Taphonomic signature of Eurasian eagle owl (Bubo bubo) on fish remains

Authors: Guillaud, Emilie, Lebreton, Loïc, and Béarez, Philippe

Taphonomic signature of Eurasian eagle owl (*Bubo bubo*) on fish remains

Emilie GUILLAUD[1,2]*, Loïc LEBRETON[3] and Philippe BÉAREZ[1]

[1] *Unité Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements (AASPE), Muséum National d'Histoire Naturelle, CNRS, CP 56, 57 rue Cuvier, 75005 Paris, France; e-mail: emilie.guillaud@mnhn.fr*

[2] *Unité Histoire Naturelle de l'Homme Préhistorique (HNHP), Institut de Paléontologie Humaine, Muséum National d'Histoire Naturelle, CNRS, Paris, France*

[3] *Unité Histoire Naturelle de l'Homme Préhistorique (HNHP), Université de Perpignan Via Domitia, CNRS, EPCC Centre Européen de Recherches Préhistoriques, Tautavel, France*

Abstract. Fish bones are often found in Palaeolithic cave deposits, but the origin of their accumulation is generally poorly known. Knowledge of the accumulator is essential to understand the role of fish in human subsistence activities, and the Eurasian eagle owl (*Bubo bubo*) is frequently recognized as an accumulator of skeletal remains on archaeological sites.
We analyzed 27 Eurasian eagle owl pellet samples from Tautavel (Pyrénées Orientales) in southern France. From this sample, we identified 1812 fish remains distributed across seven species: allis shad (*Alosa alosa*), European eel (*Anguilla Anguilla*), gudgeon (*Gobio gobio*), roach (*Rutilus rutilus*), Mediterranean barbel (*Barbus meridionalis*), chub (*Squalius cephalus*) and tench (*Tinca tinca*). These remains were characterised by relatively complete skeletal representation, minimal bone fragmentation and low digestive surface damage. On the basis of surface modification, we produced a set of criteria to be applied to the fossil record in order to highlight the role of this owl in cave fish deposits.

Key words: Palaeolithic, nocturnal raptor, fish remains, taphonomy, diet

Introduction

The origin of small fish bone deposits in caves occupied by human populations during Palaeolithic times is a recurrent problem. There are multiple predators that can have frequented or occupied the cave, and the different types of alteration observed on bones can illustrate the action of either human or non-human predators, like carnivores or birds. It is important to document these agents as they can accumulate and/or modify the deposit and potentially alter the surface structure of the bone. In the case of fish remains, very few studies have been done to identify the bone accumulator or verify the contribution of each predator, and further experimental work needs to be conducted.

The natural disintegration of pellets produced by raptors can be an important process of accumulation. Birds produce regurgitation pellets containing bones that display varying degrees of damage and digestion (Andrews 1990). One of them, the Eurasian eagle owl

(*Bubo bubo*), is a nocturnal raptor of the Strigidae family that accumulates pellets under perching and nesting sites (Penteriani et al. 1999, Cochard 2008). Considered the largest nocturnal raptor in Europe, it lives mainly in rocky and mountain areas or on the escarpments bordering river valleys, alternating between wooded and open areas. It hunts preferentially in open spaces (Jürgen 1995). It is present from Europe to North Africa and East Asia. In France, it is found mainly in the southern regions. *Bubo bubo* is a dietary opportunist that feeds on carrion as part of a varied diet. Its diet consists mainly of medium mammals such as hedgehog, lagomorphs, and rodents, but also includes birds, reptiles and amphibians (Géroudet 1984, Cramp 1985). Several studies have mentioned fish consumption in its diet (Bocheński 1960, Hiraldo et al. 1975, Malafosse 1984, Bayle et al. 1987, Le Gall 1999, Penteriani et al. 2002).

Despite its behaviour and opportunistic subsistence, the Eurasian eagle owl has been considered a

* Corresponding Author

potential accumulator of fish remains in cave deposits (Nicholson 1991, Le Gall 1999, Laroulandie 2002, Rambaud et al. 2008, Russ 2010, Russ & Jones 2011), its presence is documented during the Palaeolithic (Mourer-Chauviré 1975, Louchart & Soave 2002).

The aim of this article is to present a taphonomic analysis of the diet and damage related to digestion in the Eurasian eagle owl in the south of France. This will constitute an aid for understanding archaeological fish accumulations and will provide supplementary data to previously existing taphonomic references.

Material and Methods

Samples were collected near the River Verdouble, close to Tautavel (42°48′55″ N, 2°44′50″ E, altitude 194 m, Pyrénées Orientales, France) between June and August 2016. This river has woody riparian vegetation and is classified as "2ⁿᵈ category". It is populated with cyprinids like the Mediterranean barbel (*Barbus meridionalis*), chub (*Squalius cephalus*), common carp (*Cyprinus carpio*) and carnivores such as northern pike (*Esox lucius*). Samples were collected from the inside of a small cavity (Fig. 1), a European eagle owl nesting place, and from the immediate area outside of the cavity (under the porch). This material was not exposed to the weather for a prolonged time, therefore, the remains did not display any sign of weathering or of having been disturbed by scavengers. The remains from these two zones are recognizable by the different colouration of the bone's surface.

