Agency for Research [ANR TRIDENT, ANR-13-JSV7-0008-01, PI: G. Merceron], the Polish National Science Centre [Grant No N N304 301940], the WP 1.3 of the LabEx DynamiTe (University Paris 1 Panthéon-Sorbonnes) and the PCR “Du Dernier Maximum Glaciaire à l'optimum climatique dans le Bassin parisien et ses marges” [2019-2021; P.I.: Sylvain Griselin, Ludovic Mevel].

Authors are grateful to Kristian Murphy Gregersen, Centre for Geogenetics, responsable of the Quaternary Zoology Collections (Zoological Museum of Copenhagen - Denmark) and Daniel Klingberg Johansson, from the collections staff, responsible of the Mammals and Amphibians Collection (Zoological Museum of Copenhagen - Denmark), and the staff of the Zoological Collection of Mammal Research Institute, Polish Academy of Sciences in Białowieża. The authors also thank Vebjørn Veiberg and Olav Strand from the Norwegian Institute for Nature Research (NINA) for giving us access to Norwegian material at NINA, G. Reynaud and L. Painault (PALEVOPRIM, Poitiers, France) for administrative guidance, Sabine Riffaut for artwork of the figure 2, M. Colyn and A. Ramdarshan for discussion. Finally, the authors would like to thank I. Calandra and an anonymous reviewer as well as the guest editor T. Tütken, who helped to improve the quality of this manuscript.

Data Availability

Research data are available upon request to the corresponding author.

References

- Ackermans, N.L., Winkler, D.E., Martin, L.F., Kaiser, T.M., Clauss, M., Hatt, J.-M., 2020. Dust and grit matter: abrasives of different size lead to opposing dental microwear textures in experimentally fed sheep (*Ovis aries*). *Journal of Experimental Biology* 223. doi:10.1242/jeb.220442
- Andersen, R., 1991. Habitat deterioration and the migratory behaviour of moose (*Alces alces* L.) in Norway. *Journal of Applied Ecology* 28, 102–108.
- Andersen, R., Saether, B.-E., 1992. Functional response during winter of a herbivore, the moose, in relation to age and size. *Ecology* 73, 542–550.
- Apollonio, M., Belkin, V.V., Borkowski, J., Borodin, O.I., Borowik, T., Cagnacci, F., Danilkin, A.A., Danilov, P.I., Faybich, A., Ferretti, F., 2017. Challenges and science-based implications for modern

management and conservation of European ungulate populations. *Mammal research* 62, 209–217.

Azorit, C., Tellado Ruiz, M.S., Oya, A., Moro, J., 2012. Seasonal and specific diet variations in sympatric red and fallow deer of southern Spain: a preliminary approach to feeding behaviour. *Animal Production Science* 52, 720–727.

Ball, J.P., Nordengren, C., Wallin, K., 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology* 7, 39–47.

Berlio, E., 2017. Écologie alimentaire et paléoenvironnements des cervidés européens du Pléistocène inférieur: le message des textures de micro-usure dentaire (PhD Thesis). Université de Poitiers, France.

Berlio, E., Azorit, C., Blondel, C., Tellado Ruiz, M.S., Merceron, G., 2017. Deer in an arid habitat: dental microwear textures track feeding adaptability. *Hystrix, the Italian Journal of Mammalogy* 28, 222–230.

Bignon-Lau, O., Catz, N., Berlio, E., Veiberg, V., Strand, O., Merceron, G., 2017. Dental microwear textural analyses to track feeding ecology of reindeer: a comparison of two contrasting populations in Norway. *Mammal Research* 62, 111–120.

Borowik, T., Cornulier, T., Jędrzejewska, B., 2013. Environmental factors shaping ungulate abundances in Poland. *Acta Theriologica* 58, 403–413.

Borowik, T., Wawrzyniak, P., Jędrzejewska, B., 2016. Red deer (*Cervus elaphus*) fertility and survival of young in a low-density population subject to predation and hunting. *Journal of Mammalogy* 97, 1671–1681.

