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On the taphonomic origins of Vistulian bird remains from cave deposits in Poland

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Abstract. The species composition of 23 assemblages of birds whose remains come from Vistulian deposits of 10 caves in southern Poland was compared with that of birds found in the diet of contemporary European Eagle Owls, from 20 sites, and Snowy Owls, from 13 sites. Several similarities were found to occur between bird assemblages from those deposits and from pellets of Eagle Owls. Most of the Vistulian bird remains under analysis seem to come from victims of Eagle Owls. A small proportion of these assemblages may have a different origin; potential sources are indicated.

Key words: Vistulian (Weichselian), fossil bird remains, cave deposits, pellets, Eagle Owl (*Bubo bubo*), Snowy Owl (*Nyctea scandiaca*).

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I. INTRODUCTION

Vistulian bird remains are known in Poland from less than 20 sites, almost exclusively cave deposits and rock shelters. Only the remains coming from the Younger Vistulian, about 50,000 years BP (BOCHEŃSKI 1993) are relatively abundant. Assemblages of those remains, and particularly the more diversified in terms of species, are used to reconstruct palaeoenvironments, and more rarely palaeoclimates (BOCHEŃSKI 1974a, 1981, 1988; MADEYSKA 1981; BOCHEŃSKI jun. 1990b; TOMEK & BOCHEŃSKI 1995; CYREK et al. 2000; TOMEK et al. 2003; LORENC 2001a,b, 2004, in preparation; TOMEK & BOCHEŃSKI 2005). In palaeoenvironmental and palaeoclimatic studies that rely on fossil faunal remains it is essential to know the origins of the remains. The occurrence of the bird bones in cave deposits and the nature of their preservation shows that they largely come from the pellets of owls that inhabited the cave sites, or their vicinity, in the past (BOCHEŃSKI 1974a, 1983, 2000). However, not all owls live in rocky environments. In Europe those that do include the Eagle Owl *Bubo bubo*, Tawny Owl *Strix aluco* and Little Owl *Athene noctua*. The fossil assemblages of bird remains discussed in the present study show a great predominance of bones of large and medium-sized birds, mostly galliforms, and more rarely anatids. These are birds whose size precludes them from falling prey to the Tawny Owl and Little Owl. Predominant among their victims are small birds, mostly passerines. Galliforms and anatids, however, are commonly found in the diet of contemporary Eagle Owls (UTTENDÖRFER 1939; GLUTZ & BAUER 1980; MIKKOLA 1983; CRAMP &

SIMMONS 1985; LORENC 2003b, 2004). This suggests that Eagle Owls are the chief 'suppliers' of the bird bones to the cave deposits. The origins of bird remains in cave deposits as being primarily Eagle Owl prey has been suggested before e.g. for the abundant and highly species-rich bird assemblage from the rock-shelter in Krucza Skała (BOCHEŃSKI & TOMEK 2004), and outside Poland, in Bazhukovo III in the Middle Ural Mountains (BOCHEŃSKI & NEKRASOV 2001). However, galliforms and anatids are also found among the prey of modern Snowy Owls, although in much smaller numbers than among those of Eagle Owls (UTTENDÖRFER 1939; GLUTZ & BAUER 1980; MIKKOLA 1983; CRAMP & SIMMONS 1985; LORENC 2003a, 2004). Hence, theoretically, bird remains from the Vistulian cave deposits could also have belonged to victims of Snowy Owls. True enough, Snowy Owls do not nest in caves today, but one cannot altogether dismiss the possibility of their using the caves under study in the Vistulian e.g. as shelters. The contemporary breeding range of the Snowy Owl does not cover areas abounding in caves, hence no direct analogy is possible. That is why Snowy Owls were included in the research alongside Eagle Owls.

Thus, the main aim of the present article is to find answers to the following questions:

– Do the bone remains of birds known from the Vistulian cave deposits in Poland mainly represent the victims of Eagle Owls?

– What contribution to the assemblages were made by Snowy Owls?

– Is it possible to identify other significant sources for the bird remains?

One source of information concerning the origin of bones in cave deposits are results of taphonomic studies, e.g. the nature of bone damage and the extent of preservation of the individual elements of the skeleton (BOCHEŃSKI et al. 1993; BOCHEŃSKI & TOMEK 1997; BOCHEŃSKI 1997, 2005; BOCHEŃSKI & NEKRASOV 2001). The present research, however, was conducted exclusively on the basis of a faunal analysis of the Vistulian assemblages of birds.

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II. MATERIAL AND METHODS

The material for the present study consists of lists of identified bone remains of birds from Vistulian cave deposits published in works on the individual sites, and published lists of the prey species of contemporary Eagle Owls and Snowy Owls. Crucial for the research was the identification of the minimum number of individuals (MNI) for each of the species listed. In the case of two caves (Raj and Mamutowa), the MNI was determined on the basis of an unpublished inventory of all the bird bones identified there (BOCHEŃSKI – unpublished data). Also, in the case of two sites in Finland, that have provided the data on the contemporary diet of Eagle Owls, use was made of unpublished data made available to the present author (SULKAVA – unpublished data). The bones of birds from the caves and rock shelters under analysis have been deposited in the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow. For both the lists of fossil bird remains and of modern prey of Eagle Owls and Snowy Owls, only those assemblages were used that consisted of at least 10 species. With reference to the fossil material, the analysis was carried out on assemblages coming from sedimentary layers from identified stratigraphies. In this way the study embraces thanatocenoses from 10 sites. They are: Raj Cave, Komarowa Cave, Deszczowa Cave, the Upper Rock Shelter of the Deszczowa Cave, the Cave in Dziadowa Skała, the rock-shelter in Krucza Skała, Sąspowska Zachodnia Cave, Mamutowa Cave, Obłazowa Cave, and Obłazowa 2. The location of the individual sites is presented in Figure 1. The age of the deposits which contained the remains from the literature is given in Table I. Some sites have material that comes from layers of various ages and such assemblages were analysed separately. Therefore, the total number of assemblages of bird fossil remains examined during the research is 23.

