Acta zoologica cracoviensia, **45**(special issue): 341-355, Kraków, 29 Nov., 2002

Owls, multirejection and completeness of prey remains: implications for small mammal taphonomy

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Received: 11 Sep., 2001
Accepted for publication: 21 Dec., 2001

LAUDET F., DENYS Ch., SENEGAS F. 2002. Owls, multirejection and completeness of prey remains: implications for small mammal taphonomy. In: Proceedings of the 4th Meeting of the ICAZ Bird Working Group Kraków, Poland, 11-15 September, 2001. *Acta zoologica cracoviensia*, **45**(special issue): 341-355.

Abstract. For more than twenty years, taphonomic studies have focused on bone and teeth modifications from owl prey remains due to digestion (fragmentation, dissolution by gastric juices) in order to recognize which predator(s) has (have) originated fossil bone assemblages and which bias could have occurred in terms of paleoenvironmental and archaeological interpretations. Such studies have neglected the fact that meals, particularly when large prey individuals are eaten, are sometimes spread within several pellets. This study aims to estimate the occurrence and the taphonomic consequences of prey multirejection within modern Barn Owl pellet samples recovered in the wild from France and South Africa, and establish their different diets. The taphonomic observation of the contents of each pellet has displayed patterns of completeness of prey skeleton proportionate to the size of prey per pellets. In the African owl pellets 60% of the largest rodents are represented by the postcranial parts without the skull and/or some complete limbs, or are represented by the skull only. The pattern for small prey species is less than 20%. The pellets from France include remains of small rodents and shrews, the skeletons of which rarely exhibit the pattern observed in the African pellets and are more complete, apart from 20% of them represented by only 1 to 4 elements (instead of 13% in African pellets). These bone distributions could indicate a frequent multi-rejection of prey skeletons according to the size and the number of swallowed mammals. This means that the diet and the quality of pellets recovered or preserved through time, could strongly influence the occurrence or the bone representation of some species – particularly the largest ones – within a fossil or modern pellet assemblage, with palaeoecological, ecological (by over-estimation or under-estimation of the number of species) and taphonomic implications (large variations in skeletal representation or digestion criteria). We suggest the development of such an approach in order to obtain accurate taphonomic referentials from modern pellet assemblages.

Key words: taphonomy, *Tyto alba*, small mammal, multirejection, prey, South Africa, France.

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I. INTRODUCTION

A large part of research in small mammal taphonomy aims to understand the role of predators in the formation of bone assemblages, and its consequences to palaeontological interpretations. Remains of small vertebrates from modern raptors have been particularly studied (MAYHEW 1977; DODSON & WEXLAR 1979; KORTH 1979; DENYS 1985; BRAIN 1981; HOFFMAN 1988; KUSMER 1990; HOCKETT 1991; BOCHEŃSKI & TOMEK 1994; DENYS et al. 1996; HOCKETT 1996; BOCHEŃSKI et al. 1997, 1998; POKINES & KERBIS-PETERHANS 1997; SAAVEDRA & SIMONETTI 1998; PINTO & ANDREWS 1999; STEWART et al. 1999), because of the ability of these birds to concentrate rejected pellets around their roost site. Indeed, according to the intensity of bone and tooth damage and loss due to ingestion and digestion (breakages, dissolution by gastric juices), raptors have been classified within 5 categories (ANDREWS 1990; FERNANDEZ-JALVO & ANDREWS 1992). Nocturnal raptors, which cause little damage, are ranked into categories 1 (weakest modifications: e.g. *Tyto alba*), 2 (e.g. *Bubo capensis*) and 3 (e.g. *Strix aluco, Bubo bubo*) while diurnal raptors, because of the higher degree of digestion and breakage of prey remains, are spread within the two last categories. However, studies are still not numerous and samples have rarely contained more than 30 pellets. Some parameters have not been, or are rarely, considered and quantified in terms of taphonomic modifications, like occasional feeding habits (decapitation and dismembering, richness of meal, owlets feeding, seasonal needs of calcium, age of prey individuals (ERRINGTON 1930; CHITTY 1938; RACZYŃSKI & RUPRECHT 1974, VEIN & THEVENOT 1978; LOWE 1980) or the differential survival of prey remains subjected to digestion (DENYS et al. 1996; SAAVEDRA & SIMONETTI, 1998). Furthermore, owl diet specialists sometimes mention that meals could be spread within several pellets (eg. BAUDVIN et al. 1995; GANEY 1992; BRUCE & MC LEAN 1986; SOUTHERN 1954), particularly when the mammalian prey is large, although this fact has never been quantified. This last point has focused the attention of one of us, following the observation of remains from a sample of *Bubo bubo ascalaphus* SAVIGNY, 1809 pellets: skeletons of large gerbils were the best preserved if they were rejected alone in a pellet, whereas skulls or postcranial parts of rodents distributed among several prey pellets were more frequently absent. These results suggested that multirejection of prey individuals could be more frequent than is thought, and in this case, the representation of remains (and dietary estimations) could vary highly according to the quality of pellet sample recovery (LAUDET & HAMDINE 2001). This new study aims to test this hypothesis with a largest sample of pellets of one of the less destructive raptor, the Barn Owl *Tyto alba* (SCOPOLI, 1769). Taphonomic modifications for two kinds of diet are compared with each other: one is composed of minute mammals to large rodents, and the other includes only small rodents and shrews. Taphonomic implications of these observations will be particularly discussed.

Aknowledgements. The authors express their thanks to P. ANDREWS, T. O'CONNOR & J. R. STEWART for their suggestions and improving English corrections. A part of this work has been undertaken during two PhD theses at the laboratory of Paleontology ("paleontologie fondamentale" team), University of Montpellier II.

II. MATERIAL AND METHOD

101 fresh, intact pellets have been selected from two neighbouring localities in South Africa in the region of Gauteng (SENEGAS 2000), and from a locality in Southwestern France. Both sites are karstic formations, where owls rest, and where rich bone concentrations are often preserved in the fossil record.

The first south African sample includes 40 pellets deposited close to the fossil locality of Bolt's Farm (SENEGAS & AVERY 1998), 3 km SW of the famous hominid site of Sterkfontein. They derive from two accumulations of pellets separated by a few meters within the same karstic fissure (pellets were numbered x.1 and y.2).

The second South African sample consists of 33 pellets deposited in a fissure near the fossil site of Drimolen (KEYSER 2000), 7 km from Sterkfontein.

The last sample is made of 28 pellets recovered at the French locality of Pech Crabit (South of the Quercy region, near Limogne) in the bottom of a fissure infilling, whose sediments are famous for their richness in Lower Oligocene small mammals (LAUDET 2000).

