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Bird procurement by humans during the Middle and Early Upper Paleolithic of Europe: New data for the Aurignacian of southwestern France

Véronique Laroulandie^{a*}, Eugène Morin^{b, a}, Marie-Cécile Soulier^c, Jean-Christophe Castel^{d, a}

a - Université de Bordeaux, PACEA UMR 5199 du CNRS, B2, Allée Geoffroy St-Hilaire CS 50023, 33615 Pessac CEDEX, France. veronique.laroulandie@u-bordeaux.fr

b - Trent University, Department of Anthropology, DNA Block C, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada. eugenemorin@trentu.ca

c - Université de Toulouse Jean-Jaurès, TRACES UMR 5608 du CNRS, Maison de la Recherche, 5, allées Antonio Machado, 31058 Toulouse cedex 9, France. mariecsoulier@gmail.com

d - Musée d'histoire naturelle de Genève, Département d'archéozoologie, CP6434, Route de Malagnou 1, 1211 Genève 6, Switzerland. jean-christophe.castel@ville-ge.ch

* corresponding author

Abstract

Recently, the development of taphonomically-oriented studies of avifaunal assemblages have contributed towards renewing our perceptions of the complexity of Neandertal behavioral adaptations in Europe. In contrast, few studies have been conducted on bird samples dated to the Early Upper Paleolithic. Here, we provide new data for three archeological sites (Isturitz, le Piage, Abri Cellier) from southwestern France that have produced Aurignacian material. Evidence of bird processing, use of raptor talons and that bird bones served as raw material aid in enlarging our knowledge of how birds were exploited during the Aurignacian. Overall, the available information shows a clear focus on scavenging birds and points to only marginal changes in the way humans used birds during the Mousterian and Early Upper Paleolithic.

Keywords

Paleolithic; Symbolism; Raptors; Corvids; Feathers; Talons

1. Introduction

In Europe, the period between 45,000 and 35,000 years ago was the scene of major changes that coincided with the replacement of Middle Paleolithic (Mousterian) technologies by Upper Paleolithic ones. In addition, this period is important because it saw the demic expansion of anatomically modern humans into Europe, a process that led to the demise of the local Neandertal populations. This series of events, which took place after the Mousterian and before or during the onset of the Aurignacian, is associated with several so-called “transitional” industries (e.g., Châtelperronian, Uluzzian, Szeletian). However, the nature, timing and geographical variability of these changes have been—and still are—a subject of heated debate in paleoanthropology, debates that also extend to the biology and cultural affinities of the human populations involved in this transition (e.g., d’Errico et al., 1998; Bar-Yosef and Bordes, 2010; Benazzi et al., 2011, 2015; Discamps et al., 2011, 2015; Higham et al., 2014; Villa and Roebroeks, 2014; Zilhão et al., 2015; Gravina et al., 2018; Villa et al., 2018). Despite some advances, the small number of human remains available for this period, problems of chronology and stratigraphic provenience, combined with sometimes conflicting paradigms continue to be a major source of concern for the interpretation of these events.

In the last few years, paleogenomic data have been used to argue for episodes of admixture between Neandertal and anatomically modern human populations (e.g., Sankararaman et al., 2014; Fu et al., 2015). In addition, new archeological evidence has highlighted the behavioral “complexity” of the Middle Paleolithic Neandertals, contributing to a change of perspective with respect to their cognitive abilities. This evidence includes indications that the European Neandertals buried their dead (e.g., Maureille and Van Peer, 1998; Rendu et al., 2013; Maureille et al., 2016), made bone tools (Soressi et al., 2013; Tartar and Costamagno, 2016), used pigments (e.g., Soressi and d’Errico, 2007), collected marine shells (Zilhão et al., 2010) and stones for aesthetic purposes (e.g., Radović et al., 2016) and engraved and painted abstract signs in caves (Rodríguez-Vidal et al., 2014; Hoffmann et al., 2018), all independently from modern human influence.

