Pattern of bird bone fragmentation in pellets of the Long-eared Owl Asio otus and its taphonomic implications

Zbigniew M. BOCHEŃSKI and Teresa TOMEK

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Abstract. Fragmentation of bird bones in pellets of *Asio otus* was studied and compared with that in pellets of *Strix aluco* and *Bubo bubo*. The MNI obtained with the ulna and humerus found in *A. otus* pellets was higher than that obtained with any other bird bone. Each of the three owl species compared damages bones of its bird victims in a different way, which may help with determining the origin of fossil assemblages.

Key words: taphonomy, bird bones, pellets, Asio otus.

Zbigniew M. BOCHEŃSKI and Teresa TOMEK, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Slawkowska 17, 31-016 Kraków, Poland.

I. INTRODUCTION

It is the second paper of a series designed on bird taphonomy. The main purpose of the studies is to provide quantitative data on the damage to the bones of birds preyed upon by various owl species, and to compare the results with the patterns of bird bone fragmentation in fossil assemblages. Since birds may sometimes constitute up to 80% of the Long-eared Owl's diet (CRAMP 1985), it seemed advisable to study the fragmentation of their bones in its pellets. Similar studies of the relations between owls' diets and fossil assemblages were carried out on mammalian prey (e. g. BAYLE 1993; FERNANDEZ-JALVO & ANDREWS 1992); they resulted in pointing to the predator responsible for the accumulation of the fossil materials.

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II. MATERIAL AND METHODS

Pellets of Long-eared Owls Asio otus (LINNAEUS, 1758) were collected several times at their winter roost site, 10 km west of Kraków, Poland, in the winters of 1990/91 and

1993/94 (dates of collecting: 16 Mar. 91; 10 Oct. 93; 2 Feb. 94; 1 Apr. 94). At that time up to 40 owls were observed there on single occasions, so the pellets must have been cast by many individuals. At first all pellets were collected and then bird bones were chosen, which was a very time-consuming task. Next, only the pellets which included bird bones were collected (bird bones often protrude from pellets).

No attempt was made to determine the bird bones; a great many of them belonged to prey of the tit/sparrow size.

The fragmentation of bird bones in A. otus pellets was evaluated in the way described by BOCHEŃSKI et al. (1993). The fragmentation categories distinguished are also the same as proposed for S. aluco and B. bubo (BOCHEŃSKI et al. 1993: Figs. 1-5). The number of bones (fragments) in each category was counted irrespective of whether they came from the left or from the right side of the body.

In order to compare the proportion of whole long bones with that of broken ones, the numbers of whole bones were multiplied by two. This was necessary for statistical reasons, since after its breakage each bone is represented by at least two pieces: a proximal and a distal. In other words, each whole bone was given two points, and each fragment of a bone one point. For further statistical analysis, the points – and not the numbers of bones – were used.

When comparing the total numbers of proximal and distal parts, the numbers of fragments, and not the points, were used (i. e. whole bones plus proximal parts versus whole bones plus distal parts).

The minimum number of individuals (MNI) was calculated for each bone separately. The results are presented in two ways: as absolute numbers and as percentages of the number of the most numerous sort of bone, in our case the ulna. The MNI values are certainly somewhat underestimated since the bones were not determined and, for the sake of simplicity, the proximal and distal parts were not fitted together. Instead, the number of whole bones and that of proximal or distal parts of the left or right side – whichever was more numerous – were taken. The error resulting from this procedure is believed to be the same for each kind of bone.

The present results for Asio otus were compared with those for Strix aluco and Bubo bubo (BOCHEŃSKI et al. 1993). Chi-square test was used to evaluate the statistical significance of differences within each pair of species (A. otus/S. aluco and A. otus/B. bubo). All the cases analysed were characterized by one degree of freedom (df=1). Although in many cases the levels of statistical significance were higher than reported, we decided to set them at 0.05 (*) or 0.01 (**). All statistical analyses were performed using the StatSoft CSS: Statistica package.