In total, we studied 27 samples of undigested and regurgitated material (pellets – samples may contain one or more pellets, as some of them were disintegrated before collection). Several samples also contained the remains of birds (MNI = 106), lagomorphs (MNI = 82) and rodents (MNI = 132). First, the samples were dry-cleaned to separate the bones by taxon; then each category of bone was sent to the specific expert. However, this study only reports on the fish remains. Each bone was identified by anatomic and taxonomic comparison with the reference collection of freshwater fishes from the Muséum National d'Histoire Naturelle (MNHN, Paris) and the Institut Royal des Sciences Naturelles de Belgique (IRSNB, Bruxelles). We also used published keys (Lepiksaar 1994, Radu 2005). All the remains were examined both macroscopically and microscopically. A binocular microscope was used for the identification of small skeletal elements and for the observation of digestion marks. For the quantitative analysis, we used the number of identified specimens (NISP) and the minimum number of individuals (MNI). The MNI was estimated from the number of

first vertebrae or paired bones and according to the differences in the size of the bones (Poplin 1976) by sample and by spatial localization (inside or outside the cavity). Prey sizes were estimated by direct comparison with specimens from the osteological reference collection of the MNHN. Following the methodology used in a previous study (Guillaud et al. 2017), surface modification was classified following Nicholson (1991). The percentage of visible surface was adapted from Villa & Mahieu (1991). The proportions of bone damage on bone surface were divided into five categories of digestion: null, light, moderate, heavy and extreme (Fernández-Jalvo & Andrews 2016). Damage to the bone surface caused by beak hit was noted and counted. Percentage of bone representation was calculated using the formula
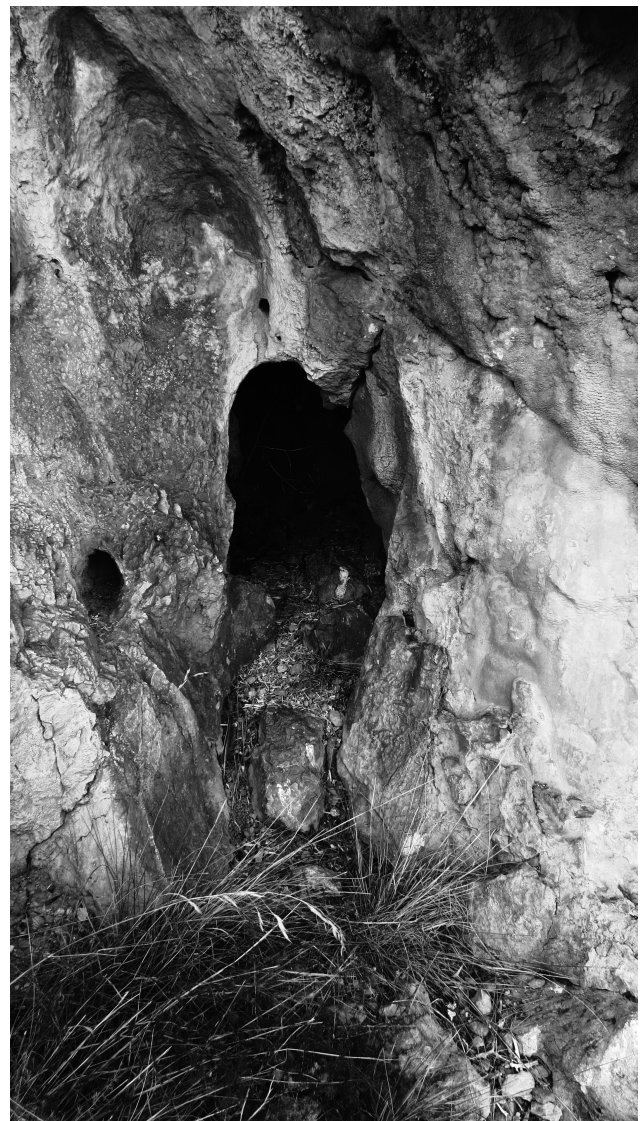

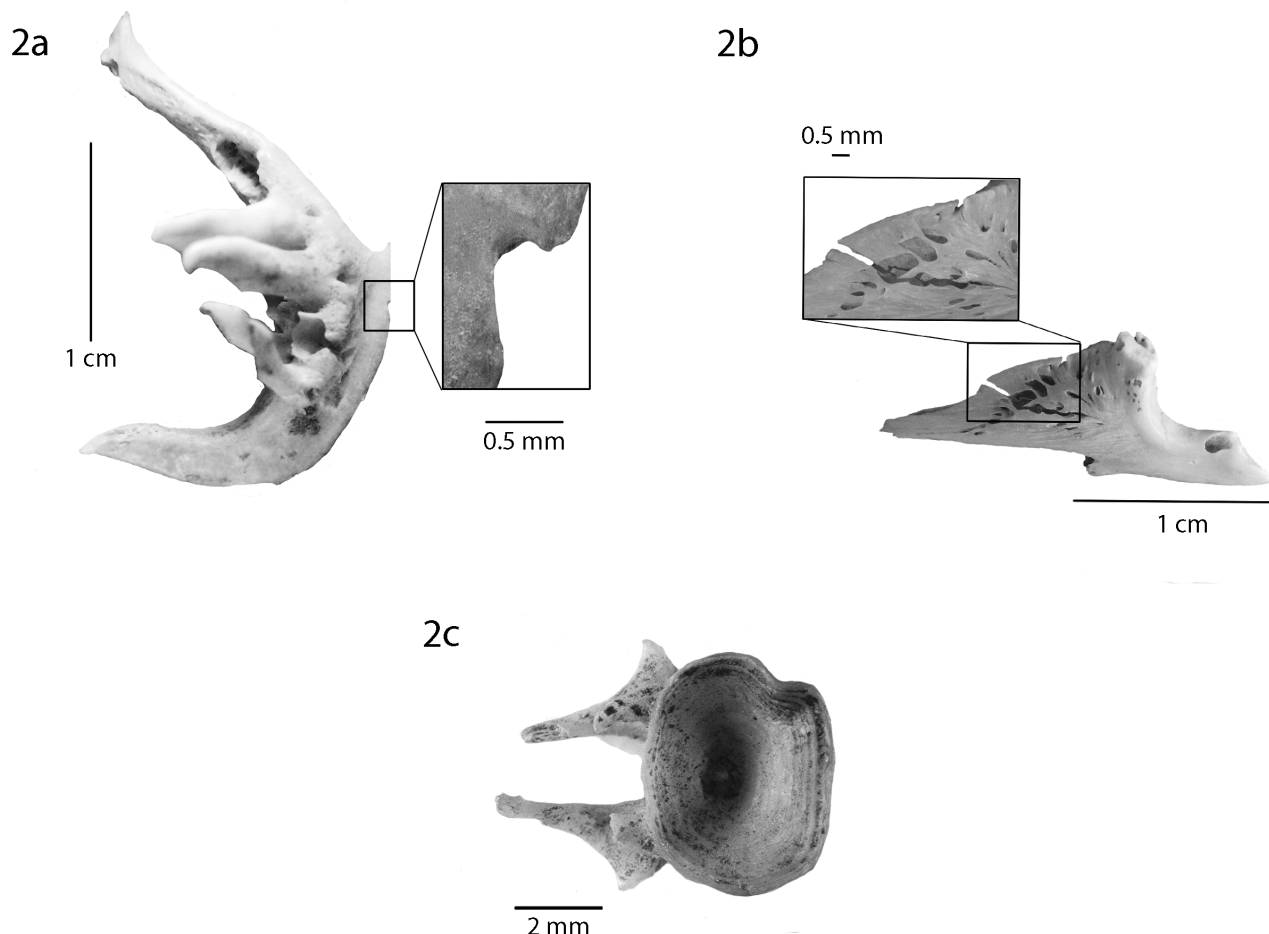**Fig. 1.** Small cavity used by a European eagle owl for nesting and from where samples were collected.