Studies of bird remains have significantly added to the debate by providing new light on the behavioral adaptations of Neandertals. However, ornitho-archeological studies are few and often geographically and/or chronologically biased. The goal of the present paper is to contribute towards closing this gap by presenting new information on the use of birds during the Early Upper Paleolithic of Europe. These new data derive from the long-studied region of Southwestern France, where three sites containing bird remains have recently been excavated. These sites comprise occupations attributed to the Protoaurignacian (PA) and Early Aurignacian (EA). The PA and EA are two successive technocomplexes from the European Early Upper Paleolithic that have been distinguished using criteria relating to lithic and bone tool production (e.g. Bon, 2002; Teyssandier and Liolos, 2008; Teyssandier et al. 2010). The earliest of these—the PA—starts around 42 kyrs cal BP. This technocomplex would have been replaced by the EA, which have an estimated time range of 40–37 kyrs cal BP (Banks et al. 2013). The data provided here allow for a fuller appreciation of processes of change, convergence and continuity in human-bird interactions during these pivotal periods, as evaluated from the perspective of ornitho-archeozoology. However, before presenting these data, we first give a brief overview of the current state of our knowledge on human exploitation of birds during the Middle and Early Upper Paleolithic.

2. The contribution of ornitho-archeozoology

2.1 *Mousterian*

In recent years, detailed taphonomic studies have clarified the potential role played by humans in the accumulation of bird remains in Middle Paleolithic sites (e.g., Laroulandie et al., 2016; Rufà et al., 2016a, 2016b, 2018; Romero et al., 2017; Lloveras et al., 2018). In Southern France and Iberia, archeozoological analyses of Mousterian collections have shown that Neandertals regularly obtained large mammals and, to a lesser extent, small fast game such as rabbits (e.g., Cochard et al., 2012; Blasco et al., 2013; Morin et al., 2019) and birds. With respect to birds, a wide range of species was exploited, including pigeons, Corvidae, Phasianidae and diurnal raptors, as well as Anseriformes and small passerines (see synthesis in Gómez-Olivencia et al., 2018, table S7 and fig. 1). Fowling was apparently a frequent activity, at least in some sites such as Gorham's cave (Blasco et al., 2014, 2016) and Cova Negra (Martínez Valle et al., 2016). Interactions between Neandertals and scavenging birds (e.g., corvids, large diurnal raptors)—especially the golden eagle (*Aquila chrysaetos*)—were probably more common than what is suggested by the frequency of cutmarked remains, as these birds are relatively well represented in Middle Paleolithic avifaunal samples (Finlayson et al., 2012, 2019; Finlayson and Finlayson, 2016). Overall, without dwelling overly on the variability that is beginning to emerge, it seems clear that Neandertals exploited edible and/or non-edible bird resources on relatively broad geographical (a roughly triangular tract of land minimally formed by Gibraltar, Germany and Croatia) and chronological (at least from Marine Isotope Stage [MIS] 9 to MIS3) scales. According to microscopic observations of cutmarks and other taphonomic evidence, Middle Paleolithic humans looked for blood, meat, tendons, bones, feathers and raptor talons (Peresani et al., 2011; Finlayson et al., 2012; Morin and Laroulandie, 2012; Blasco et al., 2014, 2016; Romandini et al., 2014, 2016; Radovčić et al., 2015; Fiore et al., 2016; Laroulandie et al., 2016; Martínez Valle et al., 2016; Majkić et al., 2017; Gómez-Olivencia et al., 2018, Lloveras et al., 2018). Feather residues identified on stone tools at the site of Payre and Abri Maras (Hardy and Moncel, 2011; Hardy et al., 2013) may, if confirmed by additional experiments and observations (Pedergnana and Blasco, 2016), be consistent with this interpretation. In essence, marks indicative of feather and raptor talon exploitation support the hypothesis that Neandertals had already evolved complex, symbolically-mediated behavior by at least MIS5, if not earlier.