III. RESULTS

Skull: Fragments of the skull were relatively numerous in the pellet material of A. otus (Table I). They consisted mostly of the category "whole beak", which formed 85% of all the skull fragments found. It is worth noting that no whole skull was found

Table I

Fragmentation of the skull and beak in pellets of A. otus expressed as percentages of the total number of skull fragments found (see BOCHEŃSKI et al. 1993: Fig. 1). MNI (%) is the percentage of the highest value of the MNI (obtained with ulna), formed by the number of individuals estimated on the basis of a given bone

Number of fragments	Whole skull (%)	Skull with beak and brain case without back part	Brain case without back part (%)	Brain case (%)	Whole beak (%)	End of beak (%)	Other fragments (%)	Total of broken parts (%)	MNI (N)	MNI (%)
1	2	3	4	5	6	7	8	9	10	11
N=96	0	2	4	0	85	0	9	100	83	59

(column 2), and that all the brain cases which were not broken to pieces (columns 2, 3, 4 and 5 jointly) lacked the back part up to the condylus occipitalis (columns 3 and 4).

Comparison with S. aluco and B. bubo (BOCHEŃSKI et al. 1993): As shown in Table II, the number of beaks in relation to the number of all other skull fragments (Table I: columns 2, 3, 6, 7 jointly versus 2, 3, 4, 5, 8 jointly) differs significantly between A. otus

Table II

Statistically significant differences in the proportion of beaks and other skull fragments found (table I: columns 2, 3, 6, 7 jointly versus 2, 3, 4, 5, 8 jointly) calculated for each pair of species. A. otus – present data; S. aluco and B. bubo – after BOCHEŃSKI et al. (1993). * – p<0.05; ** – p<0.01

and the second of the second of	S. aluco	B. bubo
A. otus	rans a A off the to	** $\chi^2 = 11.23$
S. aluco	i iX pronsi z sitzeristik	** $\chi^2 = 6.04$

and *B. bubo*, whereas between *A. otus* and *S. aluco* the difference is not significant. In the three owl species under comparison beaks are the most numerous fragments of the skull. Whole skulls were found only in pellets of *S. aluco*, but even there they were rather scarce. The percentage of the characteristically damaged brain cases (i. e. without back parts) in relation to the total number of brain cases except those broken to pieces, was the highest in *A. otus* (100%) and followed by *S. aluco* (70%). The pellets of *B. bubo* from the basic material of BOCHEŃSKI et al. (1993) lacked that category of damage, which however formed 32% in their additional material. It should be stressed, anyhow, that brain cases (whether damaged or not) were never numerous in any of the owls.

Mandible: Fragmentation of mandibles in pellets of A. otus is presented in Table III.

Table III

Fragmentation of the mandible in pellets of A. otus expressed as percentages of the total number of mandibular fragments found (see BOCHEŃSKI et al. 1993: Fig. 2). For MNI (%) – see Table I

Number of fragments	Whole (%)	One branch (%)	Articular part (%)	Tip of mandibula (%)	Middle part of branch (%)	Total of broken parts (%)	MNI (N)	MNI (%)
1	2	3	4	5	6	7	8	9
N=149	16	28	31	25	0	84	103	74

Comparison with S. aluco and B. bubo (BOCHEŃSKI et al. 1993): Table IV shows that these three owl species differ in the number of whole mandibles versus the total number of their broken fragments (Table III: column 2 versus 7). The percentage of whole mandibles was the highest in S. aluco (39%), followed by A. otus (16%) and B. bubo (2%). The percentages of articular parts (Table III: column 4) were almost equal in all the three owl species (29-35%), whereas the other categories of damage showed more differences.

Table IV

Statistically significant differences in the proportion of the total number of whole and broken mandibles (Table III: colum 2 versus 7) calculated for each pair of species. A. otus – present data; S. aluco and B. bubo – after BOCHEŃSKI et al. (1993). * – p<0.05; ** – p<0.01

1.73	S. aluco	B. bubo		
A. otus	** $\chi^2 = 25.58$	** $\chi^2 = 6.95$		
S. aluco		** $\chi^2 = 27.06$		

Sternum: Table V shows the fragmentation of sterna in A. otus pellets. The fragments without the rostrum sterni prevailed slightly over those with the rostrum (column 4 versus 2 and 3 jointly).

