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Preliminary taphonomic studies on damage to bird bones by Snowy Owls *Nyctea scandiaca*, with comments on the survival of bones in palaeontological sites

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Abstract. Fragmentation of bird bones and their digestion by Snowy Owls *Nyctea scandiaca* were studied in a feeding experiment in Zurich Zoo, Switzerland. Victims' heads were ingested by the owls and remains of their skulls were often found in pellets. Humeri were the best bone for the calculation of the MNI. With the exception of ulnae, only up to 50% of articular parts of long bones were affected by digestion. The problem of bone survivorship (species-specific patterns versus mechanical properties of bones) is discussed. It is postulated that taphonomic analyses of fossil materials should be based on a variety of factors including fragmentation of bones and their survivorship, traces of digestion, representation of species and chemical alteration of bone tissues.

Key words: taphonomy, bird bones, pellets, *Nyctea scandiaca*.

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I. INTRODUCTION

Although Snowy Owls *Nyctea scandiaca* feed mainly on lemmings and voles, birds may dominate their prey under certain conditions (BROOKS 1929, GLUTZ VON BLOTZHEIM & BAUER 1980, PORTENKO 1972, WILLIAMS & FRANK 1979). In some areas particularly the species of *Lagopus* belong to their substitute food (GROSS 1944 – after DUFRESNE 1922, WATSON 1956, PORTENKO 1972). Remains of both *Lagopus* species are very abundant in the late Pleistocene and Early Holocene sites of the Palearctic (TYRBERG 1995). Although nowadays Snowy Owls are restricted to northern parts of the Palearctic, in the late Pleistocene and Holocene they had a much more southern distribution (BOCHEŃSKI 1974), and therefore they could prey upon the birds whose fossil remains are now found in the Palearctic. Fossil remains of *Lagopus* species have already been attributed to the activities of Snowy Owls (BAALES 1992). However, BAALES based his attribution only on the frequency of skeletal elements in fossil materials. As little is known about damage caused to bird bones by Snowy Owls, I seek to clear this situation in this study to better assess the predator responsible for accumulation of fossil deposits.

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II. MATERIAL AND METHODS

A pair of Snowy Owls *Nyctea scandiaca* LINNAEUS, 1758, were fed with eight adult quail *Coturnix coturnix* at the Zurich Zoo, Switzerland. The experiment was carried out between 8-26 May, 1995. One dead but otherwise untouched quail was offered to the owls at a time. The owls did not eat the whole quail at once. They would have probably finished it later but uneaten remains were removed from the aviary by small mustelids at night (quail feathers, 4 wings and a fragment of pelvis with the proximal part of a femur were found outside the aviary). Standard food consisting of freshly killed mice and a few-day-old chicks (the size of a sparrow) was also available to the owls. The female Snowy Owl incubated throughout the experiment. Pellets were collected on feeding days and on the subsequent two days.

The fragmentation of quail bones was evaluated in the way described by BOCHEŃSKI et al. (1993) and BOCHEŃSKI & TOMEK (1994). Damage to the bone surface was studied under the SEM and light microscope, applying categories of damage proposed by BOCHEŃSKI & TOMEK (in print).

Bone ratio of the wing to leg elements was calculated as the number of wing fragments (humerus, ulna, carpometacarpus) divided by the sum of wing and leg bone fragments (femur, tibiotarsus, tarsometatarsus), expressed as percent (ERICSON 1987, LIVINGSTON 1989). Ratios for other species than the Snowy Owl were calculated from raw data from previous papers (BOCHEŃSKI et al. 1993, BOCHEŃSKI & TOMEK 1994). Chi-square tests were used to check whether the frequencies of wing and leg elements differed significantly from the expected 1:1 proportion.

The minimum number of individuals (MNI) was calculated for each bone separately. The results are presented as absolute numbers and as percentages of the number of the most numerous sort of bone, in this case the humerus. The procedure was the same as in the previous studies (BOCHEŃSKI et al. 1993, BOCHEŃSKI & TOMEK 1994) – i. e. the MNI was computed for the whole material (not for separate pellets) and without fitting proximal and distal parts together.

Due to the small amount of experimental material available (8 quail that successfully went through veterinary examinations), the results may not be statistically significant. Therefore the present study has only a preliminary character and we may say only of tendencies in damaging victims' bones – i. e. describe it qualitatively rather than quantitatively.