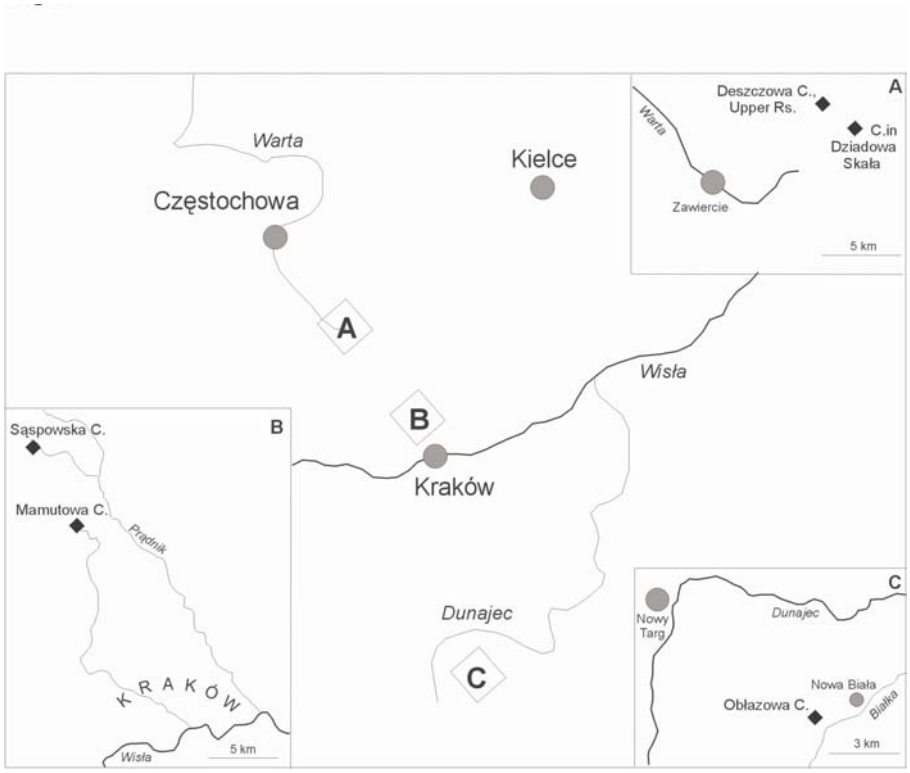

Fig. 1. Location of sites that yielded the bird remains from the Vistulian (abbreviations used: C. – cave, Rs. – rockshelter).

As to contemporary prey of Eagle Owl and Snowy Owl, only data from Europe was considered. The Eagle Owl data come from 20 localities in northern, central and western Europe. The distribution of those sites is presented in Figure 2. The information on the Eagle Owl diet derives from the breeding season. The material from southern Europe was disregarded because the climatic and environmental conditions in this area are different from those that are thought to have occurred in Poland during the Vistulian. The Snowy Owl data come from 13 localities in northern and north-western Europe, from the breeding and non-breeding seasons. The location of those sites is presented in Figure 3.

The lists of avian prey species of present-day Eagle Owl and Snowy Owl were compared with those of birds from cave deposits to identify similarities and differences, mainly in the amounts of remains, their species diversity, and especially the presence of birds from the same families and orders. Special attention was paid to the families and orders found regularly and dominant in terms of bird numbers. It was assumed that marked similarities between those assemblages might indicate that the origin of the fossil remains was mainly from the prey of Eagle Owls or Snowy Owls. This meant adopting the assumption that such aspects of the biology of Eagle Owls and Snowy Owls as the nesting and feeding environments as well as their diets have not changed significantly between the Vistulian and the present. To minimise possible errors that might result from these assumptions, the group of bird assemblages compared were suitably large and highly diversified in terms of species. A possibility that was also taken into consideration was that the Vistulian bird remains could have originated from other sources. Hence, attention was paid to those species represented by the fossil remains that do not occur, or do so only sporadically, in the diet of contemporary Eagle Owls and Snowy Owls.