Borowik, T., Ratkiewicz, M., Maślanko, W., Duda, N., Rode, P., Kowalczyk, R., 2018. Living on the edge—The predicted impact of renewed hunting on moose in national parks in Poland. *Basic and Applied Ecology* 30, 87–95.

Borowik, T., Ratkiewicz, M., Maślanko, W., Duda, N., Kowalczyk, R., 2020. The level of habitat patchiness influences movement strategy of moose in eastern Poland. *PLoS ONE* 15, e0230521.

Borowik, T., Kowalczyk, R., Maślanko, W., Duda, N., Ratkiewicz, M., 2021. Annual movement strategy predicts within-season space use by moose. *Behavioral Ecology and Sociobiology* 75, 1–11.

Bridault, A., 1992. The status of Elk during the Mesolithic. *Anthropozoologica* 16, 151–160.

Calandra, I., Merceron, G., 2016. Dental microwear texture analysis in mammalian ecology. *Mammal Review* 46, 215–228.

Calandra, I., Schulz, E., Pinnow, M., Krohn, S., Kaiser, T.M., 2012. Teasing apart the contributions of hard dietary items on 3D dental microtextures in primates. *Journal of Human Evolution* 63, 85–98.

Calandra, I., Zub, K., Szafrńska, P.A., Zalewski, A., Merceron, G., 2016a. Silicon-based plant defences, tooth wear and voles. *Journal of Experimental Biology* 219, 501–507.

Calandra, I., Labonne, G., Schulz-Kornas, E., Kaiser, T.M., Montuire, S., 2016b. Tooth wear as a means to quantify intra-specific variations in diet and chewing movements. *Scientific Reports* 6, 1–9.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309, 1239–1241.

Cederlund, G., Sand, H. akan, 1994. Home-range size in relation to age and sex in moose. *Journal of Mammalogy* 75, 1005–1012.

Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., McCabe, A.M., 2009. The last glacial maximum. *Science* 325, 710–714.

Clauss, M., Kaiser, T.M., Hummel, J., 2008. The morphophysiological adaptations of browsing and grazing mammals. In: Gordon, I.J., prins, H.H.T. (Eds.), *The Ecology of Browsing and Grazing*. Springer, pp. 47–88.

Crees, J.J., Carbone, C., Sommer, R.S., Benecke, N., Turvey, S.T., 2016. Millennial-scale faunal record reveals differential resilience of European large mammals to human impacts across the Holocene. *Proceedings of the Royal Society B: Biological Sciences* 283, 20152152.