2.2 *Transitional industries*

Few studies have addressed the issue of bird exploitation by the makers of the transitional industries. Concerning the Châtelperronian—the earliest Upper Paleolithic industry of France and Northern Spain—archeozoological information on bird exploitation is limited to three sites. Tubes and by-products of tool making derived from the long bones of whooper swan (*Cygnus Cygnus*), griffon vulture (*Gyps fulvus*) and cinereous vulture (*Aegypius monachus*) were uncovered at the Grotte du Renne at Arcy-sur-Cure in France (Leroi-Gourhan and Leroi-Gourhan, 1964; d'Errico et al., 1998; Julien et al., 2017; Mourer-Chauviré, 2019). Disarticulation cutmarks on several talons of large diurnal and nocturnal raptors, respectively the white-tailed eagle (*Haliaeetus albicilla*) and the eagle owl (*Bubo bubo*), indicate that humans were interested in these specific elements (Julien et al., 2017; Mourer-Chauviré, 2019; Vanhaeren et al. 2019). The fact that remains from these taxa are few suggests that the dietary exploitation of birds was anecdotal at Arcy-sur-Cure. In Spain, a cutmarked phalanx from an Iberian imperial eagle (*Aquila adalberti*) was identified at Foradada Cave (Rodríguez-Hidalgo et al., 2019), a finding that mirrors the observation made at Arcy-sur-Cure. At La Ferrassie (France), a humerus attributed to the bearded vulture (*Gypaetus barbatus*) shows cutmarks indicative of defleshing (Mourer-Chauviré, 1984). With this notable exception, there is currently very little evidence for bird consumption during the Châtelperronian.

With respect to the Uluzzian—an Early Upper Paleolithic technocomplex documented in Italy and Eastern Europe—a small number of sites indicate that birds were also a minor component of the human diet in this region (Gala et al., 2018). At Fumane, a few bird bones attributed to the golden eagle (*Aquila chrysaetos*), alpine chough (*Pyrrhocorax graculus*) and black grouse (*Lyrurus tetrrix*) show anthropic marks suggesting that carcasses were disarticulated and defleshed (Tagliacozzo et al., 2013). Further south, at Castelcivita, human modifications have been observed on several bones from various bird species (Fiore et al., in press). This includes a crushing impact mark on a grey partridge (*Perdix perdix*) humerus resulting from the disarticulation of the wing (Fiore et al., 2015; Gala et al., 2018). Additional evidence for this site comes from a cutmarked humerus from a Eurasian hobby (*Falco subbuteo*) that may reflect feather removal (Fiore et al., 2018, in press).

2.3 Aurignacian

Like the Châtelperronian, archeozoological studies focused on birds are scarce for the Aurignacian. At the Grotte de l'Observatoire (Monaco), the Aurignacian/Gravettian material suggests that human foragers removed feathers from diurnal raptors including those from a cinereous vulture (Romandini, 2017). In contrast, several finds provide evidence for the use of bird bones as raw material during the Aurignacian. Among these are some exceptional discoveries of flutes made of bird long bones in Germany. Those from Geißenklösterle have been manufactured from a swan (*Cygnus* sp.) radius and from the bone of an indeterminate large-sized bird (Hahn and Münzel, 1995). In Hohle Fels Cave, a radius from a griffon vulture has been used as raw material in the EA (Conard et al., 2009). In France, Isturitz yielded a flute specimen made from an ulna of a large diurnal bird of prey (Passemar, 1944; Buisson, 1990). Additionally, a by-product of a tubular object made from a vulture radius was discovered at Gargas (Vercoutère, 2009).

Tubular objects decorated with notches are reported for several sites containing PA (Riparo Bombrini: Bertola et al., 2013) and EA (Gatzarria: Sáenz de Buruaga, 1991; Abri Cellier: White and Knecht, 1992; Tolmie, 2013; Les Rois: Ramirez-Rozzi et al., 2009; Isturitz: White, 2010; Les Cottés: Rigaud et al., 2014) occupations. However, because these objects have often been shaped and/or polished extensively, it is not always possible to identify the specimens to species or anatomical part, let alone as bird. In addition to these objects, a fragment of a vulture ulna from a level containing PA or EA material at Isturitz shows longitudinal cutmarks and small impacts consistent with its use as a tool (Normand et al., 2007). Three snowy owl (*Bubo scandiacus*) phalanges, including a talon with disarticulation cutmarks, have been identified in the EA from La Quina-Aval (Mallye et al., 2013). These remains are the only bird bones documented in the rich faunal assemblage from this site, which comprises at least three thousand reindeer specimens. Mourer-Chauviré (1984) identified a burned phalanx from a cinereous vulture and a cutmarked tibiotarsus from a golden eagle in an EA context at La Ferrassie. However, interpreting these modifications in terms of behavior remains difficult at this point. In France, with the possible exception of the La Ferrassie specimens, there is virtually no evidence for bird consumption during the Aurignacian. This observation contrasts with findings from other regions such as Geißenklösterle and Hohle Fels in Germany, Paglicci and Grotta del Fossellone in Italy, where ptarmigan (*Lagopus* sp.) (Conard et al., 2013), alpine chough (Tagliacozzo and Gala, 2004), grey partridge and snowy owl (Alhaique et al., 1998), respectively, have been exploited for food. However, even at these sites, birds seem to have been infrequent dietary items in comparison to ungulates. Despite this caveat, the available information clearly indicates that bird species were occasionally processed during the Aurignacian. Feather