Table I

Cave sites with their age and numbering of layers containing the bird remains under study. The stratigraphic division after KOZARSKI (1980, 1981), KOZARSKI & NOWACZYK (1999). Stratigraphy of the layers according to (abbreviations used: C. – cave, Rs. - rockshelter): **Raj C.** (KOWALSKI et al. 1972; BOCHEŃSKI 1974a; MADEYSKA 1981), **Komarowa C. (**TOMEK & BOCHEŃSKI 2005), **Deszczowa C., Upper Rs. of the Deszczowa C.** (CYREK et al. 2000; NADACHOWSKI – unpublished data), **Rs. in Krucza Skała** (BOCHEŃSKI & TOMEK 2004), **C. in Dziadowa Skała** (DYLIK et al. 1954; CHMIELEWSKI 1958; BOCHEŃSKI jun. 1990b), **Sąspowska Zachodnia C.** (MADEYSKA 1981, 1988; BOCHEŃSKI 1988, 1989), **Mamutowa C.** (BOCHEŃSKI 1974a; NADACHOWSKI 1976; MADEYSKA 1981, 1992), **Obłazowa C.** (MADEYSKA & VALDE-NOWAK 2003), **Obłazowa 2** (NADACHOWSKI et al. 1993)

Stratigraphy			Raj C.	Komarowa C.	Deszczowa C.	Upper Rs. of the Deszczowa C.	Rs. in Krucza Skała	C. in Dziadowa Skała	Sąspowska Zachodnia C.	Mamutowa C.	Obłazowa C.	Obłazowa 2
VISTULIAN (Weichselian)	Late Vistulian			B			1-8 I-V	8 7	3		I* V-II	
	Plenivistulian	Upper Plenivistulian		C	VIII VIIIa	VIII				2	VII	
		Middle Plenivistulian		D E	VIIa						XI- VIII	+
		Lower Plenivistulian	8-10 4-6									
	Early Vistulian										XIX- XIII	

* – the age of layer I was determined to be Holocene and/or Late Vistulian. It is possible for the bone material from this layer to have mixed with that of layer II (TOMEK et al. 2003). That is why layer I was examined during the research.

III. RESULTS

Analysis of the Vistulian assemblages of bird remains

Members of the following orders were found to occur regularly (in every or almost every assemblage): Galliformes, Falconiformes, Strigiformes and Passeriformes; among the last, members of the family Corvidae and the genus *Turdus* regularly occurred. It was also noted that there were birds associated with an aquatic and/or aquatic/marsh environment in all the assemblages. This group was represented by Podicipediformes, Ciconiiformes (the family Ardeidae), Anseriformes, Gruiformes (the families Rallidae and Gruidae), and Charadriiformes. Hence, these birds will be treated as one group termed waterfowl. The distribution and percentages of birds of the above systematic groups in individual assemblages are presented in Table II. The table also accommodates pigeons, Columbiformes, although their remains can only rarely be found in fossil material. This facilitates the comparison of the fossil material and modern assemblages of Eagle Owl prey. Notes to the table

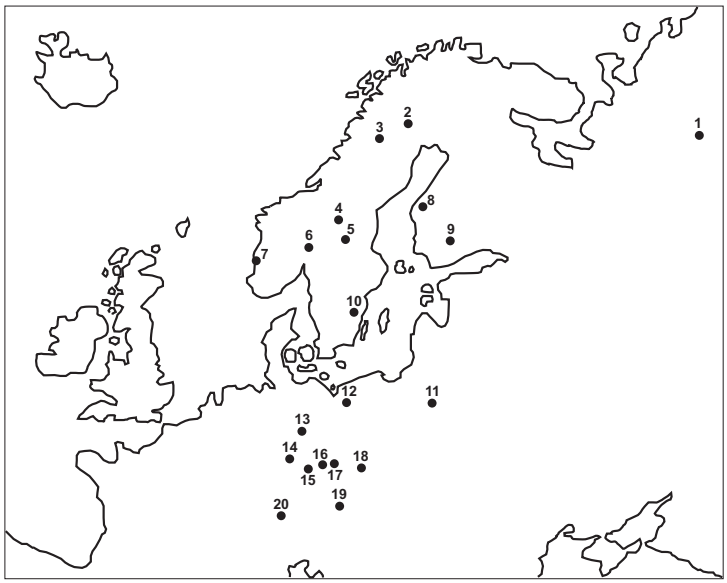

Fig. 2. Location of sites that yielded the data on the Eagle Owl diet (points 1-20). **1.** Russia: Pechora river (Ust-Unya) (TEPLOWA 1957 in: JANOSSY & SCHMIDT 1970); **2.** Sweden: Jokkmokk (HOGLUND 1966); **3.** Sweden: Laisvall (SCHAEFER 1971); **4.** Sweden: Glöte (HOGLUND 1966); **5. S**weden: Hamra (HOGLUND 1966); **6.** Norway: Hedmark (MYSTERUD & DUNKER 1982); **7.** Norway: Hordaland (WILLGOHS 1974); **8.** Finland: Vaasa (SULKAVA – unpublished data); **9.** Finland: Tampere – Lahti (SULKAVA – unpublished data); **10.** Sweden: Östergötland, SmÍland (OLSSON 1979); **11.** Poland: Podlasie (PUGACEWICZ 1995); **12.** Poland: Rogoźnica (BANZ & DEGEN 1975); **13.** Germany: Harz (KÖNIG & HAENSEL 1968), **14.** Germany: Thüringen (MÄRZ 1972); **15.** Germany: Elbsandsteingebirges (MÄRZ & PIECHOCKI 1980); **16.** Czech Republik: České středohoři (VONDRAČEK 1977), **17.** Czech Republik: Polomené hory (VONDRAČEK 1983); **18.** Czech Republik: Jeseníky (SUCHY 2003); **19.** Austria: Niederösterreich (FREY 1973), **20.** Germany: Bayern (Südbayern) (WICKL 1979).