III. RESULTS

1. Handling of food

Quail were mainly, if not wholly, taken by the male Snowy Owl (the female was incubating and went off the nest only sporadically). Thus, we may assume that most (or all) of the pellets with remains of quail were produced by the male.

Observations on the way of eating were difficult because the male always ate quail while hidden behind a large stone in a corner of the aviary. From five observations the typical feeding procedure

was: The male took a quail from where it had been laid out, and carried it in his beak back to the corner of the aviary. There, on the ground, he tore the quail up keeping it in his claws (head forward). He tore the quail's head asunder and swallowed it. Then, holding with his beak the base of the victim's wing (humerus region), he detached the wing from the carcass and swallowed it. Next, he tore off small pieces from the victim's breast. A characteristic noise of breaking bones could be heard from about ten meters. Snowy Owls were not observed to pluck quail; all torn up pieces were swallowed with feathers. After 10-15 minutes the owl stopped eating and fell asleep on a nearby roost, leaving the uneaten remains (one-half of the quail or more) on the ground. Probably the male would have finished it later if mustelids had not stolen the carcass at night.

On many occasions, when male and female Snowy Owls were observed eating mice and chicks, they always swallowed them whole, head first.

2. Fragmentation of bones

A x i a l s k e l e t o n. No whole skull was recorded, and all the brain cases, which were not broken to pieces (Table I: columns 2, 3, 4 and 5 jointly), lacked the back part with the condylus occipitalis (columns 3 and 4). Of all distinguishable skull fragments, beaks (columns 2, 3, 6, 7 jointly) were the most numerous element found.

Most of the mandibular remains found were those from the category "one branch"; only one whole mandible (8%) was present (Table II).

The fragmentation of the sterna is shown in Table III. Fragments without the rostrum sterni prevailed over those with the rostrum (column 4 versus 2 and 3 jointly).

Fragments of the pelvis were mainly from the synsacrum and acetabulum regions (Table IV).

Table I

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

Total 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 (%)	MNI (N)	MNI (%)
1	2	3	4	5	6	7	8	9	10
N = 15	–	7	13	–	33	–	47	6	86

Table II

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

Total number of fragments	Whole (%)	One branch (%)	Articular part (%)	Tip of mandibula (%)	Middle part of branch (%)	MNI (N)	MNI (%)
1	2	3	4	5	6	7	8
N = 12	8	75	8	8	–	6	86

Table III

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

Total 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 = 25	–	12	88	3	43

Table IV

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

Total 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	2	3	4	5	6	7
N = 12	8	8	42	42	3	43

L o n g b o n e s. The fragmentation of long bones is shown in Table V. There were considerable differences in the degree of fragmentation between various types of bones. Whole bones were more numerous than their fragments for ulnae, radii, carpometacarpi, phalanx I dig. maj. alae and tarsometatarsi, whereas broken parts prevailed in scapulae, coracoids, humeri, femora and tibiotarsi (column 2 versus 6).

For most bones proximal and distal ends were roughly in equal abundance but in humeri proximal ends were more numerous, and in femora distal ends were more numerous.

Shafts that were identifiable as from a particular element and without articular ends (column 5) were very rare for all types of bones. However, many unidentifiable shafts – and especially their small fragments – were found. Most of them (76%) had a broad gap along the shaft and looked like tiny pieces of flat bones at first glance (Fig. 1). Less than one-third of the fragments (24%) did not have the gap but even then most of them were short.

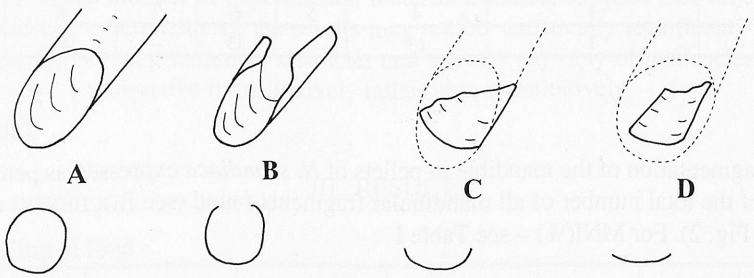

Fig. 1. Small fragments of unidentifiable shafts damaged by digestion (their numbers are listed in the last rows of Tables V and VIII). Most edges of the fragments are thinned and rounded. A cross section of each fragment is shown below it. A – no gap along the shaft; B – a stripe of shaft walls digested completely, which produced a broad gap along the shaft; C-D – large parts of shafts dissolved to the effect that the fragments look like pieces of flat bones at first glance.