residues on Aurignacian stone tools from Hohle Fels are compatible with this view (Hardy et al., 2008).

Figurative depictions provide further information on human-bird interactions during the Aurignacian. For instance, an engraved owl, possibly an eagle owl, has been identified far away from the entrance in Chauvet cave, France (Chauvet et al., 1995; Clottes dir., 2001). An alleged small depiction of a bird engraved on a flint flake has also been described at the open-air site of Cantalouette (Ortega et al., 2015). In Germany, the excavation of an Aurignacian level at Hohle Fels cave yielded a small ivory figurine representing a water bird (Conard, 2003). These separate instances emanate from three different classes of archeological places—respectively a “sanctuary” cave, a flint workshop and a habitation site—which suggests that depictions of birds were made in different contexts, possibly with varied meaning.

3. Methods and Materials

The bird remains analyzed in our study come from Isturitz, Le Piage and the Abri Cellier (fig. 1). All three sites are located in the Aquitaine Basin of Southwestern France and have recently been—or are currently being—excavated, which allows for improved stratigraphic control over earlier excavations. The sediment was systematically water-sieved at these sites, which enhances the recovery of small archaeological remains. The bird bones discussed below were all isolated during the archeozoological analysis of the faunal material. The remains were identified using the reference collections of the Université de Bordeaux (PACEA laboratory) and the Muséum national d’Histoire naturelle in Paris. Bone surfaces were inspected under a magnifying glass (30x for Abri Cellier) and a binocular microscope (magnification 10–30x for the other two sites) for marks and other taphonomic information (Laroulandie, 2000). Anthropogenic marks were interpreted in economic terms with the aid of experimental datasets (Laroulandie, 2000, 2001; Laroulandie et al., 2008; Pedergrana and Blasco, 2016; Romandini et al., 2014, 2016). The anatomical nomenclature follows Livezey and Zusi (2006).



FIG1. Location of the sites (Map from Eric Gaba – Wikimedia Commons user: Sting ; CC BY-SA 4.0).

Isturitz, the first of these sites, is a vast cave located in the Pyrenean foothills near the towns of Saint-Martin d'Arberoue and Isturitz (Pyrénées-Atlantiques). This site yielded a long archeological sequence ranging from the Mousterian to the Magdalenian. Isturitz has long been excavated, with significant work being conducted during the first half of the twentieth century by E. Passemard and R. and S. de Saint-Périer (see Normand and Cattelain, 2017 for an overview). The recent excavations by C. Normand have focused on the Aurignacian levels from the Salle Saint-Martin. The previously unpublished bird remains presented here come from the C4 d1 and C4 III levels, both attributed to the PA (Normand, 2017). At Isturitz, this technocomplex is radiocarbon-dated to between 43.3 and 40.1 kyrs cal BP (Barshay-Szmidt et al., 2018). Several thousand mammal specimens were collected in these levels and treated together as belonging to a single chronocultural phase. These remains are dominated by horse (*Equus caballus*, 59%, NISP count) and, to a lesser extent, *Bos/Bison* (16%). Carnivores are present as well, the most common species being the fox (9%) and bear (4%). Taphonomic analyses indicate that the fauna from these occupations is mostly anthropogenic (Soulier, 2013; Soulier et al., 2014). Our sample for Isturitz also includes preliminary observations made on a bird bone from level A excavated by Passemard in the same zone. According to Normand (2017), this level comprises mixed PA and EA material.