Comparison with S. aluco and B. bubo (BOCHEŃSKI et al. 1993): The percentages of all the categories of fragmentation in A. otus and B. bubo are very similar. It is also reflected in Table VI, where statistically significant differences between the number of fragments with and without the rostrum sterni, were found in the A. otus/S. aluco and S. aluco/B. bubo relations (but not between A. otus and B. bubo).

Table V

Fragmentation of the sternum in pellets of *A. otus* expressed as percentages of the total number of sternal fragments found (see BOCHEŃSKI et al. 1993: Fig. 3). For MNI (%) – see Table I

Number of fragments	More than 1/2 with rostrum (%)	Less than 1/2 with rostrum (%)	Fragments without rostrum (%)	MNI (N)	MNI (%)
1	2	3	4	5	6
N = 125	11	31	58	53	38

Table VI

Statistically significant differences in the proportion of the total number of fragments with rostrum sterni and without it (Table V: columns 2 and 3 jointly versus 4) calculated for each pair of species. A. otus – present data; S. aluco and B. bubo – after BOCHEŃSKI et al. (1993). * – p<0.05; ** – p<0.01

Althod Wolles	S. aluco	B. bubo
A. otus	** $\chi^2 = 71.48$	EL Yorks Siz 2 (8) Whe
S. aluco	. So the to much start bere	** $\chi^2 = 56.30$

Pelvis: The ilium-ischium-pubis bone occured in the largest numbers of all pelvic fragments in the pellets of A. otus. Its proportion was 71% (Table VII: columns 2 and 3 jointly). The corresponding figure for the synsacrum was 52% (columns 2 and 4 jointly).

Comparison with S. aluco and B. bubo (BOCHEŃSKI et al. 1993): Contrary to the above-mentioned results for A. otus, the most numerously represented fragment of the pelvis in S. aluco and in B. bubo was the synsacrum (77% and 49% respectively). The percentages of the fragments of the acetabulum region in A. otus and S. aluco are similar (6% and 9% respectively), whereas in B. bubo their percentage was much higher (33%).

Long bones: In A. otus, seven bones gained more points for the category "whole" (humerus, ulna, radius, carpometacarpus, phalanx I dig. majoris, femur and tarsometatarsus), whereas the remaining three bones (scapula, coracoideum and tibiotarsus) got more points for the category "broken" (Table VIII: columns 7 and 8).

The category "shaft" was never numerous; in some cases no shaft was found (Table VIII: column 5).

Comparison with S. aluco and B. bubo (BOCHEŃSKI et al. 1993): Asio otus and Strix aluco show the same tendency in the degree of bone fragmentation (number of points: whole bones versus all broken parts): in both owls the same seven bones gained more points in the category "whole", and the same three bones were more often broken. In

Table VII

Fragmentation of the pelvis in pellets of *A. otus* expressed as percentages of the total number of pelvic fragments found (see BOCHEŃSKI et al. 1993: Fig. 4). For MNI (%) – see Table I

Number of fragments	Synsacrum with 1 or 2 ilium-ischii- pubis bones (%)	Ilium-ischii- pubis bone (%)	Synsacrum whole or partial (%)	Acetabulum region (%)	MNI (N)	MNI (%)
1 8	2	3	4	5	6	7
N = 129	30	41	22	6	68	49

Table VIII

Fragmentation of long bones in pellets of *A. otus* expressed as percentages of the total number of long-bone-fragments found (see BOCHEŃSKI et al. 1993: Fig. 5). In scapula: distal part and shaft are shown jointly in the category "shaft". In coracoideum: proximal = sternal, distal = scapular. Columns 7 and 8 show points used for statistical analysis (for explanation – see "Material and Methods"). For MNI (%) – see Table I