Remains have been sorted manually after disaggregating the pellets in water. Each element contained in a pellet was separated from the others. The main skeletal parts have been counted for each prey individual within the pellets: skull elements (maxillae, mandibles and their teeth: molars and incisors), and the main postcranial elements: long bones (humerus, radius and ulna for forelimbs, femur and tibia for hindlimbs), coxal bones (scapula and pelvis). Because of their size, the astragalus and the calcaneus were also taken into account, except for smallest species (shrews and smallest mice) to avoid sampling errors.

African mammals were precisely determined from dental material, and postcranial elements were also identified if teeth were absent when it was possible, by direct comparison with complete skeletons (from other pellets). At least 13 genera and 14 species have been recognized within pellets. They were ranked into three categories according to their size: the largest rodents (the gerbil *Tatera*, the mole rat *Cryptomys*, the vlei rat *Otomys* and the black rat *Rattus*: 80 to 200g), the middle-sized mice (*Steatomys*, *Mastomys*, *Rhabdomys* and *Aethomys*: 20 to 80g), and the smallest mice (*Dendromus*, *Mus)* and shrews (*Suncus*, *Myosorex* and *Crocidura)* (less than 15g).

For Western European mammals, because of the same category of size and taxa, and difficulties of separations of postcranial parts between rodent species, the differentiation was only made between rodent remains (small murids and microtids, mainly represented by *Mus*, *Apodemus* and *Microtus*) and shrews (*Crocidura* and *Sorex*).

Digestion traces on teeth (molars and incisors) were counted (i.e. showing enamel losses: FERNANDEZ-JALVO & ANDREWS 1992), and peculiar observations on bones have also been noted.

For each sample and category of prey individuals, the maximum number of prey individuals (MNP) has been calculated. The MNP corresponds to the addition of the number of mammals individuals recognized in each pellet: it means that different skeletal parts found in several different pellets (i.e. a hindlimb in a first pellet and a skull in an other one) do not belong to a same prey individual, except in peculiar cases. The MNI is the number of individuals (prey) calculated from the best represented of the skeletal elements in the sample based on the number of bones expected from one individual [across the different pellets] (eg. 2 for long and coxal bones, 6 for molars). These MNP and MNI allow the calculation of the relative rate of representation (or relative completeness percentage) for each skeletal part.

III. RESULTS

Tables I, II and III indicate the representation of skeletal parts in pellets for each genus, and for each group of prey species.

Bolt's Farm (Table I)

1. General observations about pellet contents

The remains of 65 rodents and 12 shrews have been recognized from the 40 pellets. A bird phalanx and postcranial bones of an amphibian complete the list of prey taxa (pellet 11.2 and 3.2).

Most frequently the remains of only a single mammal are present within the pellets (n=16): 13 are those of large rodents (10 *Tatera*, 2 *Otomys* and one *Rattus*), 2 belong to the genus *Mastomys* and one to *Rhabdomys*. In general, the remains within these single-prey pellets correspond to the elements of the whole skeleton. That is except for 5 rodents, the skeletons of which are characterised by the absence of one or two hindlimb bones (and a forelimb for one of them), and one *Otomys* represented by the hindlimb bones only. All of these rodents are adult or subadult. In addition a complete skeleton of a multimammate mouse (*Mastomys*) has been rejected with a solitary ulna of another rodent of the same species (pellet 16.2), and the hindlimbs of a mole rat have been rejected with a single long bone from each of two other small mammals (13.1).

Table I

Bone representation of prey individuals in *Tyto alba* pellets from Bolt's Farm (South Africa) according to genus. In bold: residual elements from a prey individual. Grey boxes: losses of complete skull, forelimb or hindlimb. Large rodents: section A; middle-sized rodents: section B; small rodents and shrews: section C)

A – large rodents

	taxa	*Tatera*																						*Otomys*								
	n°pellet	1.1	1.1	2.1	3.1	5.1	7.1	8.1	10.1	11.1	12.1	14.1	17.1	17.1	19.1	2.2	5.2	7.2	11.2	13.2	13.2	15.2	17.2	4.1	6.1	20.1	3.2	9.2	11.2	12.2	14.2	18.2
Cranium	Maxilla	2	1	2	2	2	2	2	2	2	2	2	2	2	2	0	2	2	0	2	0	2	2	2	2	2	2	2	2	0	2	0
	Upper Incisor	2	0	2	2	2	2	2	2	2	2	2	2	2	2	**1**	2	2	0	2	0	2	2	2	2	2	2	2	2	0	2	0
	Upper Molar	2	3	6	3	5	6	6	6	6	5	4	6	6	6	0	6	5	**1**	6	0	0	6	6	6	6	6	6	6	0	6	0
Lower Jaw	mandible	2	2	1	2	2	2	2	2	2	2	2	2	2	2	0	2	1	0	2	0	0	2	2	2	2	2	2	2	0	2	0
	Lower Incisor	2	0	1	2	2	2	2	2	2	2	2	2	2	2	0	2	1	0	2	0	0	2	2	2	2	2	2	2	0	2	0
	Lower Molar	2	3	3	4	5	6	6	6	6	6	5	6	6	2	0	6	3	0	6	0	0	6	6	6	6	6	4	6	0	6	0
Forelimb	Scapula	2	1	2	2	2	2	2	2	1	2	2	2	0	2	0	2	2	0	2	0	1	1	0	2	2	2	1	2	2	2	0
	Humerus	2	1	2	2	2	2	2	2	1	2	2	2	2	2	0	2	2	0	2	0	2	0	0	2	2	2	1	2	0	2	0
	Radius	2	1	2	2	2	2	2	2	1	2	2	2	2	2	0	2	2	**1**	2	0	2	0	0	2	2	2	1	2	2	1	0
	Ulna	2	2	2	2	2	2	2	1	0	2	2	2	2	2	0	2	2	0	2	0	1	1	0	2	2	2	1	2	1	1	0
Hindlimb	Pelvis	2	0	2	2	1	0	2	2	0	0	1	2	0	2	0	2	2	0	2	0	2	0	0	2	0	0	0	0	2	0	2
	Femur	2	2	2	2	1	0	2	2	0	0	1	2	0	2	0	2	2	0	2	0	2	1	0	2	0	0	0	0	2	0	2
	Tibia	2	2	2	2	1	0	2	2	0	0	1	2	0	2	0	2	2	0	2	0	2	0	0	2	0	0	0	0	0	0	2
	Astragalus	1	0	2	2	1	0	2	2	0	0	1	2	0	2	0	2	2	0	2	**1**	2	0	0	2	0	0	0	0	0	0	2
	Calcaneus	2	1	1	2	1	0	2	2	0	0	1	2	0	1	0	2	2	0	2	0	0	0	0	2	0	0	0	0	0	0	2

