Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy

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A large and varied avifaunal bone assemblage from the final Mousterian levels of Grotta di Fumane, northern Italy, reveals unusual human modifications on species that are not clearly relatable to feeding or utilitarian uses (i.e., lammergeier, Eurasian black vulture, golden eagle, red-footed falcon, common wood pigeon, and Alpine chough). Cut, peeling, and scrape marks, as well as diagnostic fractures and a breakthrough, are observed exclusively on wings, indicating the intentional removal of large feathers by Neandertals. The species involved, the anatomical elements affected, and the unusual type and location of the human modifications indicate an activity linked to the symbolic sphere and the behavioral modernity of this European autochthonous population.

cut marks | raptors | symbolism | Middle Paleolithic

Archaeological evidence suggests that nonutilitarian human behaviors represented by coloring substances and ornamental objects made of animal bone and teeth, marine shells, and ostrich eggshells are associated with the Middle Stone Age and the Middle Paleolithic in Africa (1–4) and the Near East (5) and have been potentially ascribed to anatomically modern humans (6). In Europe, similar evidence regarding the symbolic use of teeth, marine shells, and pigments 50 ky B.P. (7–10) would seem to imply the independent emergence of behavioral modernity in autochthonous Neandertal populations, thus challenging the cognitive difference between Neandertals and anatomically modern populations as postulated in the human revolution model (11, 12). Anatomical elements extracted from hunted or scavenged animals are possible indicators of symbolic behavior when they preserve traces of unusual human intervention on their surfaces that cannot be linked to food or utilitarian purposes.

Avifaunal remains constitute a particular category of these materials, as they document a number of different utilizations according to the kind of element exploited. In Turkey, a terminal pedal phalanx of a very large raptor with a notch cut into its anterior proximal end has been found in layer B at Üçağizli Cave dated to ∼29 ky[14]C B.P., approximately the end of the early Ahmarian (13). In Europe, the use of long bones of large-sized birds (vultures, eagles, swans) to make ornamental objects or flutes appears ephemerally in the Castelperronian (7) and is well known in the archaeological record from the Aurignacian onward (14, 15). The exploitation of birds as a food resource during the Upper Paleolithic is also documented by taphonomic analyses and has been interpreted as a marker of the breadth of the human diet to support the notion that population pressure played a significant role in the evolution of Late Pleistocene human cultures (16, 17). The earliest evidence of this practice is often said to have been found in the Aurignacian of Grotta del Fossellone (18) and in the Aurignacian and Early Gravettian of Grotta Paglicci (19) in Italy, as well as in the Gravettian of Pavlov I in the Czech Republic (20). This revolution has been challenged by the discovery of a food exploitation of birds in the Middle Pleistocene at Bolomor Cave (21). A particular aspect of the use of bird bones or other elements by Neandertals has been inferred in France at Pech de l'Azé I (22, 23) and at Baume de Gigny (24), where some posterior phalanges of golden eagle (*Aquila chrysaetos*) and swan (*Cygnus cygnus*) bear striae produced by lithic

tools. A very similar find—an ungual phalanx of golden eagle with disarticulation striae, suggesting the removal of the claw (25)—was recovered in the Mousterian levels of Grotta di Fumane together with Levallois industries, sure evidence of Neandertal activity (26, 27). Specimens such as these, interpreted as ornaments, have an important symbolic value but require further confirmation based on extensive taphonomic analyses of larger assemblages. In response to this question, we submitted the avifaunal collection of some final Mousterian levels of Grotta di Fumane to a taphonomic analysis that resulted in the identification of striae produced by lithic tools on wing elements of raptors, chough, and pigeons. These findings support the hypothesis that the Neandertals had a particular interest in the feathers of these animals.

Results

Site. Grotta di Fumane is located on the southern edge of the Veneto Prealps in northern Italy and provided a dated sequence spanning from marine isotope stage (MIS) 5 to 2 (28–30) (*SI Text* and Fig. S1). Excavations have been carried out since 1988 in the cave entrance, where Mousterian, Uluzzian, and Aurignacian living floors have been identified within finely separated levels, yielding evidence of in situ human occupation with numerous lithic implements, faunal remains, hearths, and other structures (31–33).

Ornamental objects and painted stones have been found exclusively in Aurignacian levels (33). During the MIS 3, humans occupied the cave in different climatic and environmental conditions, ranging from moist temperate at the base of the final Mousterian sequence (units A11 and A10), with alternating cooling in the final Mousterian and Uluzzian levels (units A9–A3) and a shift to cooler and drier conditions in the Aurignacian sequence (units A2–D3) (25). In the final Mousterian levels the most abundant faunal remains are red deer (*Cervus elaphus*), ibex (*Capra ibex*), and roe deer (*Capreolus capreolus*), whereas chamois (*Rupicapra rupicapra*), bison (*Bison priscus*), and giant deer (*Megaloceros giganteus*) are less frequent. Moose (*Alces alces*), horse (*Equus ferus*), and wild boar (*Sus scrofa*) are very rare. All ungulate species, with the exception of horse and wild boar, bear traces of human exploitation (34). In these same phases the cave was also used by carnivores, as evidenced by the presence of gnaw marks on ungulate bones and of numerous digested fragments. Wolf (*Canis lupus*), hyena (*Crocuta crocuta*), and fox (*Vulpes vulpes*) are common; both brown bear (*Ursus arctos*) and cave bear (*U. spelaeus*) are also present. Human traces, attributable exclusively to skinning, are present on both species of bear, as well as on fox and wolf.

A5–A6 and A9 Stratigraphic Complex. The stratigraphic complex of levels A5 and A6, dated to 44.8–42.2 ky calibrated B.P. (30),

evidences accumulations of faunal remains and lithic artifacts referable to an occupation of the site shifting from intense and persistent (A6) to more ephemeral (A5). These two levels, excavated over the whole entrance area, provided evidence of a well-structured use of the living spaces (*SI Text*). Areas with combustion structures, close to dumps of combustion debris, are adjacent to areas used for Levallois flake manufacture; tool shaping and curation; butchering of ungulates; and treatment of hides and pelts. Below the sterile layer A7, level A9 has not yet provided secure radiocarbon dates. As with layers A5–A6, it records repeated site occupations over the whole entrance area, with combustion structures and zones used for flake manufacture and butchering mostly red deer and giant deer. Lithic industry in level A9 records an abrupt replacement by the discoid method.

Avifaunal Association. An analysis of the avifaunal assemblage from the final Mousterian levels A6–A5 resulted in the identification of 660 bones, belonging to 22 species of birds living in different biotopes (Table S1). Small- and medium-sized birds from open and rocky habitats (Alpine chough, *Pyrrhocorax graculus*, and corn crake, *Crex crex*) and from alpine forest habitat (black grouse, *Tetrao tetrix*) are prevalent. A large amount of specimens are Passeriformes, mainly Corvids and thrushes. Important ecological indicators, such as the water rail (*Rallus aquaticus*), the common moorhen (*Gallinula chloropus*), and the pied avocet (*Recurvirostra avosetta*), suggest the existence of humid zones close to the cave. The Galliformes are represented by the black grouse, together with the common quail (*Coturnix coturnix*), rock ptarmigan (*Lagopus muta*), and willow ptarmigan (*Lagopus* cf. *lagopus*), whereas the Columbiformes are represented only by the common wood pigeon (*Columba palumbus*).

The presence of several birds of prey should also be mentioned. The nocturnal raptors present are the long-eared owl (*Asio otus*) and the tengmalm's owl (*Aegolius funereus*). The diurnal raptors are represented by three hawks, the most common being the Eurasian kestrel (*Falco tinnunculus*), followed by the red-footed falcon (*F. vespertinus*) and the common hobby (*F. subbuteo*). Of the large accipitriformes, there are only two specimens: one of Eurasian black vulture (*Aegypius monachus*) and one of lammergeier (*Gypaetus barbatus*).

Results of the Taphonomic Analyses. The taphonomic study of bird bones from the A5–A6 stratigraphic complex revealed a clear human interest in lammergeier, red-footed falcon, common wood pigeon, and Alpine chough, although the capture and consumption of other species cannot be excluded (Table 1). Nevertheless, several bones bear modifications made by raptors or small carnivores, as indicated by the presence of scores, pits, punctures, or traces of the action of digestive juices. A microscopic analysis of the surfaces led to the recognition of traces of human intervention on five wing elements, which, given their importance, will be described in detail below.