Bones (Total number of fragments)	Whole bone (%)	Proximal part (%)	Distal part (%)	Shaft (%)	Total of broken parts (%)	Whole bone (points)	Total of broken parts (points)	MNI (N)	MNI (%)
1. 10. 10. 10. 10.	2	3	4	5	6	7	8	9	10
Scapula (N=157)	11	39	U_1 160	50	89	36	139	43	31
Coracoideum (N=175)	22	30	46	1	78	78	136	64	46
Humerus (N=277)	87	9	4	0	13	480	37	135	96
Ulna (N=273)	88	5	7	0	12	480	33	140	100
Radius (N=175)	78	10	11	1	22	274	38	79	56
Carpometacarpus (N=173)	91	6	3	0	9	314	16	89	64
Phalanx I Dig Maj. (N=57)	100	0	0	0	0	114	0	29	21
Femur (N=204)	53	23	24	0	47	218	95	81	58
Tibiotarsus (N=296)	10	56	30	4	90	58	267	98	70
Tarsometatarsus (N=233)	64	14	21	1	36	298	84	103	74

B. bubo — besides the scapula, coracoideum and tibiotarsus — the category "broken" outnumbered the category "whole" also as regards the humerus and femur. However, when the general tendency mentioned above was tested in detail, it appeared that there were more statistically significant differences between the number of whole bones and that of broken bones (Table IX). Only in two bones (coracoideum and phalanx I dig. majoris) the degree of fragmentation is the same in all the three owl species. On the other hand, four bones (humerus, ulna, radius and tibiotarsus) show statistically significant differences between all the three owls. Regarding the ten long bones examined, statistically significant differences were most often found between A. otus and B. bubo (8 bones), then between S. aluco and B. bubo (7 bones). The differences between A. otus and S. aluco were found only in 5 sorts of bones (Table IX).

The total number of proximal parts found in the material (whole bones plus proximal parts) was compared with the total number of distal parts (whole bones plus distal parts) for each long bone (Table VIII: columns 2, 3 and 4). The results of the comparison of pellets from these three owl species are shown in Table X. The biggest differences were found in the tibiotarsus, where the relative abundance of the proximal and distal parts seems to be species-specific. Similar differences were found for the radius (only in the relations A. otus/S. aluco and A. otus/B. bubo) and for the coracoideum (only between A. otus and B. bubo). The remaining bones did not show statistically significant differences. It is worth noting that although the difference in number between the proximal and the distal parts of the tibiotarsi of the A. otus and S. aluco victims was significant, the proximal parts prevailed over the distal in both owl species. On the contrary, in the Eagle Owl the distal parts of the tibiotarsus outnumbered the proximal. The differences may express some general tendencies in the medium-sized and large-sized owls, but this hypothesis calls for further studies. When comparing the relative preservation of the proximal and distal parts in the tarsometatarsus and ulna, and the sternal and scapular parts in the coracoideum in the three owl species (present data: Table VIII: columns 2, 3 versus 2, 4; BOCHEŃSKI et al. (1993): Table V: columns 2, 3 versus 2, 4), we found that the distal part of the tarsometatarsus outnumbered the proximal by 7% in A. otus, 17% in S. aluco and 13% in B. bubo. The scapular part of the coracoideum prevails over the sternal by 16% in A. otus, 30% in S. aluco and 48% in B. bubo. The proximal and distal parts of the ulna are practically equally numerous in the three owl species examined (2% differences only).

As shown in Table XI, when only broken long bones were taken into account (Table VIII: columns 3 and 4), five various kinds of bones showed significant differences between the numbers of proximal and distal parts in the A. otus/S. aluco relation (radius, carpometacarpus, femur, tibiotarsus, tarsometatarsus), five kinds of bones in the S. aluco/B. bubo relation (coracoideum, humerus, carpometacarpus, femur, tibiotarsus), and four bones between A. otus and B. bubo (coracoideum, radius, tibiotarsus, tarsometatarsus). Only in the ulna no such differences were found between any pairs of owl species.

The category "shaft" did not play any important role in any of the owl species examined.

