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ORIGINAL PAPER

Contributing to characterise wild predator behaviour: consumption pattern, spatial distribution and bone damage on ungulate carcasses consumed by red fox (*Vulpes vulpes*)

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Abstract

Neo-taphonomic studies of carnivores are commonly used to explain the formation processes of Pleistocene faunal assemblages. However, these works have been developed mostly with large carnivores—e.g. hyenas. On the contrary, small and medium-sized carnivores have been scarcely studied in spite of their presence in most of the archaeological sites. Here, we present a study trying to characterise the wild predator behaviour from a taphonomic perspective, describing consumption patterns on 23 small-sized ungulate carcasses eaten by red foxes (*Vulpes vulpes*) during a 2-year period in the Spanish Pyrenees. The aim of this work, therefore, is to characterise taphonomically this predator and to obtain data to distinguish them from other most common carnivores. For that, a combination of observational data from photo/video-trap and taphonomic analyses was compiled, allowing us to control variables like seasonality and time of consumption, as well as the spatial dispersion of skeletal remains. The initial interest by foxes lies in the disassembly of the anatomical elements and their transport to secluded places giving rise to dispersion of bones. Regarding to seasonality, bone modification increases at the end of winter/spring time, and proportionally, the time of consumption decreases. When the carcass is complete, viscera seem to be an important resource, followed by meat covering femur and humerus. This phenomenon causes significant damage on axial bones (mainly fractures and tooth marks), and to a lesser extent, on pelvis and proximal stylopodials.

Keywords Taphonomy · Actualism · Animal behaviour · *Vulpes vulpes*

Introduction

In the last decades, actualistic studies have commonly been developed to create analogical frameworks, which could be used to explain processes occurred in the past. In this respect, neo-taphonomic studies with current carnivores have become an essential tool to understand the role played by bone-modifying animals in the archaeological and paleontological records. However, this kind of studies is frequently handicapped by contextual difficulties when dealing with wild animals; for example, a long-time of observation and experimentation is required, control systems are commonly less tight than when experimenting with captive carnivores, and the subsequent results are not always satisfactory for observers. The paucity of studies with wild carnivores prevents the development of a neo-taphonomic database to be used in the correct interpretation of past faunal assemblages. In many cases, these difficulties have been overcome with studies carried out with captive carnivores, and the data thus obtained have been mechanically used to elaborate behavioural patterns for various types of carnivores (Saladié et al. 2013; Rodríguez-Hidalgo et al. 2013, 2015; Lloveras et al. 2012, 2016; Camarós et al. 2013, 2015). In this respect, Gidna et al. (2013) warn that the inappropriate use of actualism, derived from inadequate contexts and with limited variables, can lead to erroneous analogies and, subsequently,

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to unsuitable interpretations when analysing prehistoric faunal assemblages.

Despite this, many actualistic studies have been developed with free-ranging large carnivores in order to characterise their behaviour and taphonomical signature (e.g. Sala et al. 2014; Arilla et al. 2014). Furthermore, knowing the role of these predators in archaeological sites becomes crucial so as to improve the understanding about hominid-carnivore interactions in the past (e.g. Cruz-Uribe 1991; Marean and Spencer 1991; Domínguez-Rodrigo 1999; Pokines and Kerbis Peterhans 2007; Arilla et al. 2014).

Small- and medium-sized carnivores like red foxes (*Vulpes vulpes*) or badgers (*Meles meles*) are common in most European Pleistocene sites (e.g. Delpech 1983; Andrews and Fernández-Jalvo 1997; Yravedra 2001; Stimpson et al. 2016) and, unfortunately, hardly studied from a neo-taphonomic perspective (Mondini 1995; Krajcarz and Krajcarz 2014; Mallye et al. 2008; Yravedra et al. 2014; Young et al. 2015a). The comprehension of these carnivore actions can help us to enhance the manner in which we analyse archaeological sites. The predator activity of different agents, like carnivores and human groups, turns out in a complex scenario where an accurate interpretation of faunal assemblages becomes essential, bearing in mind the palimpsest phenomenon. Therefore, neo-taphonomic studies may entail a better insight about the relation between carnivores and hominins as a way to differentiate the resulting damage.

The analysis of modern fox-made bone assemblage contributes to improve the referential framework for this carnivore activity (e.g. Mondini 1995; Nasti 2000; Fernández et al. 2010; Lloveras et al. 2012; Krajcarz and Krajcarz 2014; Yravedra et al. 2014; Young et al. 2015a). The red fox is considered a highly adaptable small predator with a remarkable generalist behaviour, because it can feed on a broad food spectrum, depending on supply. Its dietary preferences focus on invertebrates (insects and worms), birds and small mammals such as rodents and lagomorphs, as well as on ungulate carrion (e.g. Fedriani 1996). An important aspect of red fox behaviour is the occupation of underground lairs where it brings skeletal portions and/or prey (e.g. Goszczyński 1974). The red fox is of interest in the interpretation of the fossil faunal assemblages because it was a common inhabitant of Pleistocene archaeological sites in Eurasia, northern Africa and North America. Thus, it is crucial to define criteria for the identification of red fox-made bone accumulations. It is worth mentioning the Mondini's (1995) study, which presents data on bone assemblage from seven fox dens in rock shelters in La Puna (Catamarca province, Argentina). The skeletal part representation shows a predominance of appendicular elements, mostly distal limbs. Yravedra et al. (2014) also tackle this topic and analyse two modern assemblages modified by foxes corresponding to a natural-death assemblage in Spain, and a den in France. These authors analyse tooth marks and fracture patterns, as well as frequencies, distribution of tooth marks on bone surface and measurements. Their results point to a transport of all anatomical sections in small ungulates, such as sheep, and a high frequency of tooth marks depending on the context—e.g. the proportion is lower in the natural-death assemblage than in the den. Gnawing damage is mainly located on appendicular elements and bone edges. Krajcarz and Krajcarz (2014) also analyse a modern fox-made bone assemblage in an inactive underground stone mine in Poland (cave-like context) and observe a high proportion of gnawing and concentrations in clusters with specific orientations. The scavenging behaviour of wild foxes and wild badgers was also recorded by Young et al. (2015a) in order to recreate and interpret crime scenes. The red fox as a generalist predator and opportunistic feeder can feed on a wide prey spectrum which allows it to adapt in a wide variety of different environments. The results of the Young et al.'s (2015a) study attribute to red fox a high capacity of dispersing skeletal remains and an increasing frequency of scavenging in colder seasons also during the earlier stages of decomposition.

However, the scarce number of direct observations of red fox bone-modifying behaviour is still insufficient to characterise these animals from a neo-taphonomic standpoint, and the works carried out until now are not comparable to the number of observations among large carnivores. Here, we present a study trying to characterise the wild predator behaviour describing consumption patterns on 23 ungulate carcasses scavenged by wild red foxes (*Vulpes vulpes*) during a 2-year period in the Spanish Pyrenees. These ethological observations and the resulting taphonomic signature can be a diagnosis which could work out for differentiating the action of these carnivores from other most common small-, medium-sized and large carnivores. The results obtained can be used to model the archaeological signature of scavenging, scattering or collecting. Furthermore, understanding the fox behaviour can help find out both, looting actions and foreign inputs in hominin campsites and as a result, improve the growing framework for a better interpretation of the archaeological bone assemblages. For that, a combination of observational data from photo/video-trap and taphonomic analyses has been compiled, allowing us to control variables like seasonality and time of consumption, as well as the spatial dispersion of the skeletal remains.

Materials and methods

This study was conducted for 2 years, during which time a total of 23 carcasses eaten by red foxes were collected in the region of Pallars Jussà (Pyrenees, Spain). The study area is a partially mountainous territory crossed from North to South by the Flamisell River, specifically a midland riparian forest (Fig. 1). The mixed forest is basically composed by a diversity

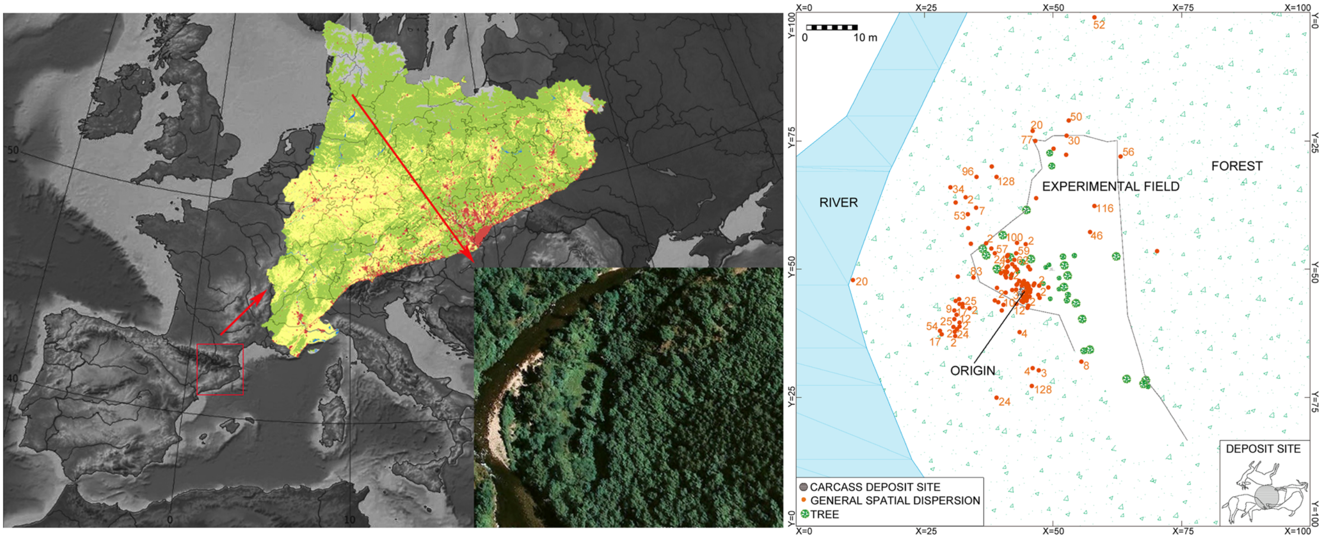


Fig. 1 Location of the neo-taphonomic study area in the Spanish Pyrenees (left), and spatial distribution graphic map using a Trimble S6 total station, Virtual References Station technique and the MiraMon system (SIG) showing the numbers of bones recovered at this point (right). Note that only those places containing more than one bone are expressed in numbers

of trees such as pine tree (*Pinus sylvestris*), oak (*Quercus robur*), holm oak (*Quercus ilex*), false acacia (*Robinia pseudoacacia*), black poplar (*Populus nigra*), willow (*Salix*) and ash tree (*Fraxinus*). The low vegetation in the area consists in a wide variety of riverside bushes expected in this territory such as hawthorn (*Crataegus monogina*), box (*Buxus sempervirens*) or blackthorn (*Prunus spinosa*) between others, having in mind that the area is located at an altitude of 735 m above the sea level. The sample consisted of 23 small-sized ungulates belonging to four different species: 1 *Capra hircus*, 9 *Capreolus capreolus*, 11 *Sus scrofa* and 2 *Ovis aries* (Table 1; Table S1). All carcasses used in our observations weight less than 100 kg [class 2 sensu Bunn 1982] and were deposited whole in the same place, but in different moments—that is, each carcass was deposited alone and corresponds to one observation period (OB). These carcasses came from road kill animals or required culling and were provided by the *Direcció General dels Agents Rurals* (*Departament d'Agricultura, Ramaderia, Pesca i Alimentació from Generalitat de Catalunya*). To minimise interference during the experimentation, we selected a specific site where human activity is rare. In all cases, the carcasses were moved to this definite place in order to document the consumption process and the spatial dispersion. The photographic trap was carried out using No Glow Infrared Trail cameras (photo- and video-trap) installed in the surroundings of the carcasses to record the predators involved in the consumption. These wildlife cameras are equipped with invisible black LED (Black Flash) that does not produce the visible red glow as a side effect. During almost weekly site reviews, the level of scavenging and the scattered remains for each carcass were described and recorded. The removal of remains was carried out when prolonged lack of visits by foxes pointed out the cessation of fox feeding. The method of searching was visual inspection. Once the fox visits ended, a group of minimum three people searched in detail an area of about 10,000m^2. Depending on the season and the vegetation coverage, the search was repeated two more times. During late spring and summer, the grass was high, this fact allowed us to follow the paths of red foxes but also could have been a problem with hidden bones. The same issue happened in autumn with fallen leaves. Snowfalls were not a problem because the snow does not last more than 2 or 3 days. The location of bones and the movement of a whole carcass or disarticulated remains from its primary deposit site were recorded using a Trimble S6 total station (Trimble R6 receptors) and VRS (Virtual References Station) technique. The data obtained have been mapped using the MiraMon system (SIG).

All the skeletal specimens were recovered and cleaned using non-aggressive techniques, such as boiling in a solution of water and non-enzymatic detergent. More resistant tissues were removed by using a wooden knife or soft pointed tools that did not compromise the bone surface. Bone damage on the selected specimens was analysed using an Olympus SZ 11 stereoscopic (magnification up to 110), together with an ESEM (FEI QUANTA 600 Environmental Scanning Electron Microscope). The classification of Haynes (1980, 1983, 1988), Binford (1981), Stiner (1994) and Blumenschine (1995) was followed for categorisation of tooth marks as pits/punctures and scores. Punctures and pits are marks caused when a tooth penetrates the cortical bone surface due to pressure. Scores are elongated marks generated by the drag of a tooth along the surface of the bone (Maguire et al. 1980; Binford 1981). Furrowing is defined as the deletion of preferably cancellous tissue on the end of long bones (Maguire et al. 1980; Binford 1981; Haynes 1980, 1988),

Table 1 General characteristics of the experimental series organised by observation periods (OB)

Observation	Season	Carnivore	No. of visits	Temporal range *per* visit (min)	Other carnivores	Ungulate carcass	Age at death	Cause of death	Exposure time[a]	Minimum distance (m)[b]	Maximum distance (m)[b]
OB. 1	Summer 2014	*Vulpes vulpes*	25	1–24	–	*Sus scrofa*	Juvenile	Required culling	24 days	0	33,322
OB. 2	Summer 2014	*Vulpes vulpes*	50	1–31	–	*Capra hircus*	Adult	Natural	28 days	0	5319
OB. 3	Autumn 2014	*Vulpes vulpes*	28	1–11	–	*Ovis aries*	Adult	Natural	37 days	0	13,932
OB. 4	Winter 2014/15	*Vulpes vulpes*	38	1–70	–	*Ovis aries*	Adult	Natural	32 days	7611	7611
OB. 5	Winter 2015	*Vulpes vulpes*	18	1–32	–	*Capreolus capreolus*	Juvenile	Accident[run over]	11 days	17,603	17,603
OB. 6	Winter 2015	*Vulpes vulpes*	108	1–36	–	*Sus scrofa*	Juvenile	Required culling	14 days	9584	9584
OB. 7	Winter 2015	*Vulpes vulpes*	185	1–52	–	*Sus scrofa*	Juvenile	Required culling	33 days	31,435	31,435
OB. 8	Winter 2015	*Vulpes vulpes*	45	1–27	–	*Sus scrofa*	Juvenile	Required culling	20 days	Not recovered	Not recovered
OB. 9	Spring 2015	*Vulpes vulpes*	65	1–25	–	*Capreolus capreolus*	Juvenile	Accident[run over]	10 days	18,432	18,432
OB. 10	Spring 2015	*Vulpes vulpes*	15	1–20	–	*Capreolus capreolus*	Juvenile	Accident[run over]	5 days	12,242	13,927
OB. 11	Spring 2015	*Vulpes vulpes*	13	1–17	–	*Capreolus capreolus*	Juvenile	Accident[run over]	6 days	18.61	55,052
OB. 12	Spring 2015	*Vulpes vulpes*	12	1–24	–	*Capreolus capreolus*	Juvenile	Accident[run over]	3 days	18,051	18,051
OB. 13	Spring 2015	*Vulpes vulpes*	18	1–15	–	*Capreolus capreolus*	Juvenile	Accident[run over]	5 days	17,339	21,521
OB. 14	Spring 2015	*Vulpes vulpes*	16	1–20	–	*Capreolus capreolus*	Juvenile	Accident[run over]	4 days	18,812	25,142
OB. 15	Spring 2015	*Vulpes vulpes*	81	1–26	–	*Sus scrofa*	Juvenile	Required culling	23 days	0	15.91
OB. 16	Summer 2015	*Vulpes vulpes*	53	1–51	–	*Sus scrofa*	Juvenile	Required culling	21 days	0	18,323
OB. 17	Autumn 2015	*Vulpes vulpes*	75	1–81	–	*Sus scrofa*	Juvenile	Required culling	39 days	0	31,374
OB. 18	Autumn 2015	*Vulpes vulpes*	63	1–183	*Gyps fulvus*	*Sus scrofa*	Juvenile	Required culling	21 days	2034	27,019
OB. 19	Autumn 2015	*Vulpes vulpes*	51	1–109	*Gyps fulvus*	*Sus scrofa*	Infantile	Required culling	6 days	12,257	15,362
OB. 20	Winter 2016	*Vulpes vulpes*	97	1–38	*Martes foina*	*Sus scrofa*	Infantile	Required culling	63 days	10,239	44.43
OB. 21	Spring 2016	*Vulpes vulpes*	62	1–43	–	*Sus scrofa*	Juvenile	Required culling	6 days	32,272	34,437
OB. 22	Spring 2016	*Vulpes vulpes*	41	1–33	*Genetta genetta*	*Capreolus capreolus*	Juvenile	Accident[run over]	11 days	22.96	22.96
OB. 23	Spring 2016	*Vulpes vulpes*	50	1–29	*Martes foina*	*Capreolus capreolus*	Infantile	Accident[run over]	18 days	29,409	29,409

[a] Total time from initial scavenging to final removal

[b] Distance data come from the final spatial registration after the exposure time

although it can be also registered in other skeletal elements (e.g. flat bones). Crushing is produced by the collapse of the cortical tissue in concentrated areas of bone in the form of short cracks and splits in the cortical areas (Binford 1981). Fractures following the lines of bone collagen lead to longitudinal cracks when the effect of the bite force is expanded. Crenulated edges show a fracture morphology outlining notches when the bite force overcomes the density and strength of the bone tissue (Maguire et al. 1980; Binford 1981). Peeling, or bone breakage by bending, can be identified by roughened surfaces with parallel grooves or fibrous texture on the transversal edges of the fractures (White 1992). According to Pickering et al. (2013), peeling is classified as classic peeling (described above) and incipient peeling, which includes fraying and bent ends. A range of measures for pits and punctures has been established to allow comparison with those provided by other researchers (Mondini 1995; Andrés et al. 2012; Krajcarz and Krajcarz 2014; Yravedra et al. 2014; Young et al. 2015b).

For skeletal region distribution and frequency damage, we show our statistical results on ternary plots (Weaver et al. 2011). In order to explore differences by seasons, a correlation coefficient (Pearson's r and Spearman's ρ) between recovered and damaged elements was calculated. The seasons were clustered considering the amount of alternative resources in the surrounding environment (e.g. vegetables, fruits, mushroom) in two main periods: (1) summer and autumn; (2) winter and spring. A correspondence analysis was used for testing the following variables: (1) recovered skeletal elements, (2) bone damage, (3) dispersion of bones by groups (anatomical connections), (4) maximum distance from the origin location of the carcass; (5) number of visits and (6) visit length (maximum time). To identify a pattern of transport/movements from the original position, the carcasses were divided into anatomical portions: (1) cranium, (2) mandibles, (3) neck, (4) thoracic cage, (5) lumbar, (6) pelvis, (7) scapula, (8) forelimb, (9) (fore) autopodium, (10) hind limb and (11) (hind) autopodium. The appendicular skeleton was considered by the sides; thus, the variables increase to 16. The method used to assess the main movements was a hierarchical cluster analysis by single linkage.