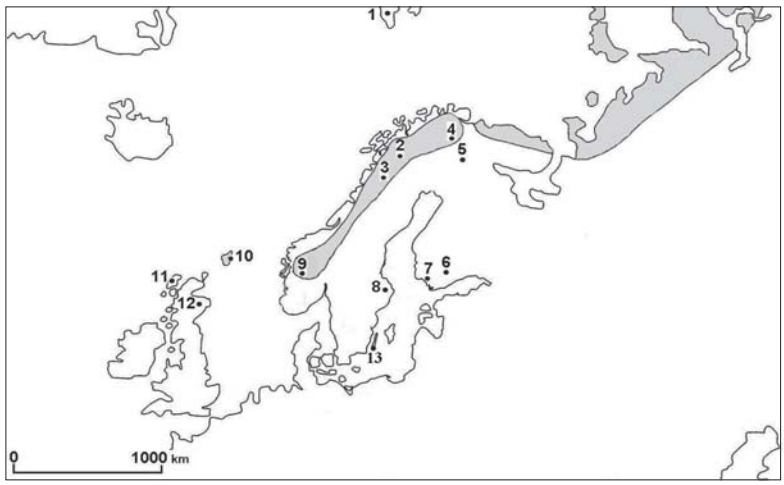

Fig. 3. Location of sites that yielded the data on the Snowy Owl diet (points 1-13) and the breeding range of this species (grey) (after VOOUS 1962; CRAMP & SIMMONS 1985). **1.** Svalbard (MEHLUM & GJERTZ 1998); **2.** Sweden: Abisko (ANDERSSON & PERSSON 1971); **3.** Sweden: Ammarnäs (ANDERSSON & PERSSON 1971); **4.** Finland: Lappland (MIKKOLA 1983), **5.** Finland: Lappland (SULKAVA & SULKAVA 1967 in: MIKKOLA 1983), **6.** Southern Finland (MIKKOLA 1983); **7.** Finland: Abo (MICHOLD 1958); **8.** Sweden: Uppsala (NAGELL & FRYCKLUND 1965); **9.** Norway: Hardangervidda: **a** (LOVENSKIOLD 1947 in: ANDERSSON & PERSSON 1971), **b** (HAGEN 1960); **10.** Shetland: island of Fetlar (TULLOCH 1968, 1969a, 1969b); **11.** Outer Hebrides: Isle of Levis (MARQUISS & CUNNINGHAM 1980); **12.** Scotland: Cairn Gorm plateau (MARQUISS et al. 1989); **13.** Sweden: Öland (LIND 1993).

Table II

Species diversity of the Vistulian bird remains and percentages of systematic groups found regularly. The percentages of birds from the systematic groups predominating in the given assemblage are given in boldface. ∑ – the number of birds identified and given systematic membership (allowing their classification in the table, i.e. without the denotation Aves sp.). In the calculations of the percentages of members of individual bird groups this number is 100%. Sources of data (abbreviations as in Table 1): **Raj C.** (BOCHEŃSKI 1974a, unpublished data), **Komarowa C.** (TOMEK & BOCHEŃSKI 2005), **Deszczowa C., Upper Rs. of the Deszczowa C.** (CYREK et al. 2000), **C. in Dziadowa Skała** (BOCHEŃSKI jun. 1990b), **Sąspowska Zachodnia C.** (BOCHEŃSKI 1988), **Rs. in Krucza Skała** (BOCHEŃSKI & TOMEK 2004), **Mamutowa C.** (BOCHEŃSKI 1974a, 1981, unpublished data), **Obłazowa C.** (TOMEK et al. 2003), **Obłazowa 2** (NADACHOWSKI et al. 1993; TOMEK et al. 2003)

Cave/rockshelter layer/layers	Number of species	Aves ∑	Galliformes	Columbiformes	Falconiformes	Strigiformes	Passeriformes			Waterfowl	Other birds
							Corvidae	Turdus	Other		
Raj C. layers 4-6	15	26	**42.3** [2]	–	–	7.7	–	3.8	26.9	19.2	–
Raj C. layers 8-10	14	23	**34.8** [1]	–	8.7	13.0	8.7	–	17.4	17.4	–
Komarowa C. layer E	42	70	**28.5** [3]	–	5.7	1.4	8.6	8.6	**28.5**	14.3	4.3
Komarowa C. layer D	58	107	25.2 [3]	0.9	6.5	0.9	4.6	11.2	**35.5**	11.2	1.8
Komarowa C. layer C	11	12	**25.0**	–	16.6	16.6	8.3	8.3	–	8.3	16.6
Komarowa C. layer B	42	67	**35.8** [3]	–	4.5	–	3.0	7.5	16.4	30.0	3.0
Deszczowa C. layersVIIa	22	29	**31.0** [3]	–	6.7	3.4	17.2	3.4	17.2	17.2 [5]	3.4
Deszczowa C. layers VIII/VIIIa	11	17	**41.2**	–	11.8	–	5.9	5.9	–	35.3 [5]	–
Upper Rs. of the Deszczowa C. layer VIII	12	22	**40.9**	–	4.5	–	13.6	–	–	**40.9** [5]	–
C. in Dziadowa Skała layers 8, 7	12	31	**51.6**	–	6.4	6.4	12.9	6.4	9.7	6.4	–
Sąspowska Zachodnia C layer 3	19	23	**21.7**	–	13.0	17.4	4.3	8.7	8.7	17.4	4.4

Table II cont.