B – middle-sized rodents

	taxa	*Rattus*	*Cryptomys*		*Mastomys*											*Steatomys*							*Rhabd*		*Undet*
	n°pellet	4.2	13.1	17.2	4.1	9.1	16.1	1.2	4.2	6.2	10.2	12.2	13.2	16.2	16.2	1.1	1.1	15.1	16.1	21.1	2.2	5.2	15.1	8.2	2.2
Cranium	Maxilla	2	0	0	2	2	4	2	0	2	2	0	**1**	2	0	1	1	2	0	4	1	2	2	2	
	Upper Incisor	2	0	0	2	2	3	2	0	2	2	0	**0**	2	0	1	1	2	0	4	0	2	2	2	
	Upper Molar	5	0	0	6	6	12	6	0	6	6	0	**3**	6	0	2	1	4	0	8	1	5	6	6	
Lower Jaw	mandible	2	0	0	2	2	4	2	0	2	2	0	0	2	0	2	2	2	0	3	1	2	2	2	
	Lower Incisor	2	0	0	2	2	3	2	0	2	2	0	0	2	0	2	2	2	0	2	0	1	2	2	
	Lower Molar	6	0	0	6	6	12	6	0	6	6	0	0	6	**1**	6	0	4	0	5	1	4	6	6	
Forelimb	Scapula	2	2	2	2	1	4	2	0	2	2	0	0	2	0	1	0	1	0	4	2	2	2	2	
	Humerus	2	2	2	2	2	4	2	0	2	2	2	0	2	0	2	0	2	0	4	2	1	2	2	
	Radius	2	1	1	2	2	3	2	0	2	2	2	0	2	0	2	0	2	0	3	2	1	2	2	
	Ulna	2	1	2	2	2	1	1	0	2	2	2	0	2	0	3	1	2	0	4	2	1	2	2	**1**
Hindlimb	Pelvis	2	0	0	2	2	4	1	2	2	2	0	**1**	2	0	0	0	2	0	4	2	2	2	2	
	Femur	2	0	0	2	2	2	2	2	2	2	1	**1**	2	0	2	1	2	0	3	2	2	2	2	**1**
	Tibia	2	0	0	2	2	4	2	2	2	2	2	0	2	0	2	2	2	**1**	3	2	2	2	2	**1**
	Astragalus	2	0	0	2	2	4	2	1	2	2	2	0	1	0	1	0	2	0	3	2	2	2	2	**1**
	Calcaneus	2	0	0	1	2	4	0	1	1	0	2	0	2	0	1	0	2	0	1	2	2	2	1	

Table I cont.

C – small rodents and shrews

	taxa	*Mus / Dendromus*									Suncus / Myosorex								
	n°pellet	4.1	4.1	13.1	2.2	5.2	6.2	9.2	11.2	14.2	4.1	6.1	13.1	14.1	15.1	18.1	19.1	12.2	14.2
Cranium	Maxilla	2	0	0	1	2	4	2	2	2	2	2	0	2	2	4	6	2	2
	Upper Incisor	2	0	0	1	2	4	2	2	2	2	2	0	2	2	4	6	1	2
	Upper Molar	4	0	0	3	6	6	6	6	5	6	6	0	6	1	12	6	3	6
Lower Jaw	mandible	2	**1**	0	1	2	4	2	2	2	2	2	0	2	2	4	6	2	2
	Lower Incisor	2	**1**	0	1	2	4	2	2	2	1	2	0	2	2	4	6	2	2
	Lower Molar	3	**1**	0	2	6	6	6	3	5	6	6	0	6	4	12	17	5	6
Forelimb	Scapula	1	0	0	0	2	3	2	2	2	2	0	0	1	2	0	2	0	2
	Humerus	1	0	0	2	2	3	2	2	1	1	0	**1**	0	2	0	4	2	1
	Radius	1	0	**1**	1	2	0	2	2	2	1	0	0	0	2	1	3	0	2
	Ulna	1	0	0	1	2	3	2	2	2	1	0	0	0	2	1	4	1	2
Hindlimb	Pelvis	1	0	0	0	2	1	2	2	2	1	0	0	1	0	1	3	2	0
	Femur	1	0	0	0	2	4	2	2	2	1	0	0	2	1	1	5	0	0
	Tibia	2	0	0	0	2	2	2	2	2	2	0	0	1	2	2	5	2	2

Indeed, 58 prey individuals (73% of the total) are spread within the other 22 pellets (55%). 7 pellets have recorded 3 prey individuals and 3 pellets contains various remains from 4 prey individuals. The maximum number of prey individuals for one pellet is 5 (pellet 4.1). 59 incisors out of 231 (25.5%), and 23 molars out of 615 (3.7%) exhibit digestion traces (Table IV).

2. Skeletal representation of large rodents (*Tatera*, *Otomys*, *Cryptomys*, *Rattus*) (Table IA and IB)

34 large rodents (22 *Tatera*, 9 *Otomys*, two *Cryptomys* and one *Rattus*) have been identified among 31 pellets. In the three cases where remains from two of these rodents are within the same pellet (n°1.1, 11.2 and 17.2), at least one of both skeletons is incomplete.

Three *Tatera* are represented by only a few elements within pellets: a unique and heavily digested incisor (pellet 2.2), one molar and a radius (11.2) and a digested calcaneus (13.2). The forelimbs alone represent the remains of both *Cryptomys* (13.1 and 17.2). Hindlimbs are the only remains of an *Otomys* individual (18.2), and another is represented only by some bones of both hindlimbs and forelimbs (12.2).

All other prey individuals are represented at least by their cranial part, but only 10 skeletons are complete (8 *Tatera*, one *Otomys* and the unique *Rattus*). Others are characterized by the loss of one or several complete limb(s).

Indeed, 4 *Tatera* and 6 *Otomys* are only represented by the anterior part of their skeletons: the pelvic girdle and their hindlimbs are completely absent from the pellets, as are the forelimbs and the scapulae for one out of these vlei rats (pellet 4.1). One hindlimb and the corresponding pelvis are absent for two other gerbil skeletons (5.1 and 14.1), while only a femur, an ulna and a scapula compose the postcranial parts of another gerbil (17.2).

2 gerbils are characterized by the absence of a complete mandible, while a third one has no mandible (15.2), and there is a loss of a maxilla, of the pelvic girdle and a part of one anterior limb for a last gerbil (1.1).

In summary, apart from the 3 gerbils represented by only one or two elements, 27 complete hindlimbs and 5 forelimbs have not been recovered within the pellets, as well as 4 complete skulls (Table IV). However, the remains of vlei rats from pellets 20.1 and 18.2 could derive from the skeleton of a same large (adult) individual.

3. Skeletal representation of middle-sized mice (*Mastomys*, *Rhabdomys* and *Steatomys*) (Table IB)

23 rodents of these genera have been recognized. One prey individual, represented by 3 bones from the hindlimb and one ulna only, could not be identified precisely.

8 skeletons out of 12 *Mastomys* and the two *Rhabdomys* are complete or nearly complete. A ninth *Mastomys* is only represented by one molar (pellet 16.2), and another one by one maxilla in addition to a pelvis and a femur (13.2). The two last *Mastomys* remains comprise the limbs alone (only the hindlimbs for one of them).

The representation of the fat rat (*Steatomys*) remains follows more varied patterns: 3 out of 8 prey skeletons are almost complete and one individual is represented by a single tibia. Among the four other rodent skeletons, one is without a forelimb; a third without one maxilla and a mandible; at least one missing mandible for another; and one maxilla and more than half of the postcranial bones are absent for the last.

4. Skeletal representation of smallest mammals (*Mus*, *Dendromus*, *Suncus*, *Myosorex*) (Table IC)

6 out of the 10 skeletons of mice are almost complete; a seventh one has lost a complete forelimb with a scapula, a pelvis and a femur (pellet 4.1). One mouse is represented by a single digested mandible (4.1) and a second one by an isolated radius (13.1). A last one is represented by one maxilla and one mandible (with digested incisors), in addition to some bones of the forelimbs (2.2).

Apart from one prey individual represented by an isolated humerus (pellet 13.1), all the shrews recovered have a preserved skull. The limb and coxal bones are absent for one of them (6.1) and four prey individuals exhibit a loss of one or two complete limbs (Table IV). All other skeletons are complete.

Drimolen (Table II)

1. General observations about pellet contents

A maximum of 55 rodents and 11 shrews has been calculated among the 33 pellets. 13 pellets have rejected the remains of only one rodent, and among them the postcranial elements of one *Otomys* individual were recovered within two pellets (21 and 24). 11 pellets contain the remains of two prey individuals, 5 pellets 3 prey individuals, and 3 pellets and 2 pellets include respectively 4 and 5 prey individuals. 27 incisors out of 180 (13.3%) show digestion traces among rodents. Only 4 prey individuals (the *Rattus* rodents and three shrews) have digested molars (n=11: 2.1%) (Table IV).

2. Skeletal representation of large rodents (*Tatera*, *Otomys*, *Cryptomys*, *Rattus*) (Table IIA)

The remains of 20 large rodents have been identified within 21 pellets: there is never more than one of these taxa in a pellet. 4 gerbils, 2 vlei rats and one mole rat exhibit a complete skeleton or without one or two long/coxal bone(s). One *Otomys* individual is characterized by the absence of one mandible and a maxilla (pellet 17), and a second one by the loss of a forelimb (51).

Postrcranial bones are all that remain of 7 prey skeletons. Among them, there are only the bones of the hindlimbs or the forelimbs. On the other hand, two rodents are only represented by a complete skull (with two postcranial bones in one case), and a third one by the skull and one forelimb. Remains of a last gerbil are characterised by the absence of one mandible, a forelimb and a hindlimb.

In summary, 7 complete skulls are absent (35% of the PR), 14 complete forelimbs (35%) with scapulae (except in two cases) and 9 hindlimbs (22.5%) with pelves (except in two cases).

3. Skeletal representation of middle-sized mice (*Mastomys*, *Rhabdomys, Aethomys* and *Steatomys*) (Table IIB)

4 unindentified prey species were represented by a single bone within 4 pellets (3, 48, 49, 51). Out of 22 identified rodents, the complete skeleton (sometimes without few bones) has been recovered for 18 of them: 12 *Mastomys* out of 14; 2 *Aethomys*; 3 *Steatomys* (from the same pellet: n°15) and 1 *Rhabdomy*s. Among the other mammals, one complete forelimb is absent from a *Mastomys* skeleton, and only one femur and one humerus in addition to the pelvic girdle represent a second mouse (pellet 19). One fat mouse is represented by its maxillae and one mandible alone (pellet 1), and 2 incisors and one molar are the only cranial parts of a striped mouse (53).

Table II

Bone representation of prey individuals in *Tyto alba* pellets from Drimolen (South Africa) according to genus. In bold: residual elements from a prey individual. Grey boxes: losses of complete skull, forelimb or hindlimb. Large rodents: section A; middle-sized rodents: section B; small rodents and shrews: section C)

A – large rodents

	taxa	*Tatera*											*Otomys*							*Rattus*	*Cryptomys*	
	n°pellet	1	2	4	6	13	14	16	23	25	26	40	3	9	17	21	24	50	51	12	7	11
Cranium	Maxilla	2	0	2	0	2	2	0	2	0	2	2	2	2	1	0	0	0	2	2	0	2
	Upper Incisor	1	0	2	0	2	2	0	2	0	2	2	2	2	1	0	0	0	2	2	0	2
	Upper Molar	3	0	6	0	6	6	0	6	0	6	5	6	6	6	0	0	0	6	6	0	6
Lower Jaw	mandible	1	0	2	0	1	2	0	2	0	2	2	2	2	1	0	0	0	2	2	0	2
	Lower Incisor	1	0	2	0	1	2	0	2	0	2	2	2	2	0	2	0	0	2	2	0	2
	Lower Molar	3	0	4	0	3	5	0	6	0	6	6	6	6	2	0	0	0	6	6	0	6
Forelimb	Scapula	0	2	2	1	0	0	0	2	0	2	0	2	1	1	0	0	1	2	0	2	2
	Humerus	0	1	2	0	0	0	0	2	0	2	2	2	2	2	2	0	1	1	1	2	2
	Radius	1	1	2	0	0	0	0	2	0	2	2	2	2	2	2	0	1	1	1	2	2
	Ulna	1	1	2	1	0	0	0	2	0	2	1	2	2	2	2	0	1	1	1	2	2
Hindlimb	Pelvis	2	0	2	2	0	1	2	2	2	2	1	2	2	2	0	2	2	2	0	0	2
	Femur	1	1	2	2	0	0	2	2	2	2	2	1	2	2	1	1	2	2	0	0	2
	Tibia	0	2	2	1	0	0	2	2	2	2	2	2	2	2	0	2	2	2	0	0	2
	Astragalus	1	1	2	0	0	0	2	2	2	1	0	2	2	2	0	2	2	2	0	0	2
	Calcaneus	1	1	2	0	1	0	2	2	1	2	1	2	2	2	0	2	2	1	0	0	2