Le Piage (Fajoles, Lot) is located at the foot of a limestone cliff, a few kilometers away from the Dordogne River. Excavated between 1958 and 1968 by F. Champagne and R. Espitalié (Champagne and Espitalié, 1981), le Piage became well known as a result of purported interstratifications of Châtelperronian and Aurignacian occupations (Bordes, 2002). More recent work has shown that these interstratifications are simple analytical artifacts, and therefore, invalid interpretations of the sequence (Bordes et al., 2008). Excavations were renewed at the site in 2004 by J.-G. Bordes and F. Le Brun-Ricalens, with the work still ongoing. Four thousand faunal specimens were identified in the EA level from the site. Except for two large bird bones, all of them belong to mammals. Reindeer (*Rangifer tarandus*) is largely dominant in the sample (89%, NISP count). *Bos/Bison* and horse (*Equus caballus*) also occur at low frequencies. Like Isturitz, the evidence indicates that humans accumulated the majority of the faunal remains at le Piage (Morin et al., 2016).

The Abri Cellier (Tursac, Dordogne) is a large rockshelter located in the Vézère Valley. Peyrony, and later, Collie excavated the site in the first decades of the twentieth century. Their work resulted in the discovery of several decorated limestone blocks, all attributed to the Aurignacian. In 2014, fieldwork led by R. White permitted the (re)discovery of modified blocks and the re-identification of the stratigraphic profile corresponding to the earlier excavations. This stratigraphic profile was used in the new excavations to obtain unbiased faunal samples. At the base of the sequence is level US 104, which is attributed to the EA and radiocarbon-dated to 37.5 kyrs cal BP (White et al., 2018). This unit yielded a single bird bone and a small sample of ungulate remains, most of which were attributed to reindeer. The scarcity of carnivore damage and the high proportion of anthropogenic marks indicate that humans were the main accumulators of the faunal remains (Soulier, 2014).

4. Results

4.1 Isturitz

Among the several thousand mammal remains uncovered during the recent excavation of the PA level, eight bird bones from five different taxa were identified (tab. 1). Except for a cranium portion, all are wing bones. Among these remains, two have cutmarks. The first cutmarked bone is an almost complete calvarium from a golden eagle. Two groups of double, short and oblique cutmarks are visible on the occipital bone. One is located on the left part of

the occipital condyle, whereas the other is found immediately right of the left *foramen veni occipitalis externus* (fig. 2). Both groups of cutmarks have the same orientation, which suggests that they result from the same operation. The duplicate sets of cutmarks indicate that the motion was performed at least twice. On the basis of the location of the cutmarks, the aim of the operation was probably to sever the head from the body. The fact that the calvarium is the only remain attributed to the golden eagle in the PA is of interest. However, because the rest of the carcass may lie in an unexcavated part of the site—only a small fraction of Isturitz has been excavated—we can only speculate at this point about the potential symbolic implications of this specimen.

Taxa	NISP	Anatomical element
<i>Aquila chrysaetos</i>	1	cranium (cut)
Charadriidae	1	carpometacarpus
<i>Pyrrhocorax</i> sp.	3	humerus, ulna, carpometacarpus
<i>Corvus corax</i>	2	humerus (cut), ulna
Passeriformes (small-sized)	1	carpometacarpus

Table 1: Bird remains from the Protoaurignacian level at Isturitz (material from C. Normand's excavations), "cut" means that the bone is cutmarked.

The second cutmarked bone is a distal fragment from a right humerus attributed to a northern raven (*Corvus corax*). The specimen shows a disarticulation cutmark just below the *processus supracondylaris dorsalis* (fig. 3). The placement of the cutmark implies that the medium and distal parts of the wing were separated from the body (Laroulandie, 2001). It is unclear whether these parts were removed because they lack meat or in order to obtain raw material, for instance the long black feathers that are attached to them. The ulna that we attributed to the same species does not show marks supporting feather exploitation. Despite some ambiguity regarding the goal of the motion, the cutmark indicates clear human involvement in raven processing.

In addition to the flute mentioned above, the Passemard collection contains a vulture humerus with signs of human modification. The specimen shows a perforation of the *fossa olecrani* indicating disarticulation of the elbow through over-extension (fig. 3). This form of damage, which only occurs on green bone, implies that the wing was at least partly articulated and relatively fresh when processed (Laroulandie et al., 2008). In contrast, it remains to be determined whether the bones used for the manufacture of the flutes were collected in a fresh state or not.



FIG2. Golden eagle cranium from Isturitz (calvarium portion, Ist09- VI 28- C4 d1g'- 17, C. Normand's excavations, currently stored in PACEA's facilities), top: dorsal view; middle: caudal view showing the positions of the cutmarks; bottom: enlarged view of the two groups of cutmarks. Scales represent 1 cm or 5 mm with 1 mm division identified. Photo. and CAD: V. Laroulandie, CNRS.

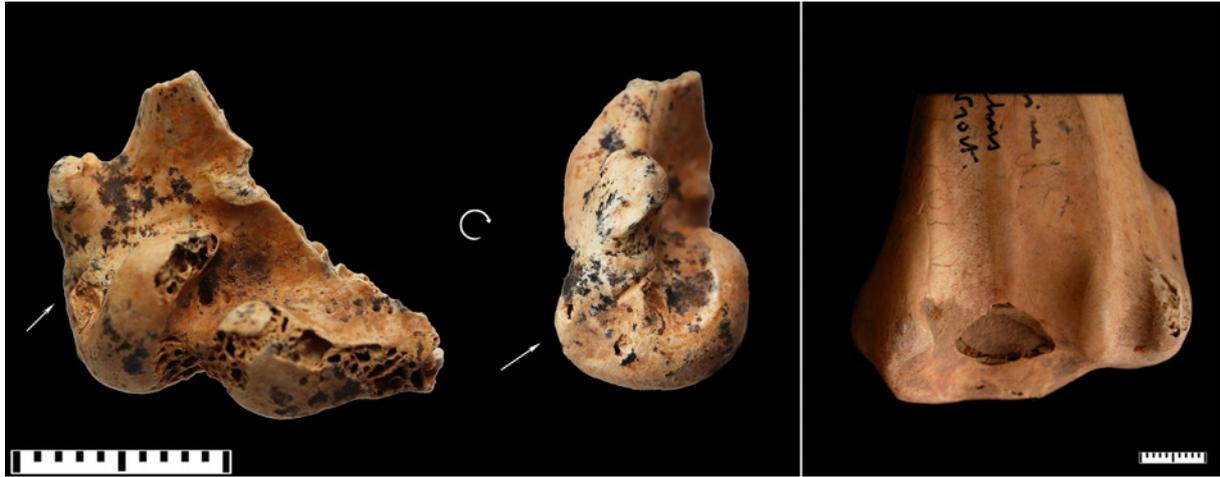


FIG3. Left: cutmarked northern raven humerus from Isturitz (Ist08- WI 29a- C4 d1g- T8; C. Normand's excavations, currently stored in PACEA's facilities), cranial and dorsal views. Right: vulture humerus from Isturitz showing squashing of the fossa olecrani resulting from the disarticulation of the wing (Passemard collection, MAN). Scales represent 1cm, with 1 mm division identified. Photo. and CAD: V. Laroulandie, CNRS.

4.2 Le Piage

The two large bird bones from the EA level at Le Piage are well preserved. However, the surface of both specimens is affected by the presence of metallic oxides (manganese), a post-depositional phenomenon frequently observed on the Le Piage specimens (Morin et al., 2016).

The first bird bone is a right digit I talon (*digitus I pedis, phalanx ungualis*). The talon has a flat plantar side and a globular and asymmetric *tuberculum flexorium* characteristic of the bearded vulture. The specimen is complete, with the exception of the extremity of the *caput phalangis* that is missing. Two groups of cutmarks were identified on the talon: one is located on the lateral side on the border of the *cotyla articularis*, whereas the other is visible from the plantar view between the margin of the articular surface and the *tuberculum* (fig. 4). Both groups of striae appear to result from the repeated contact of the cutting edge with the bone. The cutmarks differ in terms of direction, which implies a rotation of the motion while the ligaments and tendons were being sliced. Experiments have shown that these cuts occur when the talon is disarticulated from the feet, presumably for non-alimentary purposes, as this body part lacks meat (Laroulandie, 2000; Romandini et al., 2014). The fact that this specimen is the only anatomical part from the leg identified for this species may suggest differential treatment of raptor elements.

The second bird bone from le Piage is a mesial fragment from a left ulna (fig. 4). Its size, cross-section and the position of the *papillae remigales* allow its attribution to the bearded vulture. This remain shows oblique and longitudinal cutmarks, including some that are located near the papillae. According to experimental studies (Pederagnana and Blasco, 2016; Romandini et al., 2016), these cutmarks are compatible with the extraction of feathers from the wing, especially the second remiges that are tightly attached to the *papillae remigales*. In addition, this operation aids in cleaning the bone for eventual use as raw material. The fact that this part of the wing contains little meat suggests that the slicing motion was unrelated to food procurement.



FIG4. Cutmarked bearded vulture bones from le Piage (J.-G. Bordes and F. Le Brun-Ricalens' excavations, currently stored in PACEA's facilities). Top: right first talon (PG12-15D b8-1903); lateral, plantar and medial views; "a" and "b" show the location and an enlarged view of the cutmarks. Bottom: left ulna (PG08-15C b4-492); "c" and "d" show the location and an enlarged view of the cutmarks. Scales represent 1 cm or 5 mm with 1 mm division identified. Photo. and CAD: V. Laroulandie, CNRS.

4.3 Abri Cellier

A single bird bone has been uncovered during the recent excavations at the Abri Cellier. It is a mesial fragment of an ulna, likely from an immature bird, as suggested by the porous nature of the cortical bone. The large size and general morphology of the ulna is consistent with a large vulture. However, the lack of articular ends precludes a more precise taxonomic attribution. Several oblique cutmarks are visible on this specimen (fig. 5). The positions of the cutmarks are consistent with feather extraction, and possibly, defleshing, as argued for Isturitz. If the goal was to obtain feathers, the fact that the bone is from a young individual raises questions concerning the method of procurement and the type of feathers that were being sought. Was the bird caught while still a nestling or was it captured after it had left the nest? Comparisons with more complete reference collections—especially collections that cover a wide range of developmental stages—may help addressing this question in the future.



FIG5. Cutmarked vulture ulna from the Abri Cellier (CL14 -US 104- Y24- 1) (R. White's excavations), scale represents 1cm, with 1 mm division identified. Photo: M.-C. Soulier, CAD: V. Laroulandie, CNRS.

5. Discussion

Despite their small number, the bird remains presented in this study are useful as they shed new light on previously undocumented human-bird interactions during the Early Upper Paleolithic, a period for which very little information was previously available. In the PA from Isturitz, this new evidence takes the form of a processed northern raven wing and the beheading of a golden eagle. At the same site, a vulture wing was also handled while still fresh or relatively fresh, although it is not possible to assign the specimen to a specific phase of the Aurignacian. At le Piage, the data for the EA indicate the removal of a bearded vulture talon and the exploitation of an ulna for feathers and/or use as raw material. The same technocomplex at the Abri Cellier yielded an immature vulture bone indicative of processing, possibly for the same reasons.

Obviously, additional remains will be needed to ascertain whether these behaviors were isolated phenomena or habitual practices and how they varied over space and time. Regardless, there are reasons to be optimistic on these points. Despite the fact that bird remains are scarce in most Early Upper Paleolithic collections, the fact that many other assemblages remain to be studied from an archeozoological perspective means that there is still much room for new findings and for better understanding the motivations underlying the exploitation of birds during this period.

A few general observations can be drawn on the basis of the information examined here. First, in Southwestern France, there is virtually no evidence for the consumption of birds during the Early Upper Paleolithic. However, data from other regions suggest some variation on this theme. For instance, birds were probably consumed in Germany and Italy (see above), although they likely constituted a marginal part of the diet relative to ungulates. From a broader perspective, our data show no clear differences in the use of birds as food between Middle Paleolithic and Early Upper Paleolithic technocomplexes. All across Europe, birds appear to have been relatively minor dietary items, this input varying depending on the site and region. In addition, it remains unclear at this point how birds were consumed and whether this behavior varied regionally.