601 Czernik, M., Taberlet, P., Świsłocka, M., Czajkowska, M., Duda, N., Ratkiewicz, M., 2013. Fast and
 602 efficient DNA-based method for winter diet analysis from stools of three cervids: moose, red
 603 deer, and roe deer. *Acta Theriologica* 58, 379–386.
 604 Davids, C., Gwynn, J.P., Dowdall, M., 2006. Terrestrial monitoring in Øvre Dividalen (No. 42–12).
 605 Statens Straalevern.
 606 DeSantis, L.R., 2016. Dental microwear textures: reconstructing diets of fossil mammals. *Surface*
 607 *Topography: Metrology and Properties* 4, 1–12.
 608 Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri,
 609 S., Hedao, P., Noss, R., 2017. An ecoregion-based approach to protecting half the terrestrial
 610 realm. *BioScience* 67, 534–545.
 611 Estes, R., 1991. The behavior guide to African mammals. University of California Press Berkeley.
 612 European Bison Pedigree Book, Raczyński Jan. ed, 2020. Białowieża National Park. Białowieża.
 613 Francisco, A., Brunetière, N., Merceron, G., 2018. Gathering and Analyzing Surface Parameters for Diet
 614 Identification Purposes. *Technologies* 6, 75.
 615 doi:<https://doi.org/10.3390/technologies6030075>
 616 Franzmann, A.W., 1981. *Alces alces*. *Mammalian Species* 154, 1–7.
 617 Gagnon, M., Chew, A.E., 2000. Dietary preferences in extant African Bovidae. *Journal of Mammalogy*
 618 81, 490–511.
 619 Garel, M., 2005. Conséquences de la chasse et des contraintes environnementales sur la démographie
 620 des populations d'ongulés. L'exemple du mouflon méditerranéen (*Ovis gmelini musimon* ×
 621 *Ovis* sp.) en France et de l'élan (*Alces alces*) en Norvège. (PhD Thesis). Université Claude
 622 Bernard-Lyon I, France, Lyon.
 623 Gębczyńska, Z., 1980. Food of the roe deer and red deer in the Białowieża Primeval Forest. *Acta*
 624 *Theriologica* 25, 487–500.
 625 Gębczyńska, Z., Raczyński, J., 1989. Distribution, population structure, and social organization of moose
 626 in the Biebrza Valley, Poland. *Acta Theriologica* 34, 195–217.
 627 Gebert, C., Verheyden-Tixier, H., 2001. Variations of diet composition of red deer (*Cervus elaphus* L.)
 628 in Europe. *Mammal Review* 31, 189–201.
 629 Goffin, R.A., De Crombrughe, S.A., 1976. Régime alimentaire du cerf (*Cervus elaphus* L.) et du
 630 chevreuil (*Capreolus capreolus* L.) et critères de capacité stationnelle de leurs habitats.
 631 *Mammalia* 40, 355–376.
 632 Goss, R.J., 1983. Deer antlers, regeneration, evolution and function, Academic Press. ed. New York.
 633 Hagerman, A.E., Robbins, C.T., 1993. Specificity of tannin-binding salivary proteins relative to diet
 634 selection by mammals. *Canadian Journal of Zoology* 71, 628–633.
 635 Henttonen, H., Stubbe, M., Maran, T., Tikhonov, A., 2011. *Alces alces* [WWW Document]. The IUCN
 636 Red List of Threatened Species 2016. URL <http://www.iucnredlist.org>
 637 Hofman-Kamińska, E., Merceron, G., Bocherens, H., Makowiecki, D., Piličiauskienė, G., Ramdarshan,
 638 A., Berlioz, E., Kowalczyk, R., 2018. Foraging habitats and niche partitioning of European large
 639 herbivores during the Holocene—Insights from 3D dental microwear texture analysis.
 640 *Palaeogeography, Palaeoclimatology, Palaeoecology* 506, 183–195.
 641 Hofman-Kamińska, E., Bocherens, H., Drucker, D.G., Fyfe, R.M., Gumiński, W., Makowiecki, D., Pacher,
 642 M., Piličiauskienė, G., Samojlik, T., Woodbridge, J., 2019. Adapt or die—Response of large
 643 herbivores to environmental changes in Europe during the Holocene. *Global Change Biology*
 644 25, 2915–2930.
 645 Hofmann, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of
 646 ruminants: a comparative view of their digestive system. *Oecologia* 78, 443–457.
 647 Homolka, M., 1998. Moose (*Alces alces*) in the Czech Republic: Chances for survival in the man-made
 648 landscape, *Folia Zoological Monographs*. Institute of Vertebrate Biology, Academy of
 649 Sciences of the Czech Republic.
 650 Hörnberg, S., 2001. The relationship between moose (*Alces alces*) browsing utilisation and the
 651 occurrence of different forage species in Sweden. *Forest Ecology and Management* 149, 91–
 652 102.

