

# Differential representation of gerbilids in European eagle owl (*Bubo bubo ascalaphus*) pellets from Southwestern Algeria

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## Introduction

Nocturnal raptor pellets analyses are useful for different kinds of scientific purposes. For ecological and zoological studies, undigested prey remains sometimes constitute a useful source of data for small mammal taxa which could have not been observed/trapped in the field. They also allow diet analysis for predator-prey relationship studies. In these cases, preys are mainly identified and counted from skull/teeth material. Studies on skeletal material recovered from pellets are also undertaken in order to understand the origin and the paleoecological signification of small mammal fossil assemblages (MAYHEW, 1977; KORTH, 1979; DODSON and WEXLAR, 1979; DENYS, 1985, 1986; HOFFMAN, 1988; KUSMER, 1990; ANDREWS, 1990; DENYS *et al.*, 1996; SAAVEDRA and SIMONETTI, 1998). This kind of approach, i.e. taphonomic analysis, consists essentially in counting the skeletal elements representation and assessing their degradations (breakage and digestion) by different kinds of raptor species. It aims to outline criteria for recognizing predators and hence evaluate their consequences on fossil accumulation (ANDREWS, 1990; FERNANDEZ-JALVO *et al.*, 1998).

However, different raptors are able to reject several pellets within 24 hours: some are regurgitated during the day and concentrated at the roost, while others are randomly rejected and spread throughout the hunting territory during nocturnal foraging activities. Indeed, raptor roost pellets only represent a part of the diet (GUÉRIN, 1928; KORTH, 1979; GÉROUDET, 1984). Different studies have also indicated that a same meal can be rejected among several successive pellets. For instance, LOWE (1980) has noted that some bones have been kept in a tawny owl stomach during two days. CARPENTIER (1934) mentioned the simultaneous rejection of three pellets by the eagle owl, which has conducted GUÉRIN (1934) to propose that a heavy meal is rather rejected within several pellets. In fact, such observations are frequently noted for largest preys remains by those who study owls diet (e.g. BAUDVIN *et al.*, 1995; GANEY, 1992; SOUTHERN, 1954), but there is still no quantification of this pattern. In almost all studies dealing with pellets, this loss of skeletal parts is neglected for a number of skeletal elements or prey number calculation. Indeed, when the whole rejected pellets can not be examined, how is this loss of pellets and multirejection of preys likely to affect the representation of skeletal elements data for both ecological or taphonomic analyses? This pellet study is the first attempt to evaluate this problem of prey multirejection and its consequences for diet or taphonomic bias estimations.

## Material and methods

Thirty pellets of *Bubo bubo ascalaphus* have been selected for their perfect preservation state from a sample of 300 pellets. They have been recovered in December 1997 in several sites of the palm grove of Krouaa (Beni Abbès region, SW Algeria). The diet of this owl in this region is essentially composed of Gerbilids (genera *Meriones* and *Gerbillus*), which are found by one to three individuals per pellet.

The skeletal content of each pellet has been sorted manually and separated from those of other pellets. The main elements have been counted: long bones (humerus, tibia, femur, radius, ulna), flat bones (scapula and pelvis), molars and incisors, maxilla and mandibles. A skull is considered to be present if more than half of its parts is present

within a pellet, and intact if at least the different parts from nasals to frontals are joined. Teeth digestion intensity has been noted according to FERNANDEZ-JALVO and ANDREWS (1992).

Rodent remains have been separated and counted according to two different size classes: adult/subadult *Meriones* and jerboa (g. *Jaculus*) in class 1 (80-140g) and gerbils (*Gerbillus* spp.) and young *Meriones* (of which small postcranial elements could have been mistaken for gerbil ones) in class 2 (20-60g).