Table V

Fragmentation of long bones in pellets of *N. scandiaca* expressed as percentages of the total number of all 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. In the last row of the table, the name "Bone ???" includes all shafts digested so heavily that one could not tell what element they were (see also Fig. 1). For MNI(%) – see Table I

Bones (Total number of fragments)	Whole bone (%)	Proximal part (%)	Distal part (%)	Shaft (%)	Total of broken parts (%)	MNI (N)	MNI (%)
1	2	3	4	5	6	7	8
Scapula (N = 19)	–	37		63	100	4	57
Coracoideum (N = 21)	5	43	52	–	95	6	86
Humerus (N = 18)	17	55	28	–	83	7	100
Ulna (N = 8)	88	–	12	–	12	6	86
Radius (N = 9)	56	33	11	–	44	5	71
Carpometacarpus (N = 9)	78	11	11	–	22	6	86
Phalanx I dig maj. alae (N = 8)	100	–	–	–	–	6	86
Femur (N = 14)	–	36	64	–	100	5	71
Tibiotarsus (N = 17)	6	41	41	12	94	4	57
Tarsometatarsus (N = 9)	89	–	–	11	11	5	71
Bone???: without gap N = 13 with gap N = 41 Total N = 54	–	–	–	24 76 100	100		

M i n i m u m n u m b e r o f i n d i v i d u a l s. Table VI compares values of the MNI calculated on the basis of each kind of bone and expressed as percentages of the highest value for a given owl species. In *N. scandiaca*, the descending order of bones best fitted for the MNI is as follows: 1) humerus; 2) coracoid, ulna, carpometacarpus, phalanx I dig. majoris alae, skull, mandible; 3) radius, femur, tarsometatarsus; 4) scapula, tibiotarsus; 5) sternum, pelvis.

W i n g / l e g r a t i o. Mean percentages of the wing bones (fragments) as proportions of wing and leg bones from pellet materials of four owl species (see Material & Methods) were as follows:

Nyctea scandiaca 46.7%

Asio otus 49.7%

Bubo bubo 52.7%

Strix aluco 53.8%

Only the values for *S. aluco* and *B. bubo* differed significantly from the expected 50% ($p<0.01$, $df=1$, and $p<0.05$, $df=1$, respectively).

Table VI

Comparison of the MNI(%) values from pellet materials of *Nyctea scandiaca* (present data), *Strix aluco*, *Bubo bubo* (BOCHEŃSKI et al. 1993) and *Asio otus* (BOCHEŃSKI & TOMEK 1994)

Bones	*Nyctea*	*Strix*	*Asio*	*Bubo* (total)	*Bubo* (non-nest)	*Bubo* (nest)
Skull	86	96	59	22	24	14
Mandible	86	90	74	14	17	7
Sternum	43	67	38	34	30	32
Pelvis	43	56	49	36	38	26
Scapula	57	63	31	50	50	38
Coracoideum	86	76	46	58	57	45
Humerus	100	100	96	100	100	78
Ulna	86	84	100	70	75	47
Radius	71	60	56	34	31	32
Carpometacarpus	86	78	64	63	64	47
Phal. I dig. maj. alae	86	32	21	9	7	11
Femur	71	69	58	60	57	50
Tibiotarsus	57	54	70	72	54	80
Tarsometatarsus	71	76	74	96	77	100

3. Digestion of bones

Many bones were partly damaged by digestion which produced holes with rounded edges in the bone surface and rounding of green fracture (not post-deposition) breaks (Figs 2-7).

Axial skeleton

A. Surface damage

Most fragments of the head (skull and mandible) had holes with rounded edges (state B) whereas those of the sternum were usually undamaged (state A). In pelvis, undamaged fragments and those with holes with rounded edges were approximately equally numerous. Holes with sharp edges (state C) were rare and occurred only together with holes with rounded edges (Table VII).

B. Breakage

Breaks on axial elements were mostly rounded (state B). Sharp and rough breaks (state A) and variations of the two states (A+B, AB, AB+B) were less frequent (Table VII).