653 Hua, L.-C., Brandt, E.T., Meullenet, J.-F., Zhou, Z.-R., Ungar, P.S., 2015. An in vitro study of dental
 654 microwear formation using the BITE Master II chewing machine. *American Journal of Physical*
 655 *Anthropology* 158, 769–775.
 656 Hundertmark, K.J., Shields, G.F., Udina, I.G., Bowyer, R.T., Danilkin, A.A., Schwartz, C.C., 2002.
 657 Mitochondrial phylogeography of moose (*Alces alces*): late Pleistocene divergence and
 658 population expansion. *Molecular Phylogenetics and Evolution* 22, 375–387.
 659 Jędrzejewska, B., Jędrzejewski, W., 1998. Abundance of Prey. In: *Predation in Vertebrate Communities*.
 660 Springer, pp. 28–96.
 661 Jędrzejewska, B., Okarma, H., Jędrzejewski, W., Milkowski, L., 1994. Effects of exploitation and
 662 protection on forest structure, ungulate density and wolf predation in Białowieża Primeval
 663 Forest, Poland. *Journal of Applied Ecology* 664–676.
 664 Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K., Szymura, L., 2002. Kill
 665 rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland).
 666 *Ecology* 83, 1341–1356.
 667 Jones, H., Pekins, P., Kantar, L., Sidor, I., Ellingwood, D., Lichtenwalner, A., O’Neal, M., 2019. Mortality
 668 assessment of moose (*Alces alces*) calves during successive years of winter tick (*Dermacentor*
 669 *albipictus*) epizootics in New Hampshire and Maine (USA). *Canadian Journal of Zoology* 97, 22–
 670 30.
 671 Kaiser, T.M., Brinkmann, G., 2006. Measuring dental wear equilibriums—the use of industrial surface
 672 texture parameters to infer the diets of fossil mammals. *Palaeogeography, Palaeoclimatology,*
 673 *Palaeoecology* 239, 221–240.
 674 Kaiser, T.M., Clauss, M., Schulz-Kornas, E., 2016. A set of hypotheses on tribology of mammalian
 675 herbivore teeth. *Surface Topography: Metrology and Properties* 4, 014003.
 676 Karlsen, S.R., Høgda, K.A., Wielgolaski, F.E., Tolvanen, A., Tømmervik, H., Poikolainen, J., Kubin, E.,
 677 2009. Growing-season trends in Fennoscandia 1982–2006, determined from satellite and
 678 phenology data. *Climate Research* 39, 275–286.
 679 Karlsson, S., Neuvonen, S., Thannheiser, D., 2005. Plant ecology, herbivory, and human impact in
 680 Nordic mountain birch forests. Springer Science & Business Media.
 681 Kay, R.F., Hiiemae, K.M., 1974. Jaw movement and tooth use in recent and fossil primates. *American*
 682 *Journal of Physical Anthropology* 40, 227–256.
 683 Kossak, S., 1992. Foraging habits and behaviour of moose calves in virgin forest. *Acta Theriologica* 37,
 684 51–51.
 685 Kuijper, D.P.J., Devriendt, K., Bormans, M., Van Diggelen, R., 2016. Do moose redistribute nutrients in
 686 low-productive fen systems? *Agriculture, Ecosystems & Environment* 234, 40–47.
 687 Leach, R., 2013. Characterisation of areal surface texture. Springer.
 688 Leduc, C., 2012. Ungulates exploitation for subsistence and raw material, during the Maglemose
 689 culture in Denmark: the example of Mullerup site (Sarauw’s Island) in Sjælland. *Danish Journal*
 690 *of Archaeology* 1, 62–81.
 691 Leuthold, B.M., Leuthold, W., 1978. Ecology of the giraffe in Tsavo East National Park, Kenya. *African*
 692 *Journal of Ecology* 16, 1–20.
 693 Linnell, J.D., Cretois, B., Nilsen, E.B., Rolandsen, C.M., Solberg, E.J., Veiberg, V., Kaczensky, P., Van
 694 Moorter, B., Panzacchi, M., Rauset, G.R., 2020. The challenges and opportunities of coexisting
 695 with wild ungulates in the human-dominated landscapes of Europe’s Anthropocene. *Biological*
 696 *Conservation* 244, 108500.
 697 Louail, M., Ferchaud, S., Souron, A., Walker, A.E., Merceron, G., 2021. Dental microwear textures differ
 698 in pigs with overall similar diets but fed with different seeds. *Palaeogeography,*
 699 *Palaeoclimatology, Palaeoecology* 110415.
 700 Lumpkin, S., Kranz, K.R., 1984. *Cephalophus sylvicultor*. *Mammalian Species* 225, 1–7.
 701 Merceron, G., Escarguel, G., Angibault, J.-M., Verheyden-Tixier, H., 2010. Can dental microwear
 702 textures record inter-individual dietary variations? *PLoS ONE* 5, 1–9.