Cave/rockshelter layer/layers	Number of species	Aves Σ	Galliformes	Columbiformes	Falconiformes	Strigiformes	Passeriformes			Waterfowl	Other birds
							Corvidae	Turdus	Other		
Rs. in Krucza Skała layers 7-8, V	51	89	14.6	9.0	3.4	2.2	9.0	9.0	9.0	**39.3** [6]	1.1
Rs. in Krucza Skała layers 4-6, IV	63	147	29.2 [4]	6.1	2.5	4.2	7.5	2.5	8.8	**40.1** [6]	1.4
Rs. in Krucza Skała layers 3, III	24	38	34.2 [3]	5.3	5.3	2.6	15.8	2.6	–	34.2	–
Rs. in Krucza Skała layers 2/3, II/III	33	53	35.8 [3]	–	3.8	–	7.5	–	7.5	**45.3** [6]	–
Rs. in Krucza Skała layers 1-2, I, I/II	22	28	32.1 [3]	–	3.6	3.6	14.3	–	7.1	**42.9**	–
Mamutowa C. layer 2	32	69	**56.5** [2]	–	2.9	5.8	10.1	1.4	5.8	18.8	–
J. Obłazowa layers XIX-XIII	18	48	**47.9**	–	6.2	2.1	–	4.2	27.1	10.4	2.1
Obłazowa C. layers XI-VIII	44	141	**50.3** [2]	–	7.1	0.7	5.0	3.5	14.2	18.4 [6]	0.7
Obłazowa C. layer VII	19	47	**63.8** [2]	–	2.1	2.1	4.2	2.1	17.0	6.4	2.1
Obłazowa C. layers V-II	60	485	**79.0** [2]	0.2	1.4	1.0	1.8	1.6	6.2	8.2 [6]	0.4
Obłazowa C. layer I	28	75	**60.0** [2]	–	2.7	–	5.3	4.0	21.3	8.0	–
Obłazowa 2	35	64	**35.9** [2]	1.5	4.7	1.5	–	10.9	10.9	31.2 [5]	3.1

[1] – exclusively Willow Grouse *L. lagopus* and Ptarmigans *L. muta.*
[2] – Willow Grouse *L. lagopus* and Ptarmigans *L. muta* stand out for their numbers.
[3] – Willow Grouse *L. lagopus* stand out for their numbers
[4] – Willow Grouse *L. lagopus* and Black Grouse *T. tetrix* stand out for their numbers.
[5] – members of the family Anatidae stand out for their numbers.
[6] – members of the families Scolopacidae and Anatidae stand out for their numbers.

offer detailed explanations on the species or families that stand out in terms of the numbers of individual birds in those taxa (in practice this only concerns galliforms and waterfowl). Lack of such information means that it was impossible to determine the species or families represented by an outstanding number of birds. Owing to a relatively small number of all birds in a substantial propor-

tion of assemblages, percentages of specimens of individual species or families are not provided. An analysis of the data from Table II suggests the following conclusions:

Galliformes: Galliforms are the most frequently dominant group of birds in terms of numbers. They are the most numerous taxon in 18 assemblages, and their predominance over the rest of birds is usually overwhelming. In the remaining 5 assemblages galliforms come second in terms of numbers, but still their proportion is very high. The most abundant are Willow Grouse *Lagopus lagopus*, which has already been noted many times (BOCHEŃSKI 1974a,b, 2000). They are present in each bird assemblage under study, though not in all the layers of sites. There was only one assemblage, coming from layers 8-10 of Raj Cave, that did not contain bones of the Black Grouse *Tetrao tetrix*. Ptarmigan *Lagopus muta*, which were often more frequent than Black Grouse, were absent from five assemblages, while Capercaillies *Tetrao urogallus* were not found in six. Other galliforms were found only rarely and in small numbers.

Waterfowl: Where galliforms are not predominant waterfowl are usually the most abundant group of birds. They dominate in 6 assemblages (in 2 of them with galliforms), but only at two sites: the Upper Rock Shelter of the Deszczowa Cave and that in Krucza Skała. Interestingly enough, in the rock-shelter in Krucza Skała, waterfowl predominate in all the assemblages of birds studied. Two families stand out in terms of the number of their members: Anatidae and Scolopacidae.

Falconiformes: The proportion of falconiforms usually amounts to several per cent (usually less than or near 6%). There are only 3 assemblages where the percentage exceeds 10, but since they consist of a very small number of birds this higher percentage may represent the presence of a mere 2-3 individuals.

Strigiformes: The proportion usually amounts to a few per cent, with the exception of 3 assemblages where it exceeds 10%. As in the case of diurnal raptors, these are assemblages consisting of a very small number of birds. The strigiforms are usually slightly less numerous than raptors.

Corvidae: They usually constitute a few per cent, sometimes more than ten. They are more abundant than raptors or owls.

Turdus: They usually make up a few per cent, in a few assemblages slightly more. The proportion is similar to those of raptors and owls.

Other passerines: Their proportion is highly variable, from a few to more than 30%. They predominate in the assemblages from layers D and E of Komarowa Cave. It is difficult to determine the species that are most abundant in terms of numbers than other birds of this group.