Minimum number of individuals: The last columns of Tables I, III, V, VII and VIII show the MNI calculated on the basis of each kind of bone and expressed as

Table IX

Statistically significant differences in the proportion of whole and broken long bones (Table VIII: column 7 versus 8)) calculated for each pair of species. Asia ottus –

bones (Table VIII: column 7 versus 8)) calculated for each pair of species. *Asio otus* – present data; *S. aluco* and *B. bubo* – after BOCHEŃSKI et al. (1993)

Bones/species	S. al	исо	B. huho $\chi^2 = 4.85$		
A. otus SCAP x SCAP	d situ n , wode unan sangd <u>a</u>	(gorneksidis (ne go) oor sahgaliwa	*	$\chi^2 = 4.85$	
S. aluco	id a bas who	A accorded being	**	$\chi^2 = 9.17$	
A. otus COR x COR	0 A 828V056	PA - PA	(Islaed V) o dásí T) san	on le sneet in yla on le sneet in yla	
S. aluco	ni otomerudi		rikorg to s		
A. otus HUM x HUM	**	$\chi^2 = 96.35$	**	$\chi^2 = 280.13$	
S. aluco	ili ke pomegani	ės avigilas asų a	**	$\chi^2 = 99.18$	
A. otus ULNA x ULNA	**	$\chi^2 = 85.58$	**	$\chi^2 = 99.18$ $\chi^2 = 151.23$	
S. aluco			**	$\chi^2 = 22.18$	
A. otus RAD x RAD	**	$\chi^2 = 25.25$	**	$\chi^2 = 22.18$ $\chi^2 = 37.07$	
S. aluco	ound the plan		*	$\chi^2 = 5.27$	
A. otus CMC x CMC	**	$\chi^2 = 16.12$	**	$\chi^2 = 5.27$ $\chi^2 = 15.53$	
S. aluco	la l'appropriée		9 1911 <u>9</u> 11 15		
A. otus PHAL x PHAL	P vs lessos e usbiopese	ambios, v gines pagistro batiking palako pagistro	CARTO SE NO SUSSILIZA NO SUSSILIZA	at BOCHEROSTON at of the tagridated ad 13% in 8. Dan	
S. aluco	7 7 (1971) (1974)	16.16 37.84 Day	in L and	SUCCESSION AND WE	
A. otus FEM x FEM	oiboq <u>i.</u> 1970.aa 30 45		**	$\chi^2 = 24.09$	
S. aluco	soci quid be	when only brok	**	$\chi^2 = 29.08$	
A. otus TBT x TBT		$\chi^2 = 41.55$	**	$\chi^2 = 29.08$ $\chi^2 = 10.67$	
S. aluco		garana _k antanisi Suman <u>manakir</u> a	**	$\chi^2 = 7.67$	
A. otus TMT x TMT	n my Enjarent w od buent n	op oduć il basic ov osorositibile	*******	$\chi^2 = 7.67$ $\chi^2 = 6.24$	
S. aluco	y caledorae	Section to a value	**	$\chi^2 = 15.71$	

 $\label{legend: SCAP-scapula; COR-coracoideum; HUM-humerus; RAD-radius; CMC-carpometacarpus; PHAL-phalanx I dig. majoris; FEM-femur; TBT-tibiotarsus; TMT-tarsometatarsus; **-p<0.05; **-p<0.01$

Table X

Statistically significant differences in the proportion of the total number of proximal and distal parts (Table VIII: columns 2 and 3 versus 2 and 4 – i. e. whole + proximal versus whole + distal) calculated for each pair of species. Asio otus – present data; S. aluco and B. bubo – after BOCHEŃSKI et al. (1993)

Bones/species	S. aluco	B. bubo
A. otus SCAP x SCAP S. aluco	Not compared	Not compared
A. otus COR x COR S. aluco	e let _ anne serve for sec 341 to NIM observed with seculos and observed to select (six	** $\chi^2 = 7.58$
A. otus HUM x HUM S. aluco	but there were its seen that	o sa =end tenandikananik (o
A. otus ULNA x ULNA S. aluco		- ANJU x ANJU - Science
A. otus RAD x RAD S. aluco	* $\chi^2 = 4.35$	* $\chi^2 = 4.29$
A. otus CMC x CMC S. aluco	ist such data, usually can dia from various other noises incl [2] 1585, Figure Asia 1667	LICENT HOME STORES
A. otus PHAL x PHAL S. aluco	is the Tools of control of the second of the	regineral extensive and another the second s
A. otus FEM x FEM S. aluco	The site of the second	se determine MERX MER. se mated, behavious that the reasons to the house with the reasons are the second to the s
A. otus TBT x TBT S. aluco	* $\chi^2 = 6.62$	** $\chi^2 = 18.62$ * $\chi^2 = 5.42$
A. otus TMT x TMT S. aluco	u nome brey species could i ya teorgraps polici macrosso w menstresso a menstress	or committee TM Too SEAT of the order fragming of the seat fragming of the seat for

Legend: abbreviations of bone names as in Table IX; * - p<0.05; ** - p<0.01

Table XI Statistically significant differences in the proportion of proximal and distal parts (Table VIII: column 3 versus 4) calculated for each pair of species. *Asio otus* – present data; *S. aluco* and *B. bubo* – after BOCHEŃSKI et al. (1993)

Bones/species	S. aluco	B. bubo
A. otus		26000113000E
SCAP x SCAP	Not compared	Not compared
S. aluco	barsqmap solf	SCAP & SOAP
A. otus		** $\chi^2 = 14.45$
COR x COR		A. ons
S. aluco		** $\chi^2 = 7.66$
A. otus		<u> </u>
HUM x HUM		ano A
S. aluco	7	* $\chi^2 = 4.03$
A. otus	<u> </u>	
ULNA x ULNA		amo A
S. aluco		_ Art.10 x Art.10
A. otus	** $\chi^2 = 12.51$	** $\chi^2 = 9.38$
RAD x RAD		4. 0000
S. aluco		<u> </u>
A. otus	* $\chi^2 = 4.08$	
CMC x CMC		4306 A
S. aluco		** $\chi^2 = 7.47$
A. otus		103110 A.
PHAL x PHAL	Not compared	Not compared
S. aluco		LEAST X LAST
A. otus	* $\chi^2 = 5.55$	CANA SA A A A A A A A A A A A A A A A A A
FEM x FEM		AMO. A
S. aluco		** $\chi^2 = 10.68$ ** $\chi^2 = 23.29$
A. otus	* $\chi^2 = 4.95$	** $\chi^2 = 23.29$
TBT x TBT		2800 A
S. aluco		** $\chi^2 = 8.63$ * $\chi^2 = 4.52$
A. otus	* $\chi^2 = 4.12$	* $\chi^2 = 4.52$
TMT x TMT		230KL-A
S. aluco		<u></u>

percentages of the highest value (i. e. that obtained with the ulna). The sequence of bones in A. otus, from the highest MNI values to the lowest, is as follows: ulna (100%), humerus (96), mandible (74), tarsometatarsus (74), tibiotarsus (70), carpometacarpus (64), skull (59), femur (58), radius (56), pelvis (49), coracoideum (46), sternum (38), scapula (31) and phalanx I dig. majoris (21). It should be noted that the percentages of the MNI for the last five bones are below 50%.

Comparison with S. aluco and B. bubo (BOCHEŃSKI et al. 1993): Unlike A. otus, S. aluco and B. bubo at non-nest sites have the corresponding sequence of bones beginning with the humerus, and B. bubo at nest sites - with the tarsometatarsus. However, in all these cases, the sequences end with the phalanx I dig. majoris. In the material of A. otus, the humerus produced only a little worse score for the MNI than the ulna. In S. aluco and B. bubo, the percentages of the MNI obtained with the ulna were also relatively high (84% and 70%, respectively). As regards the victims' heads (skulls and mandibles), the percentages of the MNI obtained with them were the highest in S. aluco, lower (but still high) in A. otus, and very low in B. bubo. In S. aluco, only one bone showed the percentage of the MNI lower than 50%; in B. bubo there were six such bones, which is closer to the results of A. otus (five bones).