B – middle-sized rodents

	taxa	*Mastomys*														*Steatomys*		*Aethomys*		*Rhabdomys*		undetermined			
	n°pellet	8	11	19	19	20	23	26	47	48	49	49	52	53	54	1	15	6	22	5	53	3	48	49	51
Cranium	Maxilla	2	2	2	0	2	2	2	2	2	2	2	2	2	2	2	6	2	2	2					
	Upper Incisor	2	2	2	0	2	2	2	2	2	2	2	2	2	2	0	5	2	2	2	2				
	Upper Molar	6	6	6	0	6	6	5	6	5	6	5	6	6	6	4	15	6	6	6	1				
Lower Jaw	mandible	2	2	2	0	2	2	2	2	2	2	2	2	2	2	1	6	2	2	2					
	Lower Incisor	2	2	2	0	2	2	2	2	2	2	2	2	2	2	0	6	2	2	2					
	Lower Molar	6	6	6	0	6	6	4	6	6	6	6	6	6	6	2	12	6	6	6					
Forelimb	Scapula	2	2	1	0	2	2	1	2	2	2	2	1	2	2	0	6	1	2	2					**1**
	Humerus	2	2	2	**1**	2	2	2	1	2	2	2	2	2	2	0	6	2	2	2	2				
	Radius	2	2	1	0	2	2	1	1	2	2	2	2	1	2	0	6	2	2	2					
	Ulna	2	2	1	0	2	2	1	1	2	2	2	2	2	2	0	6	2	2	2	1				
Hindlimb	Pelvis	2	2	2	**2**	1	2	1	2	2	2	2	2	2	2	0	6	2	2	2	1	**1**			
	Femur	2	2	2	**1**	2	2	1	2	2	2	2	2	2	2	0	6	2	2	2	2				
	Tibia	2	2	2	0	2	2	2	2	2	2	2	2	2	2	0	6	2	2	2	2				
	Astragalus	1	2	0	0	2	2	2	1	2	1	2	1	2	1	0	3	0	2	2	1			**1**	
	Calcaneus	2	2	0	0	2	2	2	2	2	2	2	2	2	2	0	4	0	2	2	1		**1**		

Table II cont.

C – small rodents and shrews

	taxa	*Mus / Dendromus*									*Suncus / Myosorex*								
	n°pellet	9	14	15	16	17	19	26	48	49	8	9	14	16	17	40	22	49	52
Cranium	Maxilla	2	0	2	2	2	2	0	2	2	2	2	0	2	4	2	2	2	1
	Upper Incisor	1	0	2	2	2	0	**2**	2	2	1	0	0	2	4	2	2	2	0
	Upper Molar	3	0	4	4	6	3	0	6	4	6	2	0	5	12	6	6	6	3
Lower Jaw	mandible	2	0	2	2	2	1	**1**	2	2	2	2	0	2	4	2	2	2	2
	Lower Incisor	2	0	2	2	2	1	0	2	2	2	0	0	2	4	2	2	2	2
	Lower Molar	5	1	4	5	4	2	**1**	6	2	6	5	0	6	12	6	6	6	6
Forelimb	Scapula	1	0	2	2	2	1	0	2	0	1	0	4	0	2	0	0	2	0
	Humerus	2	0	2	2	2	1	**1**	0	1	2	1	3	2	3	1	2	2	1
	Radius	2	1	2	2	2	0	0	2	2	0	0	0	1	2	1	0	1	0
	Ulna	2	1	2	2	2	1	0	2	1	1	1	2	2	2	0	2	0	0
Hindlimb	Pelvis	1	2	2	2	2	0	0	2	2	2	0	2	2	4	2	2	2	0
	Femur	2	2	2	2	2	0	0	2	2	2	0	2	2	4	2	2	2	1
	Tibia	2	1	2	2	2	0	0	1	2	0	1	2	2	4	2	1	2	2

4. Skeletal representation of smallest mammals (*Mus*, *Dendromus*, *Suncus*, *Crocidura*) (Table IIC)

Out of 20 identified prey individuals, 11 skeletons are well preserved. Two others have only lost their forelimbs (excepted a humerus), while has a third individual (excepting a humerus and a radius).

The remains of two different shrews within the same pellet (n°14) are only represented by some of the limb bones, while another one is essentially represented by its skull (with 3 bones), as is another mouse (but with only one mandible). One climbing mouse is only represented by the hindlimbs with a radius and an ulna, in addition to a single molar. A mandible with upper incisors and a humerus represent a last mouse.

5. Unindentified remains

4 postcranial bones (a pelvis, a scapula, an astragalus and a calcaneus) within 4 pellets (3, 48, 49, 51) are the single remains of 4 prey individuals. They probably derived from rodents in class 3 (smallest rodents) or from young individuals of class 2 (middle sized rodents).

Pech Crabit (Table III)

1. General observations about pellet contents

A maximum of 130 prey individuals (77 rodents and 53 shrews) have counted from 28 pellets. The minimum number of prey individuals per pellet is 2 (5 pellets), the maximum is 8 (1 pellet), and half of the pellets include the remains of 4 or 6 prey individuals.

2. Preservation of rodents (Table IIIA, B)

15 individual rodent skeletons are represented by less than five elements within a pellet. Out of these, 3 are represented by only one mandible, 4 by only one postcranial bone, and one by an upper incisor and a scapula (which are particularly digested: pellet 18). A sixteenth rodent is represented by the hindlimbs alone (pellet 31).