Other birds: Present in only 12 assemblages. Their proportion is very low and about 1%. The lowest values are recorded in assemblages with a great number of bird remains, and the highest in the smallest assemblages where single specimens appear by pure chance. This demonstates that among the bird remains from the Vistulian cave deposits the bones of species not belonging to the systematic groups listed in Table II do not usually occur, or their proportions are negligible.

Analysis of the bird species composition in the diet of modern Eagle Owls

Members of the following orders were found to occur regularly (in every or almost every assemblage): Galliformes, Falconiformes, Strigiformes and Passeriformes. Among the last, members of the family Corvidae and the genus *Turdus* regularly appeared. Besides these, in all the assemblages there were birds associated with an aquatic and/or aquatic/marsh environment. They were represented by members of the same orders and families as in the fossil material (single birds from other families are only recorded sporadically) and are here treated as one group termed waterfowl. The most regular prey of Eagle Owls observed in central and western Europe includes pigeons, Columbiformes. The results of the analysis are listed in Table III. Notes for the table offer detailed data on the species or families that stand out in terms of the number of individual birds in those taxa. An analysis of the data from Table III leads to the following conclusions:

Galliformes: The most frequently dominant group of birds in terms of numbers. They are the most numerous taxon in 10 assemblages and second in two. In northern Europe, dominant among

the galliform victims are Capercaillies *Tetrao urogallus*, Black Grouse *Tetrao tetrix* or Willow Grouse *Lagopus lagopus*, while in central and western Europe, it is the Common Partridge *Perdix perdix*. The lowest percentages of galliforms (even as low as a few per cent) are recorded in the diet of Eagle Owls hunting on wetland and the seashore, where waterfowl greatly predominate as prey.

Waterfowl: Where galliforms are not predominant, they are usually the most abundant group of birds. They dominate in 7 assemblages, and particulaly among the prey of Eagle Owls hunting on wetland and the seashore. In the next 7 assemblages they are second, always after galliforms. 6 of those assemblages come from northern Europe, where the predominance of galliforms and waterfowl is especially marked (and hence the proportion of other birds is low). In northern Europe the most abundant family is always the anatids, which happens less often in central and western Europe. The lowest proportion of waterfowl (even as low as a few per cent) is recorded in the upland and mountain regions of central and western Europe.

Basically, galliforms and/or waterfowl are usually the most frequent prey of Eagle Owls in northern, central and western Europe. Their predominance is especially marked in the diet of Eagle Owls from northern Europe.

Columbiformes: In Scandinavia they are usually absent from the Eagle Owl diet, which is a result of the geographical range of pigeons (VOOUS 1962). In the diet of Eagle Owls from central and western Europe, however they occur regularly (except at one site). Their proportions varies from a few per cent to just over ten. The predominance of pigeons found among bird victims of Eagle Owls in Thuringia is exceptional (LORENC 2003a, 2004).

Falconiformes: They usually constitute a few per cent of the bird victims of Eagle Owls (usually less than or near 5%). Only at Jesioniki is their proportion much higher, which is a rare occurrence (LORENC 2003a, 2004).

Strigiformes: They usually constitute a few per cent, rarely more than ten, of Eagle Owl prey. Their proportion is usually higher than that of raptors. The predominance of owls recorded among victims of Eagle Owls at Jesioniki is an exceptional occurrence (LORENC 2003a, 2004).

Corvidae: They are only missing from two northernmost sites that lie outside the range of many corvid species (VOOUS 1962). Their proportion is usually a few per cent, but in exceptional situations can be much higher. The predominance of corvids found among victims of Eagle Owls from the Elsandsteingebirges is such a rare occurrence (LORENC 2003a, 2004).

Turdus: Their typical proportion is a few per cent, but usually lower than that of corvids.

Other passerines: Usually present, but in small numbers. Their proportion among birds hunted by Eagle Owls is typically under 3%. It is hard to indicate species that would be especially frequent or more abundant in terms of numbers than other birds of this group.

Other birds: Usually present, but their proportion among Eagle Owl prey is very low (often under 1%).

Analysis of the bird species composition in the diet of modern Snowy Owls

It is only in the case of five sites that the information about Snowy Owl diet comes from nesting birds. These are sites nos. 2, 3, 4, 9 and 10. Data from sites nos. 1, 11 and 12 also come from the breeding season, but since they are located outside the nesting area of Snowy Owls (Fig. 3), the lists include the prey of migratory Eagle Owls that passed spring and summer in those places. Other sites (nos. 5, 6, 7, 8, 13, and partly also 1) yielded exclusively autumn and winter data i.e. from migrating Eagle Owls. The percentages and species composition of birds in the diet of Snowy Owls are presented in Table IV. Even a preliminary analysis made it clear that in the diet of both, nesting and migratory Snowy Owls, birds usually constituted a negligible proportion of all victims, and their species diversity was low. No records were found of raptors and owls, or corvids among the passerines, so characteristic of the Eagle Owl diet. There were sporadic records of two taxa: columbiforms (only in the diet of migratory owls) and turdids.

Table III

Species diversity of birds in the diet of Eagle Owls From 20 sites in Europe and percentages of members of systematic groups found regularly. The percentages of birds from the systematic groups predominating in the given assemblage are given in boldface. ∑ – as in Table II. * – not all studies give the quantity of nests/territories from which data are derived. The sources of data are quoted under Fig. 2.