A distal portion of a right ulna of lammergeier (*Gypaetus barbatus*; Fig. 1) has two long striae on the medioventral face, oblique to the main axis of the element, that pass through the distal epiphysis in correspondence to the depressio radialis (Fig. 1*B*). Other shorter striae, related and parallel to the previous ones, were observed: two are close to the tuberculum carpale and are interrupted by the natural depression of the incisura of the same tuberculum, and the other marginally invades the medial surface of the sulcus intercondylaris. On the lateral portion of the ventral face, at the top of the condylus dorsalis ulnae, there are three short and deep transversal marks (Fig. 1*C*). All of the traces are latero/medially oriented, reflecting the cut of the extensor carpi and flexor carpi ulnaris muscles for the ulna-carpometacarpus disarticulation.

Traces of a lithic tool are also present on a smaller raptor, the red-footed falcon (*Falco vespertinus*). A long and deep stria is located on the condylus dorsalis humeri of the distal epiphysis of a left humerus (Fig. 2 *A* and *B*). This cut, situated on the inner side of the articulation surface, must have been made by stretching and opening the humerus-ulna articulation to separate the two bones.
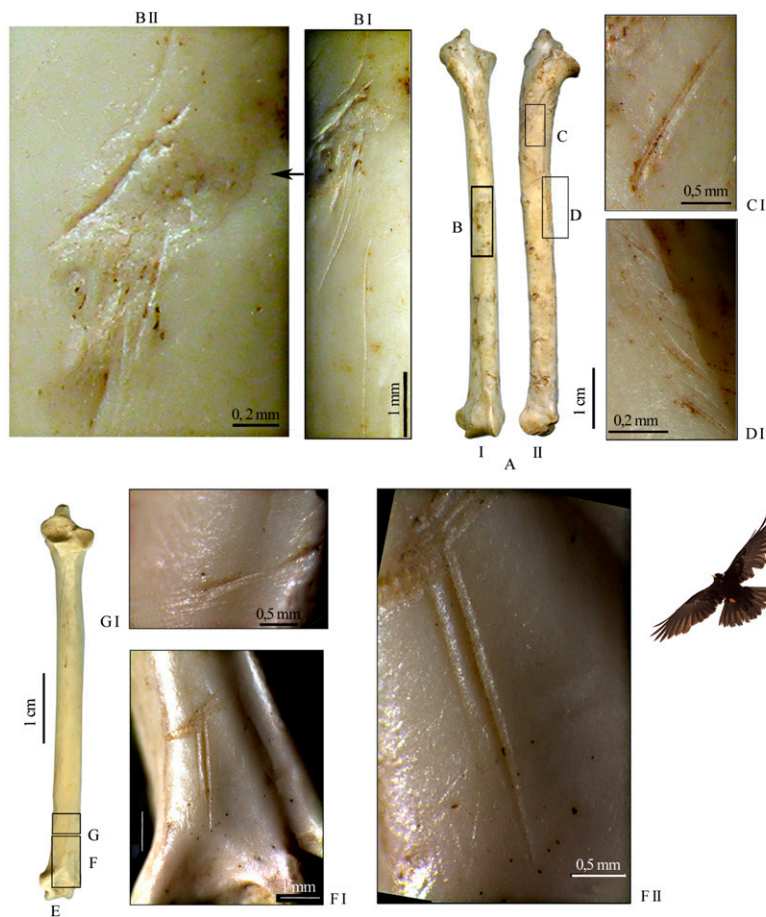
A series of oblique cuts was detected on the medial edge of the mediodistal diaphysis of an os metacarpale majus of a right carpometacarpus of common wood pigeon (*Columba palumbus*; Fig. 2 *C* and *D*). Some of these cuts—short, repeated, and at different depths—are located only on the medial edge, whereas two other marks, longer and subparallel, also affect the ventral surface. On the whole, the striae can be referred to the cutting of the insertions of the extensor carpi and interosseus ventralis muscles and, as regards their localization, they can be related to the cutting and removal of the skin for collecting the remiges.

On a complete right ulna of Alpine chough (*Pyrrocorax graculus*), there are various types of striae (Fig. 3 *A–D*). Two of these striae—short, isolated, and relatively deep—are located on the dorsal face of the olecranon on the proximal epiphysis, whereas the other is on the condylus dorsalis ulnae of the distal epiphysis. All of them can be referred to disarticulation. This activity is borne out by the presence of parallel grooves (peeling) on the ventral face of the olecranon.

On the medial face, at middiaphysis, there is a group of different types of striae. Some of these striae, located around one of the papillae remigiales ventrales, are short, oblique, curved, and referred to the same point, and are considered to be scrape marks (Fig. 3*B*). These are the origin of three other striae that are straight, long, and fine, longitudinal to the bone axis; one of them points toward the distal epiphysis, the other two to the proximal. A single short, oblique, and relatively deep stria is located close to the proximal papillae remigiales caudales dorsales (Fig. 3*C*). Further scraping traces are present in the same area on the lateral edge of the diaphysis (Fig. 3*D*). On the whole, the morphology of the striae indicates that the lithic tool was used both to cut the skin covering the ulna and for the removal of the remiges.

Table 1. Modifications identified on the analyzed bird remains from the Mousterian levels A6–A5 of Fumane Cave

Species	CTM	CTM?	PEE	ARR	BRK	FBFR	P/U	ST	DG	GW	TMOD	TNISPM
Gypaetus barbatus	1							1			2	1
*Aegypius monachus**	1					1			1	1	4	2
Falco tinnunculus									1		1	1
Falco vespertinus	1							1	1		3	2
Lagopus cf. *lagopus*		1									1	1
Tetrao tetrix						3			1	2	6	6
cf. *Tetrao tetrix*									4	1	5	5
Crex crex					1	4			2	4	11	9
cf. *Vanellus vanellus*						1					1	1
Scolopax rusticola						2					2	2
Columba palumbus	1							1			2	1
Oriolus oriolus						1					1	1
Pyrrhocorax graculus	2	1	4	1		8		4		9	29	27
cf. *Pyrrhocorax graculus*							1	2	2	1	6	6
Corvidae									1	1	2	2
Passeriformes									1		1	1
Unidentified bird			1			6			3	2	12	12
Total	6	2	5	1	1	26	1	9	17	21	89	80

CTM, cut mark; CTM?, uncertain cut mark; PEE, peeling; ARR, *arrachement*; BRK, breakthrough; FBFR, fresh bone fracture; P/U, polish/use; ST, striae; DG, digested; GW, gnawed; TMOD, total modifications; TNISPM, total no. of identified specimens modified.
*Specimen from level A9.

Fig. 1. Cut marks on the distal end of a right ulna of lammergeier (*Gypaetus barbatus*). (*A*) Different views of the ulna: (*A*, I) ventral view; (*A*, II) medioventral view; (*A*, III) dorsal view; (*A*, IV) laterodorsal view. (*B* and *C*) Localization of the cut marks; (*B*, I and *C*, I) details.

Other striae were identified on another complete left ulna of Alpine chough (Fig. 3 *E–G*). Two were identified on the medial face of the distal extremity and are subparallel and longitudinal to the bone axis (Fig. 3*F*). One of the striae is deep and long, and the other is shorter and more superficial. These striae are interrupted by transversally oriented root marks. On the dorsal edge of the same face there is a series of at least three transversal marks, two limited to the edge, and another continuing on the diaphysis with a short interruption due to the concavity of the bone (Fig. 3*G*). These striae can be related to the cutting of the flexor carpi ulnaris muscle. Finally, a short stria is present on the tuberculum carpale. On the whole, these traces may be interpreted as the result of the disarticulation of the ulna from the carpometacarpus.

Also to be noted is the recovery of another wing element of particular interest from the Mousterian level A9. This is a distal portion of the left carpometacarpus of a Eurasian black vulture (*Aegypius monachus*; Fig. 4*A*) where there is a clearly identifiable

Fig. 2. Cut marks on the left distal humerus of red-footed falcon (*Falco vespertinus*) and on the right distal carpometacarpus of common wood pigeon (*Columba palumbus*). (*A*) Cranial view of the *Falco vespertinus* humerus. (*B*) Localization of the cut marks; (*B*, I and *B*, II) details. (*C*) Ventral view of the *Columba palumbus* carpometacarpus. (*D* and *E*) Localization of the cut marks; (*D*, I and *E*, I) details.

Fig. 3. Cut marks on two ulnae of Alpine chough (*Pyrrocorax graculus*). (*A*) Different views of the right ulna; (*A*, I) medioventral view; (*A*, II) dorsolateral view. (*B* and *D*) Localization of the cut marks; (*B*, I; *B*, II; *C*, I; and *D*, I) details. (*E*) Lateral view of the left ulna. (*F* and *G*) Localization of the cut marks; (*F*, I; *F*, II; and *G*, I) details.

series of eight short striae on the ventral face, oblique to the main axis of the anatomical element, located on the neck of the epiphysis close to the synostosis metacarpalis distalis (Fig. 4*B*). Two other striae, less marked and deep, but related to the previous ones, are visible on the distal epiphysis on the facies articularis digiti minoris. All of these have a latero/medial orientation. Finally, on the dorsal face, longitudinal to the main axis of the bone and close to the sulcus interosseus, there is a proximal/distally oriented cut mark. On the whole, these striae reflect an action of disarticulation of the carpometacarpus from the phalanges involving the separation of the interosseus ventralis, interosseus dorsalis, and flexor digiti minoris muscles. The fracture edge of the dorsal face shows signs of polishing associated with microstriae and small marks (*SI Text*).