Because only 10% of the whole pellets have been sorted, the probability that one individual was recovered within several of the selected pellets (i.e. that different bones of the same prey was spread over different pellets) was very low. Indeed, the total number of preys is the sum of the number of preys counted from each pellet, whatever the latters are identified by a complete skeleton or one single bone. Relative rates of representation (relative completeness percentage),  $R_i$ , have been calculated for each element: they correspond to the total number of elements divided by the number of these elements expected if whole prey skeleton was regurgitated (i.e. 12 for molars, 4 for incisors, 2 for maxilla, mandibles, long and flat bones). Two rates of representation have been calculated:  $R_1$ , calculated from the minimum number of each kind of preys ( $R_{1a}$  for class 1 and  $R_{1b}$  for class 2), and  $R_2$ , according to the number of rejected prey (s) in the pellet ( $R_{2a}$  for one prey per pellet,  $R_{2b}$  for more). The mean relative representation for each skeletal element, calculated from the number of whole preys is noted  $Pr$ .  $Pr_2$  is the mean representation calculated from the most numerous elements (which gives the minimum number of individuals, or MNI), as it is usually made from a fossil bone or a pellet assemblage.

## Results

### *Distribution of taxa*

The content of each pellet is listed in table 1. The remains of 47 rodents have been recovered (46 gerbilids and one jerboa). Sixteen of these rodents have been rejected alone in a single pellet, 11 pellets contained the remains of two individuals and the last three, of three.



element	Rodent size :		Number of prey/pellet :				TOTAL				
	Class 1		Class 2		1 prey/pel.		> 1 preys/pel.		N	Pr	Pr2
	N	R1a	N	R1b	N	R2a	N	R2b			
<b>Humerus</b>	33	63,5	27	64,3	22	68,8	38	61,3	60	63,8	81,1
<b>Tibia</b>	37	71,2	27	64,3	27	84,4	37	59,7	64	68,1	86,5
<b>Femur</b>	39	75,0	35	83,3	27	84,4	47	75,8	74	78,7	100,0
<b>Radius</b>	38	73,1	25	59,5	24	75,0	39	62,9	63	67,0	85,1
<b>Ulna</b>	36	69,2	28	66,7	21	65,6	43	69,4	64	68,1	86,5
<b>Scapula</b>	33	63,5	17	40,5	17	53,1	33	53,2	50	53,2	67,6
<b>Pelvis</b>	37	71,2	30	71,4	24	75,0	43	69,4	67	71,3	90,5
<b>total postcr.</b>	253	69,5	189	64,3	162	72,3	280	64,5	442	67,2	85,3
<b>Maxilla</b>	40	76,9	26	61,9	29	90,6	37	59,7	66	70,2	89,2
<b>Mandible</b>	41	78,8	22	52,4	28	87,5	35	56,5	63	67,0	85,1
<b>upper molar</b>	120	76,9	51	40,5	85	88,5	85	45,7	170	60,3	76,6
<b>lower molar</b>	121	77,6	53	42,1	83	88,5	92	49,5	175	62,1	78,8
<b>total molars</b>	241	77,2	104	41,3	168	87,5	177	47,6	345	61,2	77,7
<b>upper incisor</b>	40	76,9	25	59,5	28	87,5	37	59,7	65	69,1	87,8
<i>digested up. inc.</i>	16	40,0	4	16,0	16	57,1	4	10,8	20	30,8	27,0
<b>lower incisor</b>	41	78,8	22	52,4	28	87,5	35	56,5	63	67,0	85,1
<i>digested low. inc.</i>	7	17,1	0	0,0	7	25,0	0	0,0	7	11,1	9,5
<b>total incisors</b>	81	77,9	47	56,0	56	87,5	72	58,1	128	68,1	86,5
<i>digested incisors</i>	23	28,4	4	8,5	23	41,1	4	5,6	27	21,1	36,5
<b>Skull</b>	21	80,8	13	61,9	15	93,8	19	61,3	34	72,3	91,9
<b>MNP/MNI</b>	26 / 21		21 / 18		16 / 15		31 / 24		47	37	

Table 2

Representation of the different skeletal parts according to the size (class 1 and 2 : R1a and R1b) and the number of prey per pellet (1 and 2-3 : R2a and R2b).

Twenty-six rodents have been classified in class 1. The remains of 14 of them have made up the content of a similar number of single-prey pellets. Nineteen preys of the class 2 were concentrated in 10 2/3-prey pellets, vs two in a single-prey pellet.

## **Bone and teeth representation**

Rates of representation according to size class and number of prey per pellets are detailed in table 2.

### **Skull and teeth**

Thirty-four skulls have been recovered (72% of the total preys). Among them, 21 belong to the 26 class 1 rodents (R1a = 81%), and 15 belong to single-prey pellets out of 16 (R2a = 94%). Only 13 skulls belong to the 21 detected class 2 rodents (R1b = 62%) and 19 to the 31 preys found in pellets with remains of 2 or 3 individuals (R2b = 61%).

Nineteen skulls were found intact: 11 recovered from the 16 single-prey pellets, and 17 being from class 1 rodents. Few maxilla or mandibles have lost their teeth: the consequences are a best molar representation in single-prey pellets (R2a = 87.5%) compared with 2/3- prey pellets (R2b = 47.6%), as well as for class 1 (largest) rodents (R1a = 77.2%) compared with class 2 rodents (R1b = 41.3%).

Incisors are slightly more numerous than molars, particularly for class 2 rodents (R1b = 56%) and several-prey pellets (R2b = 58.1%), but the best representation remains for class 1 incisors (R1a = 77.9%) and within single-prey pellets (R2a = 87.5%).

### **Postcranial elements**

The discrepancies of the mean representation values according to the kind of preys and pellets are less important for whole postcranial bones than teeth: R1a = 69.5% against 64.3% for R1b, but the single-prey pellets have provided 72.3% of the expected number of bones against 64.5% for the others (tabl. 2). The variation of skeletal element representation according to the size of preys is especially important for radius (R1a = 73.1%, R1b = 59.5%) and scapula (R1a = 63.5%, R1b = 40.5%). According to the number of preys per pellet, the discrepancies are important for tibia only (R2a = 84.4%, R2b = 59.2%).

Femurs are the best represented elements in all cases (Pr = 78.7%). The lowest rate of completeness is that of the scapula (between 40.5%

and 63.5%, Pr = 53.2%). Other bones are represented from around 60% to 75% of their theoretical number.

### Completeness of individuals

When the whole skeleton is considered, the representation of individuals is very variable according to the preys and the number of preys within the pellets.

– In single-prey pellets, 11 prey skeletons have only lost 23 postcranial bones (15% of total), one maxilla and two mandibles (7%). Only one individual is represented by all its postcranial parts without the skull (pellet 17), and 4 are mainly represented by their cranial parts, with three or six long or flat bones out of 14 (pellets 8, 11, 16 and 19).

– In several-prey pellets, three of class 1 rodents have no skull, but the main part of their postcranial bones (pellets 4, 10, 27). One prey is represented by its skull with only two long bones (pellet 9), and a case is intermediate (one mandible with 5 postcranial bones: pellet 23). Seven preys out of the 19 class 2 rodents in these pellets are only represented by their postcranial bones (pellets 2, 13, 18, 12, 21, and 27) and one by one maxilla and mandible with a pelvis (pellet 30). The smallest gerbils (*Gerbillus nanus*, 3 individuals) are represented in two cases by only one femur (pellet n° 20 and 30) with one broken maxilla and a mandible (pellet 30). Other gerbils are represented by a femur and a broken pelvis in one case (pellet 18), and by a single ulna in another one (pellet 21).

### Digestion

Twenty-seven incisors show digestion traces (Pr = 21.1%). Among them, 23 are from class 1 rodents in single-prey pellets. Twenty are upper incisors (74.1%). Indeed, 40% of class 1 upper incisors are digested (n = 16) vs only 16% of class 2 incisors (n = 4). All digested lower incisors are those of class 1 rodents (R1a = 17,1%).

The digestion intensity is very light (grade 1), except for three teeth (grade 2 and 3). No molar shows any digestion.

## Discussion

These results outline that losses of bones/skulls follow a peculiar pattern. The most important loss of elements is either due to the absence of skull (11 cases) or the absence of more than 50% of postcranial bones, while the skull is present (4 cases). Four individuals are represented by less than 3 bones alone in the pellets. Only one case is intermediate (with both high loss of cranial and postcranial bones). So, this absence of skull or postcranial parts is not due to digestion because bones are not particularly digested, except in two cases when two postcranial bones are the only remains of a single individual,

Selective decapitation observed in several raptor preys may sometimes explain this lack of skulls, but it concerns essentially the largest preys. *Bubo bubo ascalaphus* prey decapitation has been noted when feeding owlets: adults consume the head and let the body to their young. But in this case, pellets are mainly constituted by prey skulls (VEIN and THÉVENOT, 1978).

Indeed, a frequent multirejection of prey skeletal elements seems to be the most logical explanation. Two/three-prey pellets are particularly affected, and this deficiency in skulls underestimates the presence of the smallest preys if calculations are made from the dental/cranial material only: 13 preys are counted against 21 from postcranial elements (-33%), while this underestimation is less than 20% for the largest rodents (21 preys against 26). Adult *Meriones* and other large preys could be sufficiently large to be eaten one by one and digested in consequence. On the contrary, other preys are too light to constitute a unique meal alone: so, several preys have to be eaten to constitute a sufficient meal for the owl. As the skeletal volume of several small preys is more important than that of a large prey, a part of such small prey could then be rejected within a second pellet.

The volume of the skull is relatively important when compared with postcranial bones, and this could lead to an easy separation of the skull from the other bones when a second pellet must be elaborated by the owl. This can explain the major pattern observed in our samples (loss of the skull or postcranial elements). The rejection of different pellets is not necessarily simultaneous: the two cases where only a few bones identified an individual (pellets 18 and 20), they were more



heavily digested than other intact preys in the same pellet, certainly because of a retention in the stomach and a longer digestion.

The same law of rejection could apply if a prey is too large (e.g. pellet 11). As rodents are often decapitated when they are too large to be swallowed, one may think that if the skull and the skeleton form a too large volume for a single potential pellet, part of the bones would remain in the stomach to be rejected with the next pellet (with or without another prey). Data about *Tyto alba* largest preys in South Africa tend to confirm these observations (LAUDET, 2000). Additionally, because their skull seems to be more resistant than that of other preys (COETZEE, 1963; DENYS *et al.*, 1996), gerbilids could be particularly affected by these kinds of bias.

We can also note that teeth from single-prey pellets are more frequently digested than others: perhaps this ideal size of prey (or digestible parts) would favour prey digestion.

Consequences of these observations and hypotheses that can be drawn from them are multiple:

1) Counting preys from skull elements only is not exhaustive. The fact that different kinds of prey are not rejected in the same way can affect significantly their relative frequencies in the diet, if calculated from skulls only. The error will be dependent on the completeness of the pellets recovering. For instance, the diet of our owl (s) calculated from skulls is 62% of class 1 (n = 21) and 38% (n = 13) of class 2 rodents, while the same rates, calculated from postcranial elements pellet by pellet are 55% (n = 23) and 45% (n = 21), respectively. If the different postcranial elements are mixed and considered as a whole, the proportion of preys is quite similar to the precedent one: 54% (n = 21) of class 1 and 46% of class 2 (35 femurs, n = 18).

2) These results could also affect data in usual taphonomic analyses. Until now, taphonomic data on pellets are relatively rare, and most analyses have been made on small samples of pellets (generally around 30-50 pellets, ANDREWS, 1990), recovered from natural settings for which the number of swallowed preys is unknown. Our results show that losses of skeletal elements are not only due to digestion – which rate is useful for recognizing predators – but can vary according to the kind of preys and the quality of the recovering. Multirejection of prey hypothesis suggests that most teeth are rather lost by non-recov-

Localities	Beni Abbès	Qatar (1)	Honaine (2)	Aflou (2)	Igli (2)	Kerzaz (2)
Humerus	81,1	98,1	43,4	57,4	31,5	18,2
Tibia	86,5	67,3	44,9	100	100	100
Femur	100,0	94,2	50	98,6	84,4	66,4
Radius	85,1	88,5	14,2	20,4	9,5	7,3
Ulna	86,5	90,4	15,2	31,7	17,5	10
Scapula	67,6	80,8	8,2	16,7	5,9	3,6
Pelvis	90,5	86,6	42,2	86,8	64,4	48,2
Total postcranial	85,3	86,6	31,2	58,8	44,7	36,2
Maxilla	89,2	82,4	48,7	47,4	40,6	31,8
Mandible	85,1	80,8	99,9	83,4	99,6	99,1
Molar	77,7	23,1				
Incisor	86,5	32,7				
MNI	37	26	548	442	341	130

Table 3

Representation (in %) of skeletal parts from *Bubo bubo ascalaphus* pellets. The minimum number of individuals (MNI) was calculated from the most abundant recovered bone elements.

(1) from ANDREWS (1990), (2) from DENYS *et al.* (1996).

ering of pellets (where skulls or bones have been rejected), than by digestion only. For example, our sample has been subjected to a mean loss of 33% of bones and 39% of molars: these high losses are mainly due to the lack in our sample of the pellets where these missing cranial or postcranial parts have been "multirejected". Indeed, these results could explain the important differences observed between taphonomic studies dealing with raptors preys, and particularly *Bubo bubo ascalaphus* ones (tabl. 3).

Additional analyses should be performed to have a better idea of potential biases associated with preys and skeletal elements within pellets. These biases appear more complex than previously thought. The relative size of a predator and its preys could be the main factor explaining the distribution of skeleton parts within pellets. The size of the first prey eaten will also determine the choice of hunting for a second prey or not (thus increasing or not the probabilities of rejec-

tion of a second pellet). This also means that timing and locations of foraging activities of preys are also important factors.

In conclusion, if these observations are confirmed by further studies, they could help precise diet estimations and ecological conclusions in bringing correction factors for prey species representation. Also, they will enable to better predict taphonomic biases in fossil rodent assemblages. However, we encourage the use of postcranial bones per pellet to accurately estimate the number of preys eaten, particularly when studying small samples taken in owl roosts, and if the size spectrum of preys is relatively large.

## References

- ANDREWS P., 1990 —  
*Owls, caves and fossils*. London,  
Natural History Museum publications,  
London, 231 p.
- BAUDVIN H., GENOT J.C.  
and MULLER Y., 1995 —  
*Les rapaces nocturnes*.  
Paris, Sang de la Terre, 303 p.
- CARPENTIER C. J., 1934 —  
Le pluri-rejet quotidien de pelotes  
par *Bubo bubo ascalaphus*.  
*Oiseaux*, 4: 353-355.
- CHITTY D., 1938 —  
A lab study pellet formation in  
the short-eared owl. *Proceedings  
of the Zoological Society of London*,  
108 (A): 267-287.
- COETZEE C.G., 1963 —  
The prey of owls in the kruger  
National Park as indicated by owl  
pellets collected during 1960-61.  
*Koedoe*, 6: 115-125.
- DENYS C., 1985 —  
Nouveaux critères de  
reconnaitances des concentrations  
de microvertébrés d'après l'étude des  
pelotes de chouettes du Bostwana.  
*Bulletin du Muséum National  
d'Histoire Naturelle*, 4<sup>e</sup> série 7,  
Section A, 4: 340-349.
- DENYS C., 1986 —  
Le gisement Pliocène de Laetoli  
(Tanzanie, Afrique de l'Est): analyse  
taphonomique des assemblages  
de microvertébrés. *Paleontographica*,  
194: 69-98.
- DENYS C., DAUPHIN Y.,  
RZEBIK-KOWALSKA B.  
and KOWALSKI K., 1996 —  
Taphonomic study of algerian owl  
pellet assemblages and differential  
preservation of some rodents:  
palaeontological implications.  
*Acta Zoologica Cracoviense*,  
39 (1): 103-116.
- DODSON P. and WEXLAR D., 1979 —  
Taphonomic investigations of owl  
pellets. *Palaeobiology*, 5: 275-284.
- DUKE G.E., JEGERS A.A., LEFF G.  
and EVENSON O., 1975 —  
Gastric digestion in some raptors.  
*Comparative Biochemistry and  
Physiology*, 50 (A): 649-656.
- ERRINGTON P. J., 1930 —  
The pellet analysis method of raptor  
food habits study. *The Condor*,  
32: 292-296.

- FERNANDEZ-JALVO Y. and ANDREWS P., 1992 — Small mammal taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. *Journal of Archaeological Science*, 19: 407-428.
- FERNANDEZ-JALVO Y., DENYS C., ANDREWS P., WILLIAMS C.T., DAUPHIN Y. and HUMPHREY L., 1998 — Taphonomy and Paleocology of Olduvai Bed-I (Tanzania). *Journal of Human Evolution*, 34: 137-172.
- GANEY J. L. 1992 — Food habits of the mexican spotted owls in Arizona. *The Wilson Bulletin*, 104: 321-325.
- GÉROUDET P., 1984 — *Les rapaces diurnes et nocturnes d'Europe*. Neufchâtel, Delachaux et Niestlé, 426 p.
- GUÉRIN G., 1928 — *La vie des chouettes: Régime et croissance de l'effraie commune (Tyto alba) en Vendée*. Paris, 157 p.
- GUÉRIN G., 1934 — Le pluri-rejet quotidien de pelotes par *Bubo bubo ascalaphus* (commentaires). *Oiseaux*, 4: 356-358.
- HOFFMAN R., 1979 — The contribution of raptorial birds to patterning in small mammal assemblages. *Paleobiology* 14 (1): 81-90.
- KORTH W.W., 1979 — Taphonomy of micovertebrate fossil assemblages. *Annals of the Carnegie Museum*, 48: 235-285.
- KUSMER K., 1990 — Taphonomy of owl pellet deposition. 1990. *Paleontology*, 64: 629-637.
- LAUDET F., 2000 — *Caractérisation taphonomique des gisements oligocènes karstiques à petits vertébrés fossiles des phosphorites du Quercy (SW France)*. Thèse doct., univ. Montpellier-II, 219 p.
- LOWE V. P. W., 1980 — Variation in digestion of prey by the tawny owl. *Journal of Zoology*, 193: 283-293.
- MAYHEW D. F., 1977 — Avian predators as accumulators of fossil mammal material. *Boreas*, 6: 25-31.
- RACZYNSKI J. and RUPRECHT A. L. 1974 — The effect of digestion on the osteological composition of owl pellets. *Acta Ornithologica*, 14: 5-38.
- SAAVEDRA B. and SIMONETTI J. A. 1998 — Small mammal taphonomy: intraspecific bone assemblage comparison between South and North American barn owl, *Tyto Alba* populations. *Journal of Archaeological Science*, 25 (2): 165-170
- SANCHEZ V., DENYS C. and FERNANDEZ-JALVO Y., 1997 — Origine et formation des accumulations de microvertébrés de la couche 1a du site du Monte di Tuda (Corse, Holocène). Contribution à l'étude taphonomique des micromammifères. *Geodiversitas*, 19 (1): 129-157.
- SOUTHERN H.N. 1958 — Tawny owl and their preys. *Ibis*, 96: 384-410.
- VEIN D. and THÉVENOT M., 1978 — Étude sur le hibou Grand-Duc *Bubo bubo ascalaphus* dans le Moyen-Atlas Marocain. *Nos Oiseaux*, 34: 347-351.