Place, its numbre on the map (Fig. 2), (quantity of nests/territories)*	Number of species	Aves ∑	Galliformes	Columbiformes	Falconiformes	Strigiformes	Passeriformes			Waterfowl	Other birds
							Corvidae	Turdus	Other		
Russia: Pechora, **nr 1**	17	84	**75.0** [1]	–	4.7	3.5	–	–	–	16.6 [2]	–
Sweden: Jokkmokk, **nr 2**, (2)	15	68	**48.5** [3]	1.5	4.4	4.4	–	1.5	–	36.8 [2]	2.9
Sweden: Laisvall, **nr 3**, (2)	29	126	**38.1** [4]	–	5.5	19.0	1.6	1.6	1.6	32.5 [2]	–
Sweden: Glöte, **nr 4**, (1)	18	64	31.2 [5]	–	3.1	9.4	3.1	–	–	**51.6** [2]	1.5
Sweden: Hamra, **nr 5**, (1)	17	56	**42.8** [6]	–	5.3	5.3	7.1	3.5	1.8	33.9 [2]	–
Norway: Hedmark, **nr 6**, (3)	24	94	**33.0** [7]	–	2.1	1.0	5.3	21.2	3.2	31.5 [2]	3.2
Norway: Hordaland, **nr 7**, (16)	33	203	3.4	1.5	2.0	1.5	7.8	4.9	5.4	**74.5** [8]	–
Finland: Vaasa, **nr 8**, (27)	20	96	**35.4** [9]	1.0	–	6.2	22.9	3.1	1.0	30.2 [10]	–
Finland: Tampere-Lahti, **nr 9**, (10)	51	608	11.2 [11]	2.5	5.8	7.4	18.1 [12]	5.6	2.3	**47.0** [13]	0.6
Sweden: Östergötland, , **nr 10**	78	2774	3.2	–	3.6	4.9	5.7	1.9	2.8	**74.6** [14]	0.6
Poland: Podlasie, **nr 11**	26	94	24.5 [15]	3.2	8.5	8.5	9.6	6.4	–	**38.3** [16]	1.0
Poland: Rogoźnica, **nr 12**, (1)	29	93	4.2	–	2.1	1.1	6.4	4.3	1.1	**76.6** [17]	3.2
Germany: Harz, **nr 13**, (2)	18	61	**50.8** [18]	4.9	1.6	8.2 [2]	8.2	4.9	14.7	3.3	3.2
Germany: Thüringen, **nr 14**, (25)	44	595	18.6 [19]	**21.2** [20]	5.5	14.4	14.3	6.5	3.5	15.3 [21]	0.5
Germany: Elsandstein-gebirges, **nr 15**, (5)	35	345	20.3 [22]	9.0	11.9	12.7	**33.6** [23]	4.9	2.6	4.3	0.6
Czech Republik: České středohoři, **nr 16**, (5)	26	323	**51.4** [24]	12.4	2.8	8.3	8.6	13.0	1.2	2.8	0.9
Czech Republik: Polomené hory **nr 17**	43	734	**47.1** [25]	9.0	2.4	10.0	7.8	10.1	1.2	11.0 [26]	0.8
Czech Republik: Jeseníky, **nr 18**, (34)	47	1381	16.1 [27]	14.5	22.5 [28]	**25.3** [29]	8.5	6.1	1.7	4.0	1.2
Austria: Niederösterreich, **nr 19**, (22)	28	862	**52.4** [22]	13.9	4.7	10.8	9.2	5.3	0.1	3.2	0.2
Germany: Bayern, **nr 20**	31	155	1.9	5.2	6.4	11,6	13.5	5.8	1.9	**52.2** [30]	1.3

Table III cont.

[1] – Capercaillies *T. urogallus* constitute 75% of all galliforms.
[2] – almost exclusively anatids.
[3] – almost exclusively members of the genus *Tetrao*. Capercaillies *T. urogallus* constitute 42% of all galliforms.
[4] – Willow Grouse *L. lagopus* constitute 67% of all galliforms.
[5] – members of the genus *Tetrao* predominate. Black Grouse *T. tertrix* constitute 35% and Willow Grouse *L. lagopus* 25% of all galliforms.
[6] – members of the genus *Tetrao* predominate. Both Capercaillies *T. urogallus* and Black Grouse *T. tertrix* constitute 29% of all galliforms each.
[7] – members of the genus *Lagopus* (not determined to the species level) constitute over 80% of all galliforms.
[8] – members of the family constitute 39% of all waterfowl and next.
[9] – Black Grouse *T. tertrix* constitute 38% of all galliforms and next 23% of them Willow Grouse *L. lagopus*.
[10] – almost exclusively members of the families Anatidae and Scolopacidae.
[11] – Black Grouse *T. tertrix* of all galliforms.
[12] – Hooded Crows *C. cornix* constitute 74% of all corvids.
[13] – both members of the family Anatidae 45% of all waterfowl each.
[14] – anatids constitute 44% of all waterfowl, and next 32% of them Laridae and Sternidae together.
[15] – Common Partridges *P. perdix* of all galliforms.
[16] – anatids of all waterfowl.
[17] – anatids of all waterfowl and next 28% both members of the family Rallidae.
[18] – exclusively Common Partridges *P. perdix*.
[19] – Common Partridges *P. perdix* of all galliforms.
[20] – domestic pigeons *C. livia domestica* .
[21] – members of the family Rallidae of all waterfowl and next 30% of them constitute anatids.
[22] – Common Partridges *P. perdix* of all galliforms.
[23] – Carrion Crows *C. corone* .
[24] – exclusively Common Pheasants *P. colchicus* and Common Partridges *P. perdix*. Common Pheasant 64% of all galliforms.
[25] – exclusively Common Pheasants *P. colchicus* and Common Partridges *P. perdix*. Common Pheasants 57% of all galliforms.
[26] – members of the familyof all waterfowl.
[27] – Common Partridges *P. perdix* of all galliforms.
[28] – Common Buzzards *B. buteo* raptors.
[29] – Long-eared Owls *A. otus* and Tawny Owls *S. aluco* 46% of all owls.
[30] – both members of the family Anatidae and Rallidae constitute 42% of all waterfowl each.