Over 20 wing bones display features characteristic of fresh fracturing, and four remains bear traces typical of peeling (mainly on Alpine chough) (35, 36) and, in a single case, a breakthrough, i.e., a perforation resulting from the pressure of the olecranon of the ulna on the humerus during manual disarticulation (37). These modifications may provide a broader and better definition of human actions on bird carcasses (*SI Text* and Figs. S2–S6). Other typologies of pre- and postdepositional modifications can be related mainly to root etching, trampling, corrosion, and small carnivore gnawing (38) (Figs. S4 *D and E* and S7). On very few of the other bones, traces have been observed that are morphologically comparable with those made by a lithic implement, but uncertainties have arisen because of their small size (Figs. S2 *B and B1* and S3 *A and B1* and Table 1).

Discussion

This taphomomic study of the avifaunal assemblage from Mousterian levels of Fumane provides evidence that humans focused only on some of the species. There is no doubt that the human modifications (striae, peeling, and breakthrough) indicate an unusual significance, as they are present on rare species with no particular food utility. These are mainly birds living in open areas close to rock cliffs and caves (lammergeier, Eurasian black vulture, and Alpine chough) as well as in clearings on the edges of woods and forests (red-footed falcon and common wood pigeon). It cannot be excluded that the presence of some individuals of Alpine chough may have been due to natural causes, whereas other elements must surely have been introduced by humans, who collected them from wounded or dead animals or intentionally captured individuals.

As well as an interest in leg phalanges (25), already evident from other sites (22–24), the Neandertals from Fumane show a particular interest in wings. Their goal could have been the appropriation of the whole wing, or just the remiges—as indicated by the ulna of Alpine chough (Fig. 3*B*)—or just the bone, as the signs of polishing on the left carpometacarpus of the Eurasian black vulture from level A9 (Fig. S6) would seem to indicate. However, the use of long bones from large birds for making tools, flutes, and other products has been documented in Europe only in more recent periods (7, 12, 13, 20). The interest in wings seems to be linked neither to the size of the bird nor to a specific plumage color, in that there are several different colors, including the gray of the red-footed falcon, the blue-gray of the common wood pigeon, the orange-shaded slate gray of the lammergeyer, and the uniform black of the Alpine chough. In fact, the few remains of lammergeier and red-footed falcon (besides the common wood pigeon) are represented by front limb bones, and even in the more abundant Alpine chough, there is an overrepresentation of humeri and ulnae. This interest in wings is confirmed not only by the high percentage of bones from this portion (about 43%) in the
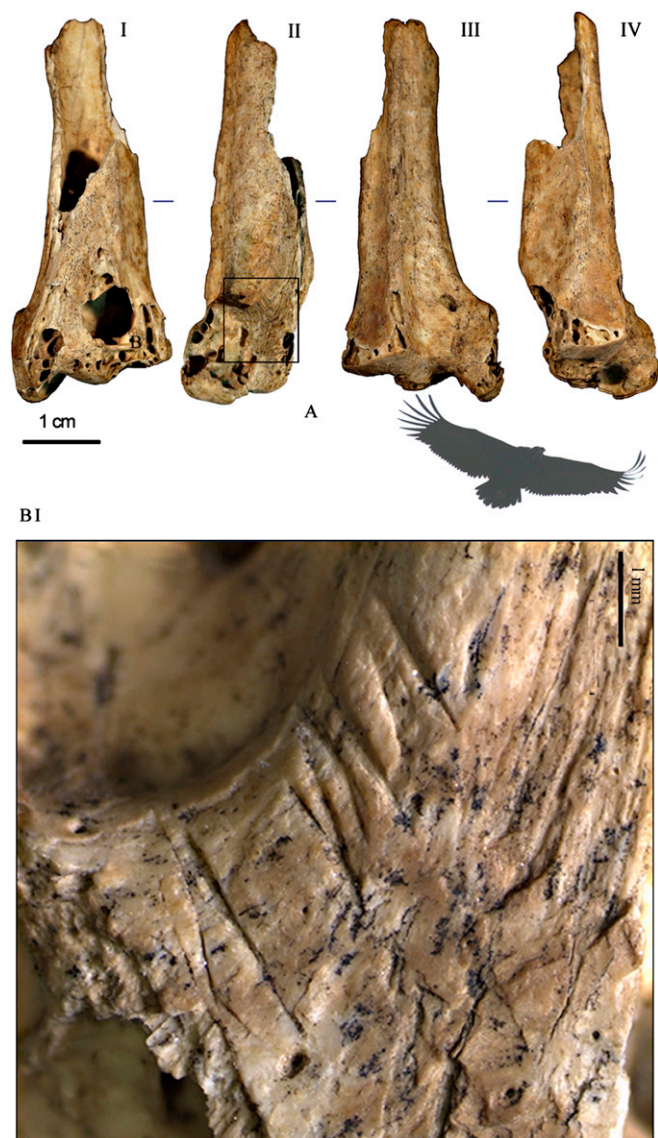
Fig. 4. Cut marks on the distal end of the left carpometacarpus of Eurasian black vulture (*Aegypius monachus*) from the Mousterian level A9. (*A*) Different views of the carpometacarpus: (*A*, I) ventral view; (*A*, II) medioventral view; (*A*, III) dorsal view; (*A*, IV) lateral view. (*B*) Localization of the cut marks; (*B*, I) detail.

osteological sample as a whole, but also by the fact that there is a high percentage of anthropic modifications (about 7%) only on these skeletal portions (*SI Text*).

Striae produced by lithic artifacts are mainly related to the action of disarticulation—of the humerus from the ulna in the case of the red-footed falcon; of the ulna from the carpometacarpus in the case of the lammergeier and the Alpine chough; and of the carpometacarpus from the phalanges in the case of the Eurasian black vulture. In the wood pigeon and Alpine chough, there is also the suggestion of the cutting and removal of the skin for the collection of the remiges. Usually, striae located on the proximal humerus, the coracoid, and the scapula in the meat-rich pectoral portion, together with those on the pelvis and femur in the thigh portion, indicate a use of the birds for food. Furthermore, it should be taken into account that the overrepresentation of wing elements in archaeological sites has also been interpreted as a consequence of capture, butchery, and food use by humans, as well as of postdepositional natural causes and of differential preservation of the bones (39).

Despite the presence of species at Fumane that were clearly of interest as food (*Lagopus, Coturnix, Rallus,* etc.), some of these being particularly numerous (*Crex* and *Tetrao*), there is only sporadic evidence of them actually being eaten, such as the *arrachement* on the ulna of *Tetrao* and the striae, albeit doubtful, on the carpometacarpus of *Lagopus*. There is also evidence of their exploitation by other predators (carnivores or birds of prey), as indicated by the traces of digestion and bites on numerous bones (Table 1). Though the traces that are definitely anthropic, referable to disarticulation, skinning, and plucking, could be related to processing for consumption as food, especially those on the carpometacarpus of pigeon, it should be underlined that they are present above all on bones from portions of the anatomy with a low meat content and from birds considered as nonedible, such as birds of prey and chough. Thus, the species involved, the anatomical elements affected, and the uniqueness of the human modifications indicate a specific Neandertal interest in the wings, and especially the feathers, of some particular birds.

This fact suggests various hypotheses on the use of the anatomical portions of birds analyzed in the study. The use of at least the longer remiges of Eurasian black vulture, lammergeier, and red-footed falcon as stabilizing elements for hunting spears, even after their reduction and preparation for fletching, does not seem possible. As well as there being uncertainties in the interpretation of the ballistic evidence on lithic tips used as armaments on the thrusting or throwing spears of Neandertals in Europe (40), the utilitarian hypothesis regarding the use of feathers for the stabilization of throwing spears does not concur with the ballistic criteria, as this stabilization is not necessary (41). A further possible use of stiff, strong feathers, including those extracted from smaller birds like Alpine chough and common wood pigeon, could have been in fletching spears launched with the aid of a spear thrower and arrows fired from a bow, as could be inferred on the basis of the earliest evidence on the invention and use of the atlatl, which, however, dates to not earlier than the Upper Solutrean, and of the bow, whose earliest remains date to the end of the Upper Paleolithic (42). Moreover, the support for the fletching hypothesis is no more than that given by ethnographic comparisons, which also attest to the use of feathers, or parts of them (e.g., the rachis), as tools or colorant containers (43).

The possibilities for the use of these anatomical elements in the social and symbolic sphere, however, are extremely abundant. Limiting the field to the recent and better-documented ethnographic contexts, it can be inferred that the use of bird feathers was very widespread and that humans have always attributed a broad and complex value to this practice, ranging from social significance and games to the production of ornamental and ceremonial objects. These objects consisted of single feathers, wings, or compositions of feathers or rachises applied on or in the body (head, ears, or nose), and also inserted in supporting material by means of elaborate feathering techniques to give form to headdresses, skirts, and hunting or war masks, or to adorn parade spears, calumets, and dancing drums (43–48).

Conclusions

The debate over the cognitive and behavioral capabilities of Neandertals, especially in the period around the first appearance of anatomically modern humans in Europe, is extensive and often based on archaeological records from a handful of pivotal sites. One of these, the Grotte du Renne site at Arcy-sur-Cure, France, provides a range of ornaments and tools usually associated with modern human industries from Châtelperronian levels, along with Neandertal teeth. Another is St. Césaire, where the relation of the Châtelperronian with Neandertals was reinforced by the discovery of a burial.

Nevertheless, a new radiocarbon dataset (49) and a reinvestigation of the available data (50) from the first and the second sites, respectively, have challenged the association between human remains and cultural assemblages. These studies, however, provide no direct evidence to invalidate the association and can, at most, be taken as implying that a minority of the symbolic

objects from the Grotte du Renne's Châtelperronian may be intrusive. The Fumane evidence on the ornamental exploitation of the feathers of large raptors and other birds strengthens the contention that the Grotte du Renne's associations are genuine and adds to the growing body of data that demonstrates the appearance of modern behavior in extinct autochthonous populations of Europe well before the immigration of modern humans (9). Moreover, the absence of evidence of this kind in the earliest Aurignacian levels at Grotta di Fumane (51) proves that, even before the Uluzzian, Neandertals achieved this level of behavioral complexity independently, and that it was not culturally transmitted or mimicked via incoming modern humans. Last, at least in southern Europe, the backdating of the acquisition of valuable elements of bird plumage opens the door to further perspectives in the exploration of the interactions that led to our extinct relatives manifesting an interest in a form of symbolic behavior.

Materials and Methods

The taxonomic determination has been based on comparison with the zoological collection of the Quaternary Paleontology and Archaeozoology Section of the Pigorini National Ethnographic Museum and Italian Institute of Human Paleontology of Rome. Microscopic analyses of the bone surfaces were carried out using Nikon 1000 stereomicroscope with 20-220 magnification range. Descriptive terms of the anatomical elements are in agreement with Livezey and Zusi (52).

1. Henshilwood C, d'Errico F, Vanhaeren M, van Niekerk K, Jacobs Z (2004) Middle Stone Age shell beads from South Africa. *Science* 304:404.
2. d'Errico F, et al. (2009) Out of Africa: Modern human origins special feature: Additional evidence on the use of personal ornaments in the Middle Paleolithic of North Africa. *Proc Natl Acad Sci USA* 106:16051–16056.
3. Texier PJ, et al. (2010) From the Cover: A Howiesons Poort tradition of engraving ostrich eggshell containers dated to 60,000 years ago at Diepkloof Rock Shelter, South Africa. *Proc Natl Acad Sci USA* 107:6180–6185.
4. Marean CW, et al. (2007) Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* 449:905–908.
5. Bar-Yosef Mayer DE, Vandermeersch B, Bar-Yosef O (2009) Shells and ochre in Middle Paleolithic Qafzeh Cave, Israel: Indications for modern behavior. *J Hum Evol* 56:307–314.
6. Mcbrearty S, Brooks AS (2000) The revolution that wasn't: A new interpretation of the origin of modern human behavior. *J Hum Evol* 39:453–563.
7. D'Errico F, Zilhão J, Baffier D, Julien M, Pelegrin J (1998) Neanderthal acculturation in Western Europe? A critical review of the evidence and its interpretation. *Curr Anthropol* 39:1–44.
8. Granger JM, Lévêque F (1997) Castelperronian and Aurignacian ornaments: A comparative study of three unexamined series of perforated teeth (Translated from French). *C Rendus Acad Sci Paris* 325:537–543.
9. Zilhão J, et al. (2010) Symbolic use of marine shells and mineral pigments by Iberian Neanderthals. *Proc Natl Acad Sci USA* 107:1023–1028.
10. Cârciumaru M, Ţuţuianu-Cârciumaru M (2009) Ochre and containers from Cioarei Cave (Translated from French). *Ann Univ Valahia Târgovişte* 11:7–19.
11. D'Errico F (2003) The invisible frontier. A multiple species model for the origin of behavioral modernity. *Evol Anthropol* 12:188–202.
12. Zilhão J (2007) The emergence of ornaments and art: An archaeological perspective on the origins of behavioural "modernity." *J Archaeol Res* 15:1–54.
13. Kuhn SL, et al. (2009) The early Upper Paleolithic occupations at Uçağizli Cave (Hatay, Turkey). *J Hum Evol* 56:87–113.
14. Fages G, Mourer-Chauviré C (1983) *Prehistoric Humans and Faunae* (Translated from French), ed Ferembach D (Soc Préhist Fr, Mémoires XVI), pp 95–103.
15. Conard NJ, Malina M, Münzel SC (2009) New flutes document the earliest musical tradition in southwestern Germany. *Nature* 460:737–740.
16. Stiner MC, Munro ND, Surovell TA, Tchernov E, Bar-Yosef O (1999) Paleolithic population growth pulses evidenced by small animal exploitation. *Science* 283:190–194.
17. Cassoli P, Tagliacozzo A (1997) Butchering and cooking of birds in the Palaeolithic site of Grotta Romanelli (Italy). *Int J Osteoarchaeol* 7:303–320.
18. Alhaique F, et al. (1998) Proc XIII Union Internationale des Sciences Préhistoriques et Protohistoriques (UISPP) Congress (ABACO, Forlì, Italy), pp 571–576.
19. Tagliacozzo A, Gala M (2005) Paglicci. The Aurignacian and the Gravettian (Translated from Italian), ed Palma di Cesnola A (Grenzi, Foggia, Italy), pp 71–90.
20. Bochenski ZM, et al. (2009) Fowling during the Gravettian: The avifauna of Pawlov I, the Czech Republic. *J Archaeol Sci* 36:2655–2665.
21. Blasco R, Fernández P (2009) Middle Pleistocene bird consumption at Level XI of Bolomor Cave (Valencia, Spain). *J Archaeol Sci* 36:2213–2223.
22. Mourer-Chauviré C (1975) The Middle and Upper Pleistocene birds of France [translated from French]. *Documents des Laboratoires de Géologie de Lyon* 64.
23. Soressi M, et al. (2008) The Paleolithic societies in the vast southwestern France: New sites, new results, new methods (Translated from French). *Mémoire Soc Préhist Fr* 47:95–132.
24. Mourer-Chauviré C (1989) The cave of Vichy (Translated from French). *Gallia Préhist* 27(Suppl):121–129.
25. Fiore I, Gala M, Tagliacozzo A (2004) Ecology and subsistence strategies in the Eastern Italian Alps during the Middle Palaeolithic. *Int J Osteoarchaeol* 14:273–286.
26. Giacobini G (1992) New discoveries of Palaeolithic humans remains in Italy. *Five Million Years, the Human Adventure*, ed Toussaint M (Ètudes et Recherche Archéologique de l'Universite de Liège, Liège, Belgium), Vol 56, pp 199–205.
27. Mussi M (2001) *Earliest Italy. An Overview of the Italian Paleolithic and Mesolithic* (Kluwer, New York).
28. Martini M, Sibilia E, Croci S, Cremaschi M (2001) Thermoluminescence (TL) dating of burnt flints: Problems, perspectives and some example of application. *J Cult Herit* 2:179–190.
29. Peresani M, et al. (2008) Age of the final Middle Palaeolithic and Uluzzian levels at Fumane Cave, Northern Italy, using ^{14}C, ESR, ^{234}U/^{230}Th and thermoluminescence methods. *J Archaeol Sci* 35:2986–2996.
30. Higham T, et al. (2009) Problems with radiocarbon dating the Middle and Upper Palaeolithic transition in Italy. *Quat Sci Rev* 28:1257–1267.
31. Peresani M. Fifty thousand years of flint knapping and tool shaping across the Mousterian and Uluzzian sequence of Fumane cave. *Quat Int*, in press.
32. Peresani M (2008) A new cultural frontier for the last Neanderthals: The Uluzzian in Northern Italy. *Curr Anthropol* 49:725–731.
33. Broglio A, et al. (2006) *The Early Upper Paleolithic of Eurasia: General Trends, Local Developments*, eds Anikovich MV, Platonova NI (Nestor-Historia, St. Petersburg, Russia), pp 263–268.
34. Cassoli P, Tagliacozzo A (1994) Paleontological, paleoeconomical and archeozoological considerations on macromammals and birds from the Late Pleistocene levels of the Fumane Rockshelter (VR) (Scavi 1988–91) (Translated from Italian). *Boll Mus Civ Stor Nat Verona* 18:349–445.
35. White TD (1992) *Prehistoric Cannibalism at Mancos 5MTUMR-2346* (Princeton Univ Press, Princeton, NJ).
36. Laroulandie V (2000) Taphonomy and archeozoology of birds in cave: Applications to the paleolithic sites of Bois-Ragot (Vienne), Combe Saunière (Dordogne) and La Vache (Ariege) (Translated from French). PhD dissertation (Université de Bordeaux, Bordeaux, France).
37. Gourichon L (1994) The snow owls of the Morin magdalenian site (Gironde). Taphonomic analysis of the remains of a night raptor hunted and exploited from prehistoric humans (Translated from French). Mémoire de Maître d'Ethnologie (Université Lumière Lyon 2, Lyon, France).
38. Lyman RL (1994) *Vertebrate Taphonomy* (Oxford Univ Press, Cambridge).
39. Bovy K (2002) Differential avian skeletal part distribution: Explaining the abundance of wings. *J Archaeol Sci* 29:965–978.
40. Villa P, Lenoir M (2009) *The Evolution of Hominin Diets*, eds Hublin JJ, Richards MP (Springer, Heidelberg), pp 59–85.
41. Hughes SS (1998) Getting to the point: Evolutionary change in prehistoric weaponry. *J Archaeol Meth Th* 5:345–408.
42. Cattelain P (1997) *Projectile Technology*, ed Knecht H (Plenum, New York), pp 212–240.
43. Catlin G (1842) Letters and Notes of the Manners, Customs, and Condition of the North American Indians (Tilt and Bogue, London), Vols 1 and 2.
44. Jenness D (1963) The Indians of Canada (National Museum of Canada, Ottawa).
45. Teit JA (1900) The Jesup North Pacific Expedition, ed Boas F. Memoir of the American Museum of Natural History (American Museum of Natural History, New York).
46. US Bureau of Ethnology Annual Report of the Bureau of Ethnology to the Secretary of the Smithsonian Institution, 1879–80 and onward (Smithsonian Inst and Government Printing Office, Washington, DC), http://www.sil.si.edu/DigitalCollections/BAE/Bulletin200/200annl.htm.
47. Sillitoe P (1988) From head-dresses to head-messages: The art of self-decoration in the highlands of Papua New Guinea. *Man (Lond)* 23:298–318.
48. Reina RE (1991) *Gift of Birds: Featherwork of Native South American Peoples*, eds Reina RE, Kensinger KM (University of Pennsylvania Museum of Archaeology and Anthropology, Philadelphia), pp 13–17.
49. Higham T, et al. (2010) Chronology of the Grotte du Renne (France) and implications for the context of ornaments and human remains within the Châtelperronian. *Proc Natl Acad Sci USA*, www.pnas.org/cgi/doi/10.1073/pnas.1007963107.
50. Bar-Yosef O, Bordes JG (2010) Who were the makers of the Châtelperronian culture? *J Hum Evol* 59:586–593.
51. Gala M, Tagliacozzo A (2005) *Proceedings IV National Congress of Archaeozoology* (Translated from Italian), eds Malerba G, Visentini P. Quaderni del Museo Archeologico del Friuli (Museo delle Scienze, Pordenone, Italy), pp 53–57.
52. Livezey BC, Zusi RL (2006) Higher order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. I. Methods and characters. *Bull Carnagie Mus Nat Hist* 37:1–544.

Supporting Information

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SI Text

Presentation of Fumane Cave. The opening of the Fumane Cave lies at the base of a rock cliff at 350 m above sea level (ASL) on the left slope of the valley of a small tributary stream flowing eastward to join the main Fumane valley in the Monti Lessini in the Veneto Prealps. This important site was already known in the 19th century, and the first explorations were carried out by the Natural History Museum of Verona in 1964 and 1982 at the bottom of a sequence exposed by a road cutting in 1950. A new series of investigations started in 1988 under the patronage of the Superintendence for the Archeological Heritage of Veneto, bringing to light a sequence of Paleolithic occupations. Excavations are conducted on a regular basis every year by the universities of Ferrara and Milan I.

The cave is part of a fossil karst complex excavated in the Ooliti di San Vigilio carbonatic sandstone (upper Lias), extensively dolomitized in the valley where the cave opens. The cave conjoins with other tunnels and was completely obstructed by sediments and by the collapse of the external vault. After this landslide was removed, between 1990 and 1996, a sheltered area of almost 60 m^2 was brought to light and extensive excavations began, with the aim of investigating evidence of the final Mousterian and Aurignacian occupations.

Sedimentary Sequence. The whole complex preserves sedimentary sequence 12 m thick, divided into four macrounits labeled S, BR, A, and D, which record the main climatic events occurring from the Early Weichselian to the second half of the Middle Weichselian. These four macrounits have been defined on the basis of their lithological composition or degree of anthropization. The base is a fill originating with the deposition of residual dolomitic sands covered by a megabreccia with partially weathered boulders. It represents the opening event preceding the Pleistocene long-term aggradation recorded, starting from macrounit S. In this first sedimentary body, dolomitic sands are prevalent, mixed with local limestone slabs in beds alternating with human occupations. Above this, the macrounit BR marks a clear lithological change due to the dramatic decrease in sands and the increase in aeolian loam with frost-shattered slabs. With the exception of the paleo living floor BR11, Mousterian occupations are evidenced only by a few dispersed lithic tools, faunal remains, and, in some cases, hearths with associated artifacts and bones interpreted as relics of specific tasks accomplished during short-term occupations. Due to intense anthropization, the overlaying macrounit A includes several horizontally layered beds from A13 to A1. Mousterian living floors range from units A11 to A5, Uluzzian from A4 to A3, and Aurignacian from A2 to A1.

The horizontally stratified final Mousterian units include frost-shattered breccia, colluvial sands (A13–A12), and aeolian matrix (A11–A4) that gradually prevail over stones to become exclusive outside the present-day cavity. The variable content in these basic lithological components and the degree of anthropization are the distinctive elements of the overall stratigraphic sequence. Furthermore, each unit contains different *facies* related to the granulometric variability, marking distinct sedimentary contexts in the cave. In detail, units A13 and A12 are loose breccia with high sand content; stones are mostly vertically arranged and outline narrow deformations that affect the overlaying unit (A11) incorporating portions of anthropic sediment. A11 and A10 are strongly anthropized levels interstratified with stony and sterile levels of frost slabs. Units A9 and A8 are still frost-shattered loose breccia with scarce-to-prevalent aeolian matrix, covered by unit A7, a sterile level with clayey-loamy matrix and smoothed coarser elements

that marks a clear, unilinear boundary with the overlaying unit (A6). This is a thin-plane anthropic horizon included in the complex described in the specific section below. The uppermost unit A4 is a breccia with slabs (A4I–A4III), which are prevalent at the cave entrance and transitional to a loamy layer outside the cavity (A4IV).

Macrounit D tops the sequence occluding the cavities and outlining the present-day slope morphology. Its origin is mainly due to several landslide events followed by stabilization and affected by crioturbation during the interval from part of OIS3 to OIS2. Human presence, still marked in the lower Aurignacian units (D3d, D3b, and D3a), becomes sporadic in the middle level D1d, where some Gravettian artifacts have been found.

Paleoecology. Macromammals, in particular hunted ungulates, indicate moist-cool climatic phases when forests extended over alpine grasslands. Nevertheless, ibex, chamois, and marmot, in addition to some birds—Alpine chough and *Lagopus muta*—indicate that open alpine environments still existed near the cave. Cervids prevail over caprids in macrounit S, although episodes of climatic cooling have been identified in S9 and in S3, where the ratio reverses. In macrounit BR a first phase records the prevalence of cervids again, with a more marked presence of caprids in BR6 up to a maximum in BR1. Cervids still prevail in A13–A12, A11–A10, and A6–A5 until the abrupt replacement by ibex and chamois in coincidence with the first Aurignacian in A2 and the spread of alpine grassland.

Anthracological investigations record a high *Pinus sylvestris/mugo* content in A11–A10 and a decrease in A9 until its disappearance from A7 upward. The percentage of *Larix decidua* remains high, and only in unit A11 does it become subordinate to *Pinus*. The anthracological association from unit A7 to A4 also includes a few broadleaf remains. Arboreal vegetation constituted a sort of parkland, variably closed during the late Mousterian. Not surprisingly, these formations were probably a sort of transition to the glacial-type herbaceous vegetation.

Final Mousterian A5–A6 Stratigraphic Complex: General Information.
Excavation and stratigraphy. The final Mousterian and Uluzzian layers have been excavated at different times since 1989 and to different extents in the area behind the present-day cave drip line and in the cave entrance (Fig. S2). The first complete stratigraphy was exposed in 1989 and 1990 in the southernmost sector; from there a northwest-to-southeast trench was opened in 1990 toward a central zone just in front of the cave entrance. Units A9 to A4 were further exposed in 1995 and 1996 in two narrow trenches dug inside the cave, before the A5–A6 complex was extensively excavated in 2000, 2001, and 2006–2008. These excavations involved several units (TettoA5, A5, A5BR, A5+A6, A6, A6BR) and brought to light combustion structures, scattered ungulate bones, flint, and other stone artifacts. All units have been excavated in 33 × 33-cm squares, with dry collection of materials (bones and lithics) and then by wet sieving. All flints ≥3 cm, macrotools on pebble, manuports, and large charcoal, as well as bones and teeth that were either identifiable or ≥5 cm have been mapped on site.

The sedimentary units of the A5–A6 complex lay over A7, a layer completely lacking in primary cultural traces, and form a homogeneous subhorizontal body with a slight east/southeast and northeast slope, just a little less than 20 cm thick. The uppermost units A4 and A3 are stony or sandy layers with few cultural remains progressively replaced by aeolian dust in the

outermost part of the cave. From the inner to the outermost zone of the cavity, aeolian dust gradually substitutes stones to become exclusive. The main units are as follows:

A6 is a layer with a dense quantity of organic matter, charcoal, fauna, and lithic artifacts as well as several combustion structures. It is 3–8 cm thick and gradually becomes thinner toward the wall, decreasing to a fine sheet of about 1–2 cm; in the inner part of the cavity it shows major variations in the form of folds, due to cryogenic/pressure structures.

A5+A6 is a loose breccia, richer in stones in the cave entrance than beyond the present-day drip-line belt. It is about 10 cm thick and systematically covers A6.

A5 is a horizon with combustion structures and dump material brought to light in the westernmost zone and gradually vanishing in the rest of the excavated area.

Field archaeological evidence. A6 is divided into three zones: the western zone, protected by the two main galleries, where there are over 20 combustion structures and localized accumulations of burnt products; a discard area characterized by the accumulation of materials derived mainly from combustion or altered by heating; and finally a large area extending to the opposite wall with dense scatters of lithic artifacts, tools, and bones modified by humans.

Combustion structures are rarely larger than 30 cm and are characterized by a reddened horizon often covered by a charcoal layer, microcharcoal, ash, and dispersed organic matter. Such structures are set directly over the sands of the sterile unit A7, but may also be within or at the top of A6. Therefore, these structures mark the aggradation of this unit and document a sequence of human frequentations that maintain the general spatial organization of the activities over time. Human occupations are more ephemeral and less intense in the above complex, where unit A5 +A6 supports the discontinuous layer A5 with its combustion structures and charcoal concentrations. Level A5 preserves a combustion area (structure A5-SIII) associated with artifacts in the immediate vicinity and partially surrounded by squared slabs.

Radiocarbon dates. >Levels A5 and A5+A6 have been recently radiocarbon dated by Oxford Radiocarbon Accelerator Unit (ORAU) using ABOX-Sc treatment. Dates are consistent for layer A5 (OxA-17980: 40150 ± 350 B.P.), structure A5-SIII (OxA-X-2275-45: 41650 ± 650), level A5+A6 (OxA-17566: 40460 ± 360 B.P.). Using a modeled Bayesian sequence generated with OxCal 4.0, Higham et al. (1) suggest that the latest Mousterian occupation of A5 took place before 43,580–42,980 BPCARIACO-HULU at 68.2% confidence.

Lithic assemblage. Thousands of artifacts have been produced using the Levallois technique; the aim was to obtain extremely functional Levallois blades with symmetrical or convergent edges using the unidirectional recurrent modality almost until the terminal phase of the reduction sequence, when it was replaced by the centripetal modality until the final discarding of the core. This type of Levallois reduction sequence was previously used in units A11, A10V, and A10, on locally provisioned flints. Levallois predetermination was not the exclusive method. A different scheme focuses on the manufacture of small flakes from polyhedral cores. A second scheme is comparable to discoid production, comparable to the discoid industry of unit A9. A third scheme involves the manufacture of a very small number of bladelets from cores and flake cores, prepared briefly with a single striking platform.

Retouched tools are mainly scrapers in contrast to points, notches, and denticulates, with the latter being rare, together with thinned simple flakes and other specimens. Of the scrapers, the simple types predominate over double, convergent, and transversal ones, as well as over scrapers with alternate or marginal retouch. Furthermore, the frequency of points and convergent scrapers in units A5 and A5+A6 and, occasionally, in unit A6,

should be noted. These are artifacts made on Levallois blades and elongated and partially cortical flakes, selected not only for their morphological and geometric regularity, but also because of their thickness. Retouchers are associated with retouched tools: more than half of the 75 recorded ones were found in layer A6. Except for an antler object from A6, only long bone and metapodial diphyseal fragments belonging to cervids and less frequently to caprids have been used. Finally, there is the exceptional presence of a scraper made on the diaphysis of a large ungulate.

Taphonomic Analysis of Bird Remains. Some of the traces detected in this study could not be referred with certainty to the action of a lithic tool. These striae, however, show some of the micromorphological features typical of cut marks, and the location on the anatomical element is also indicative of a butchering action. Also, traces such as these have been identified only on wing bones.

Of the sample analyzed, consisting of 404 elements (Table S1), wing bones (humerus, radius, ulna, carpometacarpus, and wing carpals and phalanges) constitute about 43% (Nisp 173). Of these 173 elements, 12 (about 7%) bear traces that are anthropic, or interpretable as such. These traces are present on six (22%) of the 22 species in the sample. The total number of wing elements of these six species is 141, ~9% of which bear modifications relating to wing utilizations.

Oblique traces, deep and repeated, have been identified on the lateral face of the distal epiphysis of a right ulna of *Pyrrocorax graculus*. These are wide, positioned longitudinally to the main axis of the bone and show partial recent flaking of the surface (Fig. S2 *A and B*). In addition, there is a single deeper groove with a V-shaped cross-section and two parallel traces preserved at its bottom. Traces such as these cannot be attributed with certainty to the repeated action of a lithic tool. On the opposite face, at the end of the articulation, some surface removals can be recognized, which may be related to peeling (Fig. S2 *C and D*).

A distal carpometacarpus of *Lagopus* cf. *lagopus* shows two transversally oriented striae on the diaphysis, together with a third oblique one (Fig. S3). Only the central one has a bottom and edge morphology similar to that produced by a lithic tool (Fig. S3*B*).

A right distal humerus of *Pyrrocorax graculus* shows fracture edges that may suggest fresh bone fracturing (Fig. S3*C*). On the caudal face there is a crushing (*enfoncement*) produced by the olecranon of the ulna on the sulcus musculi humerotriceps of the humerus (Fig. S3*D*). This modification is produced by forcedly flexing the two elements in the opposite direction to the natural articulation. On the caudal face of the distal epiphysis on the processus flexorius, peeling traces have also been detected at the insertion point of the triceps humeralis (Fig. S3*E*).

Other traces of peeling, as well as those on the ulna of Alpine chough with the cut marks described in the article (Fig. 3*A*) and those illustrated above (Figs. S2 *C and D* and S3*E*), have been identified on another humerus of *Pyrrocorax graculus*, localized at the same point (Fig. S4*B*), and on a fragment of tarsometatarsus of an indeterminate Aves.

Arrachement traces have been identified on a proximal ulna of *Tetrao tetrix* associated with a fresh bone fracture along the diaphysis (Fig. S5 *A–C*). The *arrachement* is a fracture of the olecranon on the proximal articulation of the ulna produced during disarticulation by forced stretching of the elbow joint.

Fractures produced by torsion as well as fresh bone fractures have been identified on several specimens belonging to different species (Fig. S5 *D and F*); in rare cases even small notches have been recognized (Figs. S4*C* and S5*D*). It is important to note that the fresh bone fracture edges are always present on specimens showing other traces (cut marks, peeling, *enfoncement*, *arrachement*) presumably produced by humans. Of particular interest, on the distal portion of a left carpometacarpus of Eurasian black vulture (*Aegypius monachus*; Fig. 4) is the cooccurrence of clear

disarticulation cut marks and polishing associated with micro-striae on the fracture edge (Fig. S6). There are also frequent specimens belonging to different species (in particular, *Pyrrocorax graculus* and *Crex crex*) that show scoring and crushing produced by the pressure of carnivore teeth (Fig. S7 *A* and *B*). Some of these gnaw marks could possibly be traces of human teeth, but at the time it was not possible to verify this hypothesis. Rare rodent gnaw marks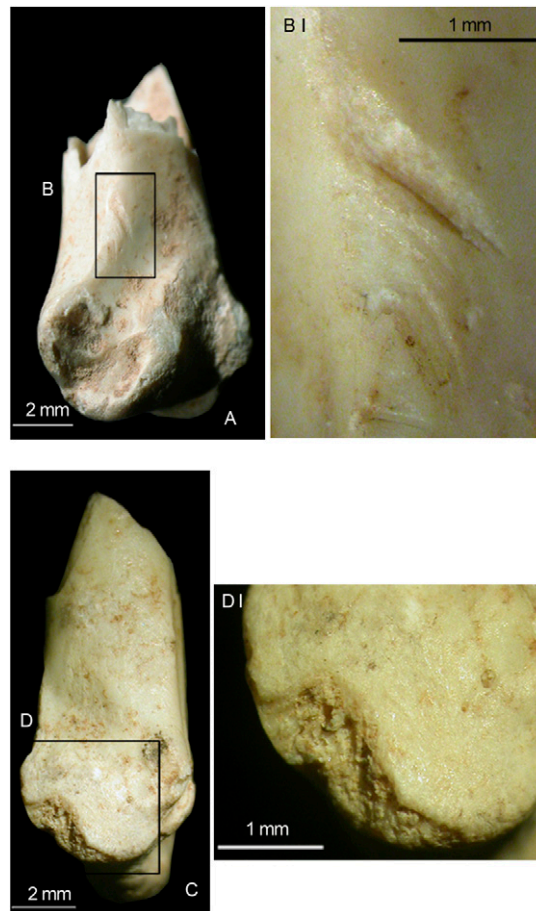 are also present. There are also bones with corrosion traces, probably produced by gastric digestive juices of carnivores and/or raptors (Fig. S7*C*).

On many specimens there are also striae of uncertain origin, isolated or in groups, superficial, very short, with variable orientation, sometimes with erosion traces that prevented the certain identification of the producing agent, although most of these striae could be the result of trampling (Fig. S4 *D* and *E*).

1. Higham T, et al. (2009) Problems with radiocarbon dating the Middle and Upper Palaeolithic transition in Italy. *Quat Sci Rev* 28:1257–1267.

Fig. S1. (*A*) Position in the north of Italy on the Monti Lessini Plateau and (*B*) the Fumane Cave. (*C*) Sketch sagittal section of the cave with evidence of the late Mousterian (A11–A5), Uluzzian (A4–A3), and earliest Aurignacian layers (A2) and of their variable content in archaeological remains (increasing from light gray to dark gray and black; by M. Cremaschi & M. Peresani, redrawn by S. Muratori; ref. 1). (*D*) Plan of the cave entrance and the lateral tunnels showing the grid and the subgrid (*Lower Right*); light gray, the excavation of the stratigraphic complex A5–A6. Solid line from squares 26–126 outlines the sagittal section. The present-day drip line is projected to the ground by the dotted line. (*E*) Large fireplace found in layer A5, squares 77–78/87–88. (*F*) Layer A6 in course of excavation in the eastern half at the cave entrance.

1. Peresani M, et al. (2008) Age of the final Middle Palaeolithic and Uluzzian levels at Fumane Cave, Northern Italy, using ^{14}C, ESR, ^{234}U/^{230}Th and thermoluminescence methods. *J Archaeol Sci* 35:2986–2996.

Fig. S2. Right distal ulna of Alpine chough (*Pyrrocorax graculus*). (*A*) Medioventral view. (*B*) Localization of the probable cut marks; (*B*, I) close-up. (*C*) Dorsal view. (*D*) Localization of the peeling traces; (*D*, I) close-up.
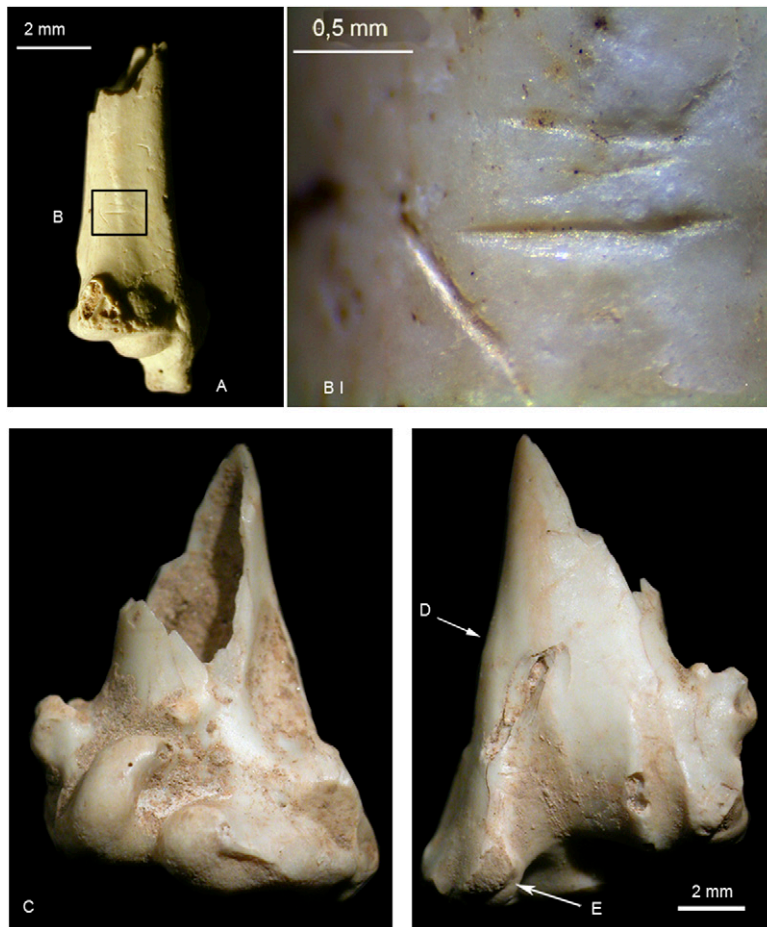
Fig. S3. (*A*) Lateral view of the right distal carpometacarpus of willow ptarmigan (*Lagopus* cf. *lagopus*). (*B*) Localization of the probable cut marks; (*B*, I) close-up. (*C*) Fracture on the cranial side of the right distal humerus of Alpine chough (*Pyrrocorax graculus*). (*D*) Localization of the *enfoncement* on the caudal side. (*E*) Localization of the peeling traces.
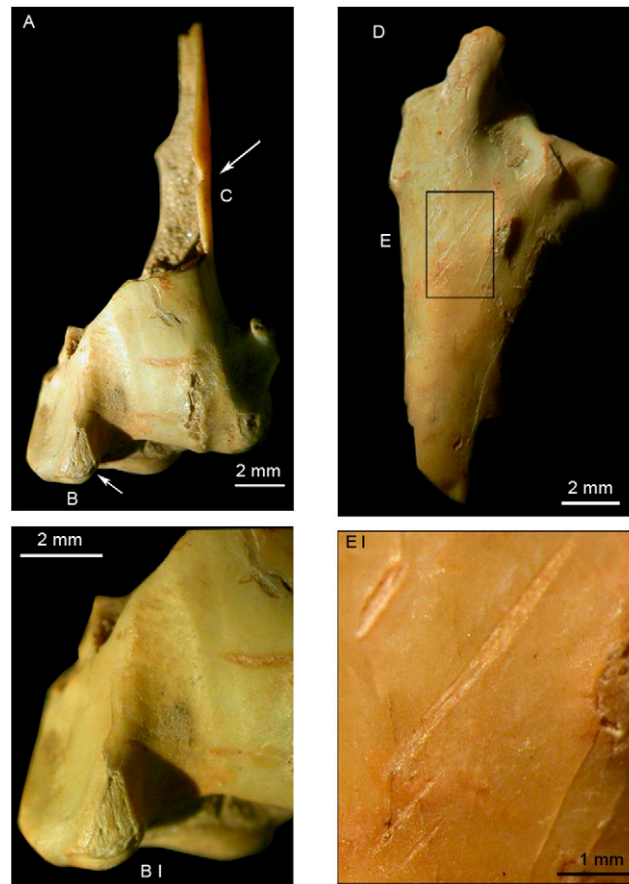
Fig. S4. (*A*) Right distal humerus of Alpine chough (*Pyrrocorax graculus*). (B) Localization of the probable peeling traces on the caudal side; (*B*, I) close-up. (C) Localization of a small notch. (*D*) Medioventral view of a right proximal ulna of Alpine chough (*Pyrrocorax graculus*). (*E*) Localization of striae of uncertain origin, probably due to trampling; (*E*, I) close-up.

Fig. S5. Right proximal ulna of black grouse (*Tetrao tetrix*). (*A*) Ventral view. (*B*) Medioventral view. (*C*) Localization of the *arrachement*; (*C*, I) close-up. (*D*) Localization of a small notch and (*E* and *F*) fresh bone torsion fractures on three diaphyses of indeterminate bird.
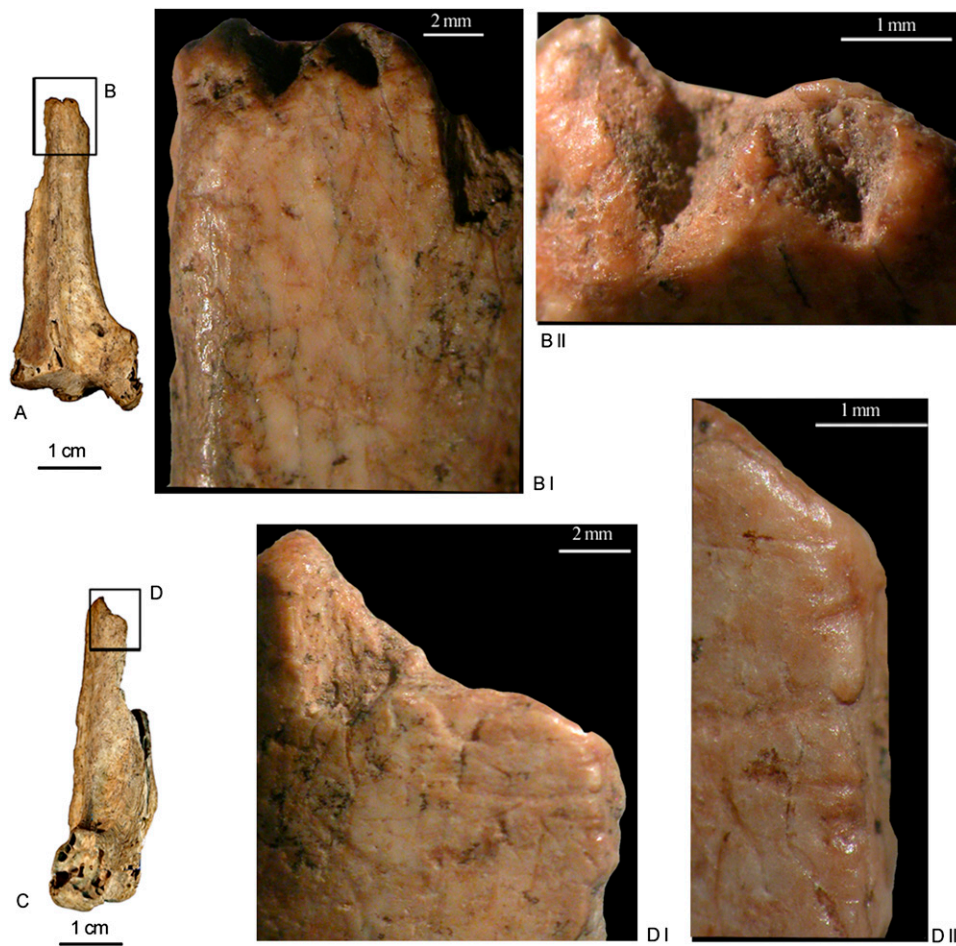
Fig. S6. Wear traces on a left carpometacarpus of Eurasian black vulture (*Aegypius monachus*). (*A*) Dorsal view. (*B*) Localization of the traces; (*B*, I and II) close-ups. (*C*) Medioventral view. (*D*) Localization of the traces; (*D*, I and II) close-ups (see also Fig. 4).
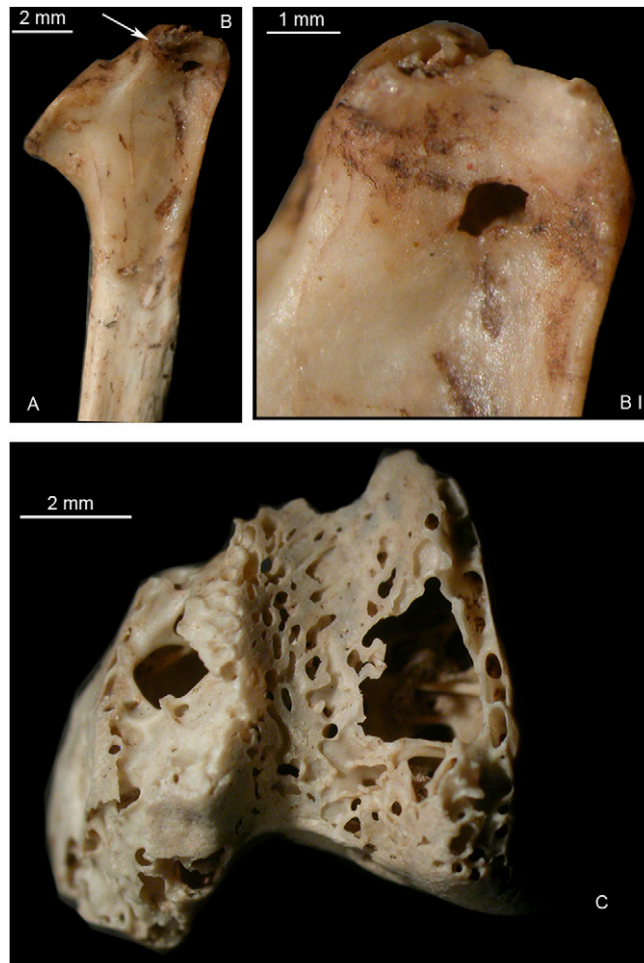
Fig. S7. (*A*) Ventral view of a right scapula of corn crake (*Crex crex*). (*B*) Localization of scoring and puncture traces; (*B*, I) close-up. (*C*) Cranial view of a right distal femur of black grouse (*Tetrao tetrix*) with corrosion traces produced by gastric digestive juices.

Table S1. Birds from the Mousterian levels and from levels A5–A6 of Fumane Cave

Species	Total NISP A6–A5	%	Total MNI A6–A5	%
Lammergeier (*Gypaetus barbatus*)	1	0.3	1	2.0
Eurasian black vulture (*Aegypius monachus*)	1	0.3	1	2.0
Common kestrel (*Falco tinnunculus*)	11	3.7	3	6.0
Red-footed falcon (*Falco vespertinus*)	5	1.7	2	4.0
Eurasian hobby (*Falco subbuteo*)	4	1.4	3	6.0
Willow ptarmigan (*Lagopus* cf. *lagopus*)	1	0.3	1	2.0
Rock ptarmigan (*Lagopus muta*)	2	0.7	1	2.0
Black grouse (*Tetrao tetrix*)	30	10.2	5	10.0
cf. Black grouse (*Tetrao tetrix*)	9	3.1		
Common quail (*Coturnix coturnix*)	2	0.7	1	2.0
Galliformes indet.	3	1.0		
Water rail (*Rallus aquaticus*)	1	0.3	1	2.0
Corn crake (*Crex crex*)	40	13.6	9	18.0
cf. Corn crake (*Crex crex*)	7	2.4		
cf. Common moorhen (*Gallinula chloropus*)	1	0.3	1	2.0
Rallidae indet.	3	1.0		
cf. Northern lapwing (*Vanellus vanellus*)	1	0.3	1	2.0
Eurasian woodcock (*Scolopax rusticola*)	3	1.0	1	2.0
Common wood pigeon (*Columba palumbus*)	1	0.3	1	2.0
Long-eared owl (*Asio otus*)	4	1.4	4	8.0
Asio sp.	2	0.7		
Tengmalm's owl (*Aegolius funereus*)	2	0.7	1	2.0
Eurasian golden oriole (*Oriolus oriolus*)	1	0.3	1	2.0
Common magpie (*Pica pica*)	3	1.0	1	2.0
Alpine chough (*Pyrrhocorax graculus*)	103	35.0	9	18.0
cf. Alpine chough (*Pyrrhocorax graculus*)	27	9.2		
Common raven (*Corvus corax*)	1	0.3	1	2.0
Corvidae indet.	7	2.4		
Common crossbill (*Loxia curvirostra*)	1	0.3	1	2.0
Passeriformes indet.	17	5.8		
Total identified birds	294	100	50	100
Identified birds	294	45		
Unidentified birds	110	16.7		
Aves being identified	256	38.8		
Total bird remains	660	100		

NISP, no. of identified specimens; MNI, minimum no. of individuals.