703 Merceron, G., Hofman-Kamińska, E., Kowalczyk, R., 2014. 3D dental microwear texture analysis of
704 feeding habits of sympatric ruminants in the Białowieża Primeval Forest, Poland. *Forest*
705 *Ecology and Management* 328, 262–269.

706 Merceron, G., Novello, A., Scott, R.S., 2016a. Paleoenvironments inferred from phytoliths and dental
707 microwear texture analyses of meso-herbivores. *Geobios* 49, 135–146.

708 Merceron, G., Ramdarshan, A., Blondel, C., Boisserie, J.-R., Brunetiere, N., Francisco, A., Gautier, D.,
709 Milhet, X., Novello, A., Pret, D., 2016b. Untangling the environmental from the dietary: dust
710 does not matter. *Proceedings of the Royal Society B* 283, 1–8.

711 Merceron, G., Colyn, M., Geraads, D., 2018. Browsing and non-browsing extant and extinct giraffids:
712 Evidence from dental microwear textural analysis. *Palaeogeography, Palaeoclimatology,*
713 *Palaeoecology* 505, 128–139.

714 Merceron, G., Berlioz, E., Vonhof, H., Green, D.R., Garel, M., Noûs, C., Tütken, T., 2020. Tooth tales told
715 by dental diet proxies: an alpine community of sympatric ruminants as a model to decipher
716 the ecology of fossil fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* 110077.

717 Modzelewska, A., Kamińska, A., Fassnacht, F.E., Stereńczak, K., 2021. Multitemporal hyperspectral tree
718 species classification in the Białowieża Forest World Heritage site. *Forestry: An International*
719 *Journal of Forest Research* 94, 464–476.

720 Moreira, L.M., Leonel, F. de P., Vieira, R.A.M., Pereira, J.C., 2013. A new approach about the digestion
721 of fibers by ruminants. *Revista Brasileira De Saúde E Produção Animal* 14, 382–395.

722 Morow, K., 1976. Food habits of moose from Augustów Forest. *Acta Theriologica* 21, 101–116.

723 Niedziałkowska, M., Hundertmark, K.J., Jędrzejewska, B., Niedziałkowski, K., Sidorovich, V.E., Górny,
724 M., Veeroja, R., Solberg, E.J., Laaksonen, S., Sand, H., 2014. Spatial structure in European
725 moose (*Alces alces*): genetic data reveal a complex population history. *Journal of Biogeography*
726 41, 2173–2184.

727 O'Connor, D.A., Butt, B., Foufopoulos, J.B., 2015. Foraging ecologies of giraffe (*Giraffa camelopardalis*
728 *reticulata*) and camels (*Camelus dromedarius*) in northern Kenya: effects of habitat structure
729 and possibilities for competition? *African Journal of Ecology* 53, 183–193.

730 Parker, D.M., Bernard, R.T.F., Colvin, S.A., 2003. The diet of a small group of extralimital giraffe. *African*
731 *Journal of Ecology* 41, 245–253.

732 Peltier, W.R., Fairbanks, R.G., 2006. Global glacial ice volume and Last Glacial Maximum duration from
733 an extended Barbados sea level record. *Quaternary Science Reviews* 25, 3322–3337.