The data from the breeding season show that in the diet of Snowy Owls nesting in Scandinavia birds are scarce. The owls catch primarily small rodents, predominantly lemmings and voles (sites nos. 2, 3, 4, 9), while the birds that fall prey to them are mainly Willow Grouse Ptarmigan *Lagopus lagopus/L. muta*. In his study of the composition of Snowy Owl prey on Norwegian uplands HAGEN (1952, after BERGMAN 1961) found small rodents predominate among them, 97.5%, as against a negligible 1.6% of birds. Outside Scandinavia (at sites nos. 1, 10, 11, 12), where lemmings do not occur and the remaining rodent groups are less numerous, the dominant victims of Snowy Owls are rabbits, hares and birds that are most readily available locally. Hence the high percentages of Snowy Owls' avian prey in the Shetlands (no. 10) and Scotland (no. 12). In the Shetlands, it is due to the great numbers of Oystercatchers *Haematopus ostralegus* nesting there, and in Scotland, of Ptarmigan *Lagopus muta*.

Observations from outside Europe confirm the dominance of rodents, especially lemmings, in the diet of nesting Snowy Owls in all areas where they occur in abundance. In Asia, on the Lena, mammals made up 98.6% of victims of those owls, while lemmings alone constituted 92%. Only two bird species were recorded there, represented by single specimens (BOLSZAKOV 1968). In northern Siberia, on the Yana-Indigirka Plain, prey other than lemmings is also a rare occurrence in

Table IV

Species diversity of birds in the diet of Snowy Owls in Europe and percentages of birds among all their victims. Site numbers and sources of data as in Fig. 3. The sites disregarded include no. 1 because of no quantitative data on owl prey existed, nos. 7 and 8 because of a small sample size, unrepresentative of all victims recorded, and no. 11 at which no birds were found among owl victims.

Species	1	2	3	4	5	6	7	8	9	10	12	13
	The share of birds (%) in diet of Snowy Owls in above sites											
	–	0.9	0.6	1.8	0.4	8.0	–	–	0.8 3.5*	27.6	58.1	64.5
Fulmarus glacialis (LINNAEUS, 1761)	+											
Anas platyrhynchos LINNAEUS, 1758						+	+					+
Anas crecca LINNAEUS, 1758												+
Somateria mollissima (LINNAEUS, 1758)	+											
Somateria spectabilis (LINNAEUS, 1758)	+											
Bucephala clangula (LINNAEUS, 1758)								+				+
Clangula hyemalis (LINNAEUS, 1758)												+
Mergus serrator (LINNAEUS, 1758)								+				
Aix sponsa (LINNAEUS, 1758)								+				
Not identified duck						+						+
Not identified goose							+					
Perdix perdix (LINNAEUS, 1758)								+				+
Lagopus lagopus (LINNAEUS, 1758)									+		+	
Lagopus muta (MONTIN, 1776)	+								+		+	
Lagopus lagopus/mutus				+	+		+		+			
Bonasia bonasia (LINNAEUS, 1758)								+				
Tetrao tetrix LINNAEUS, 1758						+		+				
Phasianus colchicus LINNAEUS, 1758								+				
Fulica atra LINNAEUS, 1758								+				
Haematopus ostralegus (LINNAEUS, 1758)										+		
Vanellus vanellus (LINNAEUS, 1758)										+		
Pluvialis apricaria (LINNAEUS, 1758)									+			
Charadrius morinellus (LINNAEUS, 1758)									+		+	
Charadrius sp.				+								
Gallinago gallinago (LINNAEUS, 1758)				+					+	+		
Numenius arquata/phaeopus										+		
Numenius phaeopus (LINNAEUS, 1758)										+		

Table IV cont.

Species	1	2	3	4	5	6	7	8	9	10	12	13
	The share of birds (%) in diet of Snowy Owls in above sites											
	–	0.9	0.6	1.8	0.4	8.0	–	–	0.8 3.5*	27.6	58.1	64.5
Tringa tetanus (LINNAEUS, 1758)										+		
Stercorarius parasiticus (LINNAEUS, 1758)										+		
Sterna hirundo LINNAEUS, 1758										+		
Not identified gull						+						
Alle alle (LINNAEUS, 1758)	+											
Uria lomvia (LINNAEUS, 1758)	+											
Columba livia LINNAEUS, