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Winter temperature and forest cover have shaped red deer distribution in Europe and the Ural Mountains since the Late Pleistocene

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1 **Winter temperature and forest cover have shaped red deer distribution in Europe and**
2 **the Ural Mountains since the Late Pleistocene**

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5 Short title: Deer distribution since Late Pleistocene

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115 *Key words: environmental niche modelling, expansion-contraction model, forest habitat,*
116 *Holocene, January temperature, Last Glacial Maximum refugia, paleoecology, radiocarbon*
117 *dating, temperate climatic zone, ungulates*

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119

120 **Abstract**

121 **Aim:** The Expansion-Contraction model has been used to explain the responses of species to
122 climatic changes. During periods of unfavorable climatic conditions, species retreat to refugia
123 from where they may later expand. This paper focuses on the paleoecology of red deer over
124 the past 54 ka across Europe and the Urals, to reveal patterns of change in their range and
125 explore the role of environmental conditions in determining their distribution.

126 **Location:** Europe and western Asia to 63° E.

127 **Taxon:** Red deer (*Cervus elaphus*)

128 **Methods:** We collected 984 records of radiocarbon-dated red deer subfossils from the Late
129 Pleistocene and the Holocene, including 93 original dates. For each deer sample we compiled
130 climatic and biome type data for the corresponding time intervals.

131 **Results:** During the last 54 ka changes in red deer range in Europe and the Urals were
132 asynchronous and differed between western and eastern Europe and western Asia due to
133 different environmental conditions in those regions. The range of suitable areas for deer
134 during the Last Glacial Maximum (LGM) was larger than previously thought and covered
135 vast regions not only in southern but also in western and eastern Europe. Throughout the
136 period investigated the majority of specimens inhabited forests in the temperate climatic
137 zone. The contribution of forests in deer localities significantly decreased during the last 4 ka,
138 due to deforestation of Europe caused by humans. Mean January temperature was the main
139 limiting factor for species distribution. Over 90% of the samples were found in areas where
140 mean January temperature was above -10° C.

141 **Main conclusions:** Red deer response to climatic oscillations are in agreement with the
142 Expansion-Contraction model but in contradiction to the statement of only the southernmost
143 LGM refugia of the species. During the last 54 ka red deer occurred mostly in forests of the
144 temperate climatic zone.

145

146 **1. Introduction**

147 Climatic oscillations during the Pleistocene, involving alternating periods of glacial and
148 interglacial cycles with irregular intervals of varying durations, had a major impact on
149 demographic changes and the distribution of plant and animal species in Europe (Hewitt,
150 2004). Many European temperate species survived the unfavorable environmental conditions
151 in refugial areas (Hewitt, 1999, 2004; Provan & Bennett 2008). According to the expansion-
152 contraction model (EC), the ranges of temperate species shrank to cover Mediterranean
153 regions, and during postglacial periods the species recolonized temperate and boreal areas
154 (Hewitt 1999, 2000, and references therein; Sommer & Zachos 2009). However, in the case of
155 some temperate mammals, archaeozoological evidence has revealed that they also existed
156 during glaciations outside the Mediterranean refugia e.g. around the Carpathian Mountains

157 (Davison et al., 2011; Deffontaine et al., 2005; Herman et al., 2016). In addition to latitudinal
158 changes, there were also range expansions in east-west directions, or changes in body forms,
159 as species adapted to different environmental conditions related to climatic humidity
160 (Matosiuk et al., 2014; Stewart, Lister, Barnes, & Dalen, 2010 and reference therein;).

161 The red deer (*Cervus elaphus*) is a widely distributed game species in Europe (Milner
162 et al., 2006; Zachos and Hartl, 2011), which can survive in diverse habitats such as
163 woodlands, moorlands, meadows, and at different altitudes, including mountains (Dolan,
164 1988; Geist, 1998; Heptner, Nasimovich, & Bannikov, 1961). The current distribution of red
165 deer is assumed to be strongly influenced primarily by colonization history during the Late
166 Pleistocene and the early Holocene (Sommer et al., 2008) and also by human activities (e.g.
167 Carden et al., 2012; Doan et al., 2017; Fernández-García et al. 2014). The red deer is also one
168 of the most abundant large mammal species in archaeological sites dated to the Late
169 Pleistocene across Europe (Sommer & Nadachowski, 2006). According to Geist (1998), the
170 European red deer is a savannah-type deer with a mixed feeding strategy, but the majority of
171 present-day red deer populations in Europe inhabit forests rather than open areas (Apollonio,
172 Andersen, & Putman, 2010 and references therein). The EC model of species response to
173 long-term environmental changes assumes a high degree of niche conservatism (i.e. the
174 tendency of species to retain their niche-related ecological traits over time), especially with
175 regards to the abiotic, climate-related dimension of a species niche (Wiens et al., 2010 and
176 references therein).

177 The history of red deer may have been more complex than explained by a simplistic
178 EC model. Studies by Sommer et al. (2008), Meiri et al. (2013) and Queiros et al. (2019)
179 suggest that red deer could have also survived during glacial times outside southern European
180 peninsular refugia, especially in northern areas of western Europe. Furthermore, the
181 distribution of western (European) and eastern (Asian) genetic lineages of red deer shifted

182 alongside climatic changes, as indicated by studies on ancient Crimean red deer populations
183 (Doan et al., 2018; Stanković et al., 2011). After the LGM when the climate became warmer,
184 western red deer populations expanded in Europe. The eastern lineage – a more cold-adapted
185 open-country grazer (Geist, 1998) – disappeared from previously occupied areas (Doan et al.,
186 2018).

187 In addition to natural environmental change, human wildlife management over recent
188 centuries has affected red deer populations via selective hunting, translocations, isolation of
189 deer in enclosures, and through the creation of barriers resulting in habitat fragmentation
190 (Carden et al., 2012; Hartl, Zachos, & Nadlinger, 2003; Niedziałkowska, Jędrzejewska,
191 Wójcik, & Goodman, 2012). From a biogeographic perspective, translocations and
192 introductions may be the main factors that could have led to erroneous conclusions about
193 postglacial recolonization routes of the red deer.

194 In this study, we analysed Late Pleistocene and Holocene red deer samples to
195 investigate the complex population history of this species across Europe and the Ural
196 Mountains since 54 ka. There are still many questions and hypotheses that need to be verified,
197 as previous studies mainly concentrated on the southern and western parts of the continent
198 (Meiri et al., 2013; Queiros et al., 2019; Sommer et al., 2008). During the Last Glacial
199 Maximum (LGM), glacial extent reached its southern limit in western Europe much earlier
200 (about 23 ka cal BP) and extended further south than in eastern Europe (Patton, Hubbard,
201 Andreassen, Winsborrow, & Stroeve, 2016; Patton et al., 2017). Therefore, larger areas were
202 available for boreal and temperate species in eastern Europe and western Asia than in western
203 Europe. Using fossil records and paleobotanical data Markova, Simakova, & Puzachenko
204 (2009) showed that during the LGM there were large areas of land with environmental
205 conditions suitable for many boreal and temperate species including red deer in eastern and
206 south-eastern Europe. However, until now few studies have demonstrated that eastern parts of

207 Europe could have played important roles as LGM refugia for temperate and boreal species
208 (Korbut, Rusin, Neumann, & Banaszek, 2019; Niedziałkowska 2017; Sommer et al., 2009).
209 We expect that, although the changes in distribution of red deer in Europe and the Urals
210 during the last 50 ka years can be explained to large extent by EC model, the species survived
211 the LGM in larger areas than previously thought. We suppose that the the potentially suitable
212 areas for deer included not only the well-known southern refugia but also vast regions of
213 eastern Europe and western Asia. We also put a hypothesis that although the European red
214 deer is ecologically flexible species, it has been best adapted to temperate climate conditions
215 and forested habitats.

216 The aims of this study were to: (i) describe changes in red deer distribution before and
217 after the LGM, (ii) identify potentially suitable areas for deer during the LGM in eastern
218 Europe and the Ural Mountains, and (iii) analyse the response of red deer to changes in
219 climate and habitat availability during the last 54 ka. These aims were addressed by collating
220 existing geolocated radiocarbon dates from the literature and supplementing them with new
221 measurements on previously undated red deer material. These were used to assess the climatic
222 conditions and habitats occupied by red deer through the last 54 ka and investigate the
223 species' ecological flexibility, alongside environmental niche modelling to assess the potential
224 niche for red deer through time in Europe and the Urals.

225

226 **2. Methods**

227 **2.1. Sampling**

228 We obtained red deer subfossil teeth and fragments of bones from zoological and
229 archeological collections in Europe and the Ural Mountains in agreement with the collection
230 owners. Species identification was based on comparative macroscopic and morphometric
231 analyses and confirmed by genetic analyses (sequencing of cytochrome b of mtDNA, see
232 Doan et al., 2017 for details). In the next step, 93 samples were radiocarbon-dated using

233 accelerator mass spectrometry (AMS) at the Gliwice Absolute Dating Methods Centre
234 (GADAM, Poland).

235 Literature searches were performed to source additional data on red deer distribution
236 in the Late Pleistocene and Holocene in Europe and western Asia. Records analysed in this
237 study also derive from the Faunal Database of the Stage Three Project
238 ([https://www.esc.cam.ac.uk/research/research-groups/research-projects/stage-three-](https://www.esc.cam.ac.uk/research/research-groups/research-projects/stage-three-project/stage-three-project-database-downloads)
239 [project/stage-three-project-database-downloads](https://www.esc.cam.ac.uk/research/research-groups/research-projects/stage-three-project/stage-three-project-database-downloads)) and data collected by the authors of this
240 manuscript during their earlier scientific projects. We focused specifically on records that
241 have been radiocarbon-dated either directly or indirectly, i.e. dates derived from charcoal,
242 humus, or bones of other animals found in the same layer as red deer fossils. Samples that
243 were not radiocarbon-dated, were excluded from the analysis.

244 All radiocarbon dates were calibrated using OxCal v. 4.2 (Bronk Ramsey, 2009) and
245 the IntCal13 calibration curve (Reimer et al., 2013). Hereafter, the ages are provided as cal
246 BP, i.e. calibrated age in years before AD 1950, using medians of the calibrated radiocarbon
247 dates.

248 **2.2. Spatial and temporal analyses**

249 The radiocarbon dataset used in this study (N = 984, including 93 new measurements,
250 Appendix 1: Table S1) covers Europe as well as western Asia up to 63° E (Figure 1, Appendix
251 2: Figure S1) and extends from the Late Pleistocene (54 000 calibrated years BP – 54 ka cal
252 BP) until modern times (0 cal BP). The largest number of records originated from the periods
253 >34-26 ka cal BP (253 samples) and 54-34 ka cal BP (239 samples). The smallest number of
254 samples were dated to the most recent time period (>4 - 0 ka cal BP; 98 samples) and the
255 LGM (>26-18 ka cal BP; 99 samples). The chosen time periods reflect episodes when
256 significant climatic and environmental changes occurred (Figure 2). The first period
257 represents the time prior to the LGM, the second represents the pre-LGM period, when

258 temperature started to decrease, the third spans the LGM, the fourth represents the time after
259 the LGM, when temperature started to increase, the fifth covers the early Holocene, and the
260 sixth period corresponds to the time period with clear signs of human-caused deforestation
261 across Europe (Fyfe, Woodbridge, & Roberts, 2015). The approximate northern limits of red
262 deer in different time periods were determined based on the distribution of red deer samples in
263 the above mentioned time intervals. The present red deer range was created based on IUCN
264 data (Lovari et al., 2018), published data on red deer distribution (Albayrak, Pamukoğlu, &
265 Kaya 2007; GBIF.org 2020; Loggers, Thévenot, & Aulagnier, 1992; Milner et al., 2006;
266 Niedziałkowska et al., 2011) and the Atlas of Mammals in Russia
267 (<http://rusmam.ru/atlas/map>).

268 We tested the latitudinal shifts of the northern edge of red deer range among the
269 studied periods with the Generalized Linear Model (GLM) using Gamma error structure.
270 Before modelling, for each considered period, we selected the most northern localities
271 (sample sites ≥ 0.9 quantile), which represented the northern limit of the species range. In the
272 GLM sample site latitude was set as a continuous response variable, while the studied period
273 (categorical variable) served as explanatory factor. The analysis was done in R ver. 3.5.2 (R
274 Core Team, 2018).

275 Sea level and the shape of coast lines in each of the defined time periods were mapped
276 based on data published by Waelbroeck et al. (2002) and applying GEBCO bathymetric
277 model of the World's oceans (Weatherall et al., 2015). Changes in the Baltic Sea level were
278 mapped based on Björck (1995) for the period 13-8 ka BP and Lambeck, Purcell, Zhao, &
279 Svensson (2010) for the period before the LGM. The extent of the Fennoscandian Ice Sheet
280 was drawn based on the database of Hughes, Gyllencreutz, Lohne, Mangerud, & Svendsen
281 (2016; 10-30 ka BP) and Lambeck et al. (2010; 39 ka and 49 ka BP).

282 **2.3. Climatic and environmental analyses**

283 Climatic (mean annual, mean January, mean July temperatures, and mean annual
284 precipitation) and biome data were obtained from the FAMOUS database (FAst Met. Office
285 and UK Universities Simulator) (Smith & Gregory, 2012, Appendix 1: Table S2). The
286 FAMOUS database was downscaled to the spatial resolution of 2.5' using the WorldClim
287 database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) as a baseline (current climate
288 data). Biome data were used in their original resolution ($5.00^\circ \times 7.50^\circ$). In our analyses, we
289 merged the biome categories from the FAMOUS database into the following categories
290 (Appendix 1: Table S2): Tundra (Tun), Forest (coniferous, mixed, deciduous, montane – For),
291 Sclerophyl woodland (Scl wood), Xerophytic shrub (Xer shr), Grassland and Desert (Grass
292 Des). More details on the methods used to extract climatic and biome data are given in
293 Appendix 3.

294 Additional information on the relative abundance of different land cover types
295 throughout the Holocene (for the period 11-0 ka BP) was obtained from a pollen-inferred land
296 cover change database (after Fyfe et al., 2015, Appendix 1: Table S3). This database contains
297 pan-European land cover classification for the last 11 ka years at 200-year temporal resolution
298 and was created by applying the pseudobiomization (PBM) method (Fyfe et al. 2010) to
299 almost 1000 fossil pollen records from across Europe. Land cover types were extracted
300 around the red deer data points, similarly to the approach taken to extract climatic data, using
301 ArcGIS 10.3.1 software (ESRI 2015, Appendix 3). To determine the potential distribution of
302 red deer in the six time periods, we created environmental niche models using Maxent
303 software (Phillips, Anderson, & Schapire, 2006) using deer records as occurrence data and
304 mean January temperature as an environmental variable (for more details concerning the
305 modelling approach see Appendix 3). All statistical analyses were performed in
306 STATISTICA 7.1. (StatSoft, 2005).

307 **3. Results**

308 **3.1. Changes in red deer distribution since the Late Pleistocene**

309 In general, the range of red deer shrank during the colder periods (54-18 ka cal BP) and
310 expanded after the LGM (18-0 ka cal BP), when the climate became warmer (Figures 2, S1
311 and 3). The changes in the northern limits of deer occurrence (statistically significant in most
312 cases; Table S4) were in agreement with the predictions of the EC model.

313 However, the scale of these changes was different in western and eastern parts of the
314 continent (Figures 2 and S1). For the earliest studied time period (54-34 ka cal BP), the
315 northernmost deer records were found above 60° N latitude in the Urals and above 52° N in
316 western Europe (present-day Ireland). Between 54 and 26 ka cal BP the red deer disappeared
317 from their northern areas moving about 200 km in a southerly direction (on average about 14
318 km ka⁻¹) in western Europe (distance measured along longitude 0° WE) and 950 km (on
319 average about 68 km ka⁻¹) in western Asia (along longitude 60° E) (Figures 2 and S1). Before
320 and during the LGM (> 34-18 ka cal BP) red deer became extinct in large areas of Europe and
321 the species' range shifted 750-800 km (on average about 100 km ka⁻¹) further to the south in
322 western Europe, but remained stable in the eastern part of the continent and the Urals. During
323 the LGM (>26-18 ka cal BP) the species range was at its minimum covering areas up to about
324 44° N latitude in present-day France and Italy, 48° N latitude in Moldova, 55° N in the Urals
325 (Figures 2 and S1).

326 After the LGM, red deer started to recolonize the European continent in a northerly
327 direction (Figures 2, 3, S1, Appendix 2: Table S4). However, the recolonization was notably
328 faster in the western than in the eastern part of the continent. Red deer started to expand from
329 the south-west towards the north and north-east. Between the end of the LGM and 11 ka BP
330 the range edge moved 1500 km northward (measured along the longitude 0°E, on average 200
331 km ka⁻¹) and 1800 km north-east (on average 240 km ka⁻¹, measured along a line from 0°WE,
332 50°N to 20°E, 60°N) in western Europe. In the eastern part of the continent and the Urals, the
333 range expansion of deer (measured longitudinally between 30°E and 60°E and along lines

334 from 30°E, 50°N to 50°E, 60°N and from 40°E, 50°N to 60°E, 60°N) was smaller (0-250 km;
335 rate 0-33 km ka⁻¹). After the LGM red deer rapidly surpassed the northern limits from the pre-
336 LGM period (54-26 ka cal BP, comp. Figures 2 (upper and middle panels), 3, S1 and Table
337 S4).

338 In the Holocene (between 11-2 ka cal BP, prior to human translocations of red deer),
339 the range of red deer continued to shift significantly (Figures 2,3, S1, Table S4) in a northerly
340 direction. The edge of species occurrence moved from 350 km to 1450 km (rate 64-264 km
341 ka⁻¹) to the north (measured along 40°E and 0°WE respectively) and 400-2000 km (rate 73-
342 364 km ka⁻¹) to the north-east (measured from 20°E, 50°N to 40°E, 60°N and from 40°E, 50°N
343 to 60°E, 60°N, respectively). In both Europe and the Urals red deer crossed 60°N (Figures 2
344 and S.1). In comparison to the contemporary red deer range, the range recorded around 2 ka
345 cal BP extended much further to the east, north-east and south (comp. Figures 1, 2 and S1).
346 Around 400 cal BP red deer still occurred in the Urals (Table S1). The present-day eastern
347 border of the continuous red deer distribution ends in the west of the European part of Russia
348 (Figures 1, S1).

349 **3.2. Climatic conditions in red deer sample locations**

350 We compared climatic variables in the red deer record site locations for the six time
351 periods. Mean annual and mean July temperatures were significantly different among the
352 studied periods, especially between the Late Pleistocene and the Holocene periods (Figures 4
353 and S.2). Median annual temperatures varied between 7.8 and 9.5°C and those of July
354 temperatures between 14.4 and 18.2°C. Annual temperature in the earlier periods (54 - 26 ka)
355 was lower than in more recent times, especially when compared with the period prior to 11-0
356 ka (Figure S2). Median July temperature in deer sample locations decreased from > 54-34 ka
357 reaching a minimum at the LGM, and then increased until the present (Figure 3, upper panel).
358 However, we found no statistical differences in the mean January temperatures among the

359 study periods (Figure 4, upper panel). Median January temperatures were between -1° and
360 1°C in all six time periods (Figure 4, upper panel). As many as 67% of all deer records were
361 found in locations with mean January temperature between -5 and 5°C (Figure 4, lower panel)
362 and more than 90% of samples occurred in locations where mean January temperature range
363 was above -10°C (Figure 4, lower panel).

364 Annual precipitation in deer sample locations varied through time (Figure S2). During
365 the LGM and postglacial periods ($>18-11$ ka BP) it was significantly higher than in earlier
366 periods (54-34 ka BP) and the Holocene (Figure S2). Median annual precipitation was highest
367 during the LGM (720 mm) and lowest in the period 54 - 34 ka BP (about 600 mm) and the
368 Holocene (Figure S2).

369

370 **3.3. Habitat niche of red deer in Europe**

371 The biome type identified around each of the dated deer records are presented in Figure S1.
372 The majority of all samples (57%) were located in forests of different types (coniferous,
373 mixed and deciduous) (Figures 4 lower panel, S1 and S3). The second biome most frequently
374 occupied by red deer was sclerophyllous woodland (29% of samples) in southern and western
375 Europe. Less than 10% of samples were found in other categories of biomes such as tundra,
376 xerophytic shrub, grassland or desert (Figures 4 lower panel, S2 and S3). The combination of
377 different biomes, to which the samples were assigned, varied among time periods (Figure S3).
378 The share of forest was lowest (about 35%) in the pre-LGM period ($>34-26$ ka cal BP) and
379 highest in the Holocene (77% to 84%). The pre-LGM and postglacial ($>18-11$ ka cal BP)
380 samples were slightly more often assigned to sclerophyll woodland than to forest.

381 Based on more detailed data on forest cover in Europe during the Holocene (Fyfe et al.,
382 2015) derived from fossil pollen data, we identified that mean forest cover \pm SE (standard
383 error) was $62\% \pm 0.8$ (range 37-80) in locations of red deer records before 4 ka BP (11-4 ka

384 BP) and $46\% \pm 1.5$ (range 27-71) after 4 ka BP (4-0 ka BP). These differences in forest cover
385 between the two periods were statistically significant (Mann-Whitney test, $U = 2299$, $p <$
386 0.0001).

387 All environmental niche models (Figure S4) generally had good predictive ability with
388 AUC values (explained in Appendix 3) for training data between 0.8 and 0.9 (the lowest
389 $AUC=0.809$ for 0-4 ka BP and the highest $AUC=0.896$ for 18-26 ka BP). The results of
390 modelling showed that during the LGM the most suitable conditions for red deer occurred in
391 western and southern Europe, in areas surrounding the Black Sea and in Asia Minor. The
392 model for the most recent time period (4-0 ka BP) corresponds very well with the
393 contemporary geographic range of European red deer (comp. Figure 1 and the last panel in
394 Figure S4). The only outliers consistently located in the unsuitable modelled habitat were deer
395 specimens found in easternmost Europe and the Urals (Figure S4).

396 **4. Discussion**

397

398 **4.1. Contraction and expansion of deer range**

399 During the last 54 ka the range of red deer has shifted according to the EC model, which
400 reveals range contraction during colder period and expansion during warmer episodes
401 (Sommer et al., 2008; Meiri et al., 2013). However, the scale of red deer range oscillations
402 were different in western Europe in comparison with eastern Europe and western Asia. This
403 pattern is still evident when uncertainty in the distribution of red deer in eastern parts of
404 Europe due to lower sample coverage (less material available) in that region is taken into
405 account.

406 During the oldest time period investigated (between 54 ka BP and 34 ka BP), the northern
407 boundary of the red deer range was located more northwards in the eastern part of the
408 continent than in western regions. Although, just before and during the LGM, a much greater
409 loss of red deer range occurred in western Europe, where the southern extent of the ice sheet

410 about 23 ka cal BP crossed 50° N latitude. In the eastern part, the ice sheet extended from 53°
411 N in eastern Poland to 75° N to the north of the Urals (Patton et al., 2017) and it reached its
412 southern limit much later than in central and western Europe (Patton et al., 2016).

413 The northernmost remains of red deer dated to the LGM were found in Moldova (48° N
414 latitude) and in western Asia (up to 55° N in the Urals), but not further than 44° N in western
415 Europe. This indicates that large previously unrecognized refugial areas of red deer existed in
416 eastern Europe. Markova et al. (2009) also identified that during the LGM large areas
417 provided suitable habitats for many mammal species in this region. However, analyses of
418 ancient DNA (aDNA) of red deer from eastern Europe and western Asia, dated to the LGM,
419 are necessary to answer questions concerning phylogenetic assignment of those animals and
420 their contribution to the contemporary deer populations.

421 Radiocarbon dated subfossil remains (Sommer et al., 2008; this study), genetic data
422 from red deer and a climatic suitability model for this species indicated that during the LGM
423 the species also occurred in south-western and western regions of France and possibly even in
424 southern Ireland (Meiri et al., 2013; Queiros et al., 2019). After the LGM, red deer started to
425 recolonize western Europe rather fast, which may be due to the fact that prior to 17.8 ka BP
426 deglaciation was more rapid in the western margins of the ice sheet than in its central and
427 eastern parts (Patton et al., 2017). Furthermore, sea level was much lower, so in the early
428 Holocene more land was available to terrestrial animals in western and northern Europe than
429 is available today. This recolonization process is evident in the contemporary distribution of
430 mtDNA lineages of red deer: the majority of individuals inhabiting western, northern and
431 central parts of Europe belong to the western mtDNA clade (called haplogroup A,
432 Niedziałkowska et al. 2011; Skog et al., 2009). During the Holocene, red deer extended their
433 range to almost the whole of western and central Europe (excluding the very most northern
434 parts).

435 Red deer in eastern Europe underwent rather different process. In the mid-Holocene a
436 clear disjunction is apparent in their eastern range (comp. Figures 2 and S1). Firstly in the
437 lower and middle Volga River region, where the most recent deer remains were dated (by
438 archaeological context) to 5 ka BP (P. Kosintsev, pers. communication). By 1.5 ka BP red
439 deer disappeared from the Ufa region, west of the southern Ural Mountains (Sungatov &
440 Levchenko, 2014). It was only in the Urals and Western Siberia that red deer survived until
441 the 18th – mid 19th century (Kirikov, 1959). The most likely causes for such a large-scale
442 extinction of red deer from its eastern most range during the Holocene were changes in
443 climate (towards more continental) and habitats (aridization) (Bolikhovskaya & Kasimov,
444 2010; Khokhlova, Morgunova, Khokhlov, & Golyeva, 2019). Furthermore, the contemporary
445 eastern border of the European red deer range, stretching from the Baltic States to the
446 Caucasus Mountains, runs parallel to the isoline of mean January temperature between -10°
447 and -15°C (see e.g. DWD, 2019), which is consistent with the 50-ka-long climatic limits
448 (mean January temperature below -10°C) of red deer found in this study.

449 The results of our study confirmed our hypothesis that the species survived the LGM
450 not only in the well-known southern European refugia, but also in more northern areas of
451 western and eastern Europe and in the Urals. The environmental niche modelling was to a
452 large extent in agreement with these results, yet the model indicated that the environmental
453 conditions in the easternmost Europe and in the Urals, where several red deer samples were
454 found, were unsuitable for the species. This apparent discrepancy can be explained by the fact
455 that in the easternmost Europe two major lineages of deer, the western (European) and the
456 eastern (wapiti *C. el. canadensis*), co-occurred in the past (Doan et al., 2018; Meiri, et al.
457 2018). Results of an ancient DNA study performed by Doan (2017) showed that 11 out of 15
458 red deer samples analysed in our paper belonged to the wapiti mtDNA lineage. According to
459 Geist (1998) the eastern red deer has been better adapted to cold and dry climate than the

460 western lineage. This was also supported by the study of Stepanova (2010), who indicated
461 that the wapiti deer occurred in Yakutia (Eastern Siberia), where mean January temperature
462 was -36.8°C. The EC model for the more cold-tolerant eastern red deer would probably be
463 different than the model for the western red deer, however, a more detailed study is needed to
464 recognize the pattern of occurrence of wapiti in the Late Pleistocene and Holocene.

465 **4.2. Ecological niche of red deer during the last 54 ka years**

466 According to the Köppen-Geiger climate classification (e.g. Peel, Finlayson, &
467 McMahon, 2007), since the Late Pleistocene red deer have occurred mainly in the temperate
468 and partly also in the cold climate zones. The reconstructed measures of precipitation, annual
469 and July temperatures in red deer sampling sites strongly varied among the studied periods,
470 especially between the Late Pleistocene and the Holocene, thus testifying to high tolerance of
471 red deer to those climatic variables. The truly limiting factor for the species was mean January
472 temperature, the only climatic index which was generally stable in all time periods
473 investigated and throughout the highly variable deer range. The majority of red deer samples
474 (92%) were found in areas where mean January temperature was not lower than -10°C. The
475 optimal winter temperature (indicated by the largest proportion of red deer samples found)
476 was between 0 and 5°C, which means that the temperate zone was most suitable for red deer
477 for at least the last 54 ka. Also, the study by Borowik, Cornulier, & Jędrzejewska (2013)
478 showed that mean January temperature is one of the most important factors limiting
479 contemporary red deer abundance in Poland.

480 The majority of the analysed red deer samples were found in sites where mean July
481 temperature was above 10°C. The isotherm 10°C of the warmest month is an indicator for the
482 treeline extent (Tuhkanen, 1993), which is consistent with the results of biome analyses in our
483 study. The majority of deer records occurred in places where different types of forest were
484 modelled in a given period. This is also consistent with the habitat preferences of

485 contemporary red deer, which is a forest-dwelling species (Borowik et al., 2013; Heptner et
486 al., 1961). Although red deer are able to exist in open areas, e.g. in the Scottish Highlands
487 (Perez-Espona et al., 2008), in most of its European range the species inhabits forests
488 (Apollonio et. al., 2010) and its abundance positively correlates with forest cover (Borowik et
489 al., 2013; Wawrzyniak et al., 2010;). Forest played an important role in enhancing gene flow
490 among populations of this species in the lowlands of north-east Poland (Niedziałkowska,
491 Fontaine, & Jędrzejewska, 2012).

492 Biome types inhabited by red deer in some periods studied (e.g. sclerophyllous
493 woodland before and after the LGM) were probably connected with the availability of
494 different biomes during those times, as determined by temperature and precipitation.
495 Generally, the representation of forest biomes was much higher in deer sites dated to the
496 Holocene than in those from the Late Pleistocene. Interestingly, among deer samples dated to
497 the Late Pleistocene, the largest proportion of records were found in forests during the LGM,
498 when red deer range was restricted to the warmest parts of Europe and western Asia. In the
499 Holocene, forest cover represented at deer sites significantly declined after 4 ka BP, which
500 reflects the human-induced deforestation of Europe (Fyfe et al., 2015).

501 The results of our study showed that during the last 54 ka the range of European red deer
502 was restricted mainly to the temperate climatic zone with -10°C January temperature as the
503 limiting factor. Forests were the preferred habitats of deer. Within the context of large-scale
504 and long-term changes in climate and habitat availability, the European red deer tracked the
505 environmental characteristics to which it has been well adapted.

506 **5. Conclusions**

507 During the last 54 ka, the range of red deer in Europe and the Ural Mountains changed
508 in response to climate oscillations, generally decreasing in cooler periods and expanding in
509 warmer periods to a large extent in agreement with the EC model. However, these processes

510 were asynchronous and differed in western and central regions when compared to eastern
511 parts of Europe and the Ural Mountains. In all analysed time periods the results of
512 environmental niche modelling were in concordance with the distribution of radiocarbon
513 dated red deer samples in most of Europe, except its easternmost parts and the Urals, where
514 more cold-tolerant subspecies of *C. elaphus* – wapiti deer - had occurred. In the LGM, the
515 range of red deer was more extensive than previously thought and included large areas north
516 and east of the southern European peninsulas. A major limiting factor for European red deer
517 distribution was mean January temperature (below -10°C). Throughout the entire study
518 period, the majority of deer records were found in forests. The temperate climate zone with
519 mean January temperature between -5°C and 0°C, and forests as the dominating vegetation
520 type, has been the optimal habitat for European red deer throughout the last 54 thousand
521 years. The results of this study will be valuable in modeling changes in the spatial distribution
522 of deer in relation to present and future climate changes.

523

524 **Data availability statement**

525 Data used in the analyses are provided in the Supporting Information.

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Figures

725 Figure 1. Spatial distribution of radiocarbon-dated red deer (*Cervus elaphus*) samples from
726 the Late Pleistocene and Holocene covering Europe and the Urals. Mercator projection.

727

728 Figure 2. Changes in the northern limits of red deer (*Cervus elaphus*) ranges in the given time
729 intervals before and during the Last Glacial Maximum (upper panel) and during and after the
730 LGM (middle panel) in Europe and the Urals. The extent of the ice sheet for given time
731 periods (ka BP). Lower panel: Antarctic (data from the Vostok ice core) temperature
732 oscillations in the study period (source: FAMOUS database; Smith and Gregory 2012). See
733 Figure S1 for maps of deer records in each time period. Maps in Mercator projection.

734

735

736 Figure 3. Mean (+/- SE) latitudes of the most northern red deer (*Cervus elaphus*) study sites
737 (localities ≥ 0.9 quantile) reflects the contraction (before the LGM) and expansion (after the
738 LGM) of red deer range. N from 6 to 10 localities. Time periods as in Figure 2. See Table 4
739 for the statistics.

740

741 Figure 4. Upper panel: Mean January (left) and mean July (right) temperatures for the red
742 deer (*Cervus elaphus*) sample locations across Europe and the Urals in the six periods
743 investigated. Significant differences among time periods are marked by horizontal lines with
744 asterisks: *** $p < 0.001$, **** $p < 0.0001$ (Kruskal-Wallis test). N from 98 to 255 deer
745 samples. Lower panel, left: Numbers and percentages of red deer samples (N = 984) in
746 relation to reconstructed mean January temperature and the radiocarbon date of each deer
747 sample in Europe and the Urals; Lower panel, right: Percentages of red deer records in
748 different reconstructed biomes in Europe and the Urals, which have been assigned to each
749 sample location and radiocarbon date (N = 984 samples).

750 **Biosketch:**

751 Magdalena Niedziałkowska is a scientist at the Mammal Research Institute, Polish Academy
752 of Sciences in Białowieża, Poland. Her interests concern the population ecology, genetic
753 diversity and phylogenetics of mammals (ungulates, large carnivores and rodents) at regional
754 and continental scales, and factors which affect them, such as landscape structure, and the
755 history and origin of populations. M.N., K.D., K.S., B.J., P.M. and A.S. conceived
756 the ideas and applied for the financial support; M.N., K.D., K.S., M.S., B.R., U. Sch., P.K.,
757 D.M., M.Ch., D.K., E.R., U.S., M.A., N.M., V.V.T., P.H., A.B., K.T., U.D., O.K., J.W., T.O.,
758 G.L., and A.A. collected the red deer samples; M.N., K.D. and U. Sch. gathered the red deer
759 records, N.P., S.P. and M.S. radiocarbon-dated the samples. R.F. and J.W. produced the land
760 cover reconstruction from fossil pollen datasets, M.G. extracted the environmental data,
761 performed the GIS analyses and prepared the maps, M.N., K.D. and B.J. analysed the data,
762 M.N., B.J. and M.G. wrote the paper. All authors contributed to data interpretation and
763 revisions to the manuscript.
764

765 **Supporting Information**

766 **Appendix 1.** Data used in the analyses.

767 Table S1. A list of red deer records used in this study.

768 Table S2. Climatic and biome data determined for each of the red deer records used in this
769 study.

770 Table S3. Land cover data extracted for each of the Holocene red deer records' locations
771 using European pollen-inferred land cover change data (after Fyfe et al., 2015).

772 **Appendix 2.** Spatial distribution of red deer records and results of spatial and environmental
773 analyses in the six studied time periods. Maps in Mercator projection.

774 **Appendix 3.** Methods of spatial analyses.