Table VII

Percentage of bones of the axial skeleton affected by digestion in pellets of *Nyctea scandiaca*. Categories of damage follow those described by BOCHEŃSKI & TOMEK (in print). B+C – both states (rounded and sharp) present on the same bone; A+B – both states (sharp and rounded) present on the same bone; A&B variations include states: AB (intermediate) and AB+B (both)

Bones	Bone surface			Breakage			
	A undamaged	B rounded	B+C rounded+ sharp	A sharp	B rounded	A+B both	A&B variations
Skull N=15	27	60	13	–	60	40	–
Mandible N=12	–	100	–	17	58	25	–
Sternum N=25	60	36	4	–	64	28	8
Pelvis N=12	42	50	8	8	67	17	8
Total N=64	38	56	6	5	62	28	5

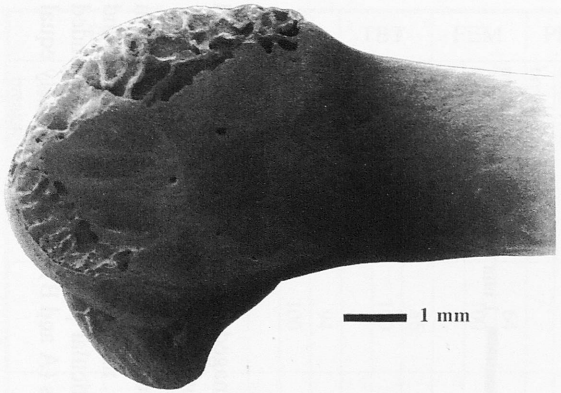

Fig. 2. Distal femur heavily affected by digestion.

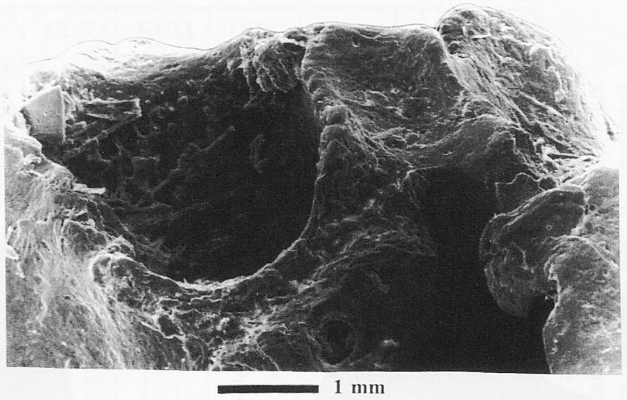

Fig. 3. Detail of Fig. 2 – digested holes with rounded edges.

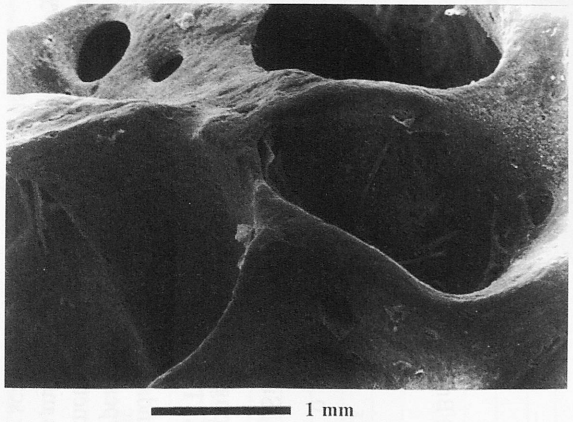

Fig. 4. Digested holes with rounded edges on proximal femur.

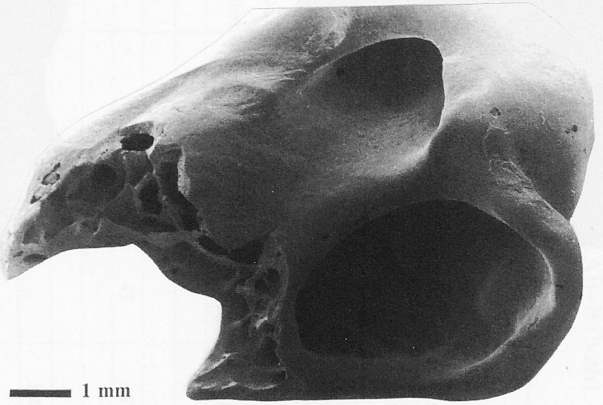

Fig. 5. Partly rounded breakage of humerus.