IV. DISCUSSION AND CONCLUSIONS

Although the literature on the food of the Long-eared Owl is enormous, there is not a single paper dealing with damage to bird bones in its pellets. Many authors do not even say, which elements of the skeleton they used for determining the number of individuals eaten by owls. Those who give such data, usually calculated the MNI from the number of beaks and, besides beaks, from various other bones including the humerus, sternum or tarsometatarsus (e. g. CRAIG et al. 1985, HEITKAMP 1967, KÄLLANDER 1977, TINBERGEN 1933, YALDEN & YALDEN 1985). Only NILSSON (1981) says that "... humeri were particularly useful for estimating both the number and weights of eaten birds", which is closest to our results. Also PHARISAT (in print) admits that humeri are often well-preserved and covered with soft tissue. This paper is probably the first one which points to the importance of the ulna and humerus, in the first place, followed in this respect by the mandible and tarsometatarsus. Beaks are also important to determining the MNI but the results obtained exclusively with them are greatly underestimated. It seems that the reason why beaks (and sometimes humeri) were used for calculating the MNI was that beaks are relatively easy to identify and humeri differ so much from other bird bones that even a non-specialist can separate them from the others. That is probably the only sound explanation why, so far as we know, the ulna has never been used for calculating the MNI. Although it is possible, yet very unlikely, the differences in fragility of the ulna and the other skeletal elements in various prey species could be responsible for those results. PHARISAT (pers. comm.) says that in his pellet material of A. otus from France (containing bird prey of the Garrulus/Turdus size - i. e. bigger than in our material), the best results in the calculation of the MNI were obtained with the humerus; the ulna provided only a little worse score (ca. 93% of the MNI calculated for humeri). Taking into account the differences in prey size, this corresponds surprisingly well with our results. Thus, we may conclude that humeri and ulnae provide the most reliable data of all the skeletal elements on the MNI in *A. otus* pellets. Similarly to our results, the remaining kind of bird bones from *A. otus* pellets in France (PHARISAT: pers. comm.) provided much worse results in this respect. According to PHARISAT (pers. comm.), even the MNI obtained with the most numerous bone (in his case the humerus), is underestimated by about 25% in relation to the MNI calculated for all the skeletal elements jointly and determined to the species-level. It should be stressed that even the MNI obtained with all the bones is most probably underestimated since the loss of bones digested by owls is 21% in *A. otus* (RACZYNSKI & RUPRECHT 1974 – data for mammalian and bird prey jointly).

Apart from being plucked (GROSS 1943; TICEHURST 1939), small birds are usually decapitated and torn up by Long-eared Owls (TICEHURST 1939). Heads are probably not always eaten since the MNI calculated from skulls and mandibles is lower than that obtained with the ulna and/or humerus. This would agree with TICEHURST's observation concerning bird prey that "... fairly often no skull is recoverable". Damage done to the skull (brain cases crushed into pieces or, at least, lacking the back part) suggests that the owl kills its prey by hitting it on the head with the beak. Such behaviour was described in the case of *Athene noctua* (OLEŚ 1961, KULCZYCKI 1964), *Tyto alba* (KULCZYCKI 1964) and – indirectly – in *Strix aluco* and *Bubo bubo* (BOCHEŃSKI et al. 1993; RÄBER 1949).

As regards the relative preservation of the fragments of the victims' heads (skulls and mandibles) in A. otus pellets, our results were confirmed by PHARISAT (pers. comm.). Also in his material, "whole beaks" (BOCHEŃSKI et al. 1993: Fig. 1, E), forming about 63% of the all skull fragments found, were the most numerous category of damage to the skull. He also did not find any whole skull (BOCHEŃSKI et al. 1993: Fig. 1, A) in his pellet material of A. otus and says that mandibles were more numerous than beaks. Although the percentages given by him differ from those from our results, the tendencies are the same in both studies.