It is interesting to note that, in our sample, all the bird species that show marks of human involvement are scavengers, although the relevant taxa differ in the extent of this behavior. According to Finlayson and Finlayson (2016), vultures are “obligate scavengers”, whereas the northern raven and golden eagle are “opportunistic” and “seasonal” scavengers, respectively. From this viewpoint, the similarity between the Middle Paleolithic (e.g., Finlayson et al., 2012; Finlayson and Finlayson, 2016) and the Early Upper Paleolithic (Mourer-Chauviré, 1984, 2019; Tagliacozzo et al., 2013; Rodríguez-Hidalgo et al., 2019) is striking. The predatory and scavenging behavior of these birds—which overlaps in terms of habitats with humans—may, in part, explain why they were targeted by Middle and Early Upper Paleolithic foragers (e.g., Finlayson and Finlayson, 2016).

Along with raptors and scavengers, there is evidence that Paleolithic foragers were interested in other bird species, including small corvids, Phasianidae and Anseriformes (see above). The available data for these species reveal no significant differences between Middle and Early Upper Paleolithic technocomplexes, particularly when local variation in species availability is taken into account. Pigeons may represent an exception to this trend, as they were hunted during the Mousterian, a practice that is not currently reported for the beginning of the Upper Paleolithic.

The use of raptor talons and feathers from large diurnal birds is interesting because it is documented all across the Pleistocene, including the Early Upper Paleolithic. However, because examples of talon and feather exploitation remain few for this period and because our understanding of their symbolic implications is currently too limited, no strong case for “cultural continuity” can be made at present between these periods. Further studies will be needed to confirm whether eagles talons were used during the Early Upper Paleolithic in manners reminiscent of the Mousterian. In the meantime it is important to emphasize that humans have used diurnal raptor claws very early in prehistory, at least as early as 130,000 years ago at Krapina (Radovčić et al., 2015), through the present day. It is tempting to infer that humans perceive these objects as a medium for acquiring the behavioral characteristics—majesty, highness, swiftness—of the raptors that shared the space with them (e.g., Morin and Laroulandie, 2012; Finlayson et al., 2019). The use of bird bones as raw material, sometimes with repetitive motifs, is documented in the Middle (Fiore et al., 2016; Majkić et al., 2017) and Upper Paleolithic (see above), although the evidence is considerably richer for the latter period. In these comparisons, we note that the practice of sawing bird long bones to produce tubes seems specific to the Aurignacian and Châtelperronian.

Perhaps the most significant change from the viewpoint of ornitho-archeozoology is the emergence of rare figurative depictions of birds during the Aurignacian. These depictions form a small part of a more general pattern of animal depiction during this time period that might have materialized profound changes in the way people perceived the world, including animals. Given recent claims for abstract Middle Paleolithic art (Rodríguez-Vidal et al., 2014; Hoffmann et al., 2018), it remains to be seen whether these forms of expression also occasionally included animals such as birds.

6. Conclusion

The application of ornitho-archeozoological approaches to Paleolithic contexts has the potential of illuminating long term trends in human-bird interactions. In the present paper, we provided an overview of our current knowledge of human exploitation of birds during the European Middle and Early Upper Paleolithic and presented new data for three Aurignacian avifaunal samples from Southwestern France. At a broad scale, comparisons between techno-complexes reveal only minor differences in patterns of bird exploitation over time. Scavenging birds were exploited for feathers and talons during both the Middle and Early Upper Paleolithic. When local availability is accounted for, only small differences are seen in the use of birds as food during these periods, a practice that appear to have remained marginal in the study region.

There is little doubt that forthcoming archeozoological analyses will improve our understanding of patterns of bird exploitation during the Paleolithic, perhaps by emphasizing unsuspected variability, as recently experienced with Middle Paleolithic avifaunas. We hope that future studies will continue to pay due attention to bird taphonomy and site formation processes. Further developments in methodological research and additional experiments should also contribute in refining our knowledge of past human-bird interactions.

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