RESEARCH ARTICLE

High-resolution isotopic evidence of specialised cattle herding in the European Neolithic

Claudia Gerling[1]*, Thomas Doppler[1], Volker Heyd[2], Corina Knipper[3], Thomas Kuhn[4], Moritz F. Lehmann[4], Alistair W. G. Pike[5], Jörg Schibler[1]

1 Institute of Prehistory and Archaeological Science, Department of Environmental Sciences, University of Basel, Basel, Switzerland, **2** Department of Archaeology & Anthropology, University of Bristol, Bristol, United Kingdom, **3** Curt-Engelhorn Centre Archaeometry, Mannheim, Germany, **4** Biogeochemistry, Department of Environmental Sciences, University of Basel, Basel, Switzerland, **5** Department of Archaeology, University of Southampton, Southampton, United Kingdom

* claudia.gerling@unibas.ch

Citation: Gerling C, Doppler T, Heyd V, Knipper C, Kuhn T, Lehmann MF, et al. (2017) High-resolution isotopic evidence of specialised cattle herding in the European Neolithic. PLoS ONE 12(7): e0180164. https://doi.org/10.1371/journal.pone.0180164

Editor: John P. Hart, New York State Museum, UNITED STATES

Received: March 30, 2017

Accepted: June 9, 2017

Published: July 26, 2017

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: The research leading to this article was part of the project CR12I2_143815/1 funded by the Swiss National Science Foundation (www.snf.ch). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Abstract

Reconstructing stock herding strategies and land use is key to comprehending past human social organization and economy. We present laser-ablation strontium and carbon isotope data from 25 cattle (*Bos taurus*) to reconstruct mobility and infer herding management at the Swiss lakeside settlement of Arbon Bleiche 3, occupied for only 15 years (3384–3370 BC). Our results reveal three distinct isotopic patterns that likely reflect different herding strategies: 1) localized cattle herding, 2) seasonal movement, and 3) herding away from the site year-round. Different strategies of herding are not uniformly represented in various areas of the settlement, which indicates specialist modes of cattle management. The pressure on local fodder capacities and the need for alternative herding regimes must have involved diverse access to grazing resources. Consequently, the increasing importance of cattle in the local landscape was likely to have contributed to the progress of socio-economic differentiation in early agricultural societies in Europe.

Introduction

Understanding herding practices of cattle (*Bos taurus*) and territorial land use is key for comprehending human social organization and economy, particularly in Europe of the 4th and 3rd millennium BC when the first stratified societies emerged [1] and the use of secondary products gained in importance [2]. In addition to meat production, secondary husbandry products, such as milk, hair, manure and animal power, became the main motivation for keeping cattle [3]. A higher demand and the efficient exploitation of these products necessitated the maintenance of larger herds [4]. In turn, larger herds increased the pressure on local grazing resources and may have been associated with the advent of more complex herding strategies and enhanced mobility. Such mobility, e.g., in the form of transhumance, allowed the most fertile land in close vicinity to the settlements to be utilized exclusively for the production of crops [5] and fodder for overwintering animals [6]. Extensive mobile cattle herding thus permits optimal resource management of different types of grazing grounds in varying altitudes and distances from the permanent settlement. As a consequence, this exploitation triggered the colonization of poor soils, dense woodlands and higher altitudes by human settlers. The enhanced mobility forged new ways of life, which fundamentally altered customs and material cultures [7], and formed the European landscape [8]. Different mobility regimes have been demonstrated for historical times [9], and from ethnographical records [10], but conclusive evidence for prehistoric cattle mobility is rare: The seasonal movement of domesticates away from the settlement to areas of open pasture (e.g., uplands) was a strategy which has been suggested for the European Neolithic [11, 12]. In prehistoric Switzerland, indirect archaeological and archaeobiological evidence for human and animal mobility includes settlement structures at high altitudes (e.g., huts, pens) and the finding of alpine plant and animal remains (e.g., alpine speedwell, alpine ibex) in lowland settlements of the late Neolithic [13].

Arbon Bleiche 3 is an ideal site to explore direct (isotopic) evidence for Neolithic cattle mobility at a time when the systematic utilization and exploitation of secondary husbandry products likely gained in importance. The settlement, located at Lake Constance (NE Switzerland; Fig 1), was occupied for only 15 years (3384–3370 BC) [14–16]. Ground plots for 27 houses were identified. 26 of them could be dated precisely by dendrochronology, providing a unique temporal context for studying Neolithic cattle management down to the level of single houses (Fig 2; Supporting Information (SI), section I).

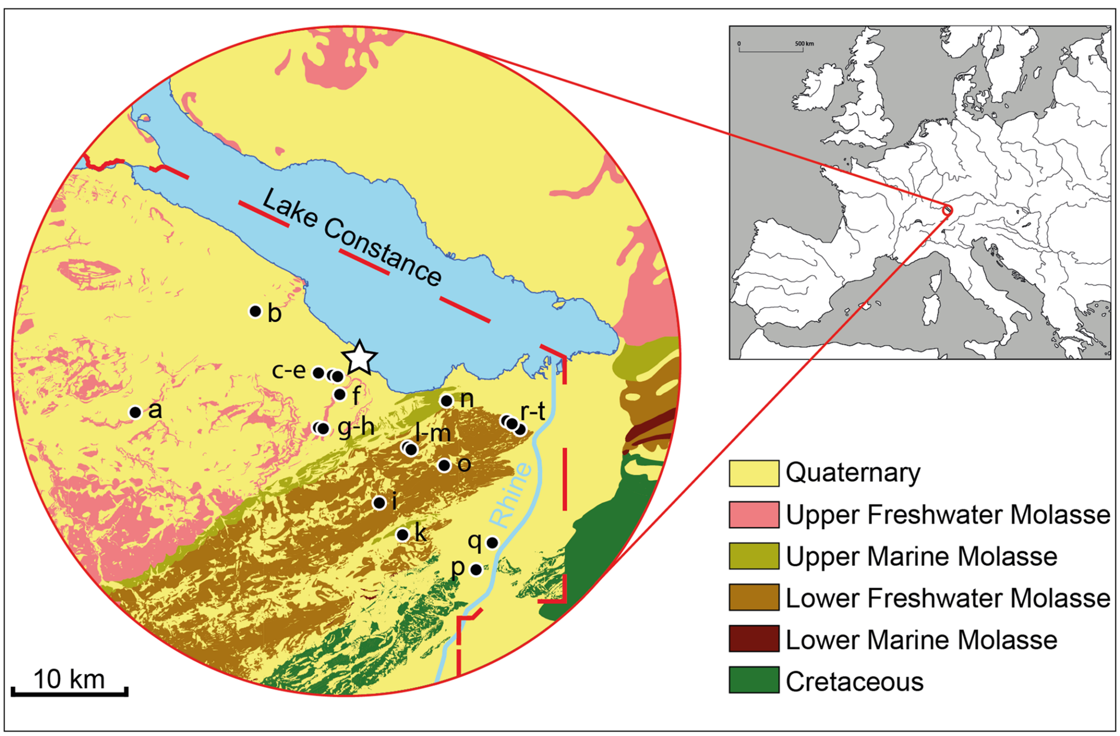

Fig 1. Geology of the study area. The location of Arbon Bleiche 3 (white star) in Central Europe with major bedrock units [17, 18] in a 30 km perimeter. The baseline sampling for bioavailable $^{87}Sr/^{86}Sr$ determination (black dots; SI section III) covered all geological units in this area, with some samples also collected outside the mapped circle (cf. S2 Table). The $^{87}Sr/^{86}Sr$ ranges are as follows: Quaternary (0.7086–0.7104, n = 8), Upper Freshwater Molasse (0.7082–0.7091, n = 4), Upper Marine Molasse (0.7084–0.7094, n = 2), Lower Freshwater Molasse (0.7084–0.7118, n = 6), Lower Marine Molasse (0.7082, n = 1), Cretaceous (0.7077–0.7085, n = 5).

https://doi.org/10.1371/journal.pone.0180164.g001

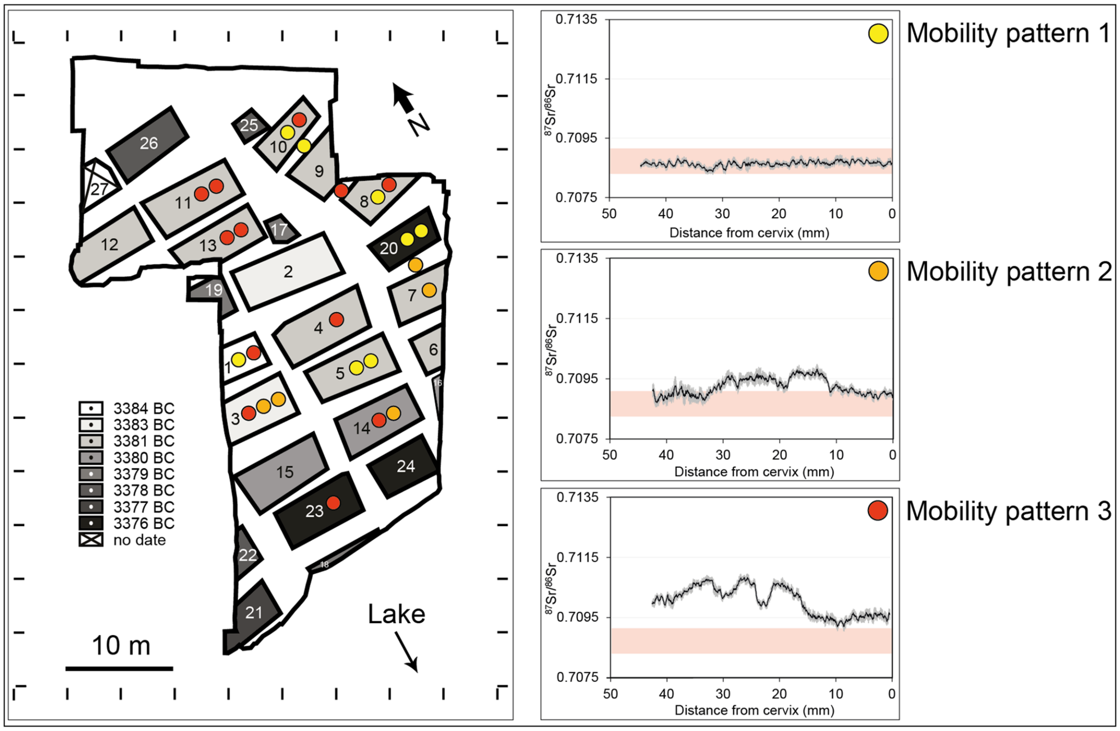

Fig 2. Cattle mobility patterns at Arbon Bleiche 3. Settlement plan with reconstructed houses (modified after [15]) and distribution of cattle mobility patterns (MP) 1–3 (left). The grey-shading represents dates of construction. $^{87}Sr/^{86}Sr$ laser ablation profiles (right) illustrate representative patterns of Sr isotope ratio variations along the tooth enamel for each mobility regime (complete data set in S1 Fig).

https://doi.org/10.1371/journal.pone.0180164.g002

Strontium isotope ($^{87}Sr/^{86}Sr$) analysis is a key method for reconstructing past human and animal mobility [19–21], which has been successfully applied to cattle remains [11, 22, 23]. Sr isotope measurements are traditionally conducted on bulk enamel samples or on micro-drilled sequential samples, usually by thermal-ionization mass spectrometry (TIMS). More recently, laser-ablation multi-collector inductively-coupled plasma mass spectrometry (LA-MC-ICP-MS) has become a highly promising approach for identifying the differences in the $^{87}Sr/^{86}Sr$ along tooth crowns, at very high temporal resolution [24, 25]. Often in combination with light stable isotope analyses ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$), recent Sr isotope studies have been used to investigate the links between cattle management, birth seasons and dairying activities [26, 27]. Here, we use LA-MC-ICP-MS strontium isotope ratio measurements along the growth axis of cattle tooth enamel as indicators of mobility to reconstruct patterns of herding. The approach makes use of the fact that the Sr isotopic compositions of geological units, soils, plants, and the hard tissues of the mammals in the same environment are closely related. The Sr isotopic signatures may be highly characteristic and can vary over relatively short geographic distances. The local $^{87}Sr/^{86}Sr$ signature is passed along the food chain and is incorporated into the teeth of animals during enamel mineralization, with negligible fractionation [20]. Provided that the $^{87}Sr/^{86}Sr$ values in the environment are indeed sufficiently different, enamel Sr isotope measurements may allow the identification of potential pasture areas at and nearby former settlements, and cattle mobility across geological units. The landscape around Arbon Bleiche 3 is dominated by Quaternary moraine deposits and outcrops of Tertiary Upper Freshwater molasse (Fig 1). To the south and east (<15 km), additional geological units of the Tertiary Upper Marine and Lower Freshwater molasse crop out. The sediments of the molasse are, with respect to their Sr-isotopic composition, clearly distinguishable from the closest high-alpine mountain chains even further south, which are dominated by Cretaceous (Alpstein and Churfirsten) and Permian sediments (south of Walensee) (SI, section II). To test also whether potential pasture grounds varied ecologically, e.g., forest pasture vs. open habitats [28, 29], C isotope measurements were conducted on mandibles or maxillae of the sampled cattle. As bone is constantly remodeled throughout the lifetime of mammals [30, 31], carbon isotope ratios measured in bone collagen reflect the protein component of the animal's diet averaged over several years. Hence, it is important to note that the C isotope data do not correspond directly to the Sr isotope ratio records measured in tooth enamel.

Materials and methods

At Arbon Bleiche 3, 39 permanent molar teeth (M1, M2, M3) from 25 cattle were selected for high-resolution $^{87}Sr/^{86}Sr$ LA-MC-ICP-MS analyses (Table 1). The teeth were associated with twelve of the 27 houses, predominantly in the northern part of the site where most of the cattle remains were excavated (Fig 2; SI, section I) [15, 32]. Although tooth enamel mineralization is a complex process [33, 34], cattle molar crowns form sequentially, progressing from the cusp to the cervix [35–37]. First molars (M1) start mineralizing *in utero*, and mineralization ends at the age of ~2 to 3 months. Second molars (M2) mineralize between the age of 1 and 12–13 months, and third molars (M3) between 9–10 months and 23–24 months [38, 39]. For twelve cattle it was possible to perform analyses on rows of teeth (2 or 3 consecutive molars), yielding expanded time-series data sets of up to two years.

Strontium isotope analysis (LA-MC-ICP-MS) of cattle teeth

Cattle teeth were provided by the Archaeological Service of the Canton Thurgau in Frauenfeld, Switzerland. Sampled skeletal elements were investigated for age at death at the Institute of Prehistory and Archaeological Science (IPAS), University of Basel, and published in 2004 [40]. An archaeozoological MNI-based approach to sampling was undertaken to ensure that the teeth and bones originated from different cattle. For Sr isotope analysis sample preparation in Basel, the surface of each tooth was carefully cleaned using a dental burr and hand drill. An enamel transect (~2 mm thick), covering the complete growth axis of the tooth, was cut out using a diamond-impregnated dental disk. The enamel was fixed in a round PTFE mount and embedded in epoxy resin (Biodur® E12 + Biodur® E1 hardener 100:28). After 12 hours under vacuum and subsequent hardening in an oven at 35˚C for 48 hours, the surface of the resin of the sample mount was ground to expose the surface of the enamel, which was then polished with SiC paper (P1200). The prepared sample mount was then transferred to the National Oceanography Centre in Southampton (NOCS) for Sr isotopic analysis, which was performed on a Finnegan Neptune multi-collector ICP-MS with a New Wave 193 nm ArF homogenized excimer laser. Plasma conditions were optimized for low oxide formation by ensuring $^{254}(UO)^+/(^{238}U^+) < 0.1\%$ [24, 25] to reduce the isobaric interference at m/z 87 primarily due to $^{40}Ca^{31}P^{16}O^+$ [41–43], which is a major constituent of the enamel matrix. Additional isobaric interferences can derive from doubly-charged rare-earth elements (REE), calcium-calcium and calcium-argide dimers, ^{87}Rb or ^{86}Kr. Contribution from ^{86}Kr was corrected for by running gas blanks, and an ^{87}Rb correction was applied assuming an $^{87}Rb/^{85}Rb$ ratio of 0.385617. Dimer interferences were monitored via the $^{84}Sr/^{86}Sr$ and ^{89}Y was measured as a proxy for REEs. Sr isotope time-series data were obtained by continuous laser ablation along the tooth's growth axis (at 20 or 25 μms^{-1}, depending on the size of the tooth). The laser pulse repetition was 15 Hz, the spot size was 150 μm, and laser fluence was 8.6 Jcm^{-2}. Prior to the actual analysis, the laser track was laser-cleaned using the identical repetition rate and spot size, but at a

Table 1. Contextual information for sampled cattle (*Bos taurus*) specimens. Listed are the length of tooth enamel (as an indicator of tooth wear), age at death (n.a. = not assigned), house attribution, mobility pattern (MP), $^{87}Sr/^{86}Sr$ data (tooth enamel) and $\delta^{13}C$ data (bone collagen).

Ind.	Skeletal element	Age at death (y)	House	Built (y BC)	MP	Lab ID	Tooth/ Bone	Enamel (mm)	$^{87}Sr/^{86}Sr$ Mean	$^{87}Sr/^{86}Sr$ Min	$^{87}Sr/^{86}Sr$ Max	$^{87}Sr/^{86}Sr$ Range	Coll %	%C	%N	C/N	$\delta^{13}C$‰ (vs. VPDB)
ARB 2	Maxilla left	c. 9	1	3384	1	ARB 2.2.1	M2	41.9	0.70836	0.70745	0.70911	0.00166					
						ARB 2.3.1	M3	44.2	0.70831	0.70745	0.70917	0.00172					
						ARB 2.1	Bone						24.3	44.1	15.7	3.3	-23.9
ARB 10	Maxilla right	c. 2–3	3	3383	2	ARB 10.2.1	M2	46.4	0.70925	0.70808	0.71055	0.00247					
						ARB 10.1	Bone						19.7	44.7	15.8	3.3	-23.2
ARB 14	Mandible right	c. 2–3	3	3383	2	ARB 14.2.1	M2	45.5	0.70924	0.70808	0.71052	0.00244					
						ARB 14.3.1	M3	52.6	0.70919	0.70799	0.71067	0.00269					
						ARB 14.1	Bone						11.3	43.7	15.6	3.3	-22.8
ARB 16	Maxilla left	c. 2–3	4	3381	3	ARB 16.3.1	M1	32.7	0.71054	0.70962	0.71203	0.00241					
						ARB 16.2.1	M2	42.5	0.71001	0.70855	0.71264	0.00409					
						ARB 16.1	Bone						19.4	45.1	16.0	3.3	-22.3
ARB 19	Mandible left	c. 9	5	3381	1	ARB 19.2.1	M3	46.7	0.70858	0.70795	0.70933	0.00138					
						ARB 19.1	Bone						19.9	44.5	16.0	3.3	-23.4
ARB 22	Mandible left	c. 6.5	7	3381	2	ARB 22.2.1	M2	38.7	0.70905	0.70790	0.71033	0.00243					
						ARB 22.1	Bone						16.0	44.0	15.9	3.2	-23.9
ARB 23	Maxilla right	c. 6.5	8	3381	3	ARB 23.2.1	M2	46.8	0.70968	0.70874	0.71066	0.00192					
ARB 25	Mandible right	c. 11.5	9/10	-	1	ARB 25.2.1	M3	44.6	0.70864	0.70808	0.70928	0.00120					
ARB 26	Mandible	n.a.	10	3381	1	ARB 26.2.1	M2?	52.3	0.70871	0.70792	0.70951	0.00158					
ARB 27	Mandible right	c. 2–3	11	3381	3	ARB 27.2.1	M2	26.4	0.70984	0.70866	0.71107	0.00240					
ARB 29	Mandible left	c. 1.5	11	3381	3	ARB 29.2.1	M2	44.4	0.71005	0.70873	0.71119	0.00246					
						ARB 29.1	Bone						20.7	43.4	15.5	3.3	-22.6
ARB 33	Maxilla left	c. 9	13	3381	3	ARB 33.4.1	M1	17.9	0.71204	0.71113	0.71283	0.00170					
						ARB 33.2.1	M2	27.7	0.71029	0.70886	0.71204	0.00318					
						ARB 33.3.1	M3	30.2	0.70997	0.70809	0.71192	0.00384					
						ARB 33.1	Bone						21.8	43.9	15.7	3.3	-22.5
ARB 34	Mandible left	c. 2–3	13	3381	3	ARB 34.2.1	M2	46.6	0.71007	0.70903	0.71135	0.00232					
						ARB 34.1	Bone						16.3	44.1	15.7	3.3	-22.4
ARB 43	Mandible right	c. 1.5	20	3376	1	ARB 43.2.1	M2	50.9	0.70866	0.70782	0.70982	0.00199					
						ARB 43.1	Bone						20.5	43.7	15.5	3.3	-24.6

(*Continued*)

Table 1. (*Continued*)

Ind.	Skeletal element	Age at death (y)	House	Built (y BC)	MP	Lab ID	Tooth/ Bone	Enamel (mm)	$^{87}Sr/^{86}Sr$ Mean	$^{87}Sr/^{86}Sr$ Min	$^{87}Sr/^{86}Sr$ Max	$^{87}Sr/^{86}Sr$ Range	Coll %	%C	%N	C/N	δ^{13}C‰ (vs. VPDB)
ARB 109	Mandible left	c. 6.5	14	3379	2	ARB 109.2.1	M2	26.3	0.70901	0.70826	0.71023	0.00196					
						ARB 109.1	Bone						18.2	42.9	15.3	3.3	-22.5
ARB 110	Mandible left	c. 9	8/9	-	3	ARB 110.3.1	M1	11.7	0.70956	0.70887	0.71025	0.00138					
						ARB 110.2.1	M2	18.9	0.70964	0.70859	0.71135	0.00276					
						ARB 110.4.1	M3	27.2	0.71028	0.70924	0.71130	0.00207					
						ARB 110.1	Bone						20.3	43.3	15.7	3.2	-22.4
ARB 111	Mandible right	c. 6.5	10	3381	3	ARB 111.2.1	M2	26.8	0.71002	0.70896	0.71121	0.00225					
						ARB 111.1	Bone						19.5	42.9	15.4	3.2	-23.0
ARB 112	Mandible left	c. 6.5	20	3376	1	ARB 112.2.1	M2	40.7	0.70896	0.70825	0.70960	0.00134					
						ARB 112.3.1	M3	47.3	0.70891	0.70822	0.70982	0.00160					
						ARB 112.1	Bone						20.3	42.3	15.1	3.3	-23.3
ARB 113	Mandible right	c. 6.5	5	3381	1	ARB 113.2.1	M2	39.4	0.70855	0.70799	0.70916	0.00116					
						ARB 113.3.1	M3	45.3	0.70868	0.70778	0.70983	0.00205					
						ARB 113.1	Bone						20.3	42.3	15.1	3.3	-22.8
ARB 114	Mandible left	c. 9	23	3376	3	ARB 114.2.1	M2	32.3	0.70984	0.70848	0.71188	0.00340					
						ARB 114.3.1	M3	43.1	0.71004	0.70809	0.71259	0.00450					
						ARB 114.1	Bone						18.3	42.4	15.2	3.3	-22.1
ARB 115	Mandible left	c. 9	3	3383	3	ARB 115.2.1	M2	13.6	0.71028	0.70883	0.71140	0.00258					
						ARB 115.3.1	M3	13.8	0.71002	0.70909	0.71165	0.00256					
						ARB 115.1	Bone						19.2	44.3	15.7	3.3	-22.2
ARB 116	Mandible left	c. 9	14	3379	3	ARB 116.2.1	M2	15.4	0.70982	0.70894	0.71069	0.00176					
						ARB 116.1	Bone						17.6	41.0	14.5	3.3	-22.2

(*Continued*)

Table 1. (*Continued*)

Ind.	Skeletal element	Age at death (y)	House	Built (y BC)	MP	Lab ID	Tooth/ Bone	Enamel (mm)	$^{87}Sr/^{86}Sr$ Mean	$^{87}Sr/^{86}Sr$ Min	$^{87}Sr/^{86}Sr$ Max	$^{87}Sr/^{86}Sr$ Range	Coll %	%C	%N	C/N	$\delta^{13}C$‰ (vs. VPDB)
ARB 117	Mandible left	c. 9	1	3384	3	ARB 117.2.1	M2	26.4	0.71159	0.70968	0.71426	0.00458					
						ARB 117.3.1	M3	36.3	0.71198	0.70959	0.71417	0.00458					
						ARB 117.1	Bone						20.2	44.9	15.8	3.3	-21.8
ARB 118	Mandible left	c. 6.5	8	3381	1	ARB 118.2.1	M2	32.7	0.70884	0.70766	0.70996	0.00230					
						ARB 118.3.1	M3	36.3	0.70876	0.70790	0.70988	0.00199					
						ARB 118.1	Bone						19.8	43.4	15.5	3.3	-24.7
ARB 119	Mandible right	c. 6.5	7/20	-	2	ARB 119.2.1	M2	42.0	0.70901	0.70794	0.71038	0.00244					
						ARB 119.3.1	M3	47.8	0.70959	0.70830	0.71098	0.00269					
						ARB 119.1	Bone						19.1	43.4	15.3	3.3	-22.1

https://doi.org/10.1371/journal.pone.0180164.t001

higher traverse rate (100 μms^{-1}). Analysis of an in-house ashed bovine pellet standard (BP), with three repeated measurements after every third sample, revealed a mean offset (Laser ablation-TIMS) in $^{87}Sr/^{86}Sr$ of +44±33 ppm (1σ), determined from 279 analyses over 18 months. This is similar to the offset reported by other laboratories using a similar methodology [44]. While this shows that interferences could not be completely eliminated, they have been reduced to the point that the reproducibility was much smaller than the observed inter-tooth variability of 952 ppm, and is therefore considered insignificant to our interpretation of the isotope data. The accuracy of laser-ablation-derived $^{87}Sr/^{86}Sr$ ratios was further verified by comparison with discrete analyses of micro-drilled samples using conventional TIMS (S2 Fig).

Discrete strontium isotope analysis of baseline samples

For baseline $^{87}Sr/^{86}Sr$ determination, dentine of cattle and red deer (*Cervus elaphus*) was analysed using a LA-MC-ICP-MS in the laboratory facilities at the National Oceanography Centre Southampton, UK. The laser spot was initially cleaned for 5 seconds with a laser repetition rate of 15 Hz and spot size of 150 μm. Data were collected at the same spot in 60 one-second cycles with a laser repetition rate of 10 Hz and a spot size of 150 μm.

For discrete Sr isotope analysis of vegetation samples (collected in spring 2013 and 2014), leaves were rinsed with demineralized water soon after collection, and dried overnight at 40–50˚C. Sample treatment followed established methods [45]. Briefly, dried leaves were ground manually and ashed in acid-washed crucibles at 550˚C for 12 h. An aliquot of approximately 20 mg of ashed leaves was transferred into clean PFA (Savillex™) vials and dissolved in 15 M HNO_3. 1 ml of 30% H_2O_2 was added to further dissolve the sample at 140–160˚C. Samples were evaporated to dryness and dissolved in 2 ml 3M HNO_3, ultrasonicated and centrifuged, before loading onto ion-exchange columns. Water aliquots (collected in spring 2013 and 2014) were transferred to clean PFA (Savillex™) vials. Sample preparation followed established methods [45]. Aliquots were evaporated to dryness, dissolved in 2 ml concentrated HCl and dried down. After adding 2 ml of concentrated HNO_3, samples were again dried down. Aliquots were then taken up in 1 or 2 ml 3 M HNO_3, ultrasonicated and centrifuged, prior to loading onto ion-exchange columns. The teeth of pigs (*Sus domesticus*) were sampled by cutting pieces of enamel representing the complete growth axis using a flexible diamond-impregnated dental disk and hand drill. The procedure is described in [46, 47]. Briefly, the inner and outer surfaces of the enamel were treated with a dental burr to remove any adhering contamination. Enamel samples were additionally cleaned with pure water in an ultrasonic bath, dried and then dissolved in 3 ml 7 M HNO_3. Samples were centrifuged to remove any adhering powder. The supernatant fluid was dried down and dissolved in 3 M HNO_3. An aliquot of this solution, representing 3 mg of solid enamel, was made up to 0.5 ml 3 M HNO_3, before loading onto ion-exchange columns. Dissolved Sr (from either plant, water or enamel samples) was separated using standard ion-exchange chromatography using 70 μl of Eichrom Sr spec resin (50–100 μm). Strontium was separated from the sample matrix by washing the column with 2.5 ml 3 M HNO_3 and eluted using 1.5 ml ultrapure water. After separation, the Sr-containing eluate was dried down. After dissolving in 1 μl 10% HNO_3, samples were loaded onto rhenium filaments, preconditioned with 1 μl $TaCl_5$ solution and 1 μl 10% H_3PO_4. Isotope ratios were measured on a Thermo Finnigan TRITON Thermal Ionization Mass Spectrometer (TIMS). Data were calibrated using the standard reference material NIST SRM 987 with a reported $^{87}Sr/^{86}Sr$ ratio of 0.710248 [48, 49]. All TIMS Sr-isotope measurements were performed in the laboratory facilities of the Department of Earth Sciences, University of Bristol, UK. The typical precision for $^{87}Sr/^{86}Sr$ measurements was ± 0.00001 (in archaeological tooth enamel).

Stable carbon isotope analysis of cattle bones

For carbon isotope analysis, collagen extraction followed established methods [50], with modifications [51] and omission of the ultrafiltration step [52, 53]. Chunks of bone were cut and subsamples were taken from a clean surface using a dental drill. 200–1000 mg of cleaned sample material was demineralized in 10 ml of 0.5 M HCl at 4˚C for two weeks. Samples were then rinsed with ultrapure water before treatment with 10 ml of 0.1 M NaOH at 4˚C for about 24 h. After rinsing, 4 ml of ultrapure water and 200 μl of 0.5 M HCl were added, and the samples gelatinized at 70˚C for 48 h. The solution containing the dissolved collagen was filtered using Ezee Filter separators (Elkay, UK) with a pore size of 60–90 μm, frozen at -20˚C, and lyophilized for 48 h. For carbon isotope analyses, between 0.5 and 1.0 mg of freeze-dried sample were weighed in duplicate into tin capsules, and introduced into an elemental analyser coupled to an isotope ratio mass spectrometer (EA-IRMS) (INTEGRA2, Sercon Ltd., Crewe, UK) in the laboratory facilities of the Department of Environmental Sciences, University of Basel, Switzerland. Carbon isotope data were calibrated using international reference materials (IAEA-CH-6, USGS40) and an in-house standard (EDTA), and reported in the conventional δ-notation as $\delta^{13}C$ in ‰ relative to Vienna Pee Dee Belemnite (V-PDB). Based on replicate analyses of the isotopic reference materials, our in-house standard and a selected bone collagen sample which were analysed recurrently in each analytical sequence, the analytical reproducibility for $\delta^{13}C$ was generally ≤ 0.2‰. Collagen preservation and purity was checked following established methods [54–56].

Results

$^{87}Sr/^{86}Sr$ values for sampled tooth enamel obtained through LA-MC-ICP-MS analysis range from 0.7075 to 0.7143 (based on individual laser measurements) with a mean of 0.7095 ± 0.0019 (2σ) (Fig 3 and S2 Fig). Sr isotope data from the tooth enamel of archaeological pigs, the dentine of cattle and red deer, as well as modern water and vegetation samples suggest that cattle grazing in close vicinity of the settlement site should display $^{87}Sr/^{86}Sr$ ratios between 0.7083 and 0.7091 (S3 Fig; SI, section II). A considerable number of samples with $^{87}Sr/^{86}Sr$ ratios that are well above this range therefore indicates that some cattle were pastured away from the settlement. Modern reference sampling of the vegetation in the area between Arbon Bleiche 3 and the high mountain ranges located in a distance of >30 to 50 km confirm that nearby and distant pasture grounds can be distinguished based on the isotopic composition, with $^{87}Sr/^{86}Sr$ up to 0.7130 in the more distant locations (S1 Table; SI, section II). The observed $^{87}Sr/^{86}Sr$ ratios allow us to distinguish between three different patterns of cattle mobility (Figs 2 and 3 and S2 Fig):

Mobility pattern (MP) 1: Stationary, local (n = 8 individuals): MP1 is characterized by $^{87}Sr/^{86}Sr$ trends that are essentially invariant ($\leq$0.0005) and fully consistent with the local baseline range of 0.7083–0.7091. The second and third quartiles of their boxplots are within the local range. Cattle remains that display MP1 were mainly found in the northern and central part of the settlement (ARB 2, 19, 25, 26, 43, 112, 113, 118).

Mobility pattern 2: Mobile, partly local (n = 5 individuals): Cattle assigned to MP2 exhibit mixed signals of local and non-local $^{87}Sr/^{86}Sr$ ratios. MP2 includes cattle that show a changeover from local to non-local $^{87}Sr/^{86}Sr$ values (ARB 119), from non-local to local $^{87}Sr/^{86}Sr$ values (ARB 109), or apparently alternating cycles of local and non-local $^{87}Sr/^{86}Sr$ (ARB 10, 14, 22). Samples displaying MP2 were primarily found in the central part of the settlement, and could be linked to houses that were situated close to each other.

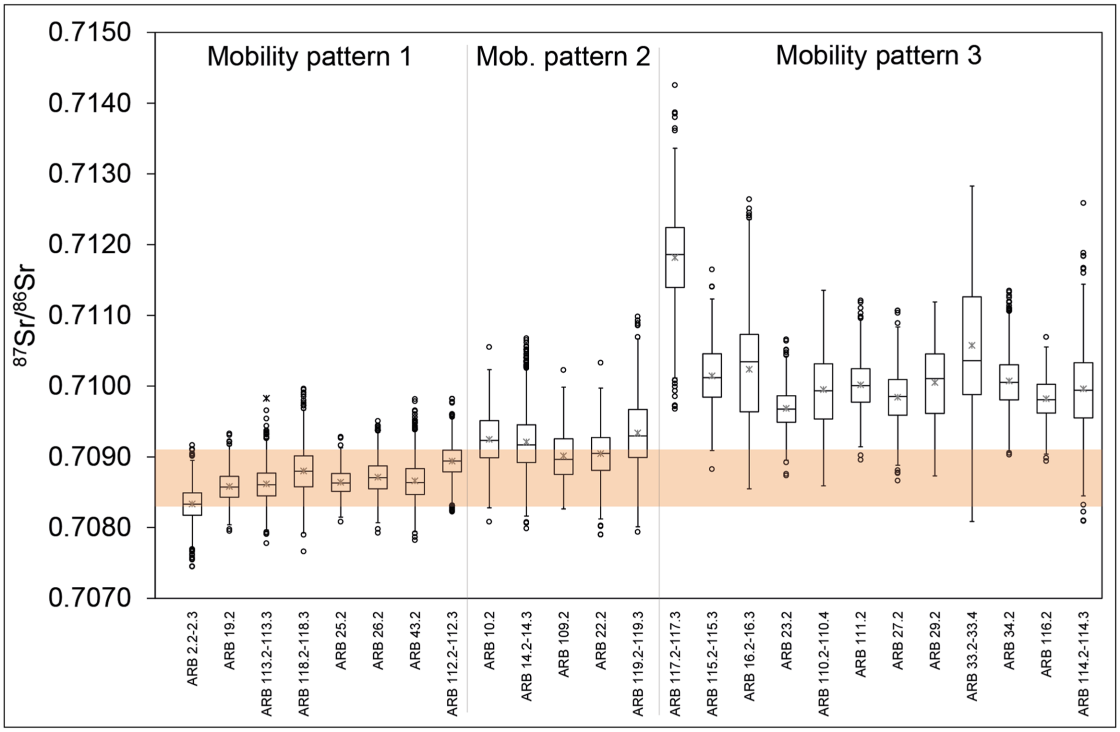

Fig 3. Box plot of $^{87}Sr/^{86}Sr$ data for cattle based on individual intra-tooth measurements. Cattle (*Bos taurus*) are grouped by mobility pattern and chronological order (cf. Table 1). The central black line in each box represents the median and the cross represents the mean. The coloured bar represents the local $^{87}Sr/^{86}Sr$ range (0.7083–0.7091).

https://doi.org/10.1371/journal.pone.0180164.g003

Mobility pattern 3: Mobile, non-local (n = 12 individuals): MP3 includes $^{87}Sr/^{86}Sr$ trends that show exclusively or mostly non-local signatures. The second and third quartiles of the boxplots lie clearly outside the expected local $^{87}Sr/^{86}Sr$ range. Samples that exhibit MP3 show $^{87}Sr/^{86}Sr$ ratios that are either persistently distinct from the local $^{87}Sr/^{86}Sr$ range of the site (ARB 23, 27, 29, 33, 34, 110, 111, 115, 116, 117), or that show dominantly non-local signatures (with some overlap with the local $^{87}Sr/^{86}Sr$ range; ARB 16, 114). MP3 specimens were found all over the settlement with a slight predominance in the northern part.

The average $^{87}Sr/^{86}Sr$ ratios of the teeth assigned to the three mobility patterns, respectively, differed significantly (Kruskal-Wallis test: $p < 0.001$; XLSTAT, version 2010). An identification and distinction of the three mobility patterns is also supported by the characteristic carbon isotope ratios of bone collagen with significantly (MP1 $\neq$ MP3; Mann-Whitney test: $p = 0.002$) different mean $\delta^{13}C$ values of -23.8 ± 0.7‰, -22.8 ± 0.6‰ and -22.4 ± 0.3‰ (1σ) for MP1, 2, and 3 respectively (Fig 4 and Table 1). The difference in the mean $\delta^{13}C$ for each pool of samples suggests that cattle mobility was associated with an apparent change in pasture grounds or grazing resources.

Cattle from the same house often displayed the same mobility pattern (houses 3, 5, 11, 13, 20). Yet for some houses, different mobility patterns were observed (houses 1, 3, 8, 10, 14). MP1 and MP2 in combination never co-occurred in the same house (Fig 2). Moreover, individual MP's were not restricted to houses with similar erection dates and they showed no clear relation to the age of the animals (Table 1).

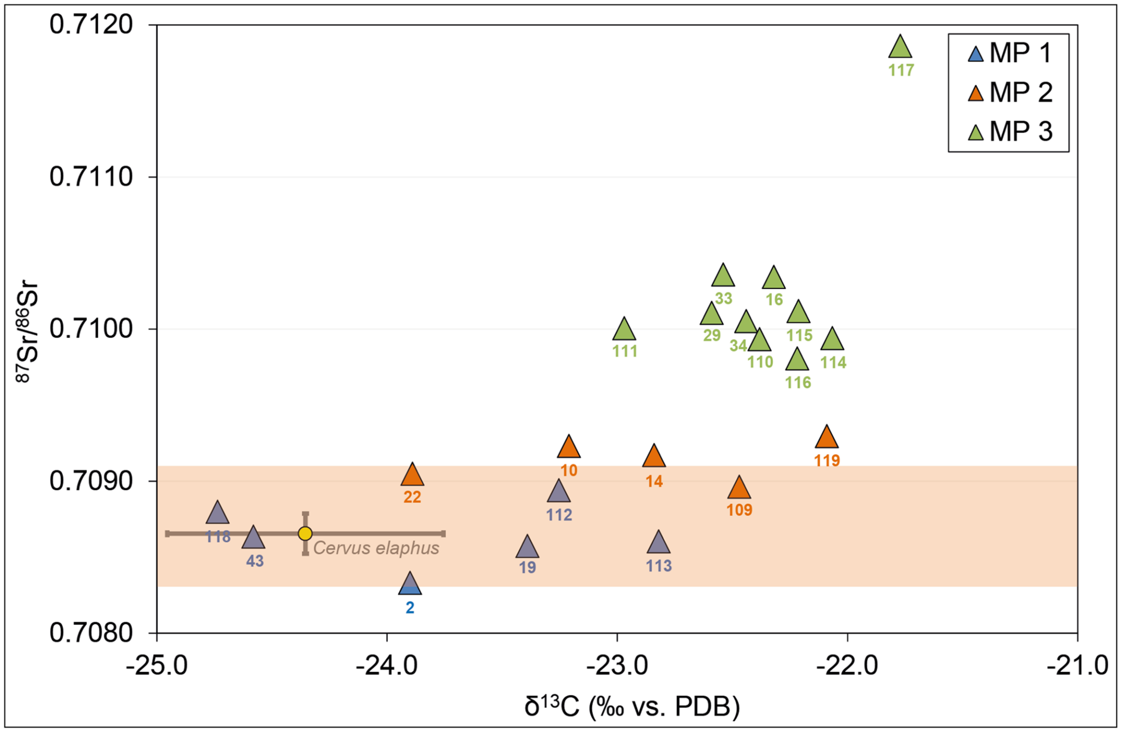

Fig 4. Scatter plot of $\delta^{13}C$ values of cattle bone collagen and average $^{87}Sr/^{86}Sr$ data of tooth enamel. $\delta^{13}C$ and $^{87}Sr/^{86}Sr$ (mean of all intra-tooth measurements for an individual) data for cattle (*Bos taurus*) are given in Table 1. Sample ID's are indicated (excl. ARB). Red deer (*Cervus elaphus*) isotopic data (n = 6; 1σ standard error) are also provided for comparison. The grey bar represents the local $^{87}Sr/^{86}Sr$ range (0.7083–0.7091).

https://doi.org/10.1371/journal.pone.0180164.g004

Discussion

The landscape and its capacity for cattle husbandry

The interpretation of the cattle movement patterns requires a detailed understanding of the Neolithic landscape and its resources around Lake Constance. The surroundings of Arbon Bleiche 3 were dominated by mixed forests of beech (*Fagus sylvatica*), oak (*Quercus* sp.), silver fir (*Abies alba*), hazel (*Corylus avellana*), ash (*Fraxinus excelsior*), and birch (*Betula* sp.) [16]. As a consequence of long-lasting human activity [14], the landscape resembled a mosaic of densely forested environments and more open settings, both natural (windfall, flood plains, lake shores) and man-made (agricultural fields, fallow ground, orchards) [16]. Human activities, with severe impact on the landscape, created new pasture grounds [57, 58], which aimed at increasing the productivity and resource capacity of the environment [59]. The multifaceted exploitation of the land around settlement sites (e.g., for timber, coppicing, pollarding, hunting, gathering, agriculture, orchards) required sustainable land management practices [58], which implies a certain limitation of land available for animal husbandry in the adjacent forests. Neighbouring settlements with additional resource demands may have created additional pressure on the landscape in the nearby surroundings [60, 61]. Plant remains found in cattle dung demonstrate the importance of wood pasture at Arbon Bleiche 3, and suggest that grazing within and at the edges of forests, and at ruderal places (including lakeshores) was common [62]. Various herding regimes for cattle may have helped to avoid or mitigate overexploitation of the available resources, and diverse (and more distant) grazing grounds were likely targeted. Herd size is an important parameter in this context. A livestock of 30–60 cattle was previously estimated based on excavated remains at Arbon Bleiche 3 [63], which implies an average of one to two co-existing animals per house. Extrapolating the calculated herd size from the excavated area to the whole settlement, we can assume a total number of 60–120 animals. Given individual requirements of approximately 17 ha of land per animal, pasture grounds of 10–20 km^2 per year were needed to sustain the settlement's combined herd (SI, section I). Ethnographic studies show that medium-sized cattle herds with more than one animal per house attest to communities that are specialised in animal husbandry or dairying, and which require elaborated herding strategies [64]. Indeed, lipid biomarker evidence on pot sherds from Arbon Bleiche 3 suggests dairying at the settlement [65, 66]. Interestingly, however, not all lactating mother cows seemed to have been kept in the immediate surrounding of Arbon Bleiche 3. Three first molars (ARB 16, 33, 110), representing the time *in utero* and shortly after birth, exhibited $^{87}Sr/^{86}Sr$ above the local range (S1 Fig), which point to some dairying in more outlying regions. We argue that the three mobility patterns in the Arbon Bleiche 3 cattle are reflective of different ecological niches utilized to sustain cattle numbers beyond the carrying capacity of the immediate environment of a settlement. This notion is supported by the observed stable carbon isotope ratios, which suggest that the exploited grazing grounds differed in their respective ecological attributes, e.g., with regards to humidity, forest cover or altitude [28, 29]. Although tooth-substance loss primarily relates to the animals' age, differences in the soil or fodder composition, relating to cattle movement, can also influence distinct tooth-wear patterns (S4 Fig and Table 1) [67, 68]. The observed Sr-isotope pattern variability between the three groups underscores that cattle management in Arbon Bleiche 3 was highly differentiated, emphasizing the complexity of herding strategies.

Local herding and seasonal movement

The Sr isotope ratios of the individuals representing MP1, accounting for approximately one third of the cattle analysed, are indicative of a static local herd. This group of animals must have been kept in the vicinity of the settlement, not more than a few km away from the site during their enamel mineralization, i.e., the first 24 months. Their C isotope ratios were lowest and most similar to those of red deer (Fig 4), and can best be explained by either leaf and twig foddering in the settlement or feeding in nearby densely forested environments [29]. The observed C isotopic signature would also be consistent with grazing grounds in humid areas [69], e.g., at the shores of Lake Constance or in flood plains. Both ecological niches were readily available in the proximity of the settlement. The absence of any summer-plant remains in cattle dung from the site confirms that there was no year-round husbandry within the actual settlement [62]. Cattle foddering nearby the settlement site implies that local supply of summer browse and winter fodder was sufficient, and that the inevitable disadvantage of losing local fertile land for cattle grazing was compensated for by the obvious benefits of maintaining a local herd (e.g., for milking, slaughtering, and traction purposes). Dairy remains in potsherds [65, 66] as well as the evidence of old animals with traction-related pathologies [40] and a wooden yoke [70] lend clear evidence to the exploitation of these benefits at Arbon Bleiche 3.

In contrast to MP1, the Sr isotope ratios of MP2 individuals suggest periods of both local and non-local grazing. The observed patterns are consistent with a herding management that involves seasonal cattle movement away from the settlement to more Sr-radiogenic catchments, and back. The associated $^{13}C/^{12}C$ ratios were higher than for MP1 individuals, consistent with a temporary cattle translocation from the local forested and rather humid environment to less humid landscapes, scattered forests or even open pastures further afield [29]. The co-existence of local cattle (MP1) and cattle displaying isotope patterns of seasonal mobility (MP2) suggests that year-round cattle fodder resources near the site were likely to be fully exploited. That local resources were insufficient to sustain all herded animals is also supported by cattle that carry MP3 (year-round herding away from the site), which represent approximately half of the individuals sampled. MP2 does not necessarily represent long-distance seasonal transhumance, as bio-available Sr with relatively high $^{87}Sr/^{86}Sr$ in the same range as observed for cattle teeth occurs within 15 km from the site (S3 Fig). Hence, $^{87}Sr/^{86}Sr$ ratios that alternate between local values and values up to 0.7105, e.g., ARB 10, 14, likely reflect periodic mobility in the hilly hinterland of Arbon Bleiche 3. Grazing spots may have varied from one year to the other, but repetitive $^{87}Sr/^{86}Sr$ shifts in the composite records suggest that certain pastures were re-visited several times (S1 Fig).

Non-local herding and alpine transhumance

Alpine mountains, i.e., the Alpstein, are located in a distance of only ~30 km from the site, rendering Arbon Bleiche 3 an ideal environment to conduct alpine transhumance (i.e., the summer exploitation of high-altitude pastures). Botanical remains of stone pine (*Pinus cembra*), alpine speedwell (*Veronica alpina*) and bone finds of the alpine ibex (*Capra ibex*) at the study site indicate that the settlers of Arbon Bleiche 3 visited high-altitude alpine regions between 1500 and 2500 m a.s.l. [16]. Moreover, the remains of Swiss clubmoss (*Selaginella helvetica*), another plant most typical for high-altitude areas (but sporadically found also at lower altitudes and in the region around Lake Constance), were identified in cattle dung [62]. In combination, these findings provide putative evidence for alpine transhumance, exploiting pastures above the timber line (estimated at 1800 m a.s.l. for the mid-4th millennium BC in the Pre-Alps [71]). The Alpstein area itself represents the closest suitable region for transhumant pasturing, but the topography is rather steep and hard to access. Moreover, isotopic values suggest it is unlikely that the Alpstein served as grazing grounds for cattle from Arbon Bleiche 3. The calcareous bedrock is characterized by $^{87}Sr/^{86}Sr$ ratios of 0.70812 ± 0.00032 (1σ) (S1 Table), inconsistent with the Sr isotope patterns observed for the MP3 cattle teeth, which are typically more radiogenic, with $^{87}Sr/^{86}Sr$ ratios of >0.7120 (ARB 16, 33, 117). Potential grazing spots with $^{87}Sr/^{86}Sr$ values of ~0.7120 are located 10–15 km southeast of the site, but they do not exceed an altitude of 1300 m a.s.l. The closest region at higher altitudes and equally high $^{87}Sr/^{86}Sr$ ratios (0.71242 ± 0.00086 (1σ)) is located south of Walensee in a distance of ~50 km from Arbon Bleiche 3 (SI, section II). Alternative pasture grounds with similarly old geological units are located east of the Alpine Rhine, slightly further away from the settlement (>60 km). Thus, the Sr isotopic patterns observed for individuals ARB 33 and especially ARB 117 may be best explained by seasonal translocation between different pastures in more Sr-radiogenic catchments, and therefore reflect a mobility pattern that is typical for alpine transhumance [72]. However, we do not see evidence for large-scale alpine cattle migration. The majority of teeth from the MP3 group show Sr isotope ratios that are consistent with grazing grounds away from, but within ~15 km distance of, the settlement site (i.e., $^{87}Sr/^{86}Sr$ values of 0.7083–0.7118), with little change in altitude. Moreover, herding grounds and food resources for animals that display MP3 appeared to be distinct from those of the MP2 and MP1 individuals, as indicated by the higher $\delta^{13}C$ of bone collagen (Fig 4). The higher $^{13}C/^{12}C$ ratios may be related to prolonged grazing in open or less humid environments. For comparison, the low $\delta^{13}C$ values determined for contemporaneous red deer are indicative of feeding grounds with a closed canopy [29]. The observed Sr isotopic fluctuations of MP3 are more complex than for MP2. Some individuals (e.g., ARB 29, 34, 114) suggest periods of stasis followed by periods of enhanced mobility on a timescale that is consistent with differential summer versus winter grazing (SI, section II). In earlier studies, ethnographic records of seasonal mobility provided evidence for complex mobility regimes, likely driven by grazing pressure and climatic constraints. Active cattle management involved multiple (3–8) herd relocations between spring and fall across different altitudes [72, 73]. Additional factors that may have contributed to the unexpectedly high number of MP3 are cattle exchange and the import of animals that had been born before the foundation of Arbon Bleiche 3, e.g., ARB 117 (house 1), ARB 16, 33 (house 3), and ARB 109 (house 14) (S5 Fig). The acquisition of animals from surrounding settlements (cattle exchange), e.g., bulls for breeding, draft animals for labour, or cattle to maintain and increase the herd size, is not unlikely, and social bonds within and beyond settlements are important for minimizing labour costs [64] and forging alliances (e.g., to gain access to land). Ritual activities, feasting, and the symbolic importance of cattle have been documented for the Neolithic and Bronze Age [22, 23, 74], and their relevance may also be indicated by bone middens and bucrania found at Arbon Bleiche 3 [40].

Specialised herding and differential access to resources

Evidence for specific mobility patterns (MP) appears to be systematically clustered within the settlement (Fig 2). MP1 was primarily observed for individuals found in the northern and central part, evidence for MP2 was focused on the central (and southern) portions of the settlement, and records of MP3 were found all over the settlement area, with a slight predominance in the north. We argue that the MP-clustering attests to differential access to resources by different individuals and groups in the settlement, and to specialised herding strategies to overcome local resource limitations. Local herding (i.e., MP1 and MP2) has likely been organized collectively, with patterns of isotopic variation being sufficiently similar to suggest the use of pastures on similar geological units. Shared herding, certainly the most efficient way of managing cattle, likely required complex interactions, cooperation and networks between the settlers or even between settlements [75–80]. We assume that social alliances were also needed to gain access to specific grazing grounds (e.g., through territorial rights) [81, 82], which apparently differed among the households in Arbon Bleiche 3, possibly depending on the period of occupation or social status. Although patterns of mobility were highly individual among MP3 animals (compared to MP1 and MP2), the range of $^{87}Sr/^{86}Sr$ ratios was similar for all cattle during periods of stasis (0.7095–0.7100) (S1 Fig). This suggests perhaps a collective overwintering strategy on the one hand, but the dispersal of animals in summer as small herds with differential access to grazing grounds on the other.

Conclusions

Our study presents the first large-scale and high-resolution approach using $^{87}Sr/^{86}Sr$ LA-MC-ICP-MS measurements to explore Neolithic cattle herding strategies more than 5400 years ago. The data from Arbon Bleiche 3 reveal distinct strontium isotopic patterns that reflect different co-existing herding practices, including localized cattle herding, seasonal mobility and permanent pasturing on distant grounds. Grazing in different environments (either at long- or short-distances) is suggested by the Sr isotope ratios in teeth, dependent on the geology, and supported by the carbon isotope values in bone collagen, dependent on the ecology, and the relation between tooth abrasion and mobility pattern which may relate to the fodder. Exploiting alternative and maybe more distant grazing grounds was necessary to relieve the pressure on local resources (carrying capacity) as a consequence of increased settlement density and larger herd sizes. A limited number of cattle show comparatively high (i.e., radiogenic) $^{87}Sr/^{86}Sr$ ratios that are consistent with translocation to, and from, nearby high-altitude areas, and thus reflect vertical (i.e., alpine) transhumance. We cannot exclude, however, that these animals predate the settlement foundation and were brought to Arbon Bleiche 3 by the first generation of settlers. The majority of the transhumant cattle were herded within 15 km of the site. Yet, the Sr isotopic data suggest a high degree of mobility within this perimeter, allowing the exploitation of patchy areas of open pasture. The individual mobility patterns suggest differential access to (presumably) the most favourable grazing grounds, which in turn have contributed to social inequalities between groups or households. But this practise also forged alliances between villages and thus fostered communication and shared values. In consequence, the increasing importance of cattle from the 4th millennium BC onwards, and the emerging complexity in keeping them, may thus be seen as a starting point for further socio-economic differentiation, which was widespread later in the European Bronze Age [83].

Supporting information

S1 File.
(PDF)

S1 Fig. ^{87}Sr/^{86}Sr LA-MC-ICP-MS data for individual cattle and analysed teeth (M1–M3), grouped by mobility pattern. Each data point denotes the mean of 10 measurements including a 2σ standard error envelope (given in grey). The coloured bar represents the local ^{87}Sr/^{86}Sr range (0.7083–0.7091). The complete data set is given in S3 Table.
(PDF)

S2 Fig. Comparison of Sr isotope analyses between LA-MC-ICP-MS (solid line) and TIMS (diamonds) of cattle tooth enamel from the Neolithic lakeside settlement of Zurich-Mozartstrasse, Switzerland. LA-MC-ICP-MS data are processed as a 10-point moving mean of the raw signal integrations with the shaded band representing a 2σ standard error of the mean. Micromilled samples (3 mg) were extracted as close as possible to the laser track of the tooth enamel and measured using standard TIMS techniques [48]. Typical errors for TIMS measurements are ± 0.00001. Both methods agree well within the analytical error showing that the potential interferences during LA-MC-ICP-MS measurements have been reduced to insignificant levels.
(TIF)

S3 Fig. ^{87}Sr/^{86}Sr baseline data. We analysed prehistoric fauna and modern local water at Arbon Bleiche 3 (left) and representative environmental ^{87}Sr/^{86}Sr data for modern vegetation in the nearby and more distant environments (right). Data are also given in S1 and S2 Tables.
(TIF)

S4 Fig. Box plot of the tooth enamel length as an indicator of tooth wear. Teeth (M2 = second molar, M3 = third molar) are grouped by mobility pattern. The central black line in each box represents the median, and the cross represents the mean.
(TIF)

S5 Fig. Chronological development of houses at Arbon Bleiche 3. Newly built houses are coloured black, existing ones are shown in grey. The last buildings were erected in 3376 BC.
(TIF)

S1 Table. Environmental ^{87}Sr/^{86}Sr baseline data from the surroundings of Arbon Bleiche 3. Calculations on the mean ^{87}Sr/^{86}Sr and ^{87}Sr/^{86}Sr ranges for geological units are based on the average values of both plants with shallow (herbs and bushes) and deep (trees) roots from each sampling location. Geological units are colour-coded according to Fig 1.
(PDF)

S2 Table. ^{87}Sr/^{86}Sr baseline data from Arbon Bleiche 3. Prehistoric fauna was analysed by LA-MC-ICP-MS (spot measurements, *Bos taurus* and *Cervus elaphus*) and TIMS (*Sus*

domesticus) and modern local water was analysed by TIMS. Water samples were collected in May 2013.
(PDF)

S3 Table. $^{87}Sr/^{86}Sr$ LA-MC-ICP-MS data for cattle teeth from Arbon Bleiche 3. The length of the laser track (distance from cervix) is shorter than the length of tooth enamel, as given in Table 1. M1 = first molar, M2 = second molar, M3 = third molar.
(PDF)

Acknowledgments

We thank Hansjörg Brem and Urs Leuzinger, Archaeological Service of Canton Thurgau, and Beat Eberschweiler and Simon Vogt, Archaeological Service of Canton Zurich, for their collaboration in sample acquisition. We are grateful to Andy Milton, National Oceanography Centre Southampton, Tim Elliott and Chris Coath, University of Bristol, for scientific and technical assistance with the isotopic analyses. Help and advice were provided by Stefanie Jacomet, Barbara Stopp and Renate Ebersbach, University of Basel, and Chris Standish, University of Southampton. The two reviewers are thanked for their helpful comments on a previous version of this paper.

Author Contributions

Conceptualization: JS VH AWGP CK CG TD MFL.

Formal analysis: CG TD.

Funding acquisition: JS.

Investigation: CG TD AWGP MFL TK CK VH JS.

Project administration: JS CG TD.

Supervision: JS AWGP MFL VH.

Writing – original draft: CG TD.

Writing – review & editing: CG TD AWGP MFL CK TK JS VH.

References

1. Renfrew C. The Emergence of Civilisation: The Cyclades and the Aegean in the Third Millennium BC. London: Methuen; 1972.
2. Sherratt A. Plough and pastoralism: aspects of the secondary products revolution. In: Hodder IG, Hammond N., editors. Pattern of the past. Studies in honour of David Clarke. Cambridge: Cambridge University Press; 1981. p. 261–305.
3. Greenfield H. Some reflections on the origins and intensification of dairying in the archaeological record. In: Greenfield H, editor. Animal Secondary Products. Domestic Animal Exploitation in Prehistoric Europe, the Near East and the Far East. Oxford: Oxbow Books; 2014. p. 20–39.
4. Schibler J, Jacomet S, Hüster-Plogmann H, Brombacher C. Synthesis. In: Schibler J, Hüster-Plogmann H, Jacomet S, Brombacher C, Gross-Klee E, Rast-Eicher A, editors. Ökonomie und Ökologie neolithischer und bronzezeitlicher Ufersiedlungen am Zürichsee. Zürich, Egg: Fotorotar; 1997. p. 329–361.
5. Bogaard A, Fraser R, Heaton THE, Wallace M, Vaiglova P, Charles M, et al. Crop manuring and intensive land management by Europe's first farmers. Proc Natl Acad Sci USA 2013; 110(31): 12589–12594. https://doi.org/10.1073/pnas.1305918110 PMID: 23858458
6. Karg S. Winter- and spring-foddering of sheep/goat in the Bronze Age site of Fiavè-Carera, Northern Italy. Environ Archaeol 1998; 1: 87–94.

7. Kristiansen K. The decline of the Neolithic and the rise of Bronze Age society. In: Fowler C, Harding J, Hofmann D, editors. The Oxford Handbook of Neolithic Europe. Oxford: Oxford University Press; 2015. p. 1093–1117.

8. Kaplan JO, Krumhardt KM, Zimmermann N. The prehistoric and preindustrial deforestation of Europe. Quaternary Sci Rev 2009; 28: 3016–3034.

9. Spindler K. Transhumanz. Preistoria Alpina 2003; 39: 219–225.

10. Davies J, Hatfield R. The economics of mobile pastoralism: a global summary. Nomadic Peoples 2007; 11: 91–116.

11. Knipper C. Die räumliche Organisation der linearbandkeramischen Rinderhaltung: naturwissenschaftliche und archäologische Untersuchungen. Oxford: Archaeopress; 2011.

12. Balasse M, Tornero C, Bréhard S, Ughetto-Monfrin J, Voinea V, Bălăşescu A. Cattle and sheep herding at Cheia, Romania, at the turn of the fifth millennium cal BC: a view from stable isotope analysis. In: Whittle A, Bickle P, editors. Early Farmers: The View from Archaeology and Science. Oxford: Oxford University Press/Proceedings of the British Academy 198; 2014. p. 115–142.

13. Della Casa P, Naef L, Reitmaier T. Valleys, pastures and passes: new research issues from the Swiss Central Alps. Preistoria Alpina 2013; 47: 17–30.

14. Leuzinger U. Die jungsteinzeitliche Siedlung Arbon-Bleiche 3. Befunde. Frauenfeld: Huber & Co. AG; 2000.

15. De Capitani A, Deschler-Erb S, Leuzinger U, Marti-Grädel E, Schibler J. Die jungsteinzeitliche Siedlung Arbon-Bleiche 3. Funde. Frauenfeld: Huber & Co. AG; 2002.

16. Jacomet S, Leuzinger U, Schibler J. Synthesis. In: Jacomet S, Leuzinger U, Schibler J, editors. Die jungsteinzeitliche Seeufersiedlung Arbon-Bleiche 3. Umwelt und Wirtschaft. Frauenfeld: Huber & Co. AG; 2004. p. 379–416.

17. Schweizerisches Bundesamt für Landestopografie. Geocatalog: GeoCover—Vector Datasets. 2014. http://www.map.geo.admin.ch.

18. Schweizerisches Bundesamt für Landestopografie. Geocatalog: Geology 500. 2008. http://www.map.geo.admin.ch.

19. Ericson JE. Strontium isotope characterization in the study of prehistoric human ecology. J Hum Evol 1985; 14: 503–514.

20. Bentley R. Strontium isotopes from the Earth to the archaeological skeleton: a review. J Archaeol Method Th 2006; 13(3): 135–187.

21. Montgomery J. Passports from the past: Investigating human dispersals using strontium isotope analysis of tooth enamel. Ann Hum Biol 2010; 37: 325–346. https://doi.org/10.3109/03014461003649297 PMID: 20367186

22. Viner S, Evans J, Albarella U, Parker Pearson M. Cattle mobility in prehistoric Britain: strontium isotope analysis of cattle teeth from Durrington Walls (Wiltshire, Britain). J Archaeol Sci 2010; 37(11): 2812–2820.

23. Sjögren K-G, Price TD. A complex Neolithic economy: isotope evidence for the circulation of cattle and sheep in the TRB of western Sweden. J Archaeol Sci 2013; 40(1): 690–704.

24. De Jong H. A strontium isotope perspective on subsistence through intra-tooth and inter-site variation by LA-MC-ICP-MS and TIMS [PhD Thesis]. University of Bristol; 2013.

25. Lewis J, Coath C, Pike AWG. An improved protocol for 87Sr/86Sr by laser ablation multi-collector inductively coupled plasma mass spectrometry using oxide reduction and a customised plasma interface. Chem Geol 2014; 390: 173–181.

26. Gron K, Montgomery J, Rowley-Conwy P. Cattle Management for Dairying in Scandinavia's Earliest Neolithic. PLoS ONE 2015; 10(7). https://doi.org/10.1371/journal.pone.0131267 PMID: 26146989

27. Towers J, Jay M, Mainland I, Nehlich O, Montgomery J. A calf for all seasons? The potential of stable isotope analysis to investigate prehistoric husbandry practices. J Archaeol Sci 2011; 38(8): 1858–1868.

28. Van der Merwe N, Medina E. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. J Archaeol Sci 1991; 18(3): 249–259.

29. Drucker D, Bridault A, Hobson K, Szuma E, Bocherens H. Can carbon-13 in large herbivores reflect the canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates. Palaeogeogr Palaeoclimatol Palaeoecol 2008; 266(1/2): 69–82.

30. Kini U, Nandeesh B. Physiology of Bone Formation, Remodeling, and Metabolism. In: Fogelman I, Gnanasegaran G, van der Wall H, editors. Radionuclide and Hybrid Bone Imaging. Berlin: Springer; 2012. p. 29–57.

31. Olsen KC, White CD, Longstaffe FJ, von Heyking K, McGlynn G, Grupe G, et al. Intraskeletal isotopic compositions (δ13C, δ15N) of bone collagen: Nonpathological and pathological variation. Am J Phys Anthropol 2014; 153(4): 598–604. https://doi.org/10.1002/ajpa.22459 PMID: 24374993

32. Marti-Grädel E, Deschler-Erb S, Hüster Plogmann H, Schibler J. Early evidence of economic specialization or social differentiation: a case study from the Neolithic lake shore settlement 'Arbon-Bleiche 3' (Switzerland). In: Jones S, O'Day S, Van Neer W, Ervynck A, editors. Behaviour behind bones: the zooarchaeology of ritual, religion, status and identity. Proceedings of the 9th ICAZ Conference, Durham 2002. Oxford: Oxbow Books; 2004. p. 164–176.

33. Montgomery J, Evans J, Horstwood MSA. Evidence for long-term averaging of strontium in bovine enamel using TIMS and LA-MC-ICPMS strontium isotope intra-molar profiles. Environ Archaeol 2010; 15(1): 32–42.

34. Zazzo A, Bendrey R, Vella D, Moloney AP, Monahan FJ, Schmidt O. A refined sampling strategy for intra-tooth stable isotope analysis of mammalian enamel. Geochim Cosmochim Ac 2012; 84: 1–13.

35. Suga S, Ohno S, Misu M, Kondo K. Progressive mineralization pattern of bovine developing enamel. Jpn J Oral Biol 1979; 21(1): 117–139.

36. Suga S. Progressive mineralization pattern of developing enamel during the maturation stage. J Dent Res 1982; 61: 1532–1542.

37. Hillson S. Teeth. Cambridge: Cambridge University Press; 2005.

38. Brown W, Christofferson P, Massler M, Weiss M. Postnatal tooth development in cattle. Am J Vet Res 1960; 21: 7–34. PMID: 13805043

39. Beasley M, Brown W, Legge A. Incremental banding in dental cementum: methods of preparation for teeth from archaeological sites and for modern comparative specimens. Int J Osteoarchaeol 1992; 2(1): 37–50.

40. Deschler-Erb S, Marti-Grädel E. Viehhaltung und Jagd. Ergebnisse der Untersuchung der handaufgelesenen Tierknochen. In: Jacomet S, Leuzinger U, Schibler J, editors. Die jungsteinzeitliche Seeufersiedlung Arbon Bleiche 3, Umwelt und Wirtschaft. Frauenfeld: Huber & Co. AG; 2004. p. 158–252.

41. Horstwood MSA, Evans JA, Montgomery J. Determination of Sr isotopes in calcium phosphates using laser ablation inductively coupled plasma mass spectrometry and their application to archaeological tooth enamel. Geochim Cosmochim Ac 2008; 72(23): 5659–5674.

42. Simonetti A, Buzon MR, Creaser RA. In-situ elemental and Sr isotope investigations of human tooth enamel by laser ablation-(MC)-ICP-MS: successes and pitfalls. Archaeometry 2008; 50(2): 371–385.

43. Irrgeher J, Galler P, Prohaska T. 87Sr/86Sr isotope ratio measurements by laser ablation multicollector inductively coupled plasma mass spectrometry: Reconsidering matrix interferences in bioapatites and biogenic carbonates. Spectrochim Acta Part B: Atomic Spectroscopy 2016; 125: 31–42.

44. Willmes M, et al. Improvement of laser ablation in situ micro-analysis to identify diagenetic alteration and measure strontium isotope ratios in fossil human teeth. J Archaeol Sci 2016; 70: 102–116.

45. Maurer A-F, Galer SJG, Knipper C, Beierlein L, Nunn EV, Peters D, et al. Bioavailable $^{87}Sr/^{86}Sr$ in different environmental samples—Effects of anthropogenic contamination and implications for isoscapes in past migration studies. Sci Total Environ 2012; 433: 216–229. https://doi.org/10.1016/j.scitotenv.2012.06.046 PMID: 22796412

46. Haak W, Brandt G, de Jong HN, Meyer C, Ganslmeier R, Heyd V, et al. Ancient DNA, Strontium isotopes, and osteological analyses shed light on social and kinship organization of the Later Stone Age. Proc Natl Acad Sci USA 2008; 105(47): 18226–18231. https://doi.org/10.1073/pnas.0807592105 PMID: 19015520

47. Gerling C, Bánffy E, Dani J, Köhler K, Kulcsár G, Pike AWG, et al. Immigration and transhumance in the Early Bronze Age Carpathian Basin: the occupants of a kurgan. Antiquity 2012; 86(334): 1097–1111.

48. Thirlwall MF. Long-term reproducibility of multicollector Sr and Nd isotope ratio analysis. Chem Geol 1991: 94(2): 85–104.

49. Avanzinelli R, Boari E, Conticelli S, Francalanci L, Guarnieri L, Perini G, et al. High precision Sr, Nd, and Pb isotopic analyses using the new generation Thermal Ionisation Mass Spectrometer ThermoFinnigan Triton-Ti®. Period Mineral 2005; 74(3): 147–166.

50. Longin R. New method of collagen extraction for radiocarbon dating. Nature 1971; 230: 241–242. PMID: 4926713

51. Knipper C, Peters D, Meyer C, Maurer A-F, Muhl A, Schöne BR, et al. Dietary reconstruction in migration period central Germany: a carbon and nitrogen isotope study. Archaeol Anthropol Sci 2013; 5(1): 17–35.

52. Jørkov MLS, Heinemeier J, Lynnerup N. Evaluating bone collagen extraction methods for stable isotope analysis in dietary studies. J Archaeol Sci 2007; 34(11): 1824–1829.

53. Sealy J, Johnson M, Richards M, Nehlich O. Comparison of two methods of extracting bone collagen for stable carbon and nitrogen isotope analysis: comparing whole bone demineralization with gelatinization and ultrafiltration. J Archaeol Sci 2014; 47: 64–69.
54. DeNiro MJ. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. Nature 1985; 317: 806–809.
55. Ambrose SH. Preparation and characterization of bone and tooth collagen for isotopic analysis. J Archaeol Sci 1990; 17(4): 431–451.
56. Van Klinken GJ. Bone collagen quality indicators for paleodietary and radiocarbon measurements. J Archaeol Sci 1999; 26(6): 687–695.
57. Akeret Ö, Rentzel P. Micromorphology and plant macrofossil analysis of cattle dung from the Neolithic lake shore settlement of Arbon Bleiche 3. Geoarchaeology 2001; 16(6): 687–700.
58. Jacomet S, Ebersbach R, Akeret Ö, Antolin F, Baum T, Bogaard A, et al. On-site data cast doubts on the hypothesis of shifting cultivation in the late Neolithic (c. 4300–2400 cal. BC): Landscape management as an alternative paradigm. Holocene; 2016.
59. Smith B. The Ultimate Ecosystem Engineers. Science 2007; 315: 1797–1798. https://doi.org/10.1126/science.1137740 PMID: 17395815
60. Billamboz A. Regional patterns of settlement and woodland developments: Dendroarchaeology in the Neolithic pile-dwellings on Lake Constance (Germany). Holocene 2014; 24(10): 1278–1287.
61. Styring A, Maier U, Stephan E, Schlichtherle H, Bogaard A. Cultivation of choice: new insights into farming practices at Neolithic lakeshore sites. Antiquity 2016; 90(349): 95–110.
62. Kühn M, Hadorn P. Pflanzliche Makro- und Mikroreste aus Dung von Wiederkäuern. In: Jacomet S, Leuzinger U, Schibler J, editors. Die jungsteinzeitliche Seeufersiedlung Arbon Bleiche 3. Umwelt und Wirtschaft. Frauenfeld: Huber & Co. AG; 2004. p. 327–357.
63. Ebersbach R. Quantitative approaches to reconstructing prehistoric stock breeding. In: Kerig T, Zimmermann A, editors. Economic archaeology: from structure to performance in European archaeology. Bonn: Habelt; 2013. p. 143–160.
64. Ebersbach R. Von Bauern und Rindern. Eine Ökosystemanalyse zur Bedeutung der Rinderhaltung in bäuerlichen Gesellschaften als Grundlage zur Modellbildung im Neolithikum. Basel: Schwabe; 2002.
65. Spangenberg J, Schibler J, Jacomet S. Chemical analyses of organic residues in archaeological pottery from Arbon Bleiche 3, Switzerland—evidence for dairying in the late Neolithic. J Archaeol Sci 2006; 33 (1): 1–13.
66. Spangenberg J, Matuschik I, Jacomet S, Schibler J. Direct evidence for the existence of dairying farms in prehistoric Central Europe (4th millennium BC). Isot Environ Health Stud 2008; 44(2): 189–200.
67. Grant A. Variation in dental attrition in mammals and its relevance to age estimation. In: Brothwell D, Thomas K, Clutton-Brock J, editors. Research Problems in Zooarchaeology, Occasional Publication. London: Institute of Archaeology; 1978. p. 103–106.
68. Ungar PS. Mammalian dental function and wear: A review. Biosurf Biotrobibol 2015; 1: 25–41.
69. Kohn M. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. Proc Natl Acad Sci USA 2010; 107(46): 19691–19695. https://doi.org/10.1073/pnas.1004933107 PMID: 21041671
70. Leuzinger U. Holzartefakte. In: De Capitani A, Deschler-Erb S, Leuzinger U, Marti-Grädel E, Schibler J. editors. Die jungsteinzeitliche Seeufersiedlung Arbon Bleiche 3, Funde. Archäologie im Thurgau. Frauenfeld: Huber & Co. AG; 2002. p. 76–114.
71. Burga C, Perret R. Vegetation und Klima der Schweiz seit dem jüngeren Eiszeitalter. Thun: Ott; 1998.
72. Davies E. The patterns of transhumance in Europe. Geography 1941; 26(4): 155–168.
73. Alther Y. Vertikal mobil. Ein Beitrag zum Verständnis alpiner Wirtschaftsformen in der Archäologie. Chur: Archäologischer Dienst Graubünden; 2014.
74. Pollex A. Comments on the interpretation of the so-called cattle burials of Neolithic Central Europe. Antiquity 1999; 73: 542–550.
75. Heyd V. Families, Prestige Goods, Warriors and Complex Societies: Beaker Groups of the 3rd Millennium cal BC along the Upper and Middle Danube. Proc Prehist Soc 2007; 73: 321–370.
76. Müller J, et al. A Revision of Corded Ware Settlement Pattern—New Results from the Central European Low Mountain Range. Proc Prehist Soc 2009; 75: 125–142.
77. Ebersbach R. My farmland − our livestock. Forms of subsistence farming and forms of sharing in peasant communities. In: Benz M, editor. The principle of sharing − Segregation and construction of social identities at the transition from foraging to farming, SENEPSE Studies in Early Near Eastern production, subsistence, and environment. Berlin: Ex Oriente; 2010. p. 159–182.

78. Bogaard A, Krause R, Strien H. Towards a social geography of cultivation and plant use in an early farming community: Vaihingen an der Enz, south-west Germany. Antiquity 2011; 85(328): 395–416.

79. Bickle P, Hofmann D, Bentley RA, Hedges REM, Nowell GM, Hamilton J, et al. Community heterogeneity in the Linearbandkeramik. Antiquity 2011; 85(330): 1243–1258.

80. Bentley RA, Bickle P, Fibiger L, Nowell GM, Dale CW, Hedges REM, et al. Community Differentiation and Kinship Among Europe's First Farmers. Proc Natl Acad Sci USA 2012; 109(24): 9326–9330. https://doi.org/10.1073/pnas.1113710109 PMID: 22645332

81. Bowles S, Choi J-K. Coevolution of farming and private property during the early Holocene. Proc Natl Acad Sci USA 2013; 110(22): 8830–8835. https://doi.org/10.1073/pnas.1212149110 PMID: 23671111

82. Borgerhoff Mulder M, Fazzio I, Irons W, McElreath RL, Bowles S, Bell A, et al. Pastoralism and Wealth Inequality. Revisiting an Old Question. Curr Anthropol 2010; 51(1): 35–48.

83. Harding A. European societies in the Bronze Age. Cambridge: Cambridge University Press; 2000.