Judging from the number of statistically significant differences in damage to the long bones (Table IX) and from the role of the head (mandible and skull) in the calculation of the MNI between various pairs of owl species, *Asio otus* and *Strix aluco* are closer to each other than any of them to *Bubo bubo*. That is in a way consistent since both of them belong to the middle-sized owls whereas *B. bubo* is much bigger. Thus, the relative differences in predator/victim size seem to play an important role here.

With the exception of the phalanx I dig. majoris, the degree of fragmentation of each skeletal element and the relative preservation of its parts provide some information on the owl species which produced the pellets [present data compared with those of BOCHEŃSKI et al. (1993): Tables II, IV, VI, IX, X, XI]. Thus, bearing in mind that bones are vulnerable to further post-depositional damage, it should be possible to ascribe some fossil assemblages to a certain owl species (predator). Such analyses of fossil assemblages could provide very interesting data; they could be done irrespective of similar analyses based on mammalian bones, so that the results obtained in both ways could be critically compared.

BOCHEŃSKI et al. (1993) noticed that the scapular parts of the coracoideum in S. aluco and B. bubo were much more numerous than the sternal parts, which could be used as an

indicator of the pellet origin of fossil assemblages. The present data provide additional data: the scapular part of the coracoideum in A. otus also outnumbers the sternal part. Moreover, the distal part of the tarsometatarsus is more often preserved than the proximal one in the three owl species. In the case of the ulna, its proximal and distal parts are nearly equally well-preserved. Similar results for tarsometatarsi and ulnae of the A. otus victims were also obtained by PHARISAT (pers. comm.). Thus, the relative preservation of proximal and distal parts in these three bones (coracoideum, tarsometatarsus and ulna) may indicate whether some fossil materials are of the pellet origin or not. However, as it was already mentioned by BOCHEŃSKI et al. (1993), this problem calls for additional studies on damage to bones under natural conditions (erosional and mechanical damage).

There are two further problems which call for additional studies. On the one hand, we still lack information on the damage to bird bones done by other large-sized owls including *Nyctea scandiaca*, *Strix nebulosa* and *S. uralensis*, which may well be responsible for the accumulation of pellets in Europe in prehistoric times. On the other hand, damage to bone surface done by the owls' digestive system as well as by depositional conditions (erosion) should be also studied.

V. FINAL CONCLUSIONS

The most characteristic differences between Asio otus and Strix aluco as well as between Asio otus and Bubo bubo in damaging their bird victims include:

- 1. Skulls and mandibles are rare in pellets of Eagle Owls, relatively numerous in Long-eared Owls and very numerous in Tawny Owls.
- 2. All recognizable brain cases of the A. otus victims lack their back part as a result of the mode of killing. Their proportion in S. aluco is somewhat smaller (70%), whereas for B. bubo such damage is much less typical (0-32%).
- 3. The proportions of beaks in the pellet material of A. otus and S. aluco are higher than that in B. bubo, which is reflected in Table II.
- 4. The proportions of the total number of whole mandibles and that of broken ones are species-specific (Table IV): S. aluco (39% of whole mandibles), A. otus (16%) and B. bubo (2%).
- 5. Sternum: more fragments with the rostrum sterni than without it are preserved in the pellets of S. aluco, and conversely in A. otus and B. bubo, which proves to be significant (Table VI).
- 6. The relations between the number of whole and broken humeri, ulnae, radii and tibiotarsi differ significantly between the three owl species. Such differences in the remaining long-bones are significant only for a given pair of owl species (Table IX).
- 7. The relations between the number of the proximal and distal parts of a given bone in pellet materials depend on the owl species and on the kind of the victims' bone (Tables X and XI).
- 8. The distal parts of the tarsometatarsus and the scapular parts of the coracoideum are more numerous than the other ends of these bones in the three owl species. Both parts

(proximal and distal) of the ulna are equally numerous in pellets. Thus, the relative abundance of the end parts of the three bones may be used as evidence of the pellet origin of fossil assemblages.

9. In A. otus the ulna and humerus provide very good results in the calculation of the MNI. In S. aluco best results are obtained with the humerus, skull and mandible. In B. bubo at non-nest sites the best bone for the determination of the MNI is the humerus, whereas at nest sites - the tarsometatarsus.

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