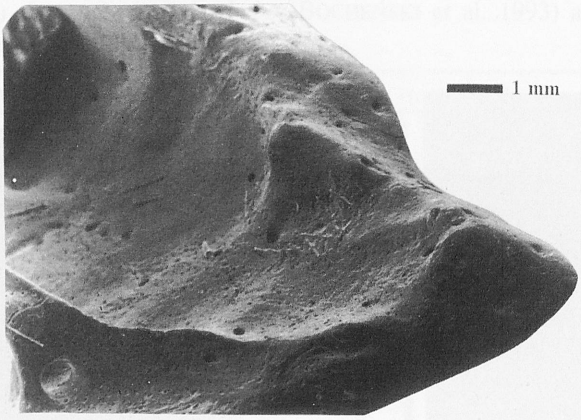

Fig. 6. Detail of Fig. 5 – breakage of humerus rounded through digestion.

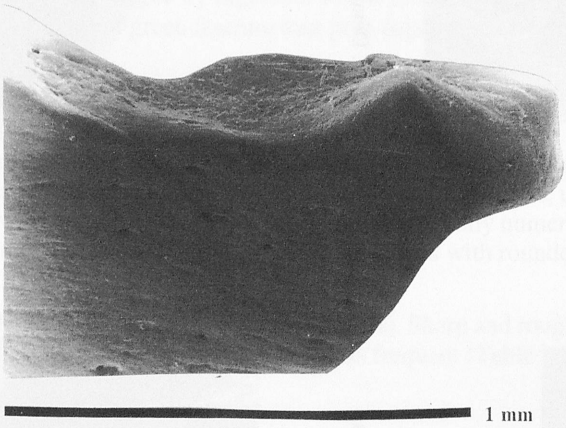

Fig. 7. Breakage of coracoid rounded through digestion.

Long bones

A. Surface damage

Long bones (articular ends and shafts) were either undamaged or they had holes with rounded edges (Table VIII). Holes with sharp edges were observed only sporadically.

Undamaged articular parts were more numerous than those with holes with rounded edges in six types of bones (radius, carpometacarpus, phalanx I dig. majoris alae, femur, tibiotarsus and tarsometatarsus). The reverse situation was in the ulna (articular parts with holes with rounded edges more numerous) whereas the frequency of both states (A and B) was approximately equal in the scapula, coracoid and humerus.

Table VIII

Percentage of long bones affected by digeston in pellets of *Nyctea scandiaca*. Categories of damage follow those described by BOCHEŃSKI & TOMEK (in print). B&C variations include states: B+C (both states present on the same bone), BC (intermediate), BC+B (both) and BC+C (both). A&B variations include: A+B (both states present on the same bone), AB (intermediate), AB+A (both) and AB+B (both). For "BONE ???" – see Table V and Fig. 1

Bones (Total number of fragments)		Bone surface				Breakage		
		A undamaged	B rounded	C sharp	B&C variations	A sharp	B rounded	A&B variations
1		2	3	4	5	6	7	8
SCAP	prox & dist N=7	43	57	–	–			
	shaft N=15	93	7	–	–			
	breakage N=29					4	72	24
COR	prox & dist N=22	41	50	–	9			
	shaft N=10	100	–	–	–			
	breakage N=20					–	55	45
HUM	prox & dist N=21	43	38	14	5			
	shaft N=9	89	11	–	–			
	breakage N=15					6	47	47
ULNA	prox & dist N=15	40	60	–	–			
	shaft N=8	88	12	–	–			
	breakage N=1					–	–	100
RAD	prox & dist N=14	71	29	–	–			
	shaft N=9	100	–	–	–			
	breakage N=4					–	100	–
CMC	prox & dist N=16	62	38	–	–			
	shaft N=9	89	11	–	–			
	breakage N=2					–	50	50
PHAL	prox & dist N=16	62	38	–	–			
	shaft N=8	75	25	–	–			
	breakage N=0					–	–	–
FEM	prox & dist N=14	64	29	–	7			
	shaft N=6	100	–	–	–			
	breakage N=14					21	43	36
TBT	prox & dist N=16	56	38	–	6			
	shaft N=9	100	–	–	–			
	breakage N=18					33	33	33
TMT	prox & dist N=16	94	6	–	–			
	shaft N=9	100	–	–	–			
	breakage N=2					–	50	50
BONE ???	without gap: items N=13 breakage N=26	69	31	–	–	8	84	8
	with gap: items N=41 breakage N=82	–	37	41	22	45	35	20
	total: items N=54 breakage N=108	17	35	31	17	36	47	17

A clear majority of shafts of all types of bones was undamaged (state A); shafts which were damaged had holes with rounded edges (state B). Only shafts of unknown types of bones did have holes (and/or gaps) with rounded and sharp edges (states B and C) which were equally numerous.