734 Percher, A.M., Merceron, G., Nsi Akoue, G., Galbany, J., Romero, A., Charpentier, M.J., 2018. Dental
735 microwear textural analysis as an analytical tool to depict individual traits and reconstruct the
736 diet of a primate. *American Journal of Physical Anthropology* 165, 123–138.

737 Ramdarshan, A., Blondel, C., Brunetiere, N., Francisco, A., Gautier, D., Surault, J., Merceron, G., 2016.
738 Seeds, browse, and tooth wear: a sheep perspective. *Ecology and Evolution* 6, 5559–5569.

739 Redjadj, C., Darmon, G., Maillard, D., Chevrier, T., Bastianelli, D., Verheyden, H., Loison, A., Saïd, S.,
740 2014. Intra- and interspecific differences in diet quality and composition in a large herbivore
741 community. *PLoS ONE* 9, e84756.

742 Renecker, L.A., Hudson, R.J., 1988. Seasonal quality of forages used by moose in the aspen-dominated
743 boreal forest, central Alberta. *Ecography* 11, 111–118.

744 Sæther, B.-E., Andersen, R., 1990. Resource limitation in a generalist herbivore, the moose *Alces alces*:
745 ecological constraints on behavioural decisions. *Canadian Journal of Zoology* 68, 993–999.

746 Sanson, G.D., Kerr, S.A., Gross, K.A., 2007. Do silica phytoliths really wear mammalian teeth? *Journal*
747 *of Archaeological Science* 34, 526–531.

748 Schmölcke, U., Zachos, F.E., 2005. Holocene distribution and extinction of the moose (*Alces alces*,
749 *Cervidae*) in Central Europe. *Mammalian Biology* 70, 329–344.

750 Schulz, E., Piotrowski, V., Clauss, M., Mau, M., Merceron, G., Kaiser, T.M., 2013a. Dietary abrasiveness
751 is associated with variability of microwear and dental surface texture in rabbits. *PLoS ONE* 8,
752 1–7.

753 Schulz, E., Calandra, I., Kaiser, T.M., 2013b. Feeding ecology and chewing mechanics in hoofed
754 mammals: 3D tribology of enamel wear. *Wear* 300, 169–179.

755 Schulz-Kornas, E., Winkler, D.E., Clauss, M., Carlsson, J., Ackermans, N.L., Martin, L.F., Hummel, J.,
 756 Müller, D.W., Hatt, J.-M., Kaiser, T.M., 2020. Everything matters: Molar microwear texture in
 757 goats (*Capra aegagrus hircus*) fed diets of different abrasiveness. *Palaeogeography,*
 758 *Palaeoclimatology, Palaeoecology* 552, 109783.

759 Scott, J.R., 2012. Dental microwear texture analysis of extant African Bovidae. *Mammalia* 76, 157–174.

760 Scott, J.R., Godfrey, L.R., Jungers, W.L., Scott, R.S., Simons, E.L., Teaford, M.F., Ungar, P.S., Walker, A.,
 761 2009. Dental microwear texture analysis of two families of subfossil lemurs from Madagascar.
 762 *Journal of Human Evolution* 56, 405–416.

763 Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental
 764 microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436,
 765 693–695.

766 Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A., 2006. Dental
 767 microwear texture analysis: technical considerations. *Journal of Human Evolution* 51, 339–
 768 349.

769 Scott, R.S., Teaford, M.F., Ungar, P.S., 2012. Dental microwear texture and anthropoid diets. *American*
 770 *Journal of Physical Anthropology* 147, 551–579.

771 Shipley, L., 2010. Fifty years of food and foraging in moose: lessons in ecology from a model herbivore.
 772 *Alces: A Journal Devoted to the Biology and Management of Moose* 46, 1–13.

773 Shipley, L.A., Blomquist, S., Danell, K., 1998. Diet choices made by free-ranging moose in northern
 774 Sweden in relation to plant distribution, chemistry, and morphology. *Canadian Journal of*
 775 *Zoology* 76, 1722–1733.

776 Singh, N.J., Börger, L., Dettki, H., Bunnefeld, N., Ericsson, G., 2012. From migration to nomadism:
 777 movement variability in a northern ungulate across its latitudinal range. *Ecological*
 778 *Applications* 22, 2007–2020.

779 Smith, C., Warren, M., 2019. GLMs in R for ecology. Smith and Warren.

780 Spitzer, R., Felton, A., Landman, M., Singh, N.J., Widemo, F., Cromsigt, J.P., 2020. Fifty years of
 781 European ungulate dietary studies: a synthesis. *Oikos* 129, 1668–1680.

782 Teaford, M.F., Glander, K.E., 1991. Dental microwear in live, wild-trapped *Alouatta palliata* from Costa
 783 Rica. *American Journal of Physical Anthropology* 85, 313–319.

784 Teaford, M.F., Oyen, O.J., 1989. Live primates and dental replication: new problems and new
 785 techniques. *American Journal of Physical Anthropology* 80, 73–81.

786 Teaford, M.F., Robinson, J.G., 1989. Seasonal or ecological differences in diet and molar microwear in
 787 *Cebus nigrivittatus*. *American Journal of Physical Anthropology* 80, 391–401.

788 Tixier, H., Duncan, P., 1996. Are European roe deer browsers? A review of variations in the composition
 789 of their diets. *Revue d'Ecologie* 51, 1–15.

790 Tixier, H., Duncan, P., Scehovic, J., Yant, A., Gleizes, M., Lila, M., 1997. Food selection by European roe
 791 deer (*Capreolus capreolus*): effects of plant chemistry, and consequences for the nutritional
 792 value of their diets. *Journal of Zoology* 242, 229–245.

793 Tixier, H., Maizeret, C., Duncan, P., Bertrand, R., Poirel, C., Roger, M., 1998. Development of feeding
 794 selectivity in roe deer. *Behavioural Processes* 43, 33–42.

795 Ungar, P.S., 2015. Mammalian dental function and wear: A review. *Biosurface and Biotribology* 1, 25–
 796 41.

797 Vivås, H.J., Sæther, B.-E., Andersen, R., 1991. Optimal twig-size selection of a generalist herbivore, the
 798 moose *Alces alces*: implications for plant-herbivore interactions. *The Journal of Animal Ecology*
 799 56, 395–408.

800 Wam, H.K., Hjeljord, O., 2010. Moose summer and winter diets along a large scale gradient of forage
 801 availability in southern Norway. *European Journal of Wildlife Research* 56, 745–755.

802 Wassen, M.J., Okruszko, T., Kardel, I., Chormanski, J., Swiatek, D., Mioduszeowski, W., Bleuten, W.,
 803 Querner, E.P., El Kahloun, M., Batelaan, O., Meire, P., 2006. Eco-hydrological functioning of the
 804 Biebrza wetlands: lessons for the conservation and restoration of deteriorated wetlands.
 805 Springer, Berlin, Heidelberg, *Ecological Studies* 191, 285–310.

806 Winkler, D.E., Schulz-Kornas, E., Kaiser, T.M., De Cuyper, A., Clauss, M., Tütken, T., 2019. Forage silica
807 and water content control dental surface texture in guinea pigs and provide implications for
808 dietary reconstruction. *Proceedings of the National Academy of Sciences* 116, 1325–1330.
809 Winkler, D.E., Schulz-Kornas, E., Kaiser, T.M., Codron, D., Leichliter, J., Hummel, J., Martin, L.F., Clauss,
810 M., Tütken, T., 2020. The turnover of dental microwear texture: Testing the “last supper” effect
811 in small mammals in a controlled feeding experiment. *Palaeogeography, Palaeoclimatology,*
812 *Palaeoecology* 557, 109930.
813 Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical
814 problems. *Methods in Ecology and Evolution* 1, 3–14.
815
816

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 ($epLsar > 5 \times 10^{-3}$), 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 ($HAsfc$) 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).

reference	pop.	tooth	sex	season	<i>Sa</i>	<i>Sp</i>	<i>Sq</i>	<i>S5v</i>	<i>Sha</i>	<i>Sda</i>	<i>Spd</i> (10 ⁻³)	<i>Vm</i> (10 ⁻³)	<i>Vmc</i>	<i>Vvc</i>	<i>Asfc</i>	<i>epLsar</i> (10 ⁻³)	<i>H81</i>	<i>Tfv</i>
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

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

856

857

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

858

859

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	3	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
aa_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

860

861

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

862

863

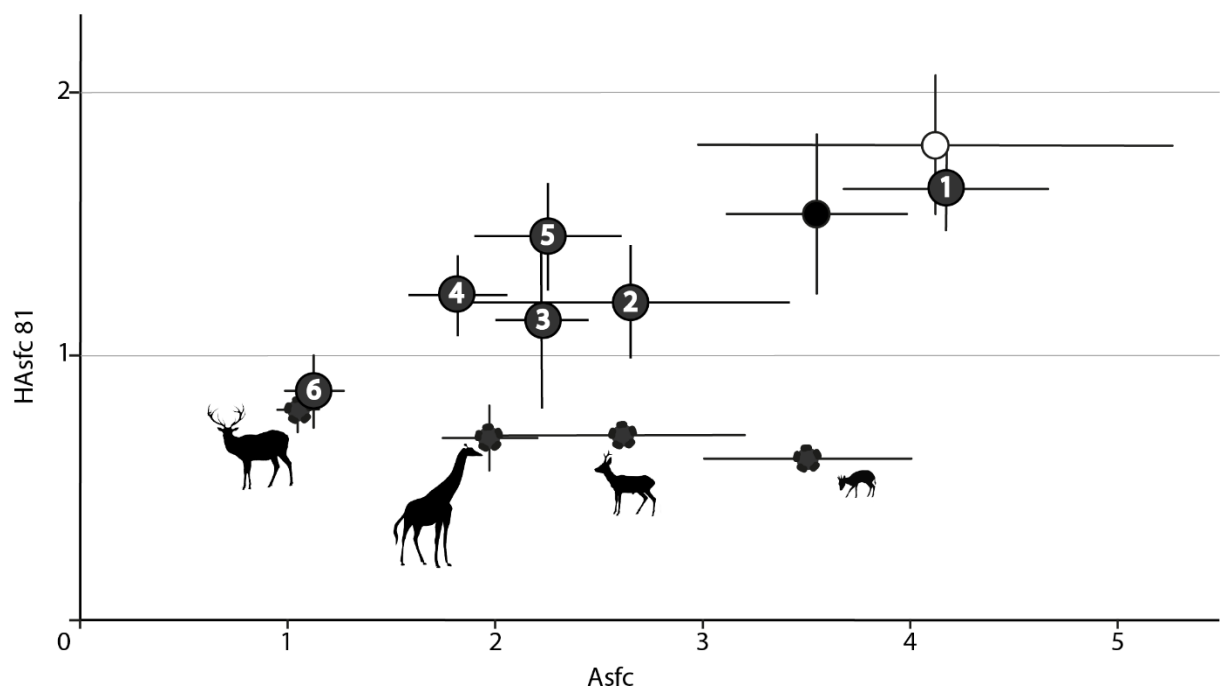
864 Table S2:

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
<i>Giraffa camelopardalis</i>	16	7	1	43.8	6.3
<i>Cephalophus silvicultor</i>	3	20	3	74.1	11.1
<i>Cervus elaphus</i>	19	1	17	5.3	89.5
<i>Capreolus capreolus</i>	18	7	13	38.9	72.2

865

866

867 Figure S1:



868

869

870 Figure S2:

