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Ravens as small mammal bone accumulators: First taphonomic study on mammal remains in raven pellets

Frédéric Laudet [a,*], Nuria Selva [b]

[a] *Unité Toulousaine d'Archéologie et d'Histoire, Université de Toulouse le Mirail, 5 allées Antonio-Machado, 31058 Toulouse cedex 1, France*
[b] *Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland*

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Abstract

The raven *Corvus corax* is one of the most common and widely distributed bird species in the northern hemisphere. Both predator and scavenger, its diet often comprises small mammals, whose bones and teeth are ejected through pellets after digestion. These pellets are frequently accumulated around the nest or roost sites, which can be used for years, even centuries. Until now, numerous studies have stressed the role of raptor pellet and mammalian scat accumulations as a source for small vertebrate palaeontological or archaeo(zoo)logical terrestrial assemblages. However, the raven, known from the Late Pliocene, has not yet been studied as a taphonomic agent. We present the first study on small mammal bone modifications from 567 raven pellets collected in Białowieża Primeval Forest (E Poland). A total of 1008 skull elements (teeth and jaws) and 812 main postcranial bones (long bones, girdles, talus, calcaneus), mainly belonging to rodents and shrews, were recovered from 129 pellets. The distinction of taphonomic features among the 5 main groups of prey (squirrels, large rodents, small rodents, shrews and moles) revealed a better representation and completeness of remains from the smallest species, and a variability in the proportion of digested teeth among different groups of prey. The global taphonomic signature of the small mammal bone assemblage appeared close to that of owls, but it placed the raven in an intermediate category of predators (between owl categories 1 to 3), according to the classification by Andrews (1990) [Andrews, P.J., 1990. Owls, caves and fossils, Natural History Museum Publications, London.]. Mineral remains from other vertebrate species (ungulates, lagomorphs, bats, birds, fish) were also frequently represented by small bone splinters (usually less than 2 cm long), egg fragments and complete elements (teeth, bones, hooves). Vegetal material, including seeds, was also frequent. The presence of such remains may be useful to distinguish a fossil bone assemblage made by raven from one originated from an owl prey accumulation. This study provides new insight to explain some small bone accumulations through Plio–Pleistocene and recent periods, particularly in mountain and cold areas. Due to its opportunistic exploitation of a wide variety of food sources, the raven may provide a more complete image of the fauna in the surrounding area of deposition than owl or small carnivore prey assemblages. Ravens associate often with open

* Corresponding author. Tel.: +33 5 61 50 25 90.
E-mail addresses: fred.laudet@voila.fr (F. Laudet), nuriaselva@poczta.onet.pl (N. Selva).

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landscapes, large carnivores and human activities, a fact that might be also relevant for archaeological or archaeozoological considerations.

Keywords: Taphonomy; *Corvus corax*; Pellets; Small mammals; Bone assemblage; Digestion; Białowieża Forest

1. Introduction

In continental environments, small vertebrate remains certainly constitute the most important part of the paleozoological record from the Eocene to the most recent periods. Numerous studies have underlined the potential role of prey accumulations as a source for small mammal fossils and archaeo(zoo)-logical assemblages (Lundelius, 1966; Mellett, 1974; Pratt, 1989; Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Fernández-Jalvo, 1995, 1996; Fernández-Jalvo et al., 1998; Matthews, 2000; Laudet, 2000; Avery, 2002; Weissbrod et al., 2005). In order to recognize the taphonomic signature of predators within a bone assemblage — and consequently to be able to make palaeontological/archaeological interpretations, modifications to bone and teeth of modern prey remains have been studied from the ejections of various predators: (a) scats from mammalian carnivores (Mellett, 1974; Andrews and Nesbit-Evans, 1983; Klippel et al., 1987; Denys et al., 1992; Schmitt and Juell, 1994; Matthews, 2000), (b) humans faeces (Crandall and Stahl, 1995), and (c) mainly pellets from nocturnal and diurnal birds of prey (Mayhew, 1977; Dodson and Wexlar, 1979; Korth, 1979; Denys, 1985; Hoffman, 1988; Kusmer, 1990; Andrews, 1990; Hockett, 1996; Denys et al., 1996; Saavedra and Simonetti, 1998; Bruderer and Denys, 1999; Laudet and Hamdine, 2001; Williams, 2001; Laudet et al., 2002). Numerous birds other than raptors are also able to eject undigestible remains through pellets or regurgitations, but only a few of them have been studied as taphonomic agents (Andrews, 1990; Emslie and Messinger, 1991). No taphonomic data are available yet for one of the most common and widely distributed bird species in the northern hemisphere: the common raven *Corvus corax* L. 1758.

Both scavenger and active predator, the raven is an omnivorous generalist that exploits a wide variety of food sources in its foraging territory (Ratcliffe, 1997; Boarman and Heinrich, 1999). Its diet has been studied mainly by pellet analysis, collected at both nesting and roosting sites (e.g. Marquiss et al., 1978; Newton et al., 1982; Engel and Young, 1989; Nogales and Hernández, 1994, 1997; Ratcliffe, 1997). This method has been sometimes combined with the analysis of prey remains (Amat and Obeso, 1989; Stiehl and Trautwein, 1991; Zawadzka, 1996) and direct observations (Cugnasse and Riols, 1987). Ravens are able to swallow the whole body of small vertebrate prey or carrion (e.g. rodents, frogs, lizards, small birds) as well as small parts of carcasses of large mammals (e.g. ungulates) and human refuse. Mammals tend to be the most important source of food (Boarman and Heinrich, 1999) and small mammals (rodents and shrews) can dominate the composition of vertebrate remains when abundant in the foraging habitat. The undigestible parts of the meal (hairs, feathers, bones, shells) are ejected through pellets which accumulate under nests and roosts. Many of these sites of pellet accumulation have been reported to be used by several successive generations of birds (Ratcliffe, 1997).