B. Breakage

Breaks of the B state (rounded) prevailed in most types of bones (scapula, coracoid, humerus, radius, femur and bones of unknown types). In tibiotarsi, sharp breaks were equally numerous as rounded breaks. Broken fragments of the remaining types of bones were too scanty to risk any analysis.

IV. DISCUSSION

1. Handling of food

Similarly to other owl species, Snowy Owls usually swallow small items whole, head-first. Larger prey is eaten piece by piece (e.g. SCHERZINGER 1974, GLUTZ VON BLOTZHEIM & BAUER 1980, MIKKOLA 1983). Small prey may also be eaten in pieces when owls are less hungry (WATSON 1956, PORTENKO 1972, SCHERZINGER 1974, GLUTZ VON BLOTZHEIM & BAUER 1980). Surplus food may be ingested later, hidden in a cache, or abandoned (WATSON 1956, TULLOCH 1968, PORTENKO 1972, SCHERZINGER 1974, MIKKOLA 1983). Thus, the same may have happened to the remainder of each quail if they had not been removed from the aviary by mustelids. Larger victims are eaten on the ground, while being held with their long axis parallel to the axis of the owl (SCHERZINGER 1974) i.e. in the way observed in the Zurich Zoo. Birds may be either ingested with bones and feathers (present data, SCHERZINGER 1974) or plucked before eating (BROOKS 1929, GROSS 1944). This seems to depend on the predator's hunger and/or the victim's size rather than to be the owls' permanent habit. The present data correspond well with those from the literature. Quail are medium-sized prey for Snowy Owls, being smaller than the *Lagopus* species that are preyed upon by the owls, but still far too large to be swallowed whole.

2. Survivorship of bones

There are various indices to calculate the relative abundance of certain skeletal elements in pellet and fossil materials (MOURER-CHAUVIRÉ 1983, ERICSON 1987, ANDREWS 1990). Their common goal is to determine agencies responsible for death of animals and subssequent accumulation of their bones. The reliability of such indices has recently been criticized (LIVINGSTON 1989, STEWART 1992). Moreover, many researchers believe that the relative robusticity and strength of skeletal elements play an important part in their survivorship (BJORDAL 1988, HARRISON & STEWART in print, LIVINGSTON 1989, WORTHY & HOLDAWAY 1994, 1996). Other factors influencing proportion of skeletal elements in fossil finds include recovery methods and physical properties of sediments (HARRISON & STEWART in print). However, the critical papers are based either on laboratory studies of mechanical properties of bones (BJORDAL 1988) or on fossil materials that have been attributed to some predators or physical agencies (the other studies). None of the studies was carried out on bone frequency in pellet material of recent raptors. Therefore we face two problems here. First, the species of predator is only a putative one, and second post-depositional breakage has been superimposed on damage done by the predator which might completely destroy the predator's "signature" (if it ever existed).

I do not doubt that relative strength and robusticity of particular types of bones are important factors in their survivorship. However, I think that the relation is not a straightforward one. For instance, of the eight long-bones of the House Sparrow *Passer domesticus* tested, the humerus and carpometacarpus were the strongest, and the radius and tibiotarsus the weakest (BJORDAL 1988). House Sparrows formed 70% of the Tawny Owls' prey items (BOCHEŃSKI et al. 1993). Yet, humeri

and radii were broken at a similar rate (whole bones constituted 55 and 58%, respectively). This can be best explained by the owls' habit of cutting off sparrows' wings (and other parts of the body) when feeding owlets. In this process robust humeri were probably broken with the beaks, whereas much more fragile and thin radii were protected by stout ulnae. Frequent damage to the humerus and coracoid result from the very strong joint between the two bones. Predators – including man – often break these bones (BOCHEŃSKI 1960, BOCHEŃSKI et al. 1993) or at least leave cut marks on them (CASSOLI & TAGLIACOZZO 1995). I believe that more humeri would remain unbroken if all prey was swallowed whole.

However, I must admit that the sequence of the MNI(%) values for bones of the Tawny Owl prey (mainly House Sparrow *Passer domesticus*) (BOCHEŃSKI et al. 1993) is similar to that of the relative strength of House Sparrows' bones (BJORDAL 1988) – with radii (tibiotarsi) and humeri at the extreme positions. Robust humeri often outnumber other bones in archaeological finds that are older than 1000 years (BJORDAL 1988: after SCHAANNING 1927 and OLSEN 1967). In this context it is surprising that the fragile radius may sometimes provide the best results (among long-bones) in the calculation of the minimum number of bones (MNB) – exceeding even much more robust and strong elements like humeri, ulnae or coracoids (WORTHY & HOLDAWAY 1994).