Table III

Bone representation of preys individuals in *Tyto alba* pellets from Pech Crabit (France) according to family (Rodents and Schrews). In bold: residual elements from a prey individual. Grey boxes: losses of complete skull, forelimb or hindlimb. Prey have been separated as precisely as possible within each pellet. Rodents: sections A and B; shrews: section C

A – rodents (1)

	n° pellet	1	1	2	2	3	4	5	7	8	9	9	12	12	14	15	15	16	16	17	17	17	18	19	21	21	22	22	23	25
	MNP	1	2	1	1	1	2	2	2	1	7	1	2	1	2	2	2	1	1	3	1	1	1	2	1	2	1	1	2	1
Cranium	Maxilla	2	4	2	2	2	4	4	4	2	14	2	4	2	4	4	4	2	2	6	0	0	2	4	2	4	2	2	4	2
	Upper Incisor	2	4	2	2	2	4	4	4	2	12	2	4	2	4	4	4	2	2	6	0	0	2	4	2	4	2	2	4	2
	Upper Molar	6	12	6	5	6	12	11	12	6	28	6	12	6	12	12	11	6	6	17	0	0	6	12	6	9	6	6	7	5
Lower Jaw	mandible	0	4	2	2	2	4	4	4	2	13	1	4	2	4	4	4	1	2	5	2	1	2	4	2	4	2	2	4	2
	Lower Incisor	0	4	2	2	2	4	4	4	2	13	1	4	2	4	4	4	1	2	5	2	1	2	4	2	4	2	2	4	2
	Lower Molar	0	12	6	2	6	12	12	12	6	31	3	12	6	12	12	5	3	6	14	6	3	6	12	6	7	6	6	8	6
Forelimb	Scapula	0	1	2	1	2	3	2	0	2	7	2	4	1	4	4	2	2	2	5	1	0	2	3	1	4	1	0	4	2
	Humerus	2	3	2	2	2	4	4	4	2	8	2	3	0	4	3	4	2	1	6	2	1	2	4	1	3	2	0	3	2
	Radius	2	4	2	1	2	2	2	4	2	11	1	4	0	1	3	2	2	0	6	2	0	2	2	1	4	1	1	4	2
	Ulna	2	4	2	2	2	3	4	3	2	7	2	4	0	4	3	4	2	1	6	2	1	1	2	0	4	1	0	4	2
Hindlimb	Pelvis	2	4	2	2	2	2	4	4	2	7	2	4	0	2	4	4	3	2	4	2	1	2	2	1	4	2	0	4	2
	Femur	2	4	2	2	1	4	4	4	2	8	2	3	0	4	3	4	2	2	5	2	1	2	4	2	4	2	0	4	2
	Tibia	2	4	2	2	2	4	4	4	2	7	2	4	0	4	4	4	2	2	5	2	1	2	3	2	4	2	0	4	2
	Astragalus	0	2	2	0	0	0	2	1	0	7	0	2	0	4	3	1	2	0	0	1	0	0	2	2	4	0	0	3	0
	Calcaneus	0	2	1	2	2	3	3	2	1	9	0	2	0	4	3	1	2	0	0	1	0	0	3	1	4	1	0	3	1

B – rodents (2)

	n° pellet	25	26	26	26	27	27	28	29	29	30	31	31	31	1	3	4	5	15	15	16	17	18	19	21	24	26	27	29
	MNP	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cranium	Maxilla	0	2	2	0	2	2	2	4	2	2	2	2	0															
	Upper Incisor	0	2	2	0	2	2	2	4	2	2	2	2	0															
	Upper Molar	0	6	6	0	6	6	6	12	4	6	6	5	0															
Lower Jaw	mandible	1	2	2	0	2	2	2	0	1	2	2	2	0		**1**								**1**	**1**				
	Lower Incisor	1	2	2	0	2	2	2	0	1	2	2	2	0		**1**								**1**	**1**				
	Lower Molar	3	6	6	0	5	6	6	0	2	6	6	2	0															
Forelimb	Scapula	0	2	2	2	2	2	2	2	0	2	0	2	0									**1**						**2**
	Humerus	0	2	2	2	2	2	2	1	0	2	2	1	0	**1**											**1**	**1**		
	Radius	0	2	2	1	2	2	2	2	0	2	0	2	0								**2**				**1**		**1**	
	Ulna	0	2	2	1	2	2	2	2	2	2	2	2	0				**1**											
Hindlimb	Pelvis	2	2	1	1	2	2	2	2	0	2	2	2	2					**1**	**1**						**1**	**1**		**1**
	Femur	1	2	2	1	2	2	2	2	0	2	2	2	2	**1**														
	Tibia	1	2	2	2	2	2	2	2	1	2	2	2	2	**2**		**1**	**1**			**1**	**1**							
	Astragalus	2	1	1	0	2	2	1	1	2	1	1	2	0												**1**		**1**	
	Calcaneus	2	0	1	0	2	0	2	2	2	1	1	2	1				**1**											**1**

Table III cont.

C – shrews

	n°pellet	4	5	8	10	12	14	15	16	18	20	22	23	24	25	27	28	29	30	4	10	12	14	18	19	21	22	26	26	29
	MNP	2	3	2	2	1	4	1	5	3	3	1	1	3	2	2	1	2	3	1	1	1	2	1	1	1	1	1	1	1
Cranium	Maxilla	4	4	2	4	2	8	2	10	6	6	2	1	6	4	2	2	4	6											
	Upper Incisor	4	4	2	3	2	8	0	10	6	6	2	1	6	4	2	2	4	6											
	Upper Molar	12	12	6	5	6	23	6	30	16	18	6	3	18	12	6	6	12	18											
Lower Jaw	mandible	4	6	2	4	2	8	2	10	6	6	2	1	4	4	2	2	4	6											**1**
	Lower Incisor	4	6	2	4	2	8	2	10	6	6	2	1	4	4	2	2	4	6											**1**
	Lower Molar	12	18	6	12	6	24	6	30	17	18	6	2	12	12	6	6	12	18											**3**
Forelimb	Scapula	3	5	0	3	2	7	2	5	0	5	1	1	2	4	4		3	4							**1**	**2**			
	Humerus	4	5	1	4	2	8	2	8	6	6	2	1	2	4	2	2	3	6	**1**										
	Radius	4	4	2	3	2	6	0	8	2	5	2	1	3	4	2		4	2							**1**				
	Ulna	3	6	2	4	2	7	2	10	4	6	2	2	5	3	2	1	3	4				**1**		**1**	**1**				
Hindlimb	Pelvis	3	6	2	4	2	7	2	9	2	6	2	1	4	4	2	2	2	6		**2**		**3**					**1**		
	Femur	3	4	2	4	2	8	2	10	5	5	2	2	5	4	2	2	3	6			**1**	**1**	**1**				**1**	**1**	
	Tibia	3	6	1	3	2	8	1	9	5	6	2	2	4	4	2	2	4	6											

All the other prey skeletons are represented by at least a part of their skull elements with some postcranial bones. Four maxillae and 10 mandibles only are completely absent from those pellets, as well as 13 forelimbs and 16 hindlimbs. Two skulls were only recovered with only one postcranial bone of the same individual, and one rodent is only represented by one mandible and a part of the hindlimbs. Teeth of this mandible are digested (giving the only digested molars of the whole sample), but digestion traces are otherwise very rare, with only 6 incisors out of 371 (1.6 %).