The genus *Corvus* (ravens and crows) is known from the Upper Miocene period (Mlíkovskí, 2000). Raven remains have been identified since the Late Pliocene, and are frequent in the Pleistocene, Holocene and more recent archaeological bone accumulations (e.g. Yalden, 2002). Therefore, providing that consumption and digestion have a low destructive efficiency on prey bones, the raven could have played an important role as a bone accumulator over geological times if these accumulations were preserved. Until now, no data about either the digestion and detailed bone occurrence of prey or carrion ingested by ravens were available in the literature. We present a first study about small mammal bone preservation from raven pellets and discuss the role of ravens as taphonomic agents.

2. Materials and methods

Białowieża Primeval Forest (BPF, approximately 1450 km^2), located on the Polish–Belarussian border land (52°30′–53°N, 23°30′–24°15′E), is one of the best preserved forest ecosystems in lowland temperate Europe. Vegetal and animal communities are among the richest in Europe. Detailed information on the vegetation and vertebrate community is given by Faliński (1986) and Jędrzejewska and Jędrzejewski (1998), respectively. The study was conducted in the Polish part of BPF (600 km^2), which includes the Białowieża National Park (100 km^2) and the commercially exploited forest (Fig. 1).

The climate of BPF is transitional between continental and Atlantic types with clearly marked cold (1 November–31 March) and warm (1 April–31 October) seasons. The mean January and July temperatures during the study period (spring 1997 to spring 2001) were −1.3 and 19.0 °C, respectively. Mean annual precipitation amounted to 578 mm. Snow cover persisted from 60 to 96 days, on average 80 days, with a maximal depth of 23 cm.

A total of 84–87 raven territorial pairs were estimated to breed in 1985–1994 in the Polish part of BPF, i.e., a breeding density of 13.8 pairs/100 km^2 (Pugacewicz, 1997). However, during the study period, raven breeding densities have declined to 7 pairs/100 km^2 (Müller, 2001) and, on average, the territory of a raven pair covered 13 km^2 (Rösner and Selva, in press). Between spring 1997 to winter 2001, around 3000 raven pellets were collected at 20 different nests (mainly during the breeding season, from February to March); at the communal roost throughout the year; and around carcasses of large ungulates, mainly in winter. A subsample of 567 pellets was randomly sorted for the taphonomic study. These analysed pellets were recovered from 15 nests of breeding pairs (361 pellets, of which 198 came from two nests), the main communal roost (185 pellets), and 11 carcasses of large ungulates (21 pellets) (Fig. 1). Raven nests were mainly located in the crown of large pine trees, often contiguous with open fields or clearings. The communal roost of immature ravens was located close to the dump of the city of Hajnówka, inside a pine plantation at the forest edge (Fig. 1). Up to 75 ravens were counted roosting together there (Rösner and Selva, in press). All the pellets were collected at accumulation places, under nesting or roosting trees and in the immediate vicinity.

Each pellet was placed in a labelled envelope, and subsequently dried, dissected and the contents identified with the help of reference material and identification keys (Romankowowa, 1963; Kowalski et al., 1981; Pucek, 1981). Main skeletal elements of small mammals were counted for each individual in a pellet. We distinguished the main skull elements (maxillae, mandibles and their teeth — molars and incisors) and 9 postcranial paired elements: (a) long bones (humerus, radius and ulna for forelimbs; femur and tibia for hindlimbs), (b) scapulae and pelvis, (c) astragalus and calcaneus. Other bones were noted (vertebra, ribs, phalanges or metapodials) whenever they were the only micromammal remains present in the pellet. Due to the difficulties in identifying the numerous bone fragments from medium-sized and large mammals and other vertebrates, we only noted the occurrence of such remains. For these remains, only teeth, long bone epiphysis and large bone splinters were counted.

For the taphonomic analysis we distinguished 5 prey/carrion categories: small rodents (voles — *Microtus*, *Clethrionomys* and mice — *Apodemus* spp.), large rodents (mainly *Rattus* spp. *and undetermined species of similar size*), squirrels (*Sciurus* spp.), shrews (*Sorex* spp.), and moles (*Talpa* spp.). For each category, the minimum number of individuals (MNI) was calculated as the highest ratio between the number of recovered skeletal elements in the total assemblage and the expected number of the same elements for one individual (2 for bone elements and upper and lower incisors, 12 for molars). The maximum number of individuals or prey (MNP, see Laudet and Hamdine, 2001) corresponded to the sum of the minimum number (or occurrence) of individuals calculated within each pellet. The MNP and the MNI values were used to calculate the relative rates of representation (as a percentage of complete elements) R1 and R2, respectively, for each skeletal part as follows:

$$R1 = \frac{100 \times N \text{ recovered elements}}{\text{MNP}},$$

and

$$R2 = \frac{100 \times N \text{ recovered elements}}{\text{MNI}}$$

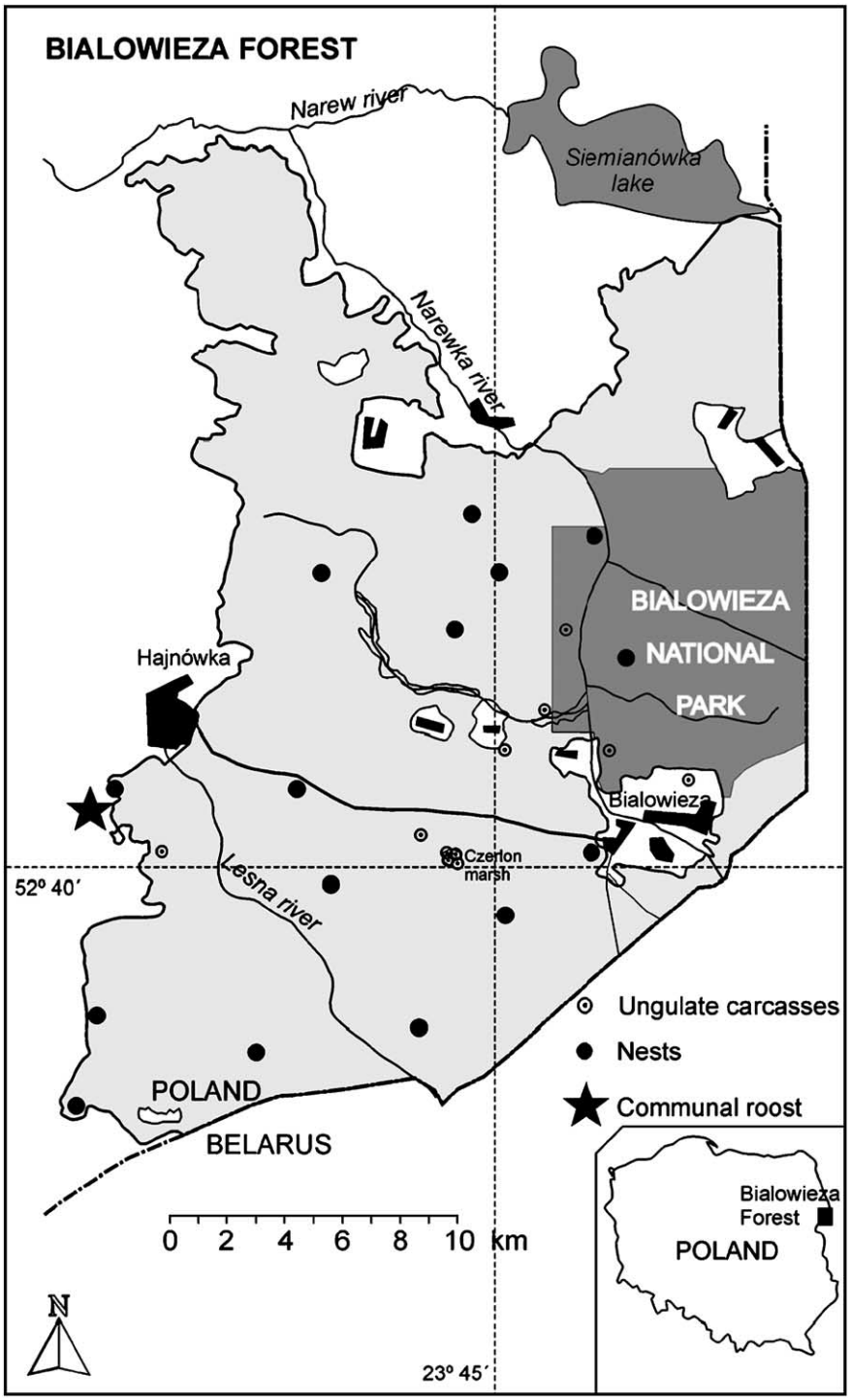

Fig. 1. Map of the study area indicating the location of the raven nests, the communal roost and the ungulate carcasses where the pellets were collected.

The values of R1 and R2 indicated the minimum and maximum representation of bones respectively (Laudet et al., 2002).

The completeness of individual skeletons in each pellet was classified into 3 main categories according to the elements represented (postcranial elements only, skull elements only, and both skull and postcranial elements present), and described in different patterns in relation to the type and number of recovered elements. The skeleton completeness may provide relevant information to explain the variability of the taphonomic signature and taxa representation in other similar assemblages in the modern or fossil record (Laudet et al., 2002). The intensity of corrosion of teeth due to digestion (grade 1: light to grade 4: heavy) was noted, according to Fernández-Jalvo and Andrews (1992), for both molars and incisors. We described the fragmentation of long bones by recording the cases when both the shaft and the bone were intact, and when long bones were represented by one epiphysis, with or without a part of the broken shaft. We also noted whether the pelvis, scapulae and mandibles were intact or not. We described whether molars and incisors were isolated in the pellet or rooted in situ in the mandible or maxilla. It was also noted whether a cranium was recovered complete or almost complete, specifying if it had postfrontal parts in anatomic connections.

3. Results

A total of 403 pellets (72.5% of the total number of pellets) contained mineralised remains (bones, teeth and eggs) from various vertebrate taxa. Bones and teeth were recovered in 343 pellets (60.5%). Small

Table 1
Representation of teeth and main bone elements recovered in the sample of raven pellets for the main small mammal prey/carrion

Skeletal element	Rodent									Shrew			Mole	Total		
	Squirrel			Large rodent			Small rodent									
	n	R1	R2	*n*	R1	R2	*n*	R1	R2	*n*	R1	R2	*n*	*n*	R1	R2
Maxilla	1	2.3	8.3	2	5.0	20.0	59	26.8	62.8	23	35.9	57.5	1	86	22.6	53.1
Mandible	6	13.6	50.0	3	7.5	30.0	81	36.8	86.2	40	62.5	100.0	2	132	34.7	81.5
Molar	11	4.2	15.3	11	4.6	18.3	364	27.6	64.5	154	40.1	64.2	2	542	23.8	55.8
Upper incisor	8	18.2	66.7	3	7.5	30.0	87	39.5	92.6	15	23.4	37.5	0	113	29.7	69.8
Lower incisor	12	27.3	100.0	3	7.5	30.0	87	39.5	92.6	33	51.6	82.5	0	135	35.5	83.3
Scapula	7	15.9	58.3	4	10.0	40.0	22	10.0	23.4	15	23.4	37.5	1	49	12.9	30.2
Humerus	5	11.4	41.7	2	5.0	20.0	75	34.1	79.8	24	37.5	60.0	1	107	28.2	66.0
Ulna	7	15.9	58.3	4	10.0	40.0	66	30.0	70.2	20	31.3	50.0	2	99	26.1	61.1
Radius	4	9.1	33.3	3	7.5	30.0	58	26.4	61.7	12	18.8	30.0	1	78	20.5	48.1
Pelvis	1	2.3	8.3	8	20.0	80.0	81	36.8	86.2	17	26.6	42.5	3	110	28.9	67.9
Femur	5	11.4	41.7	10	25.0	100.0	89	40.5	94.7	20	31.3	50.0	5	129	33.9	79.6
Tibia	2	4.5	16.7	9	22.5	90.0	93	42.3	98.9	22	34.4	55.0	6	132	34.7	81.5
Astragalus	3	6.8	25.0	7	17.5	70.0	28	12.7	29.8	10	15.6	25.0	1	49	12.9	30.2
Calcaneus	8	18.2	66.7	7	17.5	70.0	29	13.2	30.9	11	17.2	27.5	4	59	15.5	36.4
Total no. elements	80	9.6	35.1	76	10.0	40.0	1219	29.2	68.3	416	34.2	54.7	29	1820	25.2	59.1
Total no. skull parts	38	8.6	31.7	22	5.5	22.0	678	30.8	72.1	265	41.4	66.3	5	1008	26.5	62.2
Total no. postcranial bones	42	10.6	38.9	54	15.0	60.0	541	27.3	63.9	151	26.2	41.9	24	812	23.7	55.7
Total no. long bones	23	10.5	38.3	28	14.0	56.0	381	34.6	81.1	98	30.6	49.0	15	545	28.7	67.3
Number of pellets	21			20			79			26			6	129		
Mean no of elements/pellet	3.8			3.8			15.4			16.0			4.8	14.1		
Mean no of elements/individual (MNP)	3.6			3.8			11.1			13.0			4.8	9.5		
Mean no of elements/individual (MNI)	13.3			15.2			25.9			20.8			9.7	22.5		
MNP–MNI	22–6			20–5			110–47			32–20			6–3	190–81		

The number of elements found (*n*), the relative representation (%) of different elements according to the maximum number of individual (MNP) and the minimum number of individual (MNI) respectively (R1 and R2) are indicated.

mammal remains were only identified in 129 pellets (Table 1); 87 of those pellets came from 15 different nests (53 of them just from two nests), 36 pellets from the communal roost and 6 pellets were collected close to carcasses of two European bison *Bison bonasus* and one red deer *Cervus elaphus* (Fig. 1).

3.1. Bone and teeth representation of small mammals

A total of 812 bone and 1008 teeth elements were recovered from a maximum prey number (MNP) of 190 small mammal individuals: 110 voles (mainly) and mice, 42 large rodents (including at least 22 squirrels), 32 shrews and 6 moles (Table 1). In general, the mean number of bones per pellet and per individual were low (14 and 11, respectively), and although there were some differences in relation to the type of prey, the MNI of the total assemblage ($n=78$) remains low compared to the MNP.

The different patterns of skeleton representation in each pellet for each prey type are detailed in Table 2. Twelve different patterns could be distinguished. The most frequent pattern of skeleton representation consisted of the main postcranial bones and less than half of the skull (24.0% of the individuals). Only 29 skeletons (15.2%) were represented by more than half of their main elements; all of them belonged to small mammal species (voles, mice, shrews). The only 3 skeletons recovered completely belonged to shrews. More than 40% of the individuals recovered were represented by both skull and postcranial elements, whereas 38% were exclusively represented by postcranial elements (Fig. 2a). Less than 20% individuals were represented exclusively by skull parts (Fig. 2b); in 14 cases the elements present only corresponded to isolated teeth (Fig. 2c).

Remains of rodents larger than voles and mice were identified in 41 pellets (Table 1). The completeness of their skeletons was very low (Table 2). Most of them were represented only by postcranial bones (Fig. 2a), and only 19% by skull elements. Thus, the mean number of elements recovered per pellet was

Table 2
Main patterns of skeleton completeness of individuals belonging to the main small mammal prey categories (rodents, shrews and moles) recovered in each raven pellet

Pattern of skeleton completeness	Rodent						Shrew		Mole	Total	
	Squirrel		Large rodent		Small rodent						
	n	%	*n*	%	*n*	%	*n*	%	*n*	*n*	%
Skull parts + postcranial bones											
Whole skeleton	–	–	–	–	–	–	3	9.4	–	3	1.6
Half of skull + main postcranial bones or more					22	20.0	4	12.5	–	26	13.7
Less than half of skull + main postcranial bones	3	13.6	2	10.0	28	25.5	11	34.4	1	45	23.7
Isolated teeth with postcranial bones	1	4.5	1	5.0	5	4.5	–	–	–	7	3.7
Total	4	18.2	3	15.0	55	50.0	18	56.3	1	81	42.6
Skull parts only											
Whole skull parts	–	–	–	–	2	1.8	–	–	–	2	1.1
1–3 mandible/maxilla	–	–	2	10.0	8	7.3	10	31.3	–	20	10.5
One isolated tooth only	3	13.6	–	–	4	3.6	–	–	–	7	3.7
Two isolated teeth or more only	2	9.1	1	5.0	4	3.6	–	–	–	7	3.7
Total	5	22.7	3	15.0	18	16.4	10	31.3	0	36	18.9
Postcranial elements only											
9–14 main postcranial bones	–	–	5	25.0	13	11.8	–	–	1	19	10.0
2–8 main postcranial bones	7	31.8	1	5.0	8	7.3	3	9.4	2	21	11.1
1 long bone	4	18.2	4	20.0	8	7.3	1	–	–	17	8.9
No long bones or bones from girdles	2	9.1	4	20.0	8	7.3	–	–	2	16	8.4
Total	13	59.1	14	70.0	37	33.6	4	12.5	5	73	38.4
Total occurrence (MNP)	22		20		110		32		6	190	

The number of skeletons recovered (*n*), as well as the proportion (%) of different patterns within each prey category and in the total sample are shown. Main postcranial bones correspond to long bones (humerus, ulna, radius, femur, tibia) and pelvic/thoracic girdle bones.

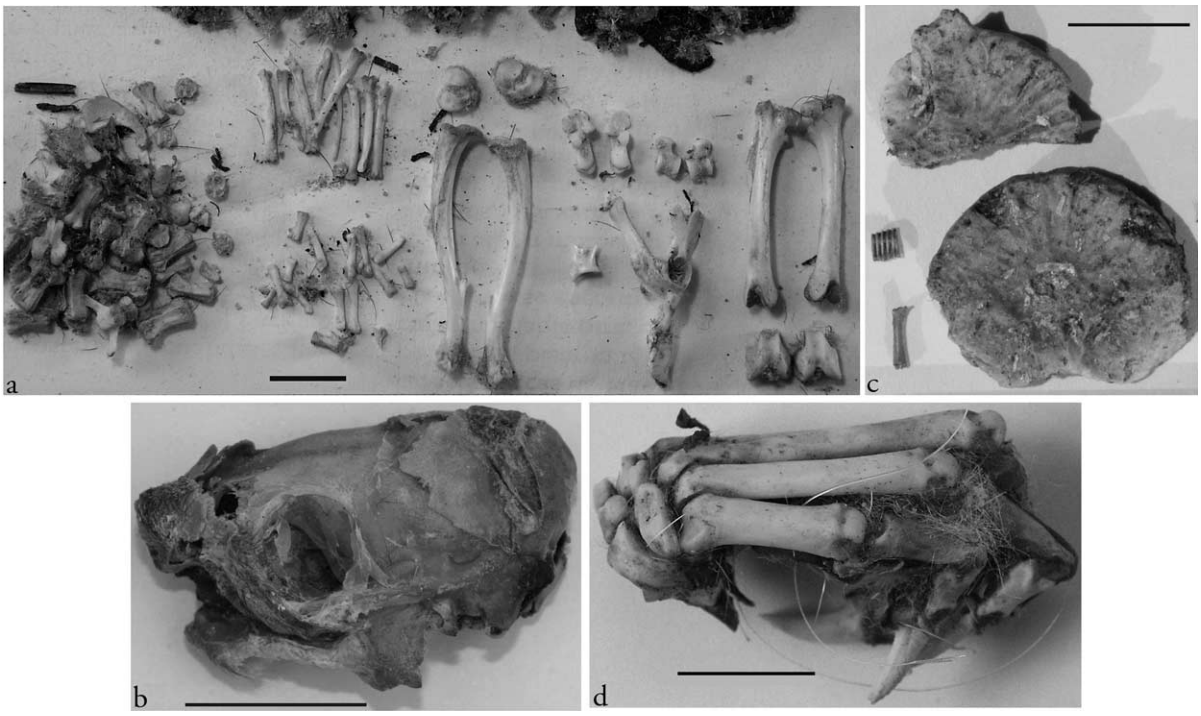

Fig. 2. Mammal remains found in raven pellets. The scale in the figures is 1 cm. a: Intact remains of the legs and tail of a rat *Rattus* spp. recovered in a same pellet. No skull elements were represented. Note the low fragmentation of long bones and the destruction of the scapula and the pelvis. b: Complete skull of a vole (*Microtus* spp.) with connected mandibles. c: Two ungulate vertebral discs recovered from a same pellet together with one isolated first lower molar of *Microtus arvalis* and an undetermined bone fragment of microvertebrate. d: Complete forefoot of a hare (*Lepus europaeus*) with connected bones recovered in a pellet.

less than 4, and the relative representation R1 of all elements was not higher from 10% (Table 1). Even the most frequent elements (lower incisor for squirrels $n=12$; molar for large rodents $n=11$) yielded a very low estimation of the MNI (MNI=6 for squirrels and 5 for other large rodents) (Table 1).

Small rodent remains constituted the main part of the assemblage (66.4% of the total number of elements). A total of 1219 remains were recovered from a maximum of 110 individuals in 79 pellets (Table 1). The mean number of remains found per pellet was 15.4, much higher than that for larger rodents. Upper and lower incisors were the most frequent skull element, whereas the tibia was the most common postcranial bone. The completeness of skeletons was also higher than for larger rodents (Table 2). Long bones from the hindlimbs were relatively more numerous than those from the forelimbs, but the relative representation of skull elements (R1=30.8%) was close to that of postcranial elements (R1=27.3%) (Table 1).

A total of 416 shrew remains were found from a maximum of 32 individuals in 26 pellets (Table 1). Shrew remains had a total representation close to that of small rodents, with a mean number of elements per pellets equal to 16. The good representation of mandibles ($n=40$) contributed to the highest value of MNI (MNI=20) in comparison to the MNP (MNP=32). Skull elements were better represented (R1=41.4%) than postcranial ones (R1=26.2%). Moles were only represented in 6 pellets by 24 postcranial bone elements, 1 mandible and two maxillae with two molars (Table 1).

3.2. Fragmentation

About 68% of the long bones recovered consisted of an unbroken shaft with one or no epiphysis (12.1%) or with both epiphyses (56.0%) (Table 3). The other long bones were represented by an epiphysis alone or with a broken shaft. Other elements

were mostly broken. Only 13.6% of the pelvis and 25.0% of the mandibles were intact, while all scapulae recovered were broken (Fig. 2a). Also cranial elements were always fragmented, with the exceptions of the intact skulls of 3 shrews and 6 voles (1 with both mandibles connected — Fig. 2b — and 5 without postfrontal parts). All the squirrel long bones were broken whereas more than half of the long bones of smaller rodents were intact. Shrew elements were the best preserved, with 68.4% of long bones intact (more than 80% of humerus and femurs were intact), and 32.5% of intact mandibles (Table 3).

Most shrew molars (96.1%) and incisors (83.3%) were rooted at the jaw (Table 4). In the case of rodents, the number of rooted teeth was lower (79.5% of molars, 62.5% of incisors), especially in squirrels whose teeth appeared usually isolated. Limbs, feet, tails and some vertebrae could appear in anatomical connection.

3.3. Digestion

In total, the teeth of 15 different individuals (equivalent to 7.9% of the MNP), distributed within 9 different pellets (7.0% of the pellets containing small mammals), showed traces of digestion. Of these, 12 individuals (8 rodents and 4 shrews) appeared in 7 pellets from raven nests, and 3 individuals (1 rodent and 2 shrews) were recovered in 2 pellets from the communal roost. The corrosion due to gastric juices affected 7.6% of the molars (40 molars recovered from 9 individuals in 7 pellets), and 8.9% of the incisors (17 lower and 5 upper incisors recov-

Table 3
Fragmentation of small mammal bones recovered in raven pellets in relation to different types of prey

	Humerus		Ulna		Radius		Femur		Tibia		Total LB		Pelvis		Scapula		Mandible	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Squirrel																		
n	5		7		4		5		2		23		1		7		7	
Intact bone	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Intact shaft	1	20.0	1	14.3	2	50.0	1	20.0	0	0.0	5	21.7						
Large rodent																		
n	2		4		3		10		9		28		8		4		2	
Intact bone	1	50.0	2	50.0	3	100.0	4	40.0	5	55.6	15	53.6	2	25.0	0	0.0	1	50.0
Intact shaft	1	50.0	3	75.0	3	100.0	4	40.0	6	66.7	17	60.7						
Small rodent																		
n	75		66		58		89		93		381		81		22		81	
Intact bone	46	61.3	39	59.1	42	72.4	40	44.9	48	51.6	215	56.4	9	11.1	0	0.0	19	23.5
Intact shaft	55	73.3	43	65.2	46	79.3	69	77.5	57	61.3	270	70.9						
Shrews																		
n	24		20		12		20		22		98		17		15		40	
Intact bone	20	83.3	14	70.0	8	66.7	16	80.0	9	40.9	67	68.4	3	17.6	0	0.0	13	32.5
Intact shaft	20	83.3	16	80.0	8	66.7	16	80.0	10	45.5	70	71.4						
Mole																		
n	1		2		1		5		6		15		3		1		2	
Intact bone	1	100.0	1	50.0	1	100.0	2	40.0	3	50.0	8	53.3	1	33.3	0	0.0	0	0.0
Intact shaft	1	100.0	1	50.0	1	100.0	2	40.0	4	66.7	9	60.0						
Total	107		99		78		129		132		545		110		49		132	
Intact bone	68	63.6	56	56.6	54	69.2	62	48.1	65	49.2	305	56.0	15	13.6	0	0.0	33	25.0
Intact shaft	78	72.9	64	64.6	60	76.9	92	71.3	77	58.3	371	68.1						

The number of elements (*n*) and the rates (%) of main bones recovered intact and without a broken shaft are indicated. Data are also presented for all long bones (LB) together.

ered from 14 individuals in 9 pellets) (Table 4). Digestive corrosion on the epiphysis of long bones was evident only in 9 elements.

In rodents, except for one slightly digested incisor (the only squirrel remain in a pellet), all digested teeth belonged to voles and mice (Table 4). The 15 digested molars of voles which were recovered (4.1% of the total number of small rodent molars) came from 3 individuals in different pellets: (a) 11 isolated molars (digestion grade 2) of the same vole from a pellet containing also digested shrew remains, (b) 2 molars (grade 1) on a mandible, and (c) 2 isolated molars (grades 1 and 2) from a third individual. Fourteen incisors (8% of the total number of small rodent incisors) from 8 voles/mice recovered in 6 pellets showed signs of digestion. Ten of them were slightly digested (8 of these incisors were found in the same pellet). Three incisors were highly digested (grade 3); one appeared isolated in a pellet with intact mole remains, whereas the other two were recovered in a pellet with two digested molars. The single extremely digested incisor (grade 4) was the only remain of a vole in a pellet and was associated with digested teeth of shrew.

All digested teeth of shrews came from 6 individuals distributed within 4 pellets. Almost all of them (84% of the molars and 100% of incisors) exhibited a high degree of digestion (grade 3) (Table 4). All these teeth were rooted at mandibles or maxillae. It is worthy to note that all teeth from the 5 mandibles of *Sorex minutus* recovered in the same pellet were strongly digested, while associated remains of *Sorex araneus* remained intact. The only 2 recovered molars of mole did not exhibit any sign of digestion.

3.4. Taphonomic remarks on other vertebrate remains

A single bat was represented by a complete but fragmented skull recovered in one pellet, containing all teeth of a single mandible and a single maxilla were moderately digested (grade 2). Identifiable mammal remains from species larger than squirrels were rare within the pellets. Isolated teeth of lagomorphs occurred in 5 pellets (7 molars and 3 incisors), all without signs of digestion. Lagomorph postcranial bone elements were found in at least 9 pellets. Two of these pellets also contained a complete forefoot of a

Table 4
Representation and digestion of teeth from small mammals recovered in raven pellets

Micromammal teeth	Rodent			Shrew	Mole	Total
	Squirrel	Large rodent	Small rodent			
No of molars	11	11	364	154	2	542
No. molars in situ	4	11	292	148	1	456
% molars in situ	36.4	100.0	80.2	96.1	50.0	84.1
No. of digested molars	0	0	15	25	0	40
% digested molars	0.0	0.0	4.1	16.2	0.0	7.4
Light digestion (grade 1)	–	–	3	1	–	4
Moderate digestion (grade 2)	–	–	12	3	–	15
Heavy digestion (grade 3)	–	–	0	21	–	21
No. of incisors	20	6	174	48	0	248
No. of incisors in situ	0	2	121	40	0	163
% incisors in situ	0.0	33.3	69.5	83.3	0	65.7
No. of digested incisors	1	0	14	7	0	22
% digested incisors	5.0	0.0	8.0	14.6	0.0	8.9
Light digestion (grade 1)	1	–	10	0	–	11
Moderate digestion (grade 2)	–	–	0	0	–	0
Heavy digestion (grade 3)	–	–	3	7	–	10
Extreme digestion (grade 4)	–	–	1	0	–	1
No. individuals with digested teeth	1	0	8	6	0	15

The number of molars and incisors recovered and the proportion of them digested and rooted at the jaw are indicated. The intensity of digestion was classified from grade 1 (light digestion) to grade 4 (heavy digestion), following Fernández-Jalvo and Andrews (1992).

hare *Lepus europaeus*, one of them with all anatomical connections, which constituted the largest mammal remain found in the sample (3.7 cm long, Fig. 2d). Two intact ulna and two intact radius with a broken acetabulum from a scapula in a pellet, and one intact tibia in another pellet were the only remains of lagomorph paired bones recovered.

Most remains of larger mammals, mainly from ungulates like roe deer *Capreolus capreolus*, red deer and wild boar *Sus scrofa*, could not be properly identified. The most frequent remains of large mammal were bone splinters, each a few millimetres long. These splinters were present in 85 pellets, and only 10 were longer than 2 cm. We also recovered 13 vertebral discs within 8 pellets (Fig. 2c). We could also identify the bud of a roe deer molar, the talus of a small carnivore and four ungulate hooves.

Bird remains were mostly represented by eggshells, which were recovered in 7.4% of the pellets. At least 24 pellets contained various bone remains from birds. These bones were frequently isolated, i.e., they were the only one bone remain present in the pellet. In only one pellet was the complete skeleton of a small passerine recovered. A few pellets ($n=11$) contained isolated frog bones. Only two of these pellets contained slightly digested frog bones. Fish bones, mainly isolated vertebrae, were present in 20 pellets (4% of the total sample).

4. Discussion

4.1. Taphonomic signature of small mammal bone assemblages created by ravens

Taphonomic data about owl prey have always underlined a clearly more frequent digestion on incisors, particularly on lower incisors, than on molars (Andrews, 1990; Bruderer and Denys 1999; Laudet and Hamdine, 2001; Laudet et al., 2002). It is worthy to note that the relative rates of digested incisors and digested molars in the total raven pellet assemblage were almost identical (7.4% and 8.9%, respectively). However, in the case of small rodent teeth, the rate of digestion was two times greater for incisors compared to molars, whereas for shrews, the whole teeth of 7 shrew mandibles were completely digested (Table 4). Additionally, most digested incisors (77%) were lower ones and digestion was considered heavy in half of the cases. These patterns of bone damage place the raven in (a) an intermediate category of owls, according to Andrews (1990), specifically between category 1 (light digestion on 8–13% of incisors, few bone breakage: barn owl *Tyto alba*) and category 2 (light digestion on 4–6% of molars: long eared-owl *Asio otus*) for rodents; and (b) between category 2 and category 3 for shrews (moderate to heavy digestion on teeth: tawny owl *Strix aluco*). However, only a few pellets yielded digestion traces; the high rate of digested shrew teeth is mainly due to the presence of 5 shrew mandibles in the same pellet, with all teeth heavily digested. These rates of digestion could vary in relation to the probability of pellet recovery (in the case of current studies) or pellet survival during fossilisation (fossil assemblage). Moreover, the presence of few digested remains associated with a majority of undigested bones in several pellets supports the argument that, like owls, some elements had a longer residence in raven stomachs, while other elements of the same meal might be ejected in previous pellets. This fact may also contribute to the observed variation in the proportion of digested remains among different modern or fossil assemblages.

Bone fragmentation and skeleton completeness in pellet assemblages may be highly dependent on bird feeding behaviour. The lack of some skeleton parts (limbs, head) in the small prey of owls is rare, even when little digestion occurs, as owls usually swallow the whole body of the rodents or shrews they kill. Only the largest prey are swallowed in several times and, thus, their parts regurgitated in several pellets (Laudet et al., 2002). In the case of raven pellets, the observed bone fragmentation (particularly scapulae and pelvis: Fig. 2a), the high destruction of skulls, and the low completeness of skeletons may be partly explained by its particular feeding habits. Personal observations with a captive raven support this hypothesis. First, the raven usually destroyed the skull of the alive domestic mouse in order to kill it. Afterwards, it started to dismember the body (mainly limbs and tail, sometimes skull elements) and eviscerate the animal. Finally, the raven was swallowing the dismembered parts of the prey and, most times, caching the rest of the body for future meals. On rare occasions, and probably when very hungry, it swallowed the whole mouse, in the same way owls do.

Because of their bigger size, large rodents such as rats, and mainly squirrels, and, of course, lagomorphs should logically be subject to heavier destruction and dismemberment of their bodies, as well as to partial consumption. Thus, the ejection of the same individual (small and large mammals) in multiple pellets may be frequent. At least in one case in our sample, different bones of squirrel, that were detected in two different pellets from the same nest, were probably originated from the same individual. This feeding behaviour may also imply that that the minimum number of largest prey calculated from the total bone assemblage can be much lower than the real number of ingested individuals, partly explaining the discrepancies in the representation (R2, Table 1) among different categories of prey/carrion. Therefore, a small mammal bone assemblage created by ravens should provide different taphonomic patterns according to the abundance and size of different prey in the diet. In a paleontological/archaeological context, the signature of the raven in small mammal bone remains only might be difficult to distinguish from nocturnal owls' signatures, particularly because of the difficulties to use fragmentation rates, which may increase through time according to postdepositionnal processes (e.g. Terry, 2004).

However, raven signature in bone assemblages may be easily distinguishable from owls when the food present is diversified. Numerous taxa represented in raven pellets are rare or completely absent from owl diets because of their large size or diurnal activities, such as squirrels, hares, fish or ungulates. Carnivores, including domestic species such as dog or cat, may be a frequent item in raven diet in forest–farmland habitats (Zawadzka, 1996), and even tortoise remains in desert environments (Camp et al., 1993). Seeds, pollen or pebbles used as gastroliths (e.g. quartz) could be also accumulated through pellets. Raven diet can be completely different among locations (see review in Ratcliffe, 1997; Boarman and Heinrich, 1999); even within the same area. In BPF, there were clear differences between the diet of nesting pairs and immature ravens; adult birds consuming considerably more rodents than immatures (Rösner et al., 2005). As suggested by this study, small mammal remains are often associated with complete bones, teeth or bone fragments of medium-sized and large vertebrates, whose length was not bigger than 3–4 cm. Ravens are known to bring much larger bones (e.g. from cattle) and prey remains than those observed in pellets into their nests (Ratcliffe, 1997; Delestrade, 2002). Therefore, the recognition of a bone assemblage created by ravens may be closely dependent on the main food type (as live prey and carrion) present in the surrounding environment.

4.2. Raven as a taphonomic agent: general considerations and perspectives

Andrews (1990), in his study of pellets from 3 corvid species other than raven, suggested that probably corvids were not important accumulators of bones; he only found four pellets of common magpie *Pica pica* containing rodent remains. However, our study emphasizes the good preservation of small mammal bones and teeth within raven pellets, little destroyed due to ingestion and digestion. Nevertheless, the low number and frequent incompleteness of micromammal skeletons in raven pellets suggests that, assuming the same number of ejected pellets, a raven pair is likely to accumulate less bones to a deposit than an owl pair. Bone accumulation may be lower particularly when large preys are frequent in the diet. For instance, 18 pellets from one nest, containing 14 rats and squirrels versus 6 voles and mice, provided only 89 bone elements. In comparison, a double number of pellets from the communal roost site — where only 2 large rodents and 2 moles out of 61 small mammals were recovered — yielded nine times more elements ($n=809$). As previously mentioned, raven feeding habits may contribute to a lower MNI estimation in relation to the actual number of killed or scavenged individuals; a fact that may increase the risk of underestimating the proportions of larger taxa in the paleoecological (or diet) analysis from raven pellet assemblages.

Bone accumulation under raven nests may be promoted by the strong fidelity of ravens to their nest site. Many of the nests monitored in this study have been used by ravens for at least the last 15 years (Pugacewicz, 1997; Müller, 2001). In other areas, some raven nests have been documented to be used for centuries (Ratcliffe, 1997). At one raven nest in BPF, 442 pellets were collected during three breeding seasons. In the case of nests located on cliffs in karstic areas, a large amount of bone mate-

rial could have been introduced in fissures or caves around the nesting sites and been preserved according to the geomorphologic and climatic evolution of the area. As an illustrative example, in a mountain area (Mont Ventoux, SE France), a large part of the small vertebrate Holocene assemblage found, associated to an exceptional concentration of brown bear bones that accidentally fell into the René–Jean pitfall (Cregut-Bonnoure and Fosse, 2001), could have been accumulated by ravens, as suggested by similar taphonomic patterns (low fragmentation and digestion) to our raven pellet assemblage (Laudet, 2005). Additionally, the richness of taxa (at least 13 rodent and insectivore species) and the simultaneous presence of fossorial (mole, subterranean vole *Pitymys*), rocky (mountain vole *Chionomys*) and forest species in this assemblage may be due to raven predation/scavenging between both lowland and upland, rather than owl hunting around the site, where a thick paleosol occurred. Moreover, because of its altitude (1650 m) and northern exposition, the site was more likely to have been occupied regularly by ravens than by owls, and ravens could have been also attracted by the carcasses of trapped bears.

Communal raven roosts may be regarded as another important site for bone accumulation in lowland environments. The number of birds gathering at roosting places is usually quite high, about 100 individuals (Hurrell, 1956; Lucid and Conner, 1974), but sometimes can exceed more than 2000 ravens (Engel et al., 1992). The permanence of night roosts is related to carcass size and duration, as well as to the temporal availability of other food resources (Boarman and Heinrich, 1999). Some roosts may last one week, especially those associated with ephemeral ungulate carcasses (Marzluff et al., 1996; Selva, 2004), while others can be used for many years (Engel et al., 1992; Boarman and Heinrich, 1999). In BPF the roosting place close to the Hajnówka dump has been used by ravens prior to the beginning of this study; a maximum of more than 200 ravens (Pugacewicz, pers. comm.) has been counted there. During February–May 2001, systematic visits to the roost allowed the recovery of more than 500 fresh pellets (Rösner and Selva, in press). As well as large bone fragments and objects carried there by the birds, the remains of dead ravens were also common on the roost site ground.

Ravens adapt well to different and changing environments, probably because of the variety of ways in which they locate food (Boarman and Heinrich, 1999). As Smith (in Ratcliffe, 1997) mentioned, raven diet ranges from a worm to a whale. The opportunistic feeding behaviour of ravens contributes to the presence of a wide variety of animal taxa in pellet accumulation sites, which owls cannot provide. Therefore, bone assemblages created by ravens may provide a good representation of the vertebrate fauna in the surroundings of the deposition area. It is also noteworthy that ravens start (and thus finish) breeding early, so often their nests are subsequently used by breeding owls, such as *Strix occidentalis* (Tishechkin et al., 1997) or *Asio otus* (Selva, pers. obs.), and raptors, like the hobby *Falco subbuteo* (Müller, 2001). This phenomenon could contribute indirectly to increase the number of prey remains around the nesting site and should be taken into account in paleontological studies. The wide distribution of ravens and their presence in all types of ecosystems, particularly in the coldest regions of the northern hemisphere, stress this bird species as a potential and relevant source of small bone accumulations in many environments, particularly in arctic or mountain areas, where the density of both nocturnal and diurnal raptors is low (e.g. Mikkola, 1983).

Ravens preferentially associate with open landscapes and human activities, particularly agriculture (Engel and Young, 1989) and cattle raising (Marquiss et al., 1978; Newton et al., 1982), a fact that could be relevant for archeological or archeozoological considerations. Ravens may benefit from pastoralism, activity that promoted raven foraging on small mammals and dung-eating insects, the deposition of domestic carcasses and the creation of garbage dumps (Delestrade, 2002). Ravens are also quite dependent on anthropogenic food sources (Marquiss et al., 1978; Restani et al., 2001). They are able to transport and accumulate human refuse (Camp et al., 1993; Delestrade, 2002), sometimes even human remains (see Cugnasse and Riols, 1987), far away from their original setting, and then modify assemblages of anthropological origins (e.g. leftovers of butchery). In regions with heavy snowfalls, ravens usually associate with large carnivores, such as wolves (Stahler et al., 2002), to feed on the leftovers of their kills. In the case of large ungulate carcasses, such as European

bison, raven pairs and flocks may utilise the same carcass continuously throughout the winter (Selva et al., 2003). Thus, ravens can provide small mammal remains close to or inside large vertebrate carcasses, and also modify kill-site assemblages. In BPF, one bison carcass located in the Czerlon marsh (Fig. 1) provided 9 pellets during one winter; four of these pellets contained almost 10% of the micromammal main elements counted in this study ($n=178$).

5. Conclusions

This work represents the first contribution to taphonomic research related to raven pellet assemblages, and emphasizes the role of ravens as important agents generating and also altering bone assemblages. As raven remains have been identified since the Late Pliocene, and they are frequent in Pleistocene, Holocene and recent archaeological bone accumulations (Yalden, 2002), ravens might represent an alternative interpretation to that concerning owls for explaining the accumulation of small bone remains through fossil and recent periods in the northern hemisphere. Further studies on taphonomic modifications on bone assemblages by ravens are needed. Particularly, data from nest and roost sites in different environmental contexts — especially karstic habitats, from feeding experiments, and also from fossil assemblages with corvid remains are needed. Such research should provide a better understanding of the role of ravens as efficient taphonomic agents on mammal fossil assemblages, and additional information to help interpreting bone accumulation through paleontological and archeological times.

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