WORTHY & HOLDAWAY (1996) point out that the survivorship of skeletal elements depends on their robusticity which varies greatly among prey species – even among prey of similar size. This hampers comparisons of materials from various sites and, especially, from different species of raptors (which catch different prey).

Bearing in mind the above mentioned difficulties, we may try to check the present results against those from literature.

Beaks are the most numerous fragments of the skull in pellets of *N. scandiaca* (present results), *S. aluco, B. bubo* (BOCHEŃSKI et al. 1993) and *A. otus* (BOCHEŃSKI & TOMEK 1994). Brain cases lacking their back parts are also frequently found in *S. aluco* and *A. otus* pellets; such damage is less typical of *B. bubo*. Of the four owl species examined, skulls and mandibles are rare only in pellets of *B. bubo*. In this respect *N. scandiaca* resembles *S. aluco* and *A. otus* rather than *B. bubo*.

However, the fragmentation of the sternum does not support the latter conclusion. Here, only in pellets of *S. aluco* do the fragments with the rostrum sterni prevail over those without the rostrum. The remaining species – including *N. scandiaca* – show the opposite state and, consequently, are more similar to one another than any of them to *S. aluco*.

For long bones, Snowy Owls (present data) and Eagle Owls (BOCHEŃSKI et al. 1993) show the same tendencies in the degree of fragmentation (whole bones versus broken parts) in all types of bones. Tawny Owls (BOCHEŃSKI et al. 1993) and Long-eared Owls (BOCHEŃSKI & TOMEK 1994) show the same tendencies as Snowy Owls in most types of bones. Differences are only in humeri and femora where Tawny Owls and Long-eared Owls showed the opposite tendency than Snowy Owls.

As in *N. scandiaca*, proximal ends of humeri are more numerous than the distal in all owl species compared (differences are only in percentages). In femora, there are different tendencies in each owl species. Eagle Owls show the same tendency as Snowy Owls (distal ends more numerous), Tawny Owls – opposite tendency, whereas in Long-eared Owls proximal and distal ends are equally numerous.

As the distal ends of the tarsometatarsi and coracoids prevailed over their proximal ends in pellets of *S. aluco, A. otus* and *B. bubo*, it has been postulated that this observation can be used as evidence of the pellet origin of fossil assemblages (BOCHEŃSKI et al. 1993, BOCHEŃSKI & TOMEK 1994). Unfortunately the material of *N. scandiaca* is too scarce to check the hypothesis.

Shafts of an unknown type of bone were not listed in pellet materials of previously examined owls. It is difficult to say whether they were not present or overlooked. Pellets of *N. scandiaca*

were collected specifically for taphonomic studies (i. e. bearing in mind the importance of all small fragments – even the unidentifiable).

Humeri and often also ulnae provide the highest MNI values in the four owl species examined (*N. scandiaca* – present data, *S. aluco* and *B. bubo* – BOCHEŃSKI et al. 1993, *A. otus* – BOCHEŃSKI & TOMEK 1994). Only under certain conditions (*B. bubo* – nest sites) do tarsometatarsi provide higher values of the MNI. Victims' heads (skulls and/or mandibles) give nearly as high scores as humeri in three owl species (*N. scandiaca*, *S. aluco* and *A. otus*) – *B. bubo* being the only exception. Good results are also obtained with tarsometatarsi in all four owl species (always above 70% of the MNI). With a few exceptions, sterna, pelvis and phalanx I dig. majoris alae usually provide poor results in the calculation of the MNI. The remaining types of bones provide various results – from poor to even very good – depending on the owl species.

ANDREWS (1990) distinguished five categories of predators on the basis of the breakage of postcrania (data for small mammals). Category one (little damage) includes – among other species – Long-eared Owls. Category two (more damage) – Snowy Owls and Eagle Owls, and category three (intermediate damage) – Tawny Owls. The division of owls is somewhat different when only bird prey is considered (present data, BOCHEŃSKI et al. 1993, BOCHEŃSKI & TOMEK 1994). The sequence of species – breaking their victims' bones from the least to the greatest extent – is as follows: Long-eared Owl, Tawny Owl, Eagle Owl and Snowy Owl. Thus, the two divisions into category of predators (based on mammalian and bird prey) differ mostly in the position of the Tawny Owl. For some reasons it produces more damage (in relation to other owls) to mammalian bones than it does to bird skeletons.