3. Preservation of shrews (Table IIIC)

12 prey individuals are only represented by a maximum of 4 elements within a pellet. For the 41 other skeletons, skull and teeth representation of each individual is rather high for most of them: only one complete forelimb and three hindlimbs are absent from the pellets, as well as the two mandibles of a skull, and one mandible and one maxilla for a second. No digested teeth have been observed.

Summary of results

Bone representation analyses for each prey individual points to at least two patterns of skeletal part losses:

The first pattern is the frequent presence of a few isolated bones or teeth as single witnesses of a swallowed prey individual (Table IV: “number of residual prey”). Such remains are more usually those of small mammals than larger ones (40 out of 43) and these are usually postcranial bones (only 3 mandibles, one incisor and two isolated molars). Some of them are more corroded by gastric juices than other bones within the same pellet.

The second pattern is the frequent absence of bones from one or several complete limb(s) (with or without scapulae/pelvic girdle), or a complete skull (Table IV), and sometimes mandibles and maxillae alone. Cases when prey remains are limited to a skull or the bones of two limbs (i.e. loss of the whole postcranial elements or the skull and some limbs) are included in this pattern. Apart from isolated remains of prey (the first pattern described above), this kind of loss mainly affects the largest mammals (Drimolen and Bolt’s Farm: 29 cases out of 51) rather than the smaller ones (35 out of 181, out of which 27 for Pech Crabit only). Indeed, the representation of the different skeletal parts calculated from the MNI is different for each sample and each category of prey (Table V). In fact, because of a low proportion of multi-rejected skulls or limbs, Pech Crabit remains give the higher values for almost all bones. At Bolt's Farm, the losses of hindlimbs from large rodents induce a lower representation of pelvis, femur and tibia than other samples, while Drimolen skull/teeth elements are less numerous than limb bones.

Table IV

Numbers of prey (MNI and MNP), teeth digestion representations, main skeletal part losses (skull, hindlimbs and forelimbs) for each sample and each kind of mammal

	Bolt's Farm				Drimolen				Pech Crabit		
class of prey	I	II	III	Total	I	II	III	Total	Rod	Shr	Total
MNP (A)	34	23	22	79	20	26	20	66	77	53	130
MNI	27	19	19	65	15	22	16	53	57	38	95
MNI/MNP	0.79	0.83	0.86	0.82	0.75	0.85	0.80	0.80	0.74	0.72	0.73
number of residual prey (B)	3	4	3	10	0	5	1	6	15	12	27
number of prey (A-B)	31	19	19	69	20	21	19	60	62	41	103
number of missing skulls	4	2	0	6	7	0	3	10	1	0	1
number of missing forelimbs	5	1	11	17	14	3	6	23	13	3	16
number of missing hindlimbs	27	1	5	33	7	2	3	12	16	1	17
Incisors (observed)	101	57	73	231	48	77	55	180	223	148	371
digested incisors	20	23	16	59	8	10	9	27	6	0	6
% digested	19.8	40.4	21.9	25.5	16.7	13.0	16.4	15.0	2.7	0.0	1.6
Molars (observed)	274	165	176	615	139	221	159	519	598	441	1039
digested molars	7	5	11	23	4	0	7	11	3	0	3
% digested	2.6	3.0	6.3	3.7	2.9	0.0	4.4	2.1	0.5	0.0	0.3

Table V

Relative rates of representation of different skeletal parts (calculated from the MNI) for each sample and each kind of mammal

	Bolt's Farm				Drimolen				Pech Crabit		
class of prey	I	II	III	mean	I	II	III	mean	Rod	Shr	mean
MNI	27	19	19	65	15	22	16	53	57	38	95
maxilla	98.1	84.2	97.4	93.8	83.3	76.9	96.9	84.8	100.0	98.7	99.5
mandible	92.6	84.2	100.0	92.3	76.7	75.0	100.0	83.0	96.5	94.3	95.6
molar	93.5	72.4	77.2	82.6	77.2	92.1	82.8	85.1	87.4	96.7	91.1
incisor	84.6	75.0	96.1	85.2	80.0	87.5	85.9	84.9	97.8	97.3	97.6
scapula	94.4	76.3	55.3	77.7	66.7	87.5	59.4	73.1	74.6	71.1	73.2
humerus	94.4	86.8	63.2	83.1	80.0	100.0	87.5	90.6	86.8	90.8	88.4
radius	94.4	81.6	52.6	78.5	83.3	85.0	56.3	75.8	79.8	72.4	76.8
ulna	90.7	81.6	63.2	80.0	83.3	90.0	71.9	82.6	84.2	93.4	87.9
pelvis	59.3	84.2	47.4	63.1	100.0	100.0	90.6	97.2	90.4	94.7	92.1
femur	64.8	89.5	60.5	70.8	96.7	100.0	96.9	98.1	91.2	100	94.7
tibia	59.3	100.0	73.7	75.4	96.7	100.0	87.5	95.3	98.2	92.1	95.8
calcaneus	55.6	84.2	*	67.4	83.3	70.0	*	75.4	49.1	*	*
astragalus	50.0	63.2	*	55.4	86.7	85.0	*	85.7	60.5	*	*

IV. DISCUSSION

Multirejection hypothesis

The presence of only one or a few bones of a prey skeleton within some pellets could be explained by the observations made by different authors about the retention of skeletal parts in the stomach by the owl. LOWE (1980) mentions that bones, especially those from the limbs, are not necessarily rejected within a single pellet. Indeed, during the pellet elaboration, some bones, especially small ones, might not have been retained by hair and could have "escaped" the first rejection, to be rejected within the following pellet (with new prey remains). A longer retention of these bones or teeth in the stomach explains also why heavily digested elements have been observed among these isolated remains, whereas other prey remains from the same pellet were not corroded.

The rejection of prey skeletons through several pellets could also explain the absence of complete limbs or skulls. This fact is sometimes observed by those who study the diet of owls, particularly for the larger mammals (e.g. BAUDVIN et al. 1995; GANEY 1992; BRUCE & MC LEAN 1986; SOUTHERN 1954). DODSON & WEXLAR (1979) note that raptors in captivity could reject more than a pellet per meal, and CARPENTIER (1934) mentions the simultaneous rejection of 3 pellets by *Bubo bubo* after swallowing 5 rodents and one bird. The weakness of gastric juices on bones could also explain why complete limbs are frequently absent from a skeleton, or represent the only remains of a skeleton: limb bones keep their anatomical connexion after digestion, and that helps the separation from the rest of the skeleton if the volume of bones and hair is too substantial to be rejected in a single pellet. In the same way, skulls, which occupy a rather large volume, are separated from the rest of the body. Sometimes, because of their large size, rodents are first decapited before ingestion. This certainly helps the ejection of a second pellet, particularly if a skull is not destroyed during ingestion or digestion.

Pellets 20 and 24 from Drimolen are the best illustration of these cases, with the multi-representation of the skeleton of the same vlei rat: one pellet contains two incisors, the forelimb bones and a femur of the same individual, and the other pellet delivers the hindlimbs bones without the former femur. The skull, if ingested, could have been rejected within a third, but unrecovered, pellet. Therefore, on the one hand, some large species could be more prone to being multi-rejected than others, because of a higher resistance of bones. For instance, it has been noted that gerbil skulls are often preserved more intact than those of other species (COETZEE 1963, DENYS et al. 1996, DAUPHIN et al. 1996, POKINES & KERBIS 1997). On the other hand, when a high number of small mammals are swallowed during a same meal, some of their bones could not be automatically ejected within the following pellet.

Other hypotheses could explain the loss of skulls or limbs. Dismembering is frequent if mammals are too large (HOCKETT 1991) or to feed the chicks (VEIN & THEVENOT 1978). Decapitation without skull ingestion by *Tyto alba* has been rarely observed in European studies (TAYLOR 1991), and there is no data about South African owls. POKINES & KERBIS PETERHANS (1997) thought that the over-representation of gerbil skulls in Barn Owl pellets from Israel is due to such a decapitation and the swallowing of the prey heads only or intensive destruction of postcranial bones. But at Bolt's farm, where the absence of hindlimbs of large rodents is particularly striking, limbs are also frequently represented within pellets, and are even the only remains of some prey skeletons. Indeed, multi-rejection of skeletons when mammals are too large or too numerous seems to be the best explanation of our observations.

Taphonomic implications

Former taphonomic observations of *Tyto alba* prey remains have provided different results in term of bone representation in numerous studies (BRUDERER & DENYS 1999, SAAVEDRA & SIMONETTI 1998, POKINES & KERBIS-PETERHANS 1997, ANDREWS 1990, KUSMER 1990, HOFFMAN 1988, KORTH 1979, DODSON & WEXLAR 1978). Losses are very important in some cases despite the fact that gastric juices of this owl are supposed to be some of the least corrosive among birds of prey (SMITH & RICHMOND 1972). Bones are mainly lightly fragmented and a low proportion of teeth exhibit signs of digestion (ANDREWS 1990). Feeding experiments on owls in captivity (i.e. the exact number of ingested prey individuals and rejected pellets with their remains are well known. Signifying that the MNP equals the MNI) have indicated that bone and skull mean losses are 7.2 % according to HOFFMAN (1988), who has examined 50 prey remains, and 17.3% according to DODSON & WEXLAR (1979) for 17 prey individuals, while bone losses in "wild" pellets can reach a mean of 60% (SAAVEDRA & SIMONETTI 1998). In our samples, bone losses of prey skeletons which have no potential multi-rejected parts could correspond to the maximum of destruction due to digestion. It is clear that the absence of bones or teeth in these cases is rather rare (e.g. postcranial parts of class 2 rodents in the African samples. Table V). This implies that bone and teeth representation varies mostly because of the multi-rejection of skeletal parts rather than destruction by gastric juices. It could explain the observations made by SAAVEDRA & SIMONETTI (1998) in the same pellets about the low number of skull and limb remains of caviomorph (100-200g), compared to cricetids (40-60g). However, data from Great Britain (ANDREWS 1990), where (small) prey rodents are similar to French ones, underline much higher losses, particularly of teeth, that multi-rejection does not explain entirely. Such losses could have been due to the feeding of chicks or bone consumption by a juvenile owl (RACZYŃSKI & RUPRECHT 1974), but in consequence, it would have also given few bone elements.

Bone completeness and number of prey individual calculations could depend on the number of larger mammals within the diet on the one hand, or on the completeness of pellet recovery relative to the real number of ejected pellets by the owl on the other. Pellet selection is rather frequent in taphonomic studies. Intact pellets are logically selected to avoid errors in bone counts but they could only represent a part of the diet, particularly if the owl ejects several pellets at different places (e.g. diurnal and nocturnal pellets). In these cases, prey remains should be counted separately in order to avoid under-estimations or over-estimations of large prey, as well as bone modifications. The use of postcranial parts to identify prey individuals is also necessary for some of these taxa. At Bolt's Farm, for example, the mole rat skulls were not recovered whereas the forelimbs of two individuals were identified; at Drimolen, 7 large rodents out of 20 would have been overlooked. Indeed, the under-estimation of prey individuals could reach 20 to 30% (Table IV: MNI/MNP). On the contrary, if unrecovered pellets containing complementary skeletal parts are preserved within a same locality, the resulting bone assemblage should give a rather high bone/taxa representation.

These new observations mean that the precise identification of nocturnal raptors responsible for a bone accumulation in the recent palaeontological record must be made according to the region and the kind of prey. The use of digestion rate must also be balanced according to the kind of prey species if samples are not important; because the presence of few species with strongly digested teeth could induce a consequent increase of this rate (cf. Table IV). The rates of incisor digestion in African pellets (25.5% and 15%) are higher than most studies of *Tyto alba* prey (13%) (Table IV), but quite similar to one of the last taphonomic study on a Mauritanian owl nest which was 23% (BRUDERER & DENYS 1999). Such discrepancies between our African samples can be explained by the digestion of the whole incisors of three *Steatomys* preys at Bolt's Farm (giving a high rate of digestion for teeth from category 2 prey), while the remains of this genus in the other sample are in small number and show no digestion traces. However, Class 1 and Class 3 mammal teeth exhibit similar rates of digested incisors in both cases (around 20% and 16.5 %: Table IV), and molar digestion is low (0.0-6.3%) in the three samples.

Nesting roosts and pellets from juvenile individuals are also needed to explain the variations of results. For the moment, the use of comparisons between bone representation patterns from modern pellets and fossil assemblages (e.g. CASTILLO et al. 2001), even if there is no postmortem modifications, could be rather speculative (see also SAAVEDRA & SIMONETTI 1998 for similar conclusions). For the same reasons, dietary studies, which are essentially made from cranial remains, could be accurate if postcranial bones are taken into account from each pellet and/or if valuations of skull losses are made according to prey species.

The quantification of bone losses within each owl pellet should bring a new light to taphonomic studies in order to understand the structure of bone assemblages due to nocturnal raptors. We encourage the development of such studies in order to elaborate a modern taphonomic reference for archaeological, paleontological and ecological applications.

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