Results

During this 2-year neo-taphonomic study, a total of 23 carcasses were placed. This represents a total of 3332 skeletal elements. From this sum, 1576 elements disappeared (47.3%) and a collection of 1756 (52.7%) anatomical elements were recovered. Of these, 645 (36.73%) showed modifications produced by the red fox, mostly located on the axial skeleton ($n = 557$; 31.72% of recovered bones) and on the girdles ($n = 33$; 1.88%) but also on the limb bones ($n = 29$; 1.65%) and on the cranial skeleton ($n = 17$; 0.97%). The rest were located on the basipodial bones ($n = 5$; 0.28%), patella/sesamoideus ($n = 3$; 0.17%) and on the acropodial bones ($n = 1$; 0.06%) (Table 2). Photo- and video-trap cameras allowed us to identify the modifying agent, as well as where this agent produced the bone damage on the carcass. This monitoring system allowed us to remove possible perturbing elements and other scavenger species in the data analysis. Figure 2 shows that the bulk of bone modification was caused by red foxes cluster on the axial skeleton (86.36% of damaged bones) and the girdles (5.12%) followed by limb bones (4.50%), cranial skeleton (2.64%), and at lesser extent on basipodial (0.78%), patella/sesamoideus (0.47%) and acropodial bones (0.16%). Compact bones are slightly modified, especially when compared to the axial, girdle and appendicular anatomical regions.

When split by season, taphonomically speaking, bone modification patterns are slightly different. The extent of damage is located on the same anatomical regions (axial skeleton followed by girdles) with regard to summer, autumn and spring season, but damage on appendicular and girdle anatomical regions declines significantly in winter (Table 3, Fig. 3). This fact is directly connected with the number of missing bones. While the average of appendicular missing bones in summer ($n = 136$; 37.16% of placed bones *per* season), autumn ($n = 209$; 56.64%) and spring ($n = 540$; 59.67%) is 51.15%, this percentage rises to 81.22% ($n = 441$) in winter. The same fact occurs with regard to girdle elements considering an average of 22.36% in summer ($n = 1$; 8.33%), autumn ($n = 3$; 18.75%) and spring ($n = 16$; 40%), while the percentage in winter gets up to 75% ($n = 18$).

The correlation tests by seasonality show a high correlation between NISP and damaged bones, mainly during winter (Pearson's $r = 0.7921879$, 95% conf., p value = 0.1101; Spearman's $\rho = 0.7$, p value = 0.2333) and spring (Pearson's $r = 0.7638974$, 95% conf., p value = 0.01011; Spearman's $\rho = 0.6808542$, p value = 0.03021). This phenomenon coincides with the seasons in which a lower quantity of alternative resources, such as vegetables, fresh fruits or mushrooms, is found in the environment. On the contrary, the same tests applied in summer (Pearson's $r = -0.752088$, p value = 0.4581; Spearman's $\rho = -0.5$, p value = 1) and autumn (Pearson's $r = 0.06343427$, 95% conf., p value = 0.9366; Spearman's $\rho = -0.6$, p value = 0.4167) show a tendency to a negative correlation, although with high p values. Here, we must consider that the low number of observations recorded during these two seasons makes the results not significant enough. A way to provide more data for these tests is to group the results from different seasons into two main periods: the period with a high proportion of alternative resources (summer and autumn) and the period with less alternative resources (winter and spring). In this case, the results seem to confirm the tendency observed previously: winter/spring (Pearson's $r = 0.7797654$, 95% conf., p value = 0.0006076; Spearman's

Table 2 Recovered bones vs. damaged bones by observations and anatomic segments split by season

Season	Carcass	Observations	Recovered bones							Damaged bones						
			Cranial	Axial	Girdles	Limbs	Basipod	Acropod	Pat/Sesam	Cranial	Axial	Girdles	Limbs	Basipod	Acropod	Pat/Sesam
Summer	*Sus scrofa*	OB. 1	3	55	4	12	18	24	16	–	6	–	–	–	–	–
	Capra hircus	OB. 2	3	53	4	12	12	18	3	–	12	–	–	–	–	–
	Sus scrofa	OB. 16	3	43	3	7	6	8	4	–	10	1	–	–	–	–
	Total		9	151	11	31	36	50	23	–	28	1	–	–	–	–
Autumn	*Ovis aries*	OB. 3	3	46	4	13	12	14	2	–	–	–	2	–	–	–
	Sus scrofa	OB. 17	3	42	4	12	18	24	16	–	4	–	–	–	–	–
	Sus scrofa	OB. 18	3	30	3	10	12	16	10	–	24	3	3	2	1	1
	Sus scrofa	OB. 19	2	1	2	1	–	–	–	1	1	2	1	–	–	–
	Total		11	119	13	36	42	54	28	1	29	5	6	2	1	1
Winter	*Ovis aries*	OB. 4	3	54	2	–	–	–	–	3	52	2	–	–	–	–
	Capreolus capreolus	OB. 5	0	6	2	–	–	–	–	–	6	2	–	–	–	–
	Sus scrofa	OB. 6	3	53	2	6	12	16	8	–	44	2	2	–	–	–
	Sus scrofa	OB. 7	1	8	0	3	6	8	4	1	8	–	1	1	–	–
	Sus scrofa	OB. 20	3	41	0	3	12	16	8	1	35	–	1	–	–	–
	Total		10	162	6	12	30	40	20	5	145	6	4	1	–	–
Spring	*Capreolus capreolus*	OB. 10	3	14	1	4	6	8	6	2	11	1	–	–	–	–
	Capreolus capreolus	OB. 11	3	53	2	6	8	8	6	2	46	2	3	2	–	2
	Capreolus capreolus	OB. 12	3	49	2	–	–	–	–	2	38	2	–	–	–	–
	Capreolus capreolus	OB. 13	3	54	3	10	18	24	14	2	45	3	3	–	–	–
	Capreolus capreolus	OB. 14	3	53	2	7	12	16	10	1	29	1	2	–	–	–
	Sus scrofa	OB. 15	3	10	4	3	–	–	–	–	9	1	1	–	–	–
	Capreolus capreolus	OB. 9	3	54	3	10	18	26	14	2	50	3	4	–	–	–
	Sus scrofa	OB. 21	3	51	3	7	12	16	10	–	48	2	1	–	–	–
	Capreolus capreolus	OB. 22	3	52	4	11	18	20	16	–	34	4	4	–	–	–
	Capreolus capreolus	OB. 23	3	51	2	3	6	8	4	–	45	2	1	–	–	–
	Total		30	441	26	61	98	126	80	11	355	21	19	2	–	2
Total			60	873	56	140	206	270	151	17	557	33	29	5	1	3

Note no anatomical element from the OB. 8 was registered; that is because the carcass was completely removed by red foxes

Basipod basipodials, *Acropod* acropodials, *Pat/Sesam* patella/sesamoideus

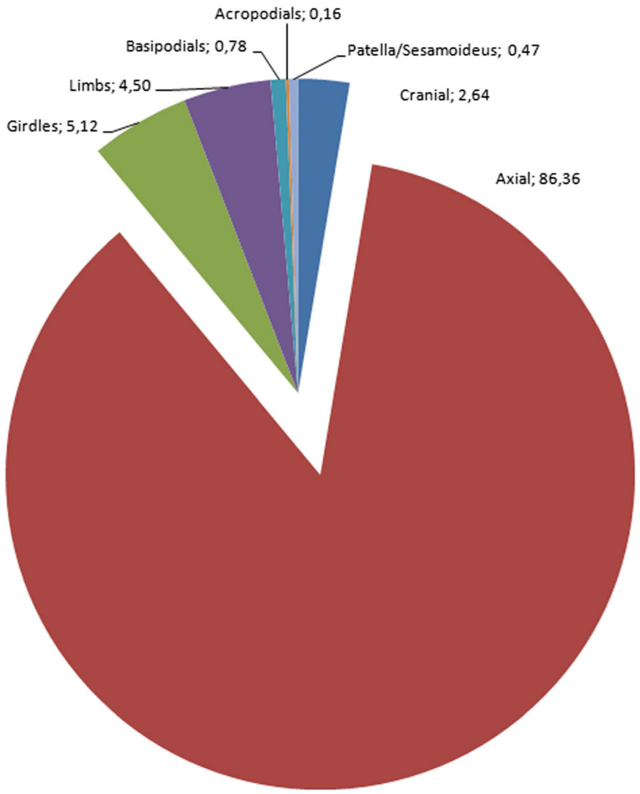


Fig. 2 Graphic describing red fox-induced damage percentages related to damaged bones split by skeletal categories

$\rho = 0.6828001$, p value = 0.005027) and summer/autumn (Pearson's $r = -0.02768607$, 95% conf., p value = 0.953; Spearman's $\rho = -0.1428571$, p value = 0.7825) (Fig. 4). Given the opportunistic and omnivorous behaviour of the red fox, it is possible to suggest a significant increase of bone damage during the seasons entailing a lower proportion of available alternative resources in the environment.

Moreover, the spread is sizeable when assessing the degree of bone damage, season and exposure time—that is, the total from initial scavenging to final removal. In this respect, the number of consumed carcasses increases progressively from the summer ($n = 3$; 13.04%) to winter season ($n = 6$; 26.09%), as does the percentage of bone modification (from 9.32 to 57.5% related to bones recovered by season), while time spent scavenging simultaneously increases smoothly (from 17.38 to 36.43%). However, in this respect, the spring and winter seasons make the difference. The number of consumed carcasses in spring rises to 43.48% ($n = 10$), while exposure time decreases abruptly (21.67%) and there is an increase in the number of damaged bones (47.45%). The increase in bone alterations can also be detected in winter (57.5%), together to a longer exposure time (36.43%) combined with a slight decrease in the number of consumed carcasses (26.09%). While the average of damaged bones reaches 5.7% in summer and autumn, the percentage of damaged bones in spring and winter climbs to 44.26%. Following the same dynamic, most of the

Table 3 Missing bones vs. recovered and damaged bones by anatomical sections and season

	Missing bones (% related to placed)				Recovered bones (*n*)				Damaged bones (% related to recovered)			
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Axial	14 (8.48)	101 (45.91)	168 (50.91)	109 (19.82)	151	119	162	441	28 (1.59)	29 (1.65)	145 (8.26)	355 (20.22)
Girdles	1 (8.33)	3 (18.75)	18 (75.00)	16 (40.00)	11	13	6	26	1 (0.06)	5 (0.28)	6 (0.34)	21 (1.2)
Limbs	17 (35.42)	28 (43.75)	84 (87.50)	99 (61.88)	31	36	12	61	–	6 (0.34)	4 (0.23)	19 (1.08)
Cranial	–	1 (8.33)	8 (44.44)	–	9	11	10	30	–	1 (0.06)	5 (0.28)	11 (0.63)
Basipodial	36 (50.00)	54 (56.25)	114 (79.17)	142 (59.17)	36	42	30	98	–	2 (0.11)	1 (0.06)	2 (0.11)
Acropodial	52 (27.08)	74 (57.81)	152 (79.17)	194 (60.63)	50	54	40	126	–	1 (0.06)	–	–
Patella/sesamoideus	31 (57.41)	53 (65.43)	91 (81.98)	105 (56.76)	23	28	20	80	–	1 (0.06)	–	2 (0.11)

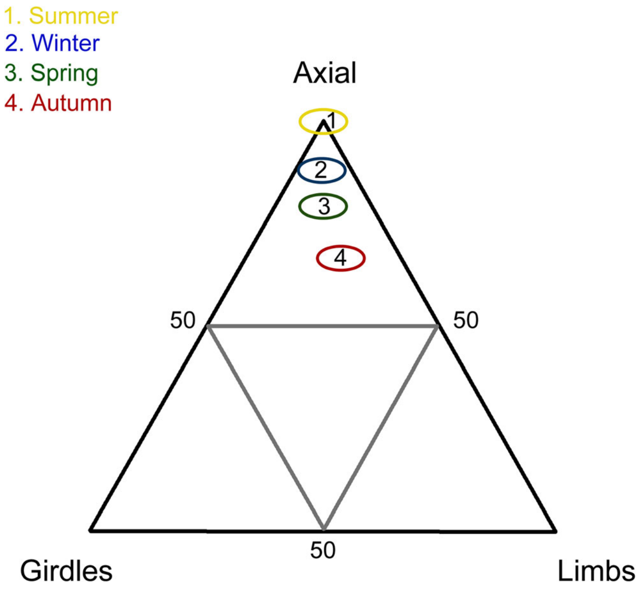


Fig. 3 Ternary-plot showing bone damage/season and classified by anatomical units. Axial skeleton = ribs and vertebrae; girdles = scapulae and pelves; limbs = humeri, radio-ulnae, femora and tibiae, but excluding metapodials, which are essentially meatless

red fox visits were conducted in winter and spring, coinciding with the highest proportion of bone damage (Table 4).

Damage such as pits, punctures, scores, furrowing, crushing, crenulated edges, fractures, longitudinal cracks and bent ends (some showing certain degree of fraying) has been identified on ungulate carcasses (Table 5, Figs. 5 and 6):

Transversal fractures Transversal fractures are the most significant damage type in the red fox-modified sample (*n* = 366; 20.84% of recovered bones). Fractures basically affect ribs (*n* = 218) and both spinous and transverse processes of vertebrae (*n* = 138), with percentages between 52.78 and 31.51%, respectively, and in relation to the recovered specimens by skeletal category. This modification is especially observed on distal and mid-shafts (*n* = 159) and, to a lesser extent, proximal shaft (*n* = 51) and on the neck (*n* = 8). Lumbar vertebrae show the highest proportions, with 52.88% (*n* = 55) of damaged items in relation to those recovered, followed by dorsal (*n* = 55; 26.31%) and cervical vertebrae (*n* = 23; 18.4%). Regarding girdles, fractures were identified on one hemi-pelvis (ilium) and on the medial border of one scapula. Three cranial elements show this alteration, the occipital condyle of one cranium and two hemi-mandible on the coronoid process and angle. Fractures were also recorded on sacra (*n* = 4) affecting the spinous process (*n* = 2), body and lateral sacral crest.

Pits, punctures and scores Tooth marks on skeletal elements in the form of pits, punctures and scores were located on 323 items (18.39%) (Fig. 5). Pits/punctures are registered on 243 bones (75.23%), scores on 9 bones (2.79%), and 71 bones (21.98%) show both alterations on the same specimens. Winter shows the highest percentage of tooth marks when split by season, with a frequency of 32.86% (*n* = 92), followed by spring (*n* = 184; 21.32%) and autumn season (*n* = 39; 12.91%), while summer season displays the lowest number of tooth marks (*n* = 8; 2.57%). Taking into account that winter is the season with the highest number of missing bones, these data should be taken only as an indicative of potential intensity of damage. Girdles are the most affected portion, with 29 tooth-marked bones (51.79% in relation to the recovered

Fig. 4 Scatter diagram resulting from the correlation coefficients between recovered elements and damaged bones by seasons

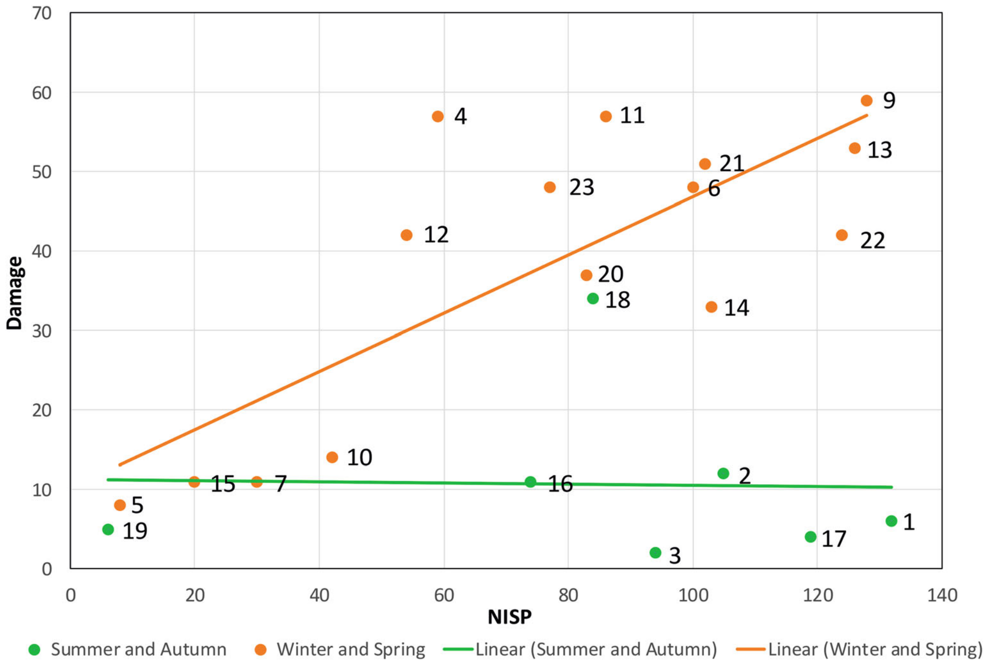


Table 4 Percentages showing the exposure time, number of ungulate carcasses, recovered and damaged bones according to seasonality data

Season	Exposure time/days	Number of visits	Carcasses	Recovered bones (% related to exposed)	Damaged bone (% related to recovered)
Summer	73 (17.38%)	128 (10.59%)	3 (13.04%)	311 (74.05%)	29 (9.32%)
Autumn	103 (24.52%)	217 (17.95%)	4 (17.39%)	303 (47.34%)	45 (14.85%)
Winter	153 (36.43%)	491 (40.61%)	6 (26.09%)	280 (29.91%)	161 (57.50%)
Spring	91 (21.67%)	373 (30.85%)	10 (43.48%)	862 (64.52%)	410 (47.56%)
Total	420	1209	23	1756 (52.7%)	645 (36.73%)

specimens by skeletal category), followed by the axial skeleton with 248 (28.38%). The cranial area is affected by a frequency of 20% (*n* = 12), and lowest percentage is correlated with the limb bones (*n* = 32; 4.17%). The pelvis is the skeletal element displaying the highest percentage of tooth marks, with a damage frequency of 63.89% mainly located on the

Table 5 Red fox-induced damage by skeletal category and season

Skeletal element	Season	Recovered bones	Pits/scores		Furrowing		Crenulated edge		Trans. fractures		Crushing		Long. cracks		Bent ends/ fraying		Pitting	
		n	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Cranial	Summer	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Autumn	11	1	9.09	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Winter	10	5	50.00	–	–	2	20.00	1	10.00	2	20.00	–	–	–	–	–	–
	Spring	30	6	20.00	–	–	6	20.00	2	6.67	2	6.67	–	–	–	–	–	–
Axial	Summer	151	8	5.30	–	–	1	0.66	14	9.27	7	4.64	5	3.31	10	6.62	–	–
	Autumn	120	25	20.83	1	0.83	6	5.00	14	11.67	1	0.83	–	–	4	3.33	–	–
	Winter	162	76	46.91	3	1.85	33	20.37	95	58.64	7	4.32	8	4.94	27	16.67	4	2.47
	Spring	440	140	31.82	1	0.23	25	5.68	236	53.64	26	5.91	42	9.55	94	21.36	–	–
Girdles	Summer	11	–	–	–	–	–	–	–	–	1	9.09	–	–	–	–	–	–
	Autumn	13	5	38.46	–	–	3	23.08	–	–	2	15.38	–	–	–	–	–	–
	Winter	6	6	100	5	83.33	2	33.33	2	33.33	–	–	–	–	–	–	2	33.33
	Spring	26	19	73.08	3	11.54	9	34.62	2	7.69	11	42.31	–	–	1	3.85	–	–
Limbs	Summer	31	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Autumn	36	4	11.11	4	11.11	–	–	–	–	–	–	–	–	–	–	–	–
	Winter	12	4	33.33	3	25.00	–	–	–	–	1	8.33	–	–	–	–	–	–
	Spring	61	15	24.59	10	16.39	–	–	–	–	2	3.28	–	–	–	–	–	–
Basipodial	Summer	36	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Autumn	42	2	4.76	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Winter	30	1	3.33	1	3.33	–	–	–	–	–	–	–	–	–	–	–	–
	Spring	98	2	2.04	–	–	–	–	–	–	–	–	–	–	–	–	2	2.04
Acropodial	Summer	50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Autumn	52	1	1.92	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Winter	40	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Spring	128	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Patella/Sesamoideum	Summer	23	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Autumn	28	1	3.57	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Winter	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Spring	80	2	2.50	–	–	–	–	–	–	–	–	–	–	–	–	2	2.50
Total		1756	323	18.39	31	1.77	87	4.95	366	20.84	62	3.53	55	3.13	136	7.74	10	0.57

Note that some remains show co-occurrence of damage, and therefore, the total number of modifications can be higher. The percentages were calculated on the number of recovered bones per skeletal category and season

Fig. 5 Some examples of red fox-induced modifications on different skeletal elements. **a** Crenulated/saw-toothed edge showing a slight arc morphology on mandible (OB. 10). **b** Pits, punctures and scores associated to fracture on pelvis fragment (OB. 12). **c** Incipient fraying and pits on rib (OB. 20). **d** Furrowing and several pits on femur (OB. 13). **e** Furrowing on distal part of immature femur (OB. 6). **f** Crushing on distal part of rib (OB. 12). **g** Puncture in association with longitudinal cracks (OB. 12). **h** Scores associated to transversal fracture (OB. 21). **i**, **j** Tooth marks on vertebrae (OB. 13). **k** Punctures (imprints) on proximal epiphysis of femur (OB. 13). Note the triangular shaped pits on some bones in panels **b** and **c**, and the co-occurrence of alterations in panels **b**, **c**, **g** and **h**. Scale = 1 cm

ilium ($n = 15$; 41.66%) and on the ischium region ($n = 14$; 38.88%), while a percentage of 35% ($n = 7$) of tooth marks is located on the scapula, mainly on the medial border ($n = 3$).

Regarding axial skeleton, modifications were found on 40.19% of the ribs ($n = 166$) and on the vertebrae ($n = 105$; 23.97%). Tooth marks on the ribs are mainly located on the distal shaft ($n = 77$; 46.38%), mid-shaft ($n = 37$; 22.29%), proximal shaft ($n = 23$; 13.86%) and on the neck ($n = 2$; 1.2%). Cervical vertebrae show the highest amount of tooth marks with a percentage of 44.76% ($n = 47$) mostly located on

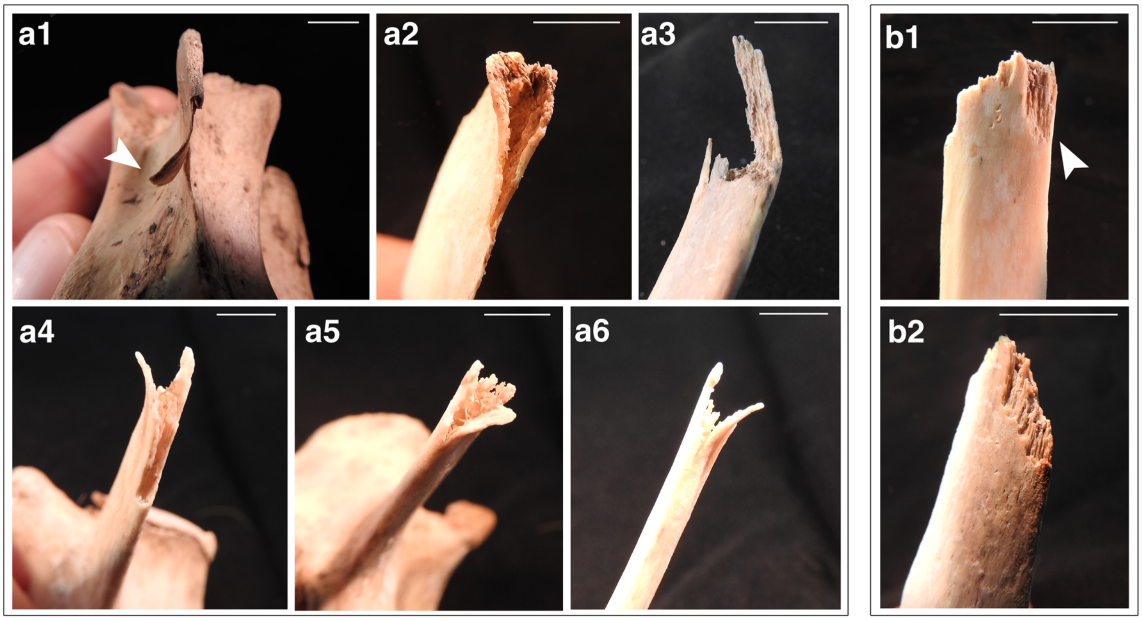


Fig. 6 Red fox-induced damage on axial bones showing bent ends (**A1** OB. 12, **A2** OB. 6; **A3** OB. 21; **A4**–**A6** OB. 12) and classic peeling (**B1** OB. 4; **B2** OB. 9). Note the co-occurrence of classic peeling and tooth pits with crescent shape on the same specimen in panel **B1**. Scale = 1 cm

the transverse process (*n* = 29; 27.62%), on the body (*n* = 17; 16.19%), and on the spinous process (*n* = 7; 6.66%). While a 29.52% of dorsal vertebrae (*n* = 31) are tooth-marked and 27 lumbar vertebrae (25.71%) display the lowest percentage of tooth marks.

Cranial elements and limb bones bear the lowest values of tooth marks. In the case of the hemi-mandible, nine elements (23.08%) show damage mainly located on the gonion (*n* = 7) and only three crania show any modification. Regarding limbs, femora show the highest number of modifications with a total of 11 elements mainly tooth-marked on the trochanter (*n* = 8) and on the head (*n* = 3). Only two elements bear modifications on the distal shaft (*n* = 2), one of them also in the proximal shaft.

All humeri show pits on their major tuberosity (head) in all cases where damage is documented (*n* = 5). No tooth marks were registered on shafts. In contrast, all modifications occur on thin cortical and cancellous tissues. Regarding compact bones, calcaneus (*n* = 5) were tooth-marked on the calcanean tuber and two patella show pits on the body. Only one residual phalanx bears tooth marks on the body and on the distal shaft. Three ulnae show damage in form of pits on their olecranon. Tibiae (*n* = 2) are tooth-marked on its lateral condyle, and only one fibula shows pits on the proximal shaft.

Figure 7 has been made taking into account the length and width of pits and punctures and the type of bone tissue (thick, thin and cancellous), and the width and number of scores on the bone tissue-type. This also takes into account the season variable for each one. The highest number of tooth mark sizes is contained within a range less than 4.5 × 4 mm. Only two imprints recorded on thin cortical (winter) and on cancellous bone (spring) have an ~ 8 × 5 mm size. In general, larger marks are located on thin cortical in winter season and on cancellous tissue in spring time. However, both pits/punctures and scores bear the highest values regarding thick cortical in autumn. Only a few number of tooth marks (*n* = 10) have been recorded in summer season, all of them located on thin cortical.

Peeling Bent ends and certain degree of fraying—which could be related to an incipient peeling—were observed on 136 bones (7.74%) and focused almost exclusively on axial skeleton (only one pelvis showed bent end). Classic peeling has also been observed on four axial bones (Fig. 6) and is included in the previous percentage as general peeling damage. A total of 79 ribs (19.13%) show this type of modification firstly on the distal shaft (*n* = 43), mid-shaft (*n* = 31) and, to a lesser extent, on the proximal shaft (*n* = 5). Vertebrae (*n* = 56; 12.78%) show damage on the spinous process (*n* = 30) and on the transverse process (*n* = 26). This category includes lumbar vertebrae which are, together to dorsal, the most affected items [*n* = 24 (42.86%); *n* = 27 (48.21%)], followed by cervical vertebrae (*n* = 5; 8.93%).

Spring time is the period in which there are more damaged items with 14.57% (*n* = 94, related to recovered bones per season), followed by winter (*n* = 27; 4.19%), summer time (*n* = 10; 1.55%) and autumn (*n* = 4; 0.62%).

Crenulated edges Fractures induced by red fox in the form of crenulated edges are registered on 4.95% of the sample (*n* = 87). These modifications were inflicted between autumn and spring, and there is only one crenulated item in

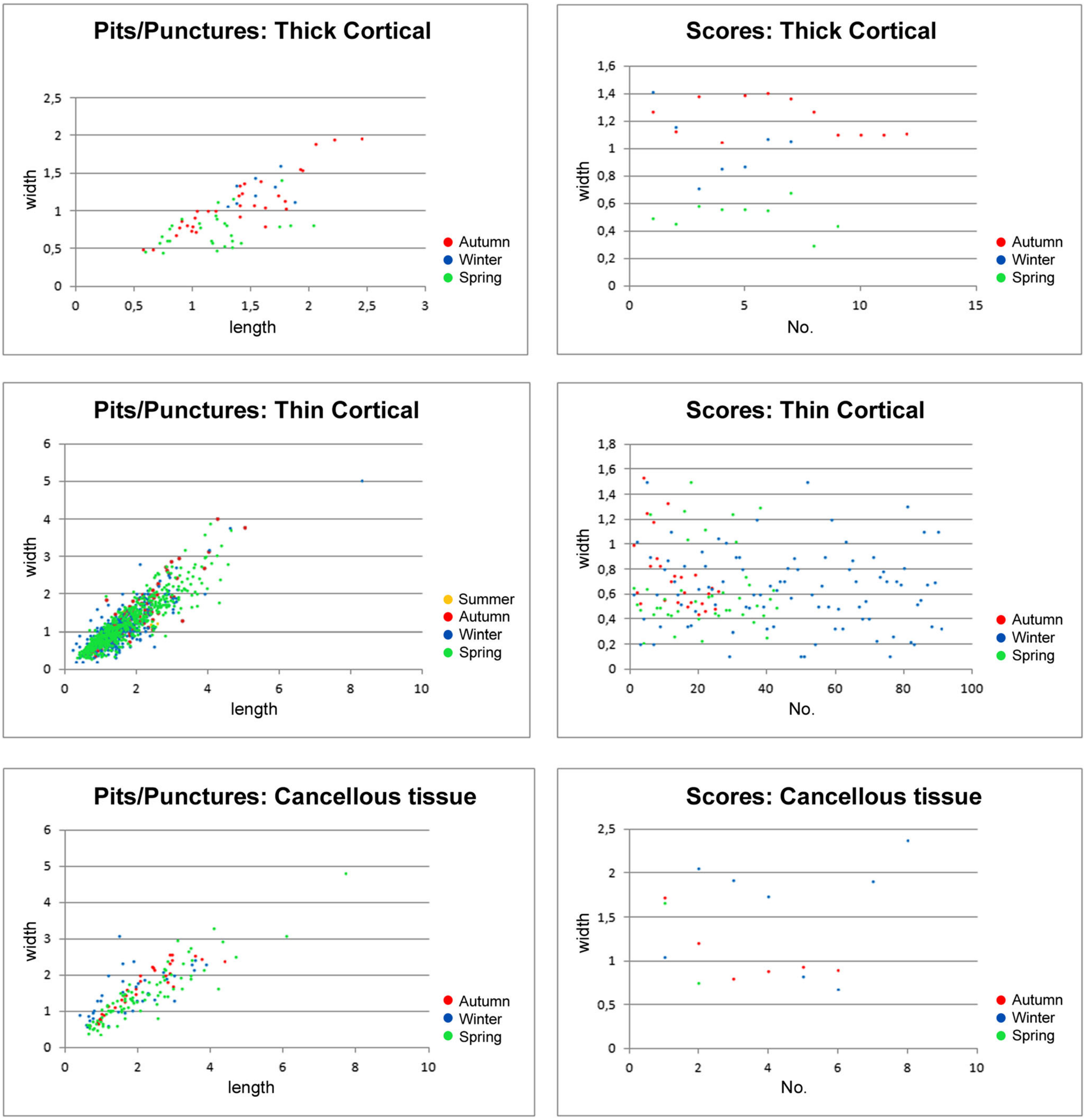


Fig. 7 Dimension of pits and scores on thick, thin and cancellous tissue classified by season

summer season. These alterations are observed mainly on girdles (*n* = 14; 25%) (Fig. 5), followed by the axial (*n* = 65; 7.45%) and cranial (*n* = 8; 13,33%) skeleton, and are absent on limb bones. In relation to girdles, all hemi-pelvis (*n* = 7) show crenulated edges on both ilium and ischium, while the medial border (*n* = 5) is the most affected part of the scapulae. Regarding axial elements, vertebrae (*n* = 55; 12.56%) show the highest percentages in relation to their elements recovered, mainly crenulated on the transverse process (*n* = 30) and on the spinous process (*n* = 25). A percentage of 2.42% of the ribs are crenulated (*n* = 10) on their distal shaft.

Crushing This alteration is mainly documented on pelvis (*n* = 14; 56%) and sacra (*n* = 5; 41.66%), followed by cranial elements (*n* = 4; 6.66%). Regarding axial elements, 4.79% of the vertebrae (*n* = 21) are crushed; among them, this alteration is observed in a preferential way on the spinous (*n* = 6) and transverse ($n = 14$) processes, and 3.63% of the ribs ($n = 15$) are crushed mainly on the mid-distal shaft.

Crushing is also observed on the medial condyle and trochanter of femur ($n = 2$) and on the lateral condyle of one tibia.

Longitudinal cracks Longitudinal cracks are represented in the sample with 55 (3.13%) modified items. We detected this alteration only on axial bones, specifically on ribs ($n = 41$), mainly located on mid-distal shaft ($n = 30$) and on vertebrae ($n = 14$), firstly on transverse process ($n = 8$) and spinous process ($n = 6$).

Furrowing This modification is detected on 1.77% of the sample ($n = 31$) (Fig. 5). Furrowing is the only type of bone damage located preferentially on limb bones ($n = 17$; 12.14%). By contrast, only 1.49% of the axial skeleton ($n = 13$ of 873 axial bones recovered) bears this type of modification. Among the axial bones, pelvis and sacrum are the most affected items ($n = 10$ of 54 items recovered; 18.52%). Ilium, ischium and pubis display all the damage on this anatomical element. Femur is the most affected appendicular element, with 12 modified bones (44.44%), followed by humeri ($n = 4$; 22.22%) and tibia ($n = 1$; 4.54%). Damage on femora clusters mainly on their trochanter ($n = 11$) and in one case on the proximal and distal shaft. Humeri display furrowing on their proximal epiphyses (greater tuberosity) in all the cases where this damage type is documented ($n = 4$). Only one case of furrowing is documented on the lateral condyle of one tibia. This damage is also located on one calcaneus showing furrowing on its tubercle.

Pitting This modification is hardly represented with 0.57% ($n = 10$) of the sample, mainly recovered in winter ($n = 6$) and spring time ($n = 4$). All the elements showing this alteration in winter season belong to axial skeleton. Among them, pelvis ($n = 2$; 3.57%) are the most affected element on the ilium, ischium and pubis, followed by the distal shaft of the ribs ($n = 4$; 0.97%). All the items that display this modification in spring time are compact bones. Patella ($n = 2$; 1.6%) is affected on the body, while calcaneus ($n = 2$; 1.49%) on the tubercle.

The video- and photo-trap cameras showed several transportations of skeletal elements and visits of other mammals and raptors. Although two small carnivores (*Genetta genetta* and *Martes foina*) scavenged on three carcasses (OB. 20, OB. 22 and OB. 23), the recorded images showed that they focused their activity on fat and soft tissues without any visible bone damage or dispersion of skeletal elements. The images showed that wild boars (*Sus scrofa*) occasionally visited the location smelling the carcasses and overlooking them—in only one case (OB. 2), a big wild boar rolled around on a carcass, moving it a few centimetres. The time of consumption was recorded in each observation period. In two cases (OB. 18 and OB. 19), the action of vultures interrupted the regular consumption sequence of the carnivores—a wake of vultures accessed the carcasses and fed on the soft tissues and viscera for approximately 4 h. This fact disrupted the red fox regular scavenging as well as the total time spent in this process. We also recorded two different birds of prey (*Buteo buteo* and *Neophron percnopterus*) scavenging on three carcasses (OB. 14, OB. 18 and OB. 19). These sporadic visits did not compromise the taphonomic study, time of consumption measurements or skeletal dispersion because the scavenger birds were only interested in small pieces of meat or maggots and flies.

Regarding general spatial dispersion, 9% ($n = 158$) of the anatomical elements remained at the initial standpoint, while 91% ($n = 1598$) were scattered by foxes. A total of 34.04% ($n = 598$) of the recovered elements were located in the first 10-m radius, while 513 skeletal remains (29.20%) were found within a 10–20-m radius. We could trace 419 (23.85%) within a 20–30-m radius, and the rest ($n = 226$; 12.86%) were found within a 30–55.05-m radius. The maximum separation distance from the origin point was the axial skeleton of a *Capreolus capreolus* (OB. 11) found in springtime at a distance of 55.05 m (Fig. 8). The mean distance of retrieved skeletal remains was 16.94 m. When split by season, the bulk of recovered elements were located within a 10-m radius during summer ($n = 290$; 93.25% related to recovered per season-time), autumn ($n = 143$; 47.35%) and winter ($n = 159$; 56.79%), whilst only six elements (0.70%) were found within the same distance in spring time. Most of the elements ($n = 379$; 43.92%) were located within a 20–30-m radius during this season. There are slight differences when dividing by skeletal categories that affect the shorter distance of 0–10 and the 20–30 m range. Both ranges show a predominance of axial elements ($n = 355$; 20.22% and $n = 264$; 15.03%, respectively) in contrast to appendicular elements ($n = 243$; 13.84% and $n = 155$; 8.83% respectively). Only eight skeletal elements (0.46%) were found in open field, while 99.54% ($n = 1748$) were recovered in secluded woodland places covered by brushwood.

Moreover, our work shows some differences during the same seasons of different years that might point out a tight relationship between climate, resource availability, and foraging efficiency/requirement. According to the National Meteorological Service from Catalonia, the temperature rate during winter/spring of 2016 was 1.5–3 °C above average, with abnormal temperatures of 5 °C above normal values in the Pyrenees—the hottest in the last 100 years. On the contrary, the recording of the previous year, winter/spring 2015, showed normal temperatures for that time and place. Our results show that between January and May of 2015, due to the adverse but normal weather conditions, red fox scavenged on 10 carcasses, while the number of carcasses decreased 60% in favourable climatic conditions, probably because of the

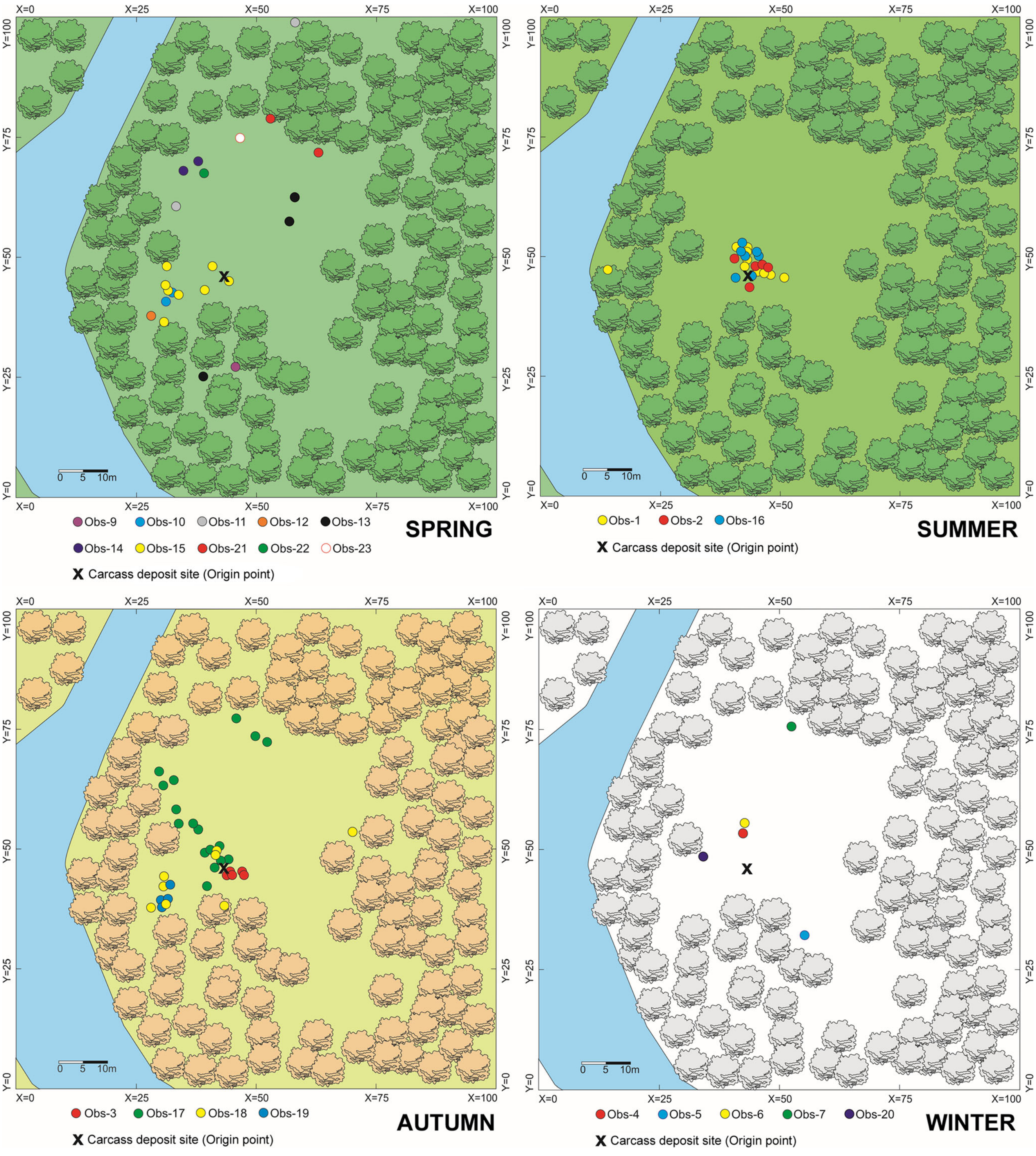


Fig. 8 Spatial dispersion of skeletal remains split by season-period

availability of natural resources. That leads to four scavenged carcasses during the same season of 2016. Taphonomically speaking, we could observe a similar difference between these two time periods, with increased bone damage in winter/spring of 2015 (*n* = 334; 19.02% related to recovered), rather than skeletal modification in the same period of the following year (*n* = 178; 10.14%).

Discussion

The research reported here adds to the growing body of knowledge on the taphonomic consequences of red fox behaviour (e.g. Mondini 1995; Nasti 2000; Fernández et al. 2010; Krajcarz and Krajcarz 2014; Yravedra et al. 2014; Young et al. 2015a; Table 6). Foxes are mainly solitary

Table 6 Major characteristic of the taphonomic samples used in this study

Carnivore	Study area	Site/functionality	Exposure time	Season	Carcass type	Skeletal profile	General damage	Tooth marks	Fragmentation	Diaphyseal cylinders	References
Red/grey fox	Puna (Camatarca), Argentina	Cave/rock shelter: den site	–	–	Camelids, ovicaprids	Appendicular	26%	–	–	No	Mondini (1995)
Red/grey fox, puma	Puna (Catamarca), Argentina	Open air site Open site	–	–	Camelids	Axial, girdles, cranial	18%	64% axial, 66% cranial, 50% girdles	Low	–	Nasti (2000)
Red/grey fox	Cholila (Chubut), Argentina	Cave/rock shelter: den site	–	–	Leporids, ovicaprids	Appendicular (leporids) Axial (ovicaprids)	12% (leporids), 11% (bovids)	40%	–	–	Fernández et al. (2010)
Red fox	Potok-Senderki, Poland	Cave/rock shelter: den site	–	–	Phasianids, leporids, cervids, canids	Appendicular, cranial	50%	50%	Low	No	Krajcarz and Krajcarz (2014)
Red fox	Ourtiaga (Pyrenees), France	Cave/rock shelter: den site	–	–	Ovicaprids, cervids, canids, equids	Appendicular	–	58% (68% appendicular)	Low	Yes	Yravedra et al. (2014)
Red fox	Ayllón (Segovia), Spain	Open air site death site	3-month period	summer	Ovicaprids	Appendicular, axial	–	39% (87% appendicular)	Low	No	Yravedra et al. (2014)
Red fox	Bovington (Dorset), UK	Open air site death site	7-month period	winter	Cervids	Axial, girdles, appendicular	–	30% (innominate)	–	No	Young et al. (2015a, b)
Red fox	Pallars Jussà (Lleida), Catalonia	Open air site death site	2-year period	All seasons	Ovicaprids, suids	Axial, girdles	36.73%	18.39% (1.65% appendicular)	20.84%	No	This study

scavengers (Cochard 2008; Cagnacci et al. 2009; Fernández et al. 2010; Krajcarz and Krajcarz 2014), and although red foxes can predate small prey, their primary instinct is to approach cautiously and inspect when facing the carcass of an ungulate (Video S1). Following our observations, their first attempt involves removing the whole carcass from the deposit site to a different, and if possible, a secluded place. The weight of a carcass is a handicap for this carnivore, so it must be dismembered for easier transportation (Yravedra et al. 2014). Even so, we could register a fox dragging a juvenile wild boar (OB. 17) for nearly five meters (Fig. 9). Skeletal dispersion exhibits a high degree of variability with a range of a few centimetres to many meters, although the majority of remote recovered anatomical elements were recovered in spring season. All categories of skeletal remains are affected by skeletal dispersion. Most of the elements of our sample were recovered from different places covered by thick vegetation and bushes, like in Young et al.'s (2015a) study. A carcass in an open landscape appeals to all types of scavengers, which quickly compete for the remains. A way to get the highest benefit is to keep out of sight of the carrion. Actually, the action of vultures (OB. 18 and OB. 19) strengthens this argument and also provides a good example about the instinctive behaviour of the Canidae family. Described as a scatter hoarder, this carnivore can

Fig. 9 Images showing a red fox dragging a juvenile wild boar (~35 kg in weight) (OB. 8)

disperse and spread food to many different sites (Vander Wall 1990). Furthermore, the red fox has a small stomach for a canine; therefore, its digestive capacity brings them to feed on their prey sparsely and store available food supplies for later consumption (Vander Wall 1990; Sklepkovychi and Montevecchi 1996; Careau et al. 2007). Foxes protect their food and will defend their catches even in the case of their own social circle (Young et al. 2015a; present study). When two or three foxes were present, we could observe a well-established level of hierarchy: One fox would scavenge the carcass, while the other foxes sat down waiting for their turn (OB. 15; OB. 17; Video S1).

Characterising foxes as a taphonomical agent and making comparisons with other predators require a sequential description of the carcass-consumption process. Our study uses a combination of data from images obtained with photo and video-trap which enable us to observe the whole procedure. The behavioural pattern related to consumption starts by tearing the weakest part of the skin, which usually matches with the lower part of the belly in the case of a whole carcass. When there is a skin wound, the skinning process starts in the affected area. The immediate purpose is to gain access to viscera. Red foxes use their molars like shears to accomplish this process, which simultaneously inflicts significant damage to axial skeleton (Video S2). The next aim of the skinning action seems to be the dismemberment and subsequent removal of different skeletal elements so as to transport it (Video S3). In some observations, these procedures take many hours to a few days depending on the season. The whole consumption process including defleshing and dismembering can lead to a high degree of bone modification (Video S4). Taphonomically speaking, fractures and tooth marks are the most common modifications in the sample, affecting mainly the axial skeleton; however, other different alterations like bent ends, crenulated edges, crushing, longitudinal cracks, furrowing and pitting were also recorded. Classic peeling damage was chiefly observed on the ribs of animals consumed by modern humans (*H. sapiens*) or chimpanzees (*Pan troglodytes*) (White 1992; Pickering and Wallis 1997; Fernández-Jalvo and Andrews 2011; Pickering et al. 2013). Despite this, we were able to register this type of modification in a previous study on a bear-modified sample (Arilla et al. 2014). The present work describes incipient peeling damage in the form of bent ends and slight fraying, and sporadic (maybe fortuitous) classic peeling as another alteration in the red fox-modified sample. The sudden movements of the fox's head combined with the insistence when biting the ends of the ribs/bones might explain this type of damage (Video S2).

Like others (Borrero 1990; Nasti 2000; Mondini 2009; Young et al. 2015a), our study shows similar rates of bone modification; however, skeletal profiles show a lower proportion of appendicular elements. The differences may lie in the type of sample; while these authors analyse damage found in the bone accumulation site made by this carnivore (as a final destination), our work focuses on the same taphonomic standpoint, but from the start of the consumption process (initial scavenging) to the bone survival analysis (as a procurement-site), considering that faunal assemblage properties can differ because of prey transport (Binford 1981). The missing bones of our sample (mostly appendicular elements) fit with the bone assemblages previously cited. Despite this, in both cases, diaphyseal cylinders are unknown.

A sample from a similar observation analysed by Yravedra et al. (2014) as a natural-death assemblage (Ayllón) shows very different results. While the percentage of recovered bones is quite similar (40.5 to 49.87% in our study), the bone damage assemblage shows substantial differences. In our sample, all long bones (LB) are complete and without fractures, while most LB lost at least one of the epiphysis or display fractures around the metadiaphyses in theirs. Conversely, they recorded a low rate of tooth marks among the axial elements and a high tooth mark frequency on the appendicular elements. As additional data, all the elements analysed in that work were recovered in summer season. When we compare the results in the same season, the differences became more apparent, displaying 1.65% of damaged bones related to recovered elements in our sample. We cannot understand the reason for the discrepancy; however, without specifying the surveillance methodology of that study, it seems probable that some other carnivore-type may have gained access to the carcasses, considering that 99% of predator actions developed at night-time in our study.

Tooth mark dimensions from our experimental sample are small, with averages of 1.37 × 1.04 mm on thick cortical, 1.63 × 1.16 mm on thin cortical and 2.01 × 1.53 mm on cancellous tissue, while the average of scores is 0.92 (thick cortical), 0.67 (thin cortical) and 1.29 (cancellous tissue). Different researchers describe similar variability of pit/score range dimensions (Mondini 1995; Krajcarz and Krajcarz 2014; Yravedra et al. 2014; Young et al. 2015b). Only two pits in our sample reach 7 mm (length); one of them on thin cortical in the winter and the other one on cortical tissue in spring.

Unfortunately, several works developed so far did not take some important variables into account, such as the total time from initial scavenging to final removal, seasonality or spatial dispersion of the anatomical elements. Some behavioural ecological models can be used to trace variables like seasonality in a bone damage assemblage (Charnov 1976; Nagaoka 2015). According to the Marginal Value Theorem (MVT) (Charnov 1976), degree and intensity of bone damage could be related to foraging efficiency and resource availability among carnivores. Furthermore, resource availability is also related to annual climate fluctuations and exposed to the rise and fall of temperature.

When split by season, our study shows considerable differences when assessing consumption degree and bone damage in the sample. Summer season displays the lowest degree of bone modification, followed by autumn (9.32 and 14.95%, respectively). Conversely, scavenging activities increase 47.45% in spring, reaching the highest level in winter (57.5%). This fact might correspond with the resource availability/climate fluctuation statement, coinciding with the period of breeding, which also determines food supply. These data are also concordant with the correspondence analysis (PCA) (Fig. 10). The plot shows two main groups of variables: (1) damage combined with number of recovered bones and maximum distance from the deposit site, and (2) groups of bones (anatomical connections) with number and duration of visits. Regarding observations, a main group can be identified. This cluster contains most of observations carried out during spring and winter, and appears to be clearly influenced by damage and, to a lesser extent, by distance and number of recovered elements. Observations during summer and autumn are scattered throughout the influence area of the second group. In this respect, significant differences between the two main periods (winter/spring and summer/autumn) can be observed. The scavenging activities during the period with less alternative resources (winter/spring) are characterised by higher damage and longer transport distances of the carcass portions. On the contrary, summer/autumn is represented by a high variability, a fact that can be related to a greater exposure time (winter/spring average = 18 days; summer/autumn average = 25 days), thus higher dispersion and number of visits.

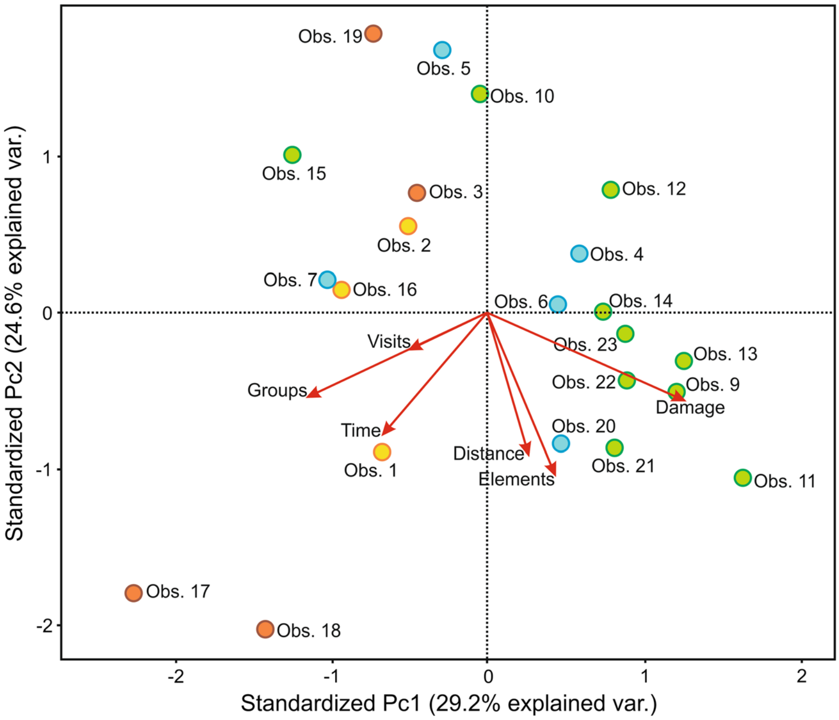
The observed dispersion of anatomical units seems to draw a general pattern for transport (Fig. 11). The hierarchical cluster analysis by single linkage shows two main groups, in which axial skeleton and hind limbs are clearly separated from forelimbs. Considering the carcass original position, forelimbs seem to be affected by a high mobility, while cranial and axial skeleton remains close to the place. On the other hand, hind limbs are usually subjected to a low mobility.

Conclusions

The present study contributes to characterise wild predator behaviour from a neo-taphonomic approach, describing consumption sequences of ungulate carcasses among red fox in the Spanish Pyrenees. A combination of observational data from photo/video-trapping and taphonomic analyses has allowed us to control three main (pre-established) variables: (1) seasonality, (2) scavenging time and (3) spatial dispersion. Regarding seasonality, the maximum activity of red fox occurs between the end of winter and spring time, when the environment availability of vegetable resources (e.g. dried fruit, nuts and fruits) is relatively scarce and also the period of breeding determines a high supply requirement. The second variable is directly affected by the former, linking this period of the year to the minimal recorded time of consumption. Therefore, as the available resources increase so does time of consumption.

The instinctive behaviour of the red fox leads to a high degree of scattering that shows a skeletal-bone dispersion from few centimetres to many meters. Although red fox

Fig. 10 Correspondence analysis showing observations by seasons: winter (blue spots), spring (green), summer (yellow), and autumn (orange)



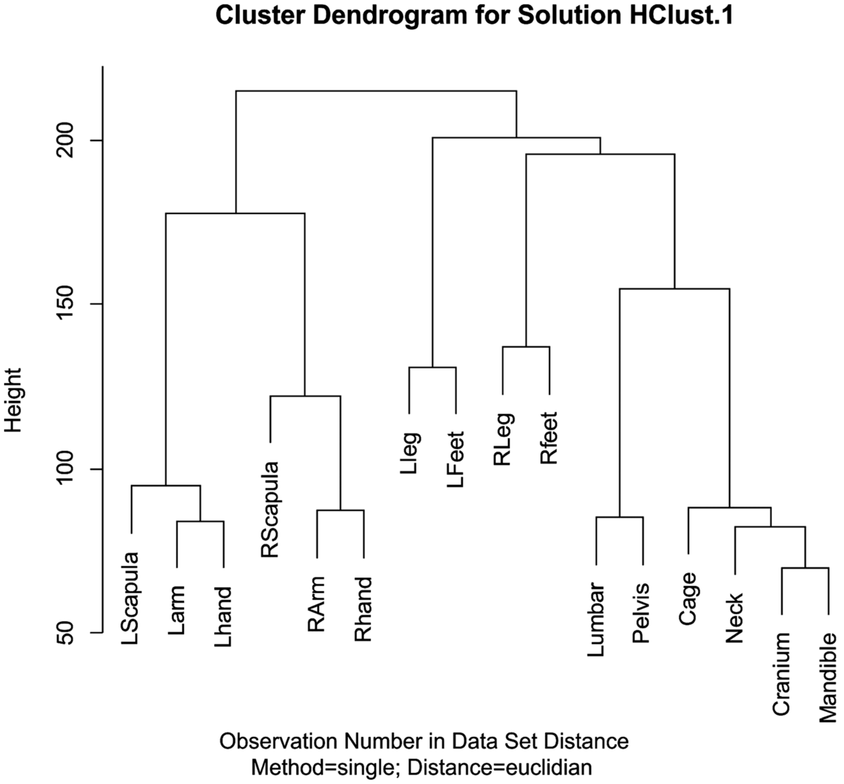


Fig. 11 Hierarchical cluster analysis (single linkage) of the distances to the carcass original position by anatomical units. The appendicular units are preceded by L (left) and R (right)

instinct when facing a small-sized ungulate carcass (< 100 kg) is to remove the whole animal, it has to be dismembered so as to transport it because of its own physical ability. Almost half of the anatomical remains disappeared, mainly appendicular elements. The bulk of recovered items were found in secluded places within a 0–30-m radius related to the initial standing point. The most significant dispersal of skeletal remains occurs in spring time. Statistical analyses show a clear transport pattern, in which forelimbs are the most affected, while cranial and axial skeleton, and to a lesser extent hind limbs, remain close to the original position.

Taphonomically, not only high bone damage on axial skeleton is identified, mainly characterised by fractures and tooth marks on distal ends of ribs and vertebrae, but also different types of alterations like bent ends, fraying, crenulated edges, crushing, longitudinal cracks, furrowing and pitting were recorded. In the case of the limb bones, some tooth marks and furrowing on proximal femur and proximal humerus were occasionally detected. No long bone breakage or shaft cylinders were documented after the consumption of ungulate carcasses in the obtaining place.

Here, we present preliminary data as the experimental project is still in progress. More data will allow us in a near future to perform significant statistic analyses including different weight categories within the small-sized ungulates. Finally, both outcomes and methodology developed here should be set out within a broader general context, mainly at geographical level. This means that more accurate field work is required, not only in the Pyrenees but also within other fox communities from different regions of Eurasia and America. As a future prospect, our results could be contrasted with other studies carried out in other areas in order to determine different or similar dynamics and, therefore, to be able to appropriately model red fox behaviour and its reflection as a taphonomic agent in the fossil record.

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