MOURER-CHAUVIRÉ (1983) says that tarsometatarsi and carpometacarpi outnumber other types of bones in remains of middle-sized prey attributed to avian predation. In larger prey they are tarsometatarsi and coracoids. Although quail may be treated as middle-sized prey for Snowy Owls, the most numerous element in their remains was the humerus which according to MOURER-CHAUVIRÉ (1983) is one of the bones indicative of human-derived deposits. In his fossil material of the *Lagopus* species, BAALES (1992) interpreted the dominance of tarsometatarsi and carpometacarpi not only as evidence of pellet origin but he also suggested that Snowy Owls produced the pellets. The present results do not support his latter conclusion because the number of fragments as well as the MNI of the two bones mentioned by him, were lower than those for the humerus. However, it still does not exclude Snowy Owls as possible predators because we know too little about post-depositional damage to bird bones.

The present data show that wing and leg bones are equally numerous in pellets of two out of the four owl species examined. The two exceptions are the Tawny Owl and the Eagle Owl in which wing bones prevailed over leg elements. According to ERICSON (1987), such proportions would be indicative of "natural bone ratio" – i. e. decomposition without human activities. It is, however, somewhat surprising that owls may produce similar bias in skeletal elements as do natural decomposition factors. The deviation from the 1:1 proportion (leg elements prevailed) in Snowy Owls was insignificant possibly only because of small sample size.

BOCHEŃSKI & TOMEK (1994) suggested that the relative abundance of the end parts of the tarsometatarsus, coracoid and ulna may be indicative of pellet origin of the material studied. The same tendencies are observed in the WORTHY & HOLDAWAY's (1995) material of parakeets' remains. Distal tarsometatarsi and scapular ends of coracoids are more numerous than the other ends of these bones, and both ends (proximal and distal) of ulnae are equally numerous. However, six other species from WORTHY & HOLDAWAY's (1996) material either contradict the rule or support it only partly. The present data on Snowy Owls are too scarce to check the hypothesis.

The difficulties mentioned above show the limited usefulness of indices based on frequency of skeletal elements. However, it still does not necessarily mean that all indices are wrong. First we

should solve the problem of "incompatibility" of various studies. Analyses of recent pellet materials include pooled data for all prey species, whereas analyses of fossil assemblages are not always able to differentiate between damage done by predators and post-depositional breakage. Although indices based on the frequency of fossil bones are not always consistent with those based on recent pellet materials, they do not exclude the possible origin of the two types of materials from a common predator. It may well happen that both "schools" are right – i. e. that raptors produce species-specific damage to bones which is later partly or completely blurred by post-depositional breakage (directly correlated with the strength of bones). Analyses of fossil assemblages attributed to the activity of avian predators seem to support the hypothesis (WORTHY & HOLDAWAY 1994, 1996). Anyway, there is great scope for experimental work on this problem.

3. Digestion

Although the pellet material of Snowy Owls is not rich enough for statistical purposes, it shows clear tendencies in the amount of bones affected by digestion. With the exception of the ulna, only 50% or less of articular ends of all long-bones had traces of digestion. Similar low percentage of affected bones was also observed in pellets of the Long-eared Owls whereas Tawny Owls and Eagle Owls produce damage recognizable on over 80% of bird bones (BOCHEŃSKI & TOMEK, in print). It corresponds well with the ANDREWS's (1990) classification of predators based on postcranial digestion of small mammals. According to him, Snowy Owls and Long-eared Owls produce little modification and belong to "category one" predators. On the other hand, Eagle Owls and Tawny Owls cause intermediate modification and are placed in "category two". The fact that shafts of long-bones are affected through digestion only sporadically, confirms that Snowy Owls belong to category one predators.

Traces of digestion on bird bones may survive long accumulation and be successfully recognized in fossil materials (STEWART 1992, WORTHY & HOLDAWAY 1994, 1996). However, attrition and soil corrosion may sometimes mimic the effects of digestion (ANDREWS 1990, BOCHEŃSKI & TOMEK in print).

Therefore it seems that taphonomic studies of fossil deposits should be based on a variety of factors – cautiously including fragmentation of bones and their survivorship, traces of digestion, representation of species and chemical alteration of bone tissues. Basing studies on only one of the factors would drastically increase the possibility of reaching wrong conclusions, but the combination of many factors is often sufficient to identify the predator.

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