Taphonomic study of Algerian owl pellet assemblages and differential preservation of some rodents: palaeontological implications

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Abstract: Taphonomic study of five Algerian *Bubo bubo ascalaphus* pellet assemblages and comparison with other *Bubo bubo* data, as well as with faunal lists for Algeria, indicates significant bias in faunal representation, bone representation and bone fragmentation. Some rodents characteristic of a given biogeographic region or vegetation zone cannot be found in the *Bubo* pellet assemblages of the corresponding region. Dipodid, gerbillid and crocidurid skulls are more digestion resistant than those of murids. The digestion biases shown here all influence the future fossilisation of such assemblages. Some palaeoenvironmental and palaeobiogeographical consequences are described. The main conclusion is that a careful taphonomic analysis must be made prior to palaeoenvironmental interpretation.

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I. INTRODUCTION

Recent developments in taphonomy have shown that most microvertebrate fossil assemblages originate from owl pellet accumulations (DENYS 1986; ANDREWS 1990; FERNANDEZ-JALVO 1992). Some criteria of bone representation, bone fragmentation and digestion are now available to identify the predator responsible for a fossil small mammal concentration (ANDREWS 1990; FERNANDEZ-JALVO & ANDREWS 1992). Together with SEM observations of bone surfaces, chemical analyses of mineral and organic content of bone allows the characterisation of some post-predation alterations of bone and determination of diagenetic processes (DAUPHIN et al. 1995). The methodology developed by ANDREWS (1990) is well adapted to the study of both modern and fossil assemblages, but thus far the number of applied studies has been limited.

In spite of existing taphonomic studies of fossil sites, there still remain unsolved problems regarding the representation of bones and teeth, which is generally lower than expected, and the surprising dominance of one or another skeletal element in the absence of traces of water sorting in the sediment. For example, it is well known that in many fossil sites mandibles are better preserved than maxillaries as well as teeth, especially incisors (Denys 1986; Denys et al. 1987). It has been shown that secondary alteration and diagenesis can play a very important part in biasing the original owl pellet concentrations (Andrews 1990). Some studies of post-predation alterations have already been published (see synthesis in Fernandez-Jalvo 1992).

Very little attention has been paid to differential preservation during the initial stage of concentration, or predation phase, of bones and teeth. Raczyński & Ruprecht (1974) have recognized differential preservation but did not attempt to estimate it. Kowalski (1990) showed the existence of faunal preservation biases and some problems in the interpretation of fossil sites. The differential preservation of skeletal elements probably appears as early as the moment of death of the animals and can be noted already during the formation of an owl pellet. In order to estimate this bias it has been necessary to obtain a collection of owl pellets from a well documented region.

Among the most studied regions with important fossiliferous localities and many owl pellet assemblages is North Africa, and especially Algeria. The small mammal fauna of this region has been the object of a comprehensive study by Kowalski & Rzebik-Kowalska (1991). The taphonomic method developed by Andrews (1990) and Denys (1985), will here be applied to some sites of Algeria. These sites have been selected for their abundance and their geographical position on an aridity gradient. The aim of this paper is to show the pattern of preservation of different taxa and different skeletal elements in such assemblages. Implications for palaeoecological studies of fossil sites will be discussed.

II. MATERIAL AND METHODS

The pellets were collected by K. Kowalski and B. Rzebik-Kowalska at five different sites in Algeria (Fig. 1). On the basis of the aspect and the size of the prey, it is evident that they all originate from *Bubo bubo ascalaphus*. The localities are (from north to south):

The site of Honaine (35°10'N, 01°39'W) is situated on the Mediterranean coast of Algeria, in a very degraded forest region. The annual rainfall in the region is between 400 and 1200 mm. This site has yielded 548 individual mammals.

The site of Aflou (34°30'N, 01°50'E) is situated 50 km north of the settlement of this name on the high plateau of the Tell Atlas, in a steppe zone receiving about 200 mm annual rainfall. Pellets have yielded 442 individual mammals.

The site of Igli (30°28'N, 01°25'W) is situated under a cliff to the north of Beni Abbès, in a desert area with some acacias. This site has yielded 341 individual mammals. This desert region receives less than 140 mm rain annually.

The site of Kerzaz (29°27'N, 01°25'W) is situated in the Sahara Desert, 3 km from a village on the road to Hadrar in a stony desert. It yielded at least 66 individual mammals.
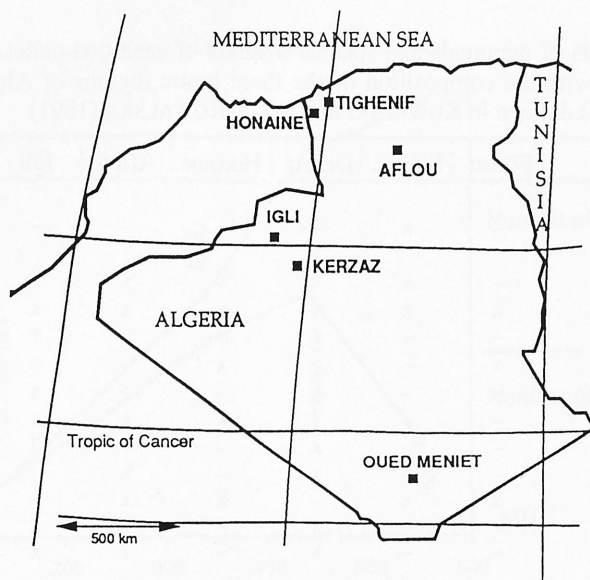
Fig. 1. Geographic position of the different owl pellet sites of Algeria.

Finally, the site of Oued Meniet (25°00'N, 04°20'E) is in the Hoggar (80 km south of Arak) and has yielded 130 individual mammals. This high montane zone of the Sahara receives slightly more rain than the central zones of this desert. Due to a collecting bias, part of the post-cranial material was missing for this site and therefore no analyses have been performed on post-cranial elements.

The taxonomic study was carried out by K. KOWALSKI (rodents), B. RZEBIK-KOWALSKA (insectivores and bats), Z. BOCHEŃSKI and J. CUISIN (birds). Comparisons have been made with faunal lists of the Recent mammal fauna of Algeria. Counts of bone frequencies and fragmentation follows the methodology explained in DENYS (1985) and ANDREWS (1990).

III. RESULTS

F a u n a l   r e p r e s e n t a t i o n

Faunal lists of mammals from different biogeographic zones of Algeria and from the *Bubo bubo* pellets of that country are provided in Table I. The highest number of mammal species (14) is found in the Honaine fauna, which has also yielded the greatest number of individuals (Fig. 2).

R o d e n t i a. Rodents are the main prey of *Bubo bubo*, both in terms of the number of species and the number of individuals (Table II).

The number of rodent species present in owl pellets is between 7 (Oued Meniet) and 11 (Aflou). There is one dominant taxon in each studied pellet assemblage: *Gerbillus pyramidum* in Igli and Aflou, *G. gerbillus* in Kerzaz, *G. nanus* in Oued Meniet and *Mus musculus* in Honaine (Table II).

The number of rodent species in the five owl pellet assemblages is lower than expected in all regions of Algeria (Table I). *Bubo bubo* is considered to be an opportunistic feeder (FRY et al. 1988), but it avoids the squirrel *Atlantoxerus getulus*, which is purely diurnal. The same observation

Table I

Faunal lists of mammals and species richness of each owl pellet assemblage. Comparison with the composition of the three biotic regions of Algeria (forest, steppe, desert) defined in KOWALSKI & RZEBIK-KOWALSKA (1991)

| Species	Forest	Steppe	Desert	Honaine	Aflou	Igli	Kerzaz	Oued M.
Sciuridae								
Atlantoxerus	–	x	–	–	–	–	–	–
Gerbilinae								
D. simoni	–	x	–	–	x	–	–	–
G. campestris	x	x	x	x	x	x	x	x
G. gerbillus	–	–	x	–	–	x	x	x
G. henleyi	x	–	–	x	–	–	–	–
G. nanus	–	–	x	–	–	x	–	x
G. pyramidum	–	–	x	–	x	x	x	x
M. crassus	–	–	x	–	–	?	?	x
M. lybicus	–	–	x	–	x	–	–	–
M. shawi	x	x	–	x	x	–	–	–
P. duprasi	–	–	x	–	–	x	x	x
P. obesus	–	–	x	–	?	x	–	–
Murinae								
A. cahirrinus	–	–	x	–	–	–	–	x
A. sylvaticus	x	–	–	–	–	–	–	–
L. barbarus	x	–	–	x	–	–	–	–
M. musculus	x	x	x	x	x	x	x	–
M. spretus	x	–	–	?	?	–	–	–
R. norvegicus	x	x	–	x	–	–	–	–
R. rattus	x	x	x	x	–	–	–	–
Gliridae								
E. quercinus	x	x	–	x	x	–	–	–
Dipodidae								
J. jaculus	–	–	x	–	–	x	x	–
J. orientalis	–	x	–	–	x	–	–	–
Hystricidae								
H. cristata	x	x	–	–	–	–	–	–
Ctenodactylidae								
C. gundi	–	x	–	–	–	–	–	–
C. vali	–	–	x	–	–	x	x	–
M. mzabi	–	–	x	–	–	–	–	–
Others								
Myotis blythi	x	x	–	–	–	–	–	–
Miniopterus schreibersi	x	–	–	x	–	–	–	–
Asellia tridens	–	–	x	–	–	x	–	–
Elephantulus rozeti	–	x	–	x	x	–	–	–
Crocidura whitakeri	–	x	–	–	x	–	–	–
Crocidura russula	x	–	–	x	–	–	–	–
Suncus etruscus	x	–	–	x	–	–	–	–
Lagomorpha indet.	–	–	–	x	–	–	–	–
Canis sp.	x	x	x	x	–	–	–	–
Total	15	16	12	14	13	11	8	7
Murinae	6	3	3	5	2	1	1	1
Gerbilinae	2	4	8	2	7	7	5	6
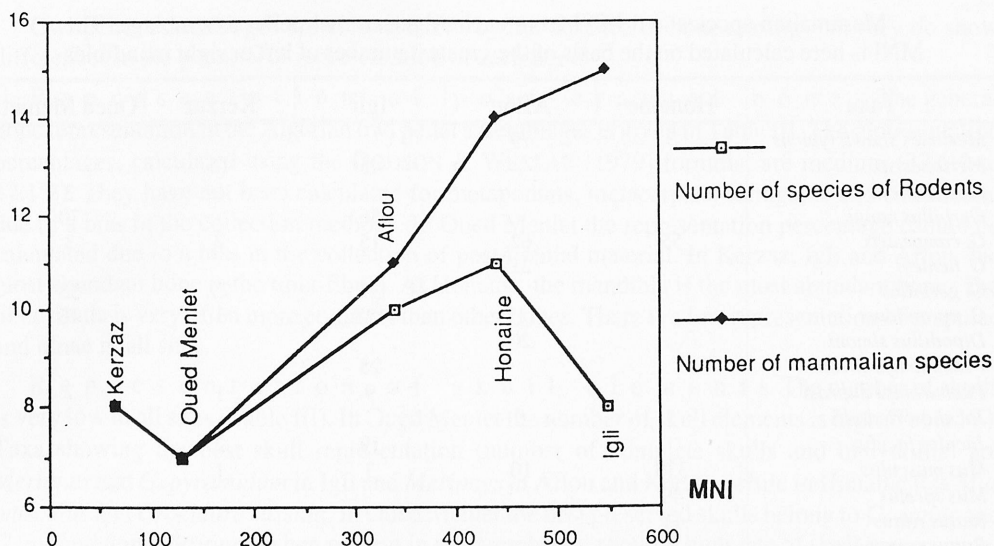
Fig. 2. Number of species of rodents (NSR) and micromammals (NlS) plotted versus the minimum number of individuals for each site. The number of rodent species is not correlated with the MNI, at least for Oued Meniet and Honaine. Nevertheless, the general number of micromammals follows the MNI.

was made by JAKSIC & MARTI (1984) for *Bubo* in Spain, Chile and California. In addition, *Bubo* does not feed on the largest African rodent, the porcupine (*Hystrix cristata*). At any given site it does not take all the available species. Among the three rodents characteristic of the steppe habitat (*Atlantoxerus, Jaculus orientalis* and *Ctenodactylus gundi*), only *J. orientalis* was found in pellets at Aflou. The forest zone is characterized by the presence of six Murinae (three of them synanthropic) and only two Gerbillinae, while the desert region has a high diversity of Gerbillinae (eight genera). It is also characterized by two Ctenodactylidae and one representative of Dipodidae (*J. jaculus*). The eight gerbilline genera have never been found together in owl pellet assemblages from the Sahara. This can be due either to the ecology of the species or to the scarcity of some prey species. If such an owl pellet assemblage were to fossilize, the environment would be interpreted to be less arid than it really was.

In order to avoid direct deductions from faunal lists, some authors have used the ratio Murinae/Gerbillinae as an indicator of aridity (JAEGER 1976; DENYS 1989). It is well known that the number of Gerbillinae increases with aridity, while the number of Murinae decreases. Since the five owl pellet assemblages studied in this paper are situated along an increasing aridity gradient (Fig. 1), we should expect an increase in Gerbillinae and a decrease in Murinae. In fact, there is an increase in Gerbillinae from Honaine to Aflou, but the two southernmost sites contain fewer Gerbillinae than expected (Table I).

C h i r o p t e r a. The number of bats found in the owl pellets is very small compared with their representation in mammalian faunas (KOWALSKI & RZEBIK-KOWALSKA 1991) (Table I). Only three species of 26 present in Algeria have been identified in the pellets. According to KOWALSKI (1995) only in rare cases do particular individuals of owls feed regularly on bats.

I n s e c t i v o r a. Except for Erinaceidae, which are rare in the diet of owls and have not been identified in localities studied in the present paper, Insectivora are well represented by *Crocidura* in the material of Honaine and Aflou, as well as by *Suncus* in the Honaine assemblage

Table II

Mammalian species and MNI from each Algerian owl pellet assemblage. The MNI is here calculated on the basis of the greatest number of left or right mandibles

Taxa	Honaine	Aflou	Igli	Kerzaz	Oued Meniet
Meriones shawi, lybicus	3	79			
Meriones sp.			45	15	
Meriones cf.*crassus*					2
Gerbillus nanus			56		70
G. campestris	55	62	15	2	3
G. henleyi		21			
G. gerbillus			37	29	35
G. pyramidum		117	128	1	16
Dipodillus simoni		20			
Psammomys obesus			25		
Pachuromys duprasi			9	1	2
Jaculus orientalis	1	6			
Jaculus jaculus			19	2	
Mus musculus	330	10	3	1	
Mus spretus	49				
Rattus rattus	11				
Rattus norvegicus	3				
Apodemus sylvaticus	19				
Lemniscomys barbarus	6				
Acomys cahirhinus					2
Ctenodactylus vali			2	5	
Eliomys quercinus	10				
Crocidura whitakeri		127			
Crocidura russula	66				
Suncus etruscus	3				
Miniopterus schreibersi	1				
Myotis blythi	5				
Asellia tridens			2		
Elephantulus rozeti	34	2			

(Tables I and II). It is noteworthy that *Crocidura whitakeri* is the most abundant mammal in the Aflou assemblage, where it is represented by a greater number of individuals that the rodent *G. pyramidum*.

L a g o m o r p h a. This order has been found in two sites only (Aflou, Honaine) in each case represented by one individual (Table II).

M a c r o s c e l i d e a. The genus *Elephantulus* is rather well represented at Honaine and Aflou (Table I).

B i r d s. Birds are absent from some sites. They are well represented at Igli, where Passeriformes as well as Columbiformes (with *Streptopelia* dominant: 11 individuals) are present. In this site 55 individuals of birds belonging to at least 22 species have been identified (J. CUISIN personal communication). At Aflou, birds are represented by 10 individuals, among them *Coturnix* sp. and Passeriformes indet. (Z. BOCHEŃSKI personal communication).

Skeletal representation

Owl pellet assemblages are characterized by the absence of bone sorting, but they do show differences in the patterns of representation of each bone.

Representation of post-cranial bones. The general bone representation in the Algerian owl pellet assemblages is given in Table III. The representation percentages, calculated using the DODSON & WEXLAR (1979) formula, are medium (37.6% to 57.1%). They have not been calculated for metapodials, metacarpals, astragalus and calcaneum, due to a bias in the collection methods. In Oued Meniet the representation percentage cannot be calculated due to a bias in the collection of post-cranial material. In Kerzaz, Igli and Aflou, the most abundant bone is the tibia-fibula. At Honaine, the mandible is the most abundant bone. The tibia-fibula is very often more common than other bones. There is a low representation of scapulae and ulnae in all sites.

Representation of skull elements. The number of skulls is very low in all sites (Table III). In Oued Meniet the number of skull elements is high (Table IV). Taxa showing the best skull representation (number of complete skulls and half-skulls) are *Meriones* and *G. pyramidum* in Igli and *Meriones* in Aflou and Kerzaz, while in Honaine it is *Mus musculus* and *Crocidura russula*. In Oued Meniet the best preserved skulls belong to *G. nanus* and *G. pyramidum*. *Meriones*, when present in an assemblage, shows a high rate of skull preservation, despite not being the most abundant mammal. In Kerzaz and Oued Meniet the dominant rodent is *G. gerbillus*, which does not have the highest proportion of skull remains. *Crocidura* also shows rather good skull representation. For *C. russula* there are 7.7% skull elements in the total of identifiable elements, while for *C. whitakeri* the proportion is 35.6% skull remains, excluding mandibles.

Maxillary vs mandibular representation. The loss of maxillaries during digestion is very significant (Table IV). The loss of maxillaries and elements of the upper part of the skull, compared with mandibles, is between 26% and 54% for the five owl pellet assemblages considered here. This represents a considerable loss, especially in Oued Meniet. Per taxon the loss is also considerable (from 19% to 63%). Despite a high number of well preserved skulls, *Meriones* shows a significant discrepancy between the representation of upper and lower jugal elements (58%), while *Jaculus* is near equilibrium (19%) (Table IV). *Crocidura* also yielded fewer maxillaries than mandibles. In *C. russula* at Honaine there are 21 upper skull elements versus 126 mandibular ones (83% loss of upper cranial elements). *C. whitakeri* in Aflou shows a loss of 34% of the upper elements due to good preservation of rostral parts of skulls.

Fragmentation

Post-cranial bones. The number of intact bones is relatively high, with better preservation being found in the pellets of Igli, Kerzaz and Honaine (nearly 57%; Table V). The assemblage of Aflou has a lower percentage of intact bones. These values correspond to those obtained by DODSON & WEXLAR (1979), the best preserved bone being the tibia with or without the fibula. Only a few tibiae have been found associated with a fibula. For other bones the preservation varies considerably from one site to the next. The fragmentation of the mandible is relatively high, as well as that of the scapula and the pelvis.

Skull fragmentation. Few studies have been devoted to differences in fragmentation in different prey taxa. This is possible only on skull remains, because the post-cranial bones cannot as yet be specifically identified. Numerous Gerbillinae (*Meriones*, *Psammomys*, *Gerbillus campestris*, *G. gerbillus*, *G. nanus*, *G. pyramidum*) and *Jaculus* are represented by complete skull remains, but in very low percentages (Table VI). Viewing all the Algerian sites together, we see that *G. pyramidum* has the highest number of intact skulls. *Crocidura russula* and

Table III

Representation percentages of bones in the *Bubo bubo ascalaphus* pellets of Algeria. PR is calculated according to the Dodson & Wexlar (1979) formula (using the NISP for calculation of the frequencies of bones rather than the MNI)

Bone	Honaine	Aflou	Igli	Kerzaz
Femur	50.00	98.6	84.4	66.4
Scapula	8.2	16.7	5.9	3.6
Pelvis	42.2	86.8	64.4	48.2
Tibia-Fibula	44.9	**100**	**100**	**100**
Humerus	43.4	57.4	31.5	18.2
Ulna	15.2	31.7	17.5	10
Radius	14.2	20.4	9.5	7.3
Mandible	**99.9**	83.4	99.6	99.1
Maxillary	48.7	47.4	40.6	31.8
Skull	9.5	28.9	33.5	22.7
NISP	486	346	278	55
MNI	548	442	341	130
PR Mean	37.6	57.1	48.7	40.7

Table IV

Cranial representation in different Algerian sites and in the most abundant taxa for all the sites together. The loss of upper skull elements is calculated first, dividing the number of upper skull (UP) fragments by the number of mandibles (MDB). The result after multiplication x100 is subtracted from 100

Bone	Honaine	Aflou	Igli	Kerzaz	Oued-Meniet
Complete skull	1	4	5	0	8
Half-skull	45	96	88	25	72
Maxillary	473	328	226	35	36
Mandible	971	577	554	109	253
Total upper parts	519	428	319	60	116
Loss= 100-UP/MD	**47%**	**26%**	**42%**	45%	**54%**
Bone	*Meriones*	*G. campestris*	*G. pyramidum*	*Jaculus*	*Mus*
Complete skull	3	2	5	3	0
Half-skull	50	22	80	11	32
Maxillary	46	124	179	41	340
Mandible	237	259	498	68	776
Total upper parts	99	148	264	55	372
Loss	**58%**	**43%**	**47%**	**19%**	**52%**
Bone	*G. nanus*	*G. gerbillus*			
Complete skull	1	2			
Half-skull	40	28			
Maxillary	49	69			
Mandible	239	189			
Total upper part	89	99			
Loss	**63%**	**48%**			

Table V

Fragmentation percentages (% intact bones versus the total number of each bone)
for different skeletal elements in the Algerian owl pellet assemblages

Bone	Honaine	Aflou	Igli	Kerzaz
Skull	0.19	2.5	1.6	0
Mandible	20.8	42.8	36.1	33.9
Humerus	**93.9**	11.8	96	80
Ulna	80	6.8	90.7	63.6
Radius	93	4.3	**100**	**100**
Scapula	6.5	86.2	15.2	0
Pelvis	0.27	0	27.1	32.1
Femur	90.5	57.7	42.6	92
Tibia-Fibula	92.4	94.8	84.2	95.2
Tibia only	86.3	87.2	79.8	65.2
% intact	56.4	39.4	57.3	56.2

Table VI

Skull and mandibular fragmentation for each species of rodent in the five
Algerian *Bubo* pellet assemblages together. HB: head and body length; IB: interor-
bital width; ZB: zygomatic width

| Species	Skull		Mandible		HB Size mm	Weight	IB mm	ZB mm
	Intact	Broken	Intact	Broken				
Gerbilinae								
D. simoni	0	30	5	23	70-85	?	5.2	45.1
G. campestris	2	137	137	215	81-115	30	5.6	14.9
G. gerbillus	2	79	86	89	80-92	16-25	4.3	13.2
G. nanus	1	89	150	79	55-77	8	6	16.5
G. pyramidum	5	260	167	203	85-120	32-36	5.5	19.5
M. crassus	3	97	48	60	115-140	40	6.4	20.7
M. shawi	0	25	78	55	115-180	60-120	6.3	22.8
P. duprasi	0	10	6	12	103-135	?	5.95	18.5
P. obesus	1	24	13	15	130-160	70+	6.6	23
Murinae								
A. cahirhinus	0	1	2	0	70-120	11-20	4.5	13.6
A. sylvaticus	0	24	15	25	30-150	15-50	4.2	12.9
L. barbarus	0	8	2	15	83-140	18-68	4.4	14.6
Mus spp.	0	384	147	74	80	15-20	3.4	10.8
R. norvegicus	0	0	0	5	80-300	200-400	4.4	17.7
R. rattus	0	24	2	28	80-250	77-108	12.4	22.8
Gliridae								
E. quercinus	0	5	13	5	100-175	45-120		
Dipodidae								
J. jaculus	1	27	5	14	70-115	55	12.4	22.8
J. orientalis	2	6	2	0	95-160	134	12.9	23
Ctenodactylidae								
Ctenodactylus sp.	0	2	2	2	165-220	45+		
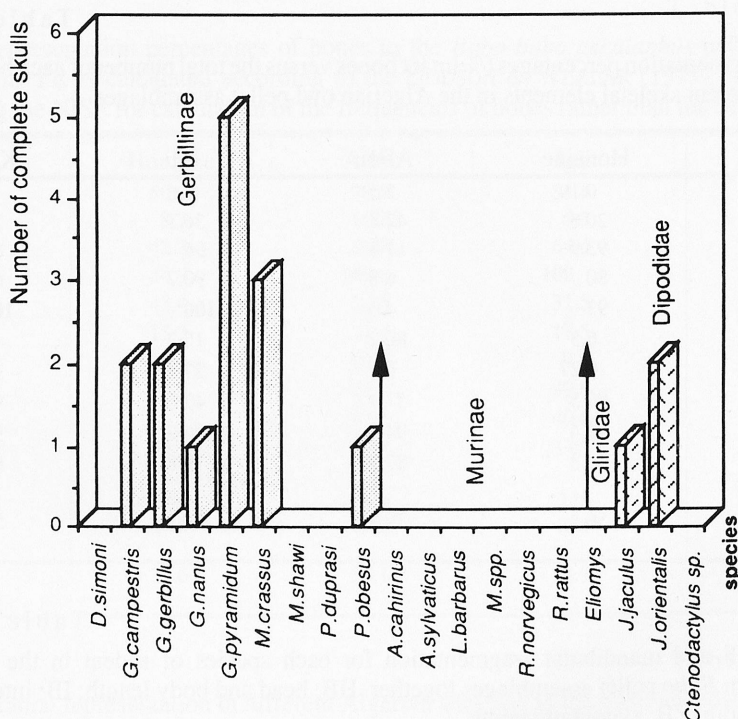
Fig. 3. Skull preservation (number of complete skulls) per species for all the Algerian pellet assemblages together. Only Gerbillinae and Dipodidae are represented by complete skulls.

C. whitakeri show one and three complete skulls, respectively . None of the Murinae is represented by a complete skull (Fig. 3).

Meriones, Gerbillus pyramidum and *Jaculus* are medium sized rodents in the prey spectrum of *Bubo bubo*. Nevertheless, they demonstrate better preservation of complete skulls and larger skull fragments than other mammals (Table VI). These three taxa will therefore have better chances of fossilization and will also be more resistant to diagenesis than others. Size is not the only factor influencing fragmentation of the skulls (Fig. 4), because it has been noted that the very small *Gerbillus nanus* is represented by a complete skull, while *Mus musculus*, a murine of the same size, is not (Table VI). Skull fragmentation is lower for Gerbillinae than for Murinae and this can affect the future fossilization of their remains. In order to investigate the effect of number of individuals on skull preservation, these two parameters have been plotted in Fig. 5. This figure shows that Dipodidae are represented by very few individuals, but with well preserved, nearly complete skulls. For Gerbillidae alone there is no correlation between the size of the sample and the number of complete skulls. *Jaculus* has the widest interorbital constriction (Table VI) and this favours a better preservation of its skull than any Gerbillinae. On the other hand, the interorbital region, which is a weak zone of the skull, is wider and more strongly built in Gerbillinae than in Murinae (Fig. 4).

There are only four nearly complete skulls of *Crocidura* preserved in Honaine and Aflou. All of these have lost the tympanic bullae. The fragmentary skulls show different types of breakage, either just behind the molar rows or behind the frontal or the parietal bone. The very small number of isolated maxillaries indicates that the skull of *Crocidura* has a good resistance to fragmentation, the back of the skull, and especially the tympanic region, being a zone of resistance for this taxon.
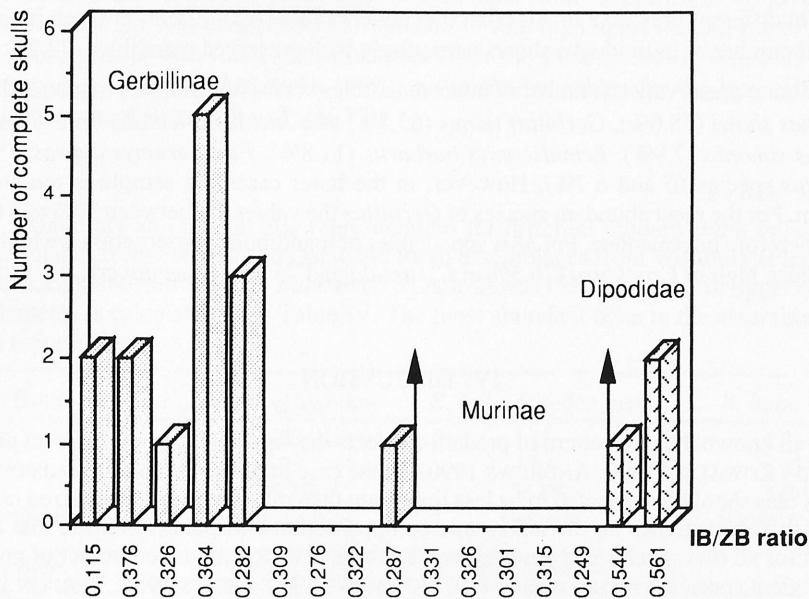
Fig. 4. Skull preservation (number of complete skulls) versus skull size (ratio IB/ZB) for all the Algerian pellet assemblages. IB: Interorbital constriction width; ZB: bizygomatic width of the skulls. Among Gerbillinae, the highest value of the ratio corresponds to the highest number of complete skulls.
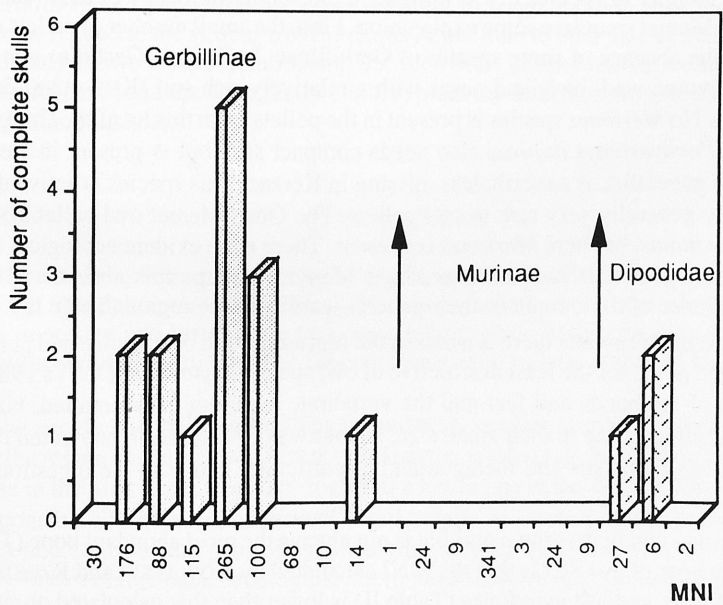
Fig. 5. Skull preservation (number of complete skulls) versus the MNI for each species for all the Algerian pellets together. It is shown here that the highest MNI does not necessary correspond to the highest number of complete skulls.

M a n d i b l e   f r a g m e n t a t i o n. The preservation rates of mandibles are different in different prey taxa in Algerian owl pellets (Table VI). *Eliomys*, which is represented by a small number of individuals, shows particularly well preserved mandibles (72.2% intact).

Mandibular preservation (number of intact mandibles versus total number of mandibles) is high in *Meriones shawi* (58.6%), *Gerbillus nanus* (65.5%) and *Jaculus orientalis* (100%), and low in *Dipodillus simoni* (17.9%), *Lemniscomys barbarus* (11.8%), *Pachyuromys duprasi* (3.3%) and both *Rattus* species (0 and 6.7%). However, in the latter cases the sample is too small to be significant. For the most abundant species of *Gerbillus* the values are between 39% and 65%. This taxon is therefore intermediate. For *Mus* spp., values of mandibular preservation are high (66.5%). They are also high in *Crocidura* (76.5% in *C. russula* and 75% in *C. whitakeri*).

IV. DISCUSSION

It is well known that the pattern of predation affects the representation of different prey taxa in owl pellets (KOWALSKI 1990; ANDREWS 1990). In the case of an opportunistic predator like *Bubo bubo*, this bias should be expected to be less important than in other, more specialized raptors. The results of different studies on the taxonomic composition of owl pellets indicate that the bias is important for all owl species and tends always towards a reduction in the number of prey species (6 to 11 rodent species, average around 8-9) (ANDREWS 1990; DENYS 1985; VERNON 1972). The highest number of species observed in some fossil cave assemblages allows us to suspect a mixing of the prey of different predators, rather than a different pattern of species abundance and diversity in the past.

It has been shown above that *Bubo bubo* does not necessary feed on the characteristic taxa of a given biogeographical region or vegetation zone. This can lead to erroneous biogeographical or palaeoecological interpretations of a fossil fauna originating from prey of such a predator.

The lower number of species of Gerbillinae in the southernmost owl pellet faunas of Algeria (Kerzaz, Oued Meniet) requires some explanation. First, the small number of pellets or individuals could explain the absence of some species of Gerbillinae. In Kerzaz, *Gerbillus nanus* is missing. This species favours wadi beds and oases with a relatively rich soil (KOWALSKI & RZEBIK-KO-WALSKA 1991). No *Meriones* species is present in the pellets from this locality. This genus requires compact soil. *Pachyuromys duprasi* also needs compact soil, but is present in Kerzaz. Finally, *Psammomys*, a generalist, is nevertheless missing in Kerzaz. This species is active during the day and is therefore generally very rare in owl pellets. The Oued Meniet owl pellet assemblage also lacks *Gerbillus nanus*, but here *Meriones* is present. There is no evident ecological reason for the absence of some gerbillids in Kerzaz or Oued Meniet. Perhaps this absence is related to the relatively small size of the sample or their general scarcity in the region (Table II).

In the Algerian owl pellets there is a bias in the representation of scapulae and pelves. This bias has already been noted for the least destructive of owl species, *Tyto alba* (DENYS 1985, 1994). The smaller bones of the hands and feet and the vertebrate have not been counted, but their loss is always very significant due to their small size. ANDREWS (1990) has already noted that the loss of small foot bones (phalanges and metapodials) in particular, is due to the ingestion mode of the predator.

In the Algerian owl pellets the mandible is not always the most abundant bone (Table III). One of the consequences of this fact is that the MNI calculated by KOWALSKI and RZEBIK-KOWALSKA on the basis of right and left mandibles (Table II) is lower than that calculated on the basis of the most abundant paired bone used for the representation percentage (Table III).

The loss of other skull elements relative to the number of mandibles is also a characteristic of differential preservation in the Algerian *Bubo bubo ascalaphus* pellets. A survey of bone abundance

in different European *Bubo bubo* pellet assemblages (data from ANDREWS 1990) gives the same result (Table VII). The loss of upper skull fragments is very high in the nesting site of *Bubo bubo* (75.5%). Comparison with fossil accumulations from the Pleistocene of Westbury (England) attributed to *Bubo bubo* by ANDREWS (1990) gives similar values for the loss of upper skull fragments, but with distinct ratios (Table VII).

Table VII

Maxillary and mandibular representation for different modern *Bubo bubo* assemblages from Sweden and Qatar and fossil assemblages from Westbury (Pleistocene, England) attributed to *Bubo bubo* by ANDREWS (1990). The loss of upper skull elements is calculated as in Table IV. The most abundant bone in the assemblages is reported here

Bone	*B. bubo* Sweden	*B. bubo* Sweden, nest	*B. bubo* Qatar
Maxillary	23	13	42
Mandible	29	53	43
Loss	**20.7%**	**75.5%**	**3.40%**
Most abundant bone	Femur	Humerus	Humerus-Radius

Bone	Westbury 11/4	Westbury 15/4	
Maxillary	320	16	
Mandible	450	92	
Loss	**29%**	**82.6%**	
Most abundant bone	Femur	Tibia	

Skull fragmentation is different from one taxon to another. According to data in this study, the skulls of Gerbillinae and Dipodidae are more resistant to fragmentation than those of Murinae. This seems to be related to the structure of the skulls rather than to their size or abundance. LYMAN (1984) has already shown a direct relationship between bone density and differential survivorship of large mammal fossils and the latter factor could explain the differential capacity for fossilisation of some small mammal taxa.

V. CONCLUSIONS

Three different biases in the preservation of Algerian owl pellets have been found in the present study. These are a faunal representation bias, a bone representation bias and a bone fragmentation bias. All are important and result from processes taking place before fossilization. They occur during predation and digestion, but have repercussions even in later stages of fossilization, such as diagenesis.

Bubo bubo ascalaphus pellet assemblages contain a smaller number of rodent species than expected for the region and indicate different faunal associations (e. g., have a higher representation of Gerbillinae in the high plateau contact zone and a lower one in the desert). Identification of the predator responsible for the accumulation of fossil faunas, evaluation of the influence of time of accumulation and study of the possibility of mixing of prey of different predators can help to estimate these biases before palaeoecological interpretations are made. Some limitations in the use of the ratio Murinae/Gerbillinae are demonstrated here, as this ratio is also biased by predation.

It is here confirmed that bone representation biases are especially characteristic of scapulae and pelves, which as a result of digestion have a lower representation percentage and a very high fragmentation rate. This confirms the observations of RACZYŃSKI & RUPRECHT (1974) and

ANDREWS (1990) for other owls. The loss of maxillaries relative to mandibles is significant and can reach 54% in *Bubo* pellets. This is a high proportion, but corresponds to the value observed in karstic fossil sites.

The main result of the present study is that Gerbillinae (and among them *Meriones*) is the taxon in which skull elements best resist digestion. Genera of this sub-family are the most common rodents in the owl pellet assemblages studied in the present paper. In the fossil fauna of Tighenif (Algeria, Middle Pleistocene), it is the dominant rodent (DAUPHIN et al. 1995). This is perhaps not an indication of a dominance of this taxon in the past, but rather of its ability to resist fossilization.

Pre-fossilization factors occurring during predation and digestion seem to affect the initial composition of future fossil small mammal assemblages rather strongly. In order to have a better estimate of palaeoecological and palaeobiogeographical biases, it is necessary to determine whether we are dealing with one predator or with a mixture of prey of different predators when studying a fossil fauna. It is also necessary to carefully evaluate the completeness and richness of a fossil fauna before any interpretation is made. A similar approach must be taken into account when studying owl pellet assemblages. The next stage of taphonomic study is that of post-depositional biases during fossilization and diagenesis. The latter would also affect the composition of the small mammal fauna. All these alterations must be kept in mind when palaeoecological or palaeobiogeographical interpretations are being made.

REFERENCES

ANDREWS P. 1990. Owls, caves and fossils. Natural History Museum Publications, London.

DAUPHIN Y., KOWALSKI K., DENYS C. 1995. Assemblage data and bone and teeth modifications as an aid to paleoenvironmental interpretations of the open-air Pleistocene site of Tighenif (Algeria). Quaternary Research, **42**: 340-349.

DENYS C. 1985. Nouveaux critères de reconnaissance des concentrations de microvertébrés d'après l'étude des pelotes de chouettes du Botswana. Bulletin du Museum national d'Histoire naturelle, 4è serie, 7, Section A, **4**: 879-933.

DENYS C. 1986. Le gisement Pliocène de Laetoli (Tanzanie, Afrique de l'Est): analyse taphonomique des assemblages de microvertébrés. Palaeontographica, **194**: 69-98.

DENYS C. 1989. Two new Gerbillids *(Rodentia, Mammalia)* from Olduvai Bed I (Pleistocene, Tanzania). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **178**: 243-265.

DENYS C. 1994. Introduction générale. Taphonomie des microvertébrés. Méthodologie et état de l'art. In: Outillage peu élaboré en os et bois de Cervidés IV. Taphonomie/Bone modification. Artéfacts, **9**: 195-206.

DENYS C., GERAADS D., HUBLIN J. J., TONG H. 1987. Méthode d'étude taphonomique des microvertébrés. Application au site Pléistocène de Tighenif (Ternifine, Algérie). Archaeozoologia, **1**: 53-82.

DODSON P., WEXLAR D. 1979. Taphonomic investigations of owl pellets. Palaeobiology, **5**: 275-284.

FERNANDEZ-JALVO Y. 1992. Taphonomia de microvertebrados del complejo carstico de Atapuerca (Burgos). Tesis Doctoral, Universidad complutense, Madrid.

FERNANDEZ-JALVO Y., ANDREWS P. 1992. Small mammal taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. Journal of Archaeological Science, **19**: 407-428.

FRY C. H., KEITH S., URBAN E. K. 1988. The birds of Africa. Vol. III. Academic Press, London and New York.

JACKSIC F. M., MARTI C. D 1984. Comparative food habits of *Bubo bubo* in Mediterranean-type ecosystems. The Condor, **86**: 288-296.

JAEGER J. J. 1976. Les rongeurs (Mammalia, Rodentia) du Pléistocène Inférieur d'Olduvai Bed I (Tanzanie). 1ère partie: Les Muridés. Fossil Vertebrates of Africa, **4**: 57-122.

KOWALSKI K. 1990. Some problems of the taphonomy of small mammals. International Symposium on the Evolution, Phylogeny and Biostratography of Arvicolids, Praha, pp. 285-296.

KOWALSKI K. 1995. Taphonomy of bats. Geobios, Mémoire Spécial, First European Congress of Palaeontology, 18: 251-256.

KOWALSKI K., RZEBIK-KOWALSKA B. 1991. Mammals of Algeria. Ossolineum, Wrocław, Warszawa, Kraków, pp. 1-367.

LYMAN R. L. 1984. Bone density and differential survivorship of fossil classes. Journal of Anthropological Archaeology, **3**: 259-299.

RACZYŃSKI J., RUPRECHT A. L. 1974. The effect of digestion on the osteological composition of owl pellets. Acta ornithologica, **14**: 5-38.

VERNON C. J. 1972 An analysis of owl pellets collected in southern Africa. Ostrich, **43**: 109-124.