144

Fig. 2. a) Beak marks on pharyngeal bone; b) fissure on the surface of an articular of cyprinid; c) beak marks on precaudal vertebra.

Table 1. Family in order of importance in the assemblage with the number of identified specimens (NISP) and minimum number of individuals (MNI) by sample and spatial localization.

Family	NISP	MNI (by sample)	MNI (by localization)	
			Interior	Exterior
Cyprinidae	751	109	65	52
Anguillidae	90	9	7	1
Clupeidae	1	1	-	1
Total	842	119	72	54

by Dodson & Wexlar (1979): PR = FO/FT × MNI, where FO is the number of elements in the sample and FT is the number of elements in the prey skeleton. This method was adapted for fish bones and gives an overview, since samples were studied together and not separately.

Results

Seven fish species were identified: allis shad (*Alosa alosa*), European eel (*Anguilla anguilla*), gudgeon (*Gobio gobio*), roach (*Rutilus rutilus*), Mediterranean barbel (*Barbus meridionalis*), chub (*Squalius cephalus*) and tench (*Tinca tinca*). The most frequently represented family was Cyprinidae, followed by Anguillidae, and Clupeidae (Table 1). Size estimations indicated that the fish eaten by the eagle owl had a fresh weight ranging between 25 and 1800g.

Anatomical representation
A total of 1812 skeletal remains were recovered from the 27 samples (Table 2). Only 46 % were identified anatomically and specifically. Among them, 36 % (300) belong to the cranial skeleton and 64 % (542) to the axial skeleton. Cranial and vertebral unidentified

145

Table 2. Number of identified fish specimens per Eurasian eagle owl samples.

Samples	Skeletal remains	Identified (%)	Unidentified (%)	NISP Anguillidae	NISP Clupeidae	NISP Cyprinidae
1	128	89 (70)	39 (30)	9	-	80
2	1	1 (100)	-	1	-	-
3	1	1 (100)	-	-	-	1
4	36	20 (56)	16 (44)	1	-	19
5	1	1 (100)	-	-	-	1
6	2	-	2 (100)	-	-	-
7	1	1 (100)	-	-	-	1
8	24	3 (13)	21 (88)	1	-	2
9	28	17 (61)	11 (39)	-	-	17
10	50	20 (40)	30 (60)	-	-	20
11	10	10 (100)	-	-	-	10
12	22	15 (68)	7 (32)	-	-	15
13	311	141 (45)	170 (55)	14	-	127
14	192	98 (51)	94 (49)	13	-	85
15	149	85 (57)	64 (43)	18	-	67
16	19	12 (63)	7 (37)	-	-	12
17	32	22 (69)	10 (31)	6	1	15
18	45	33 (73)	12 (27)	-	-	33
19	1	-	1 (100)	-	-	-
20	2	2 (100)	-	-	-	2
21	8	1 (13)	7 (88)	-	-	1
22	369	40 (11)	329 (89)	1	-	39
23	145	130 (90)	15 (10)	15	-	115
24	23	6 (26)	17 (74)	-	-	6
25	58	56 (97)	2 (3)	8	-	48
26	21	6 (29)	15 (71)	-	-	6
27	133	32 (24)	101 (76)	3	-	29
Total	1812	842 (46)	970 (54)	90	1	751

bone fragments, neural and haemal spines, and scales represented 54 % (970) of all fish remains.

For cyprinids, the entire skeleton was represented and the caudal vertebrae (25 %) were the most numerous elements. For anguillids, we observed some lack of cranial elements, and precaudal vertebrae (3 %) were the most numerous elements. For clupeids, the only remain was an opercle.

Fragmentation and loss of skeletal elements
In our sample, the Eurasian eagle owl accumulation is characterised by the simultaneous presence of complete and fragmented elements in the same pellets. The recovered elements showed a high degree of integrity. Following Andrews's (1990), the breakage degree of skeletal elements present in our sample was moderate (30 %).

Bone deformation and alteration
The deformation of skeletal elements was rare. Only two vertebrae presented post-mortem deformation. Other modifications were visible (Table 3): fissures (NISP = 7), exfoliation (NISP = 9), perforation (NISP = 7) on the surface of certain cranial bones and vertebrae (Fig. 2a) and twisted bones (NISP = 2). Damage to bone surfaces caused by beaks (NISP = 2) was also noted and counted (Fig. 2b, c). Cyprinids were most affected by these modifications.

Digestion
Damage to the bone surface was observed under a binocular microscope. Different categories of digestion damage were applied to bones and teeth (Fernández-Jalvo & Andrews 2016). Five categories of digestion were distinguished: null (0); light (1);
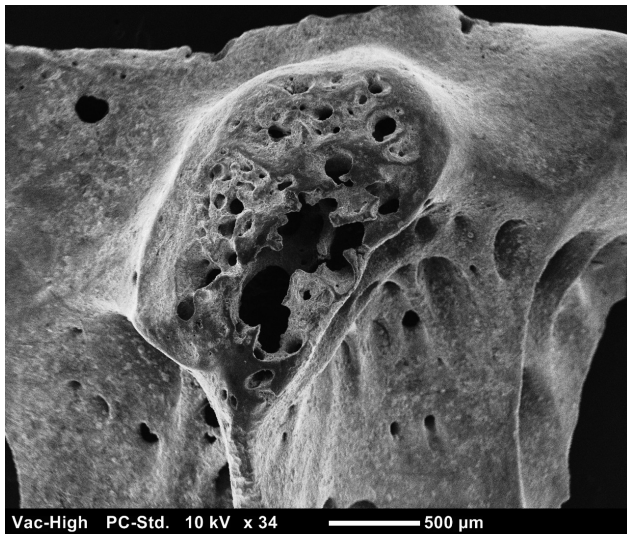
146

Fig. 3. Modification of a cyprinid basipterygium (scanning electron microscope, scale 500 µm); presence of holes and polished aspect of the spongious bone surfaces typically due to gastric juices.

moderate (2); heavy (3); and extreme (4-5). For fish bones, the digestion degrees have been illustrated in Guillaud et al. (2017).

The action of gastric juices results in a smooth and polished surface (Andrews 1990); and although the prolonged transportation of bones in water can also produce this result, only digestion could have caused these effects in our study.

The rounding and polishing of articulation edges observed on the scanning electron microscope (SEM) picture indicate advanced degradation and the presence of digestion holes (Fig. 3); this was notable in 2 % of all the remains.

Different degrees of digestion (Table 3) were observed on the surface of the skeletal remains; specifically, 5 % of the elements were altered to a light degree, 6 % to a moderate degree, and 3 % of bones suffered from moderate to heavy modification. We observed that Anguillidae and Cyprinidae remains displayed

Table 3. Percentages and classes of digestion for fish taxa according to the spatial distribution (int: interior, ext: exterior of the cavity).

				Anguillidae	Clupeidae	Cyprinidae
Bone deformation and alteration	Fissure		int	2	-	1
			ext	-	-	4
	Exfoliation		int	-	-	1
			ext	4	-	4
	Perforation		int	-	-	6
			ext	-	-	1
	Twisted bone		int	-	-	1
			ext	-	-	1
	Beak marks		int	-	-	-
			ext	-	-	2
Digestion	Bone loss absent	int	NISP	40	-	251
			%	44.44	-	33.42
		ext	NISP	23	-	261
			%	25.56	-	34.75
	Minimal digestion	int	NISP	7	-	30
			%	7.78	-	3.99
		ext	NISP	4	-	58
			%	4.44	-	7.72
	Moderate digestion	int	NISP	3	1	44
			%	3.33	100	5.86
		ext	NISP	11	-	54
			%	12.22	-	7.19
	Heavy or extreme digestion	int	NISP	1	-	22
			%	1.11	-	2.93
		ext	NISP	1	-	31
			%	1.11	-	4.13
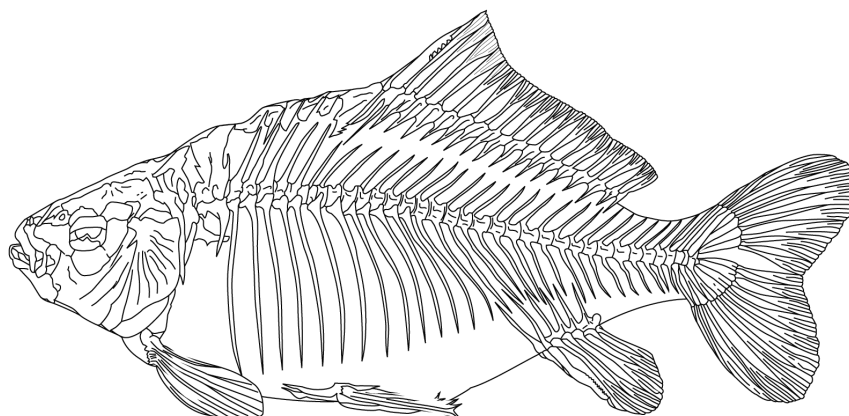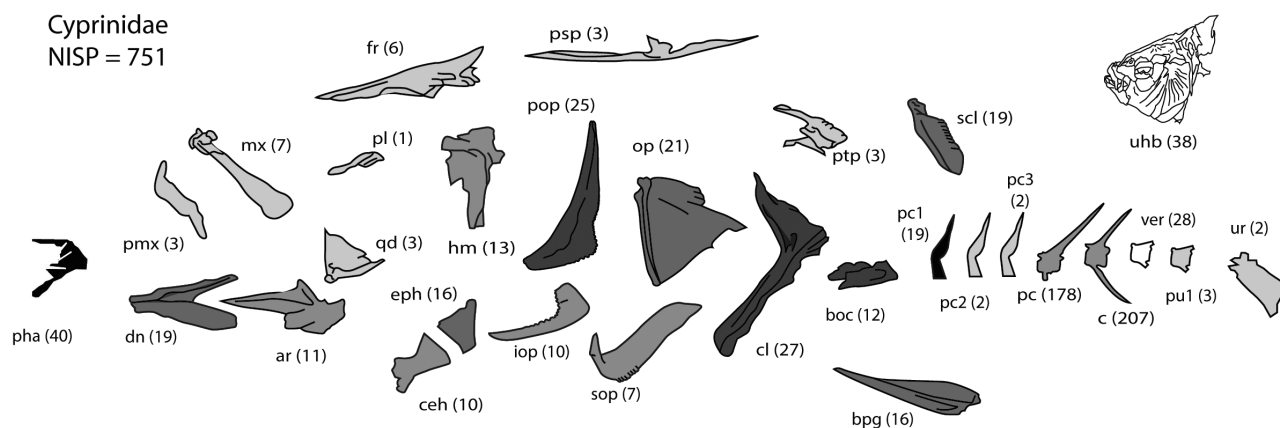
147
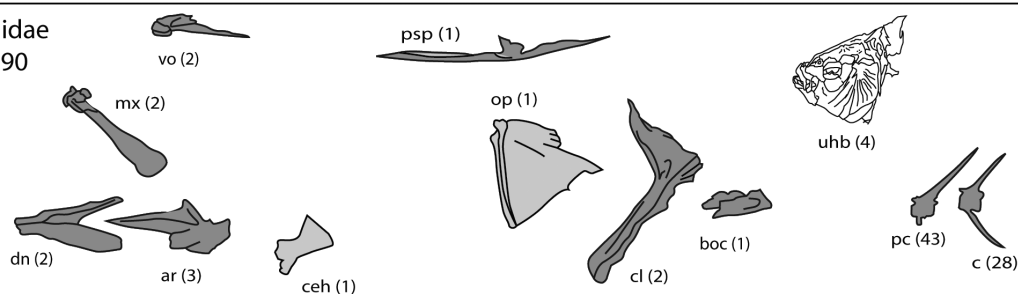
Fig. 4. Skeletal elements before and after digestion in eagle owl samples (common carp skeleton, modified from Coutureau (2005); for abbreviations see Table 4).

minimal digestion traces. Moderate digestion was observed on the only preserved remain attributed to Clupeidae (100 %), followed by Anguillidae (15 %) and Cyprinidae (13 %). Cyprinids were the most

Table 4. Number of remains by bone and fish family in the 27 Eurasian eagle owl samples.

Abbrevation	Bones	Cyprinidae	Clupeidae	Anguillidae	Total
ar	Articular	11		3	14
boc	Basioccipital	12		1	13
bpq	Basipterygium	16			16
c	Caudal vertebra	207		28	235
ceh	Ceratohyal	10		1	11
cl	Cleithrum	27		2	29
dn	Dentary	19		2	21
eph	Epihyal	16			16
fr	Frontal	6			6
hb	Head bone (unidentified)	38		4	42
hy	Hyomandibular	13			13
iop	Interopercle	10			10
mx	Maxilla	7		2	9
op	Opercle	21	1	1	23
pl	Palatine	1			1
psp	Parasphenoid	3		1	4
pha	Pharyngeal bone	40			40
ptp	Posttemporal	3			3
pc1	Precaudal 1	19			19
pc2	Precaudal 2	2			2
pc3	Precaudal 3	2			2
pc	Precaudal vertebra	178		43	221
pmx	Premaxilla	3			3
pu	Preural vertebra	3			3
pop	Preopercle	25			25
qd	Quadrate	3			3
sop	Subopercle	7			7
scl	Supracleithrum	19			19
ur	Urohyal	2			2
ver	Vertebra (unidentified)	28			28
vo	Vomer			2	2
Total		751	1	90	842

affected by heavy digestion (7 %). The localization of the remains seems to have had no impact on bone preservation.

Survival rate
In our study, 29 identified skeletal elements, from approximately 200 bones that constitute the fish skeleton, survived the digestive process (Fig. 4, Table 4). The percentage of representation (PR) was calculated according to Dodson & Wexlar (1979)

and adapted to fish osteology. The percentage of representation was characterised by good preservation of the pharyngeal bone (PR = 55.55 %) and the first vertebra (PR = 52.78 %) in cyprinids, the articular and the precaudal vertebrae in anguillids (PR = 16.67 % and 15.93 %) and the opercle in clupeids (PR = 50 %). In total, the axial skeleton represents 64 % of the studied material. Vertebrae were represented at 53 % in Cyprinidae and 9 % in Anguillidae. The cranial elements were less abundant, with 36 % for

149

Cyprinidae, 1.94 % for Anguillidae and 0.13 % for Clupeidae.

Discussion

To summarize, 27 samples produced by Eurasian eagle owls were analysed. All of them contained fish bones. Among the total remains, 46 % were identified, and the rest were unidentifiable. All skeletal elements are represented in the sample. The breakage degree of skeletal elements was very low. The degree of digestion showed that more than 86 % of bones did not suffer any modification.

The eagle owl diet has been studied in various countries such as France (Bayle 1994, Cochard 2008), Greece (Papageorgiou et al. 1993, Alivizatos et al. 2005), Italy (Marchesi et al. 2002), Slovakia (Obuch & Karaska 2010) and Spain (Cramp 1985, Lloveras et al. 2009). This nocturnal predator has a generalist diet, locally specialized in medium-sized birds and mammals but is most often opportunistic (Hiraldo et al. 1975, Donázar et al. 1989). It consumes medium mammals such as hedgehog and lagomorph but also voles, field mice, rats and other small rodents. Birds may be consumed, mostly ducks, coots or diurnal and nocturnal raptors. Consumption of frogs is rarely mentioned (Géroudet 1978, 1984, Morel & Birchker 1990).

The abundance of fish remains in our sample is consistent with the data provided by Bayle (1992), Le Gall (1999) and Riols (2009). Likewise, the species we identified were among the most frequently recorded by these authors: chub (*Squalius cephalus*) dace (*Leuciscus leuciscus*), roach (*Rutilus rutilus*), brown trout (*Salmo trutta*), followed by pike (*Esox lucius*), common carp (*Cyprinus carpio*), common nase (*Chondrostoma nasus*), burbot (*Lota lota*), perch (*Perca fluviatilis*) and barbel (*Barbus barbus*). Some studies indicate that fish have not been always eaten by the eagle owl (e.g. Bustos & Muñoz 1973, Balluet & Faure 2006, De Cupere et al. 2009, Lloveras et al. 2009); this could be the result of seasonal variation in the diet or absence of a river near the nest. Le Gall (1999) indicates that the fish eaten by eagle owls measure between a few centimetres up to 40 cm. However, the remains belonging to fishes around 200-300 g (40-80 cm depending on the species) were frequent in our sample. The presence of different body mass classes indicates a non-selectivity of prey among the fish river community. The body weight of individuals, in our sample, ranged from 25 g to 1800 g, with the largest species being the eel. It cannot be excluded that small fish have been underestimated

in this study, either because they are more sensitive to digestion or because their tiny bones were just not collected during pellet separation. Difficulties in identifying cyprinids can also cause biases. All species present in our study are coherent with the general diet of an eagle owl and with the fish fauna currently living in the River Verdouble. Our results confirm that eagle owl predation is dependent on the availability of fish population communities.

The eagle owl consumes whole fish, starting from the head. However, if the prey is too large, it may scavenge on it. These practices suggest that there is a selection of ingested body parts. Cramp (1985) noticed that the female eagle owl can dismember a prey and feed it in small pieces to their chicks. The eagle owl tends to deposit pellets at their roosts, which would suggest that any fish remains would be concentrated in the areas beneath and around the nest. The bleaching of bones also provides clear evidence of bioturbation at the cave's entrance (sun impact). For the purpose of this archaeological investigation, it was necessary to compare the spatial distribution of small mammals, birds and fish, which allowed us to make assumptions about the origin of the material deposited: anthropic *vs.* non-anthropic predator.

The number of prey bird deposit studies is expanding, and the Eurasian eagle owl has been identified as a possible accumulation agent on several archaeological sites (e.g. Andrews 1990, Sanchis Serra 2000, Laroulandie 2002, De Cupere et al. 2009). Russ (2010) studied the traces left by eagle owls during a feeding experiment at the Chestnut Centre Conservation and Wildlife Park (England). The skeletal elements recovered from pellets containing fish remains represented almost complete fish. The digestion of fish remains was minimal as they were protected: the fish being camouflaged in rats because the captive birds did not want to eat them. Broughton et al. (2006) studied 14 pellets from the modern barn owl (*Tyto alba*), and gave a general overview of the traces left on fish bones. Most of the remains (3294 remains) belonged to small sized cyprinids (< 500 g). These pellet remains were characterised by a high level of bone preservation. Digestion processes and bone modifications were characterised by a low degree of damage: rounding (16.3 %), pitting (6.9 %) and deformation (5.7 %). Following Andrews's (1990) method, the results of these two Strigiformes samples have no significant difference. Conversely, pellets coming from diurnal raptors (Falconiformes) contained less bone with a high percentage of fragmentation and a higher digestion of the bone surface than nocturnal

raptors (Mayhew 1977, Bocheński et al. 1998). Our study confirms observations made on Strigiformes: low fragmentation, beak marks on pharyngeal bones or cracking of the bone surface. Fish remains also showed signs of digestion like rounding.

The impact of digestion on vertebrate skeleton (small mammal) varies according to the enzymes and acidity of the digestive system of the predator (Denys et al. 1995, Fernández-Jalvo et al. 2016). We must not forget that the impact of digestion on the fish skeleton can also vary. The conservation of the fish bone is also correlated with its histological structure (Butler 1996, Fernández-Jalvo et al. 2002). In our study, there does not appear to be any difference in the bone conservation depending on the fish size or species. However, we did observe that the majority of the preserved bones were vertebrae; cranial bones are less compact and can be more fragmented and more rapidly digested. Andrews (1990) included eagle owl in moderate or heavy digesting concerning the tooth enamel of small mammals. According to the whole variables studied in this paper, *Bubo bubo* may be considered as an intermediate category (2) of predator modification (Andrews 1990).

Erlandson & Moss (2001) identified a large number of predator species that could potentially deposit fish remains in caves located close to the coastline: canids, bears and birds. The bone assemblages produced by raptors are characterised by their degree of digestion. Fragmentation is secondary in comparison to mammals. Some pitting was observed, and broken edges were rounded. Some of the remains showed characteristic signs of biochemical modifications like rounding and polishing.

Conclusion

The study of modern predator behaviour offers hypotheses regarding the potential accumulator in archaeological sites. During the Palaeolithic period, when caves were unoccupied by human groups, other species may have settled there and created fish bone deposits. The analysis of eagle owl pellets indicates that this owl has a diversified diet including fish when close to a river. This study of 27 pellets allowed us to characterize the damage caused to fish bones during digestion. Focusing on the taphonomic point of view, we need to take into account this species in future studies. Present work proposes a criteria for analyzing and interpreting Eurasian eagle owl pellet remains, a potential fish bone accumulator. However, because eagle owl digestion is less destructive than that of carnivores, damage produced on bone may partly or completely disappear due to the post-depositional process. Therefore, interpreting that data just on digestion is not enough; we need to combine this analysis with other criteria such as bone representation, surface modification, fractioning, fragmentation, size of fish specimens or spatial distribution. It is important to analyse the fish remains combined with other faunal and lithic remains and not separately, as it is currently the case. Although, eagle owls could have contributed to the accumulation of archaeological fish, according to the present results, it is particularly important to be prudent in the analyses of accumulations that can be created by more than one predator. The ability to determine the depositional origin of fish remains recovered from archaeological caves is crucial for the correct interpretation of deposits, but it remains challenging.

Literature

Alivizatos H., Goutner V. & Zogaris S. 2005: Contribution to the study of the diet of four owl species (Aves, Strigiformes) from mainland and island areas of Greece. *Belg. J. Zool. 135: 109–118.*

Andrews P. 1990: Owls, caves and fossils. *University of Chicago Press, Chicago.*

Balluet P. & Faure R. 2006: Le grand duc d'Europe *Bubo bubo* dans le département de la Loire. Eléments de biologie. *Nos Oiseaux 53: 195–208.*

Bayle P. 1992: Le hibou grand-duc (*Bubo bubo*) dans le Parc National du Mercantour et ses environs. *Rapport Parc National du Mercantour: 4–27.*

Bayle P. 1994: Régime alimentaire du grand-duc d'Europe *Bubo bubo* dans le Parc National du Mercantour (Alpes du Sud, France). In: Loose D. (ed.), Oiseaux de montagne. *CORA, actes du 32éme Colloque interrégional d'ornithologie, Grenoble, La Niverolle: 178.*

Bayle P., Orsini P. & Boutin J. 1987: Variations du régime alimentaire du hibou grand-duc *Bubo bubo* en période de reproduction en Basse-Provence. *L'oiseau et la Revue Française d'Ornithologie 57: 23–31.*

Bocheński Z. 1960: The diet of eagle-owl *Bubo bubo* (L.) in the Pieniny Mts. *Acta Zool. Cracov. 5: 311–332.*

Bocheński Z.M., Huhtala K., Jussila P. et al. 1998: Damage to bird bones in pellets of gyrfalcon *Falco rusticolus. J. Archaeol. Sci. 25:* 425–433.

Broughton J.M., Cannon V.I., Arnold S. et al. 2006: The taphonomy of owl-deposited fish remains and the origin of the homestead cave ichthyofauna. *J. Taphonomy 4: 69–95.*

Bustos A.R. & Muñoz I.C. 1973: Datos sobre la alimentación del *Bubo bubo* y determinación de micromamiferos en Sierra Nevada mediante egagrópilas. *Cuad. Ci. Biol. 2: 57–61.*

Butler V.L. 1996: Tui chub taphonomy and the importance of marsh resources in the western Great Basin of North America. *Am. Antiq. 61: 699–717.*

Cochard D. 2008: Discussion sur la variabilité intraréférentiel d'accumulations osseuses de petits prédateurs. *Ann. Paléontol. 94:* 89–101.

Coutureau M. 2005: Squelette de carpe commune (*Cyprinus carpio*). Dessin vectoriel, d'après photo de squelette remonté. *ArcheoZoothéque. https://www.archeozoo.org/archeozootheque/galleries/file_uploader/pdf/cyprinus_carpio.pdf*

Cramp S. (ed.) 1985: Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palearctic. IV. Terns to woodpeckers. *Oxford University Press, Oxford, New York.*

De Cupere B., Thys S., Van Neer W. et al. 2009: Eagle owl (*Bubo bubo*) pellets from Roman Sagalassos (SW Turkey): distinguishing the prey remains from nest and roost sites. *Int. J. Osteoarchaeol. 19: 1–22.*

Denys C., Fernández-Jalvo Y. & Dauphin Y. 1995: Experimental taphonomy: preliminary results of the digestion of micromammal bones in the laboratory. *C. R. Acad. Sci. 321: 803–809.*

Dodson P. & Wexlar D. 1979: Taphonomic investigation of owl pellets. *Paleobiology 5: 275–284.*

Donázar J.A., Hiraldo E., Delibes M. & Estrelia A.R. 1989: Comparative food habits of the eagle owl *Bubo bubo* and the great horned owl *Bubo virginianus* in six Palearctic and Nearctic biomes. *Scand. J. Ornithol. 20: 298–306.*

Erlandson J.M. & Moss M.L. 2001: Shellfish feeders, carrion eaters and the archaeology of aquatic adaptations. *Am. Antiq. 66: 413–432.*

Fernández-Jalvo Y. & Andrews P. 2016: Atlas of taphonomic identifications. *Vertebrate Paleobiology and Paleoanthropology Series, Springer.*

Fernández-Jalvo Y., Andrews P., Denys C. et al. 2016: Taphonomy for taxonomists: implications of predation in small mammal studies. *Quat. Sci. Rev. 139: 138–157.*

Fernández-Jalvo Y., Sánchez-Chillón B., Andrews P. et al. 2002: Morphological taphonomic transformations of fossil bones in continental environments, and repercussions on their chemical composition. *Archaeometry 44: 353–361.*

Géroudet P. 1978: Les rapaces diurnes et nocturnes d'Europe. *Les beautés de la Nature, Delachaux et Niestlé, Neuchâtel.*

Géroudet P. 1984: Les rapaces diurnes et nocturnes. *Delachaux et Niestlé, Neuchâtel.*

Guillaud E., Béarez P., Denys C. & Raimond S. 2017: New data on fish diet and bone digestion of the Eurasian otter (*Lutra lutra*) (Mammalia: Mustelidae) in central France. *Eur. Zool. J. 84: 226–237.*

Hiraldo F.J., Andrada J. & Parreños F.F. 1975: Diet of the eagle owl (*Bubo bubo*) in Mediterranean Spain. *Doñana, Acta Vertebrata 2:* 161–177.

Jürgen N. 1995: Rapaces diurnes et nocturnes. *Nathan, Paris.*

Laroulandie V. 2002: Damage to pigeon long bones in pellets of the eagle owl *Bubo bubo* and food remains of peregrine falcon *Falco peregrinus*: zooarchaeological implications. In: Bocheński Z.M., Bocheński Z. & Stewart J. (eds.), Proceedings of the 4th Meeting of the ICAZ Bird Working Group, Kraków, Poland, 11-15 September, 2001. *Acta Zool. Cracov. 45: 331–339.*

Le Gall O. 1999: Ichtyophagie et pêches préhistoriques. Quelques données de l'Europe occidentale. *Unpublished PhD thesis, Bordeaux University, France.*

Lepiksaar J. 1994: Introduction to osteology of fishes for paleozoologists. *Göteborg.*

Lloveras L., Moreno-García M. & Nadal J. 2009: The eagle owl (*Bubo bubo*) as a leporid remains accumulator: taphonomic analysis of modern rabbit remains recovered from nests of this predator. *Int. J. Osteoarchaeol. 19: 573–592.*

Louchart A. & Soave R. 2002: Changement d'ampleur de l'exploitation des oiseaux entre le Magdaléneien et l'Azilien: l'exemple du Taï 2 (Brome). *Quaternaire 13: 297–312.*

Malafosse J.-P. 1984: Quelques données sur le hibou grand-duc *Bubo bubo* dans le département de la Lozère de 1978 à 1984. *Le Grand Duc 26: 26–32.*

Marchesi L., Sergio F. & Pedrini P. 2002: Costs and benefits of breeding in human-altered landscapes for the eagle owl, *Bubo bubo. Ibis 144: E164–E177.*

Mayhew D.F. 1977: Avian predators as accumulators of fossil mammal material. *Boreas 6: 25–31.*

Morel P. & Birchler T. 1990: Ossements holocènes découverts dans l'aire d'un rapace à Melchsee-Frutt, Schrattenöhle, Wermutseingang (Kerns, OW). *Stalactite 40: 76–86.*

Mourer-Chauviré C. 1975: Les oiseaux du Pléistocène moyen et supérieur de France. *Unpublished PhD thesis, Lyon University, France.*

Nicholson R.A. 1991: An investigation into variability within archaeologically recovered assemblages of faunal remains: the influence of pre-depositional taphonomic factors. *PhD thesis, York University, U.K.*

Obuch J. & Karaska D. 2010: The Eurasian eagle-owl (*Bubo bubo*) diet in the Orava Region (N Slovakia). *Slovak Raptor J. 4: 83–98.*

Papageorgiou N.K., Vlachos C.G. & Balkaloudis D.E. 1993: Diet and nest site characteristics of eagle owl (*Bubo bubo*) breeding in two different habitats in north-eastern Greece. *Avocetta 17: 49–54.*

Penteriani V., Gallardo M. & Roche P. 2002: Landscape structure and food supply affect eagle owl (*Bubo bubo*) density and breeding performance: a case of intra-population heterogeneity. *J. Zool. Lond. 257: 365–372.*

Penteriani V., Gallardo M., Roche P. & Cazassus H. 1999: Densité, preferences en termes d'habitat de nidification, régime alimentaire, comportement vocal. *Courrier Scientifique du Parc Naturel Régional du Luberon 3: 155–165.*

Poplin F. 1976: A propos du Nombre de Restes et du Nombre d'Individus dans les échantillons d'ossements. *Cahiers du Centre de Recherches Préhistoriques 5: 61–74.*

Radu V. 2005: Atlas for the identification of bony fish bones from archaeological sites. *Asociatia romana de archeologie, studii de preistorie supplementum, Editura contrast, Bucarest.*

Rambaud D., Laroulande V., Primault J. & Béarez P. 2008: Les poissons et les oiseaux du Taillis des Coteaux (Antigny, Vienne), niveaux magdaléniens: origine naturelle ou culturelle ? In: Laroulandie V., Mallye J.-B. & Denys C. (eds.), Taphonomie des petits vertébrés: référentiels et transferts aux fossiles. *British Archaeological Reports, International Series 2269, Oxford: 167–179.*

Riols C. 2009: Le régime alimentaire du grand-duc d'Europe *Bubo bubo* dans les Corbières. In: Bourgeois M., Gilot F. & Savon C. (eds.), Gestion conservatoire des rapaces méditerranéens: retours d'expériences. *LPO, Aude & GOR: 105–123.*

Russ H. 2010: The Eurasian eagle owl (*Bubo bubo*): a fish bone accumulator on Pleistocene cave sites? *J. Taphonomy 8: 281–290.*

Russ H. & Jones A.K.G. 2011: Fish remains in cave deposits; how did they get there? *Cave & Karst Science 38: 57–60.*

Sanchis Serra A. 2000: Los restos de *Oryctolagus cuniculus* en las tafocenosis de *Bubo bubo* y *Vulpes vulpes* y su aplicación a la cararacterización del registro faunístico arqueológico. *Saguntum 32: 31–50.*

Villa P. & Mahieu E. 1991: Breakage patterns of human long bones. *J. Hum. Evol. 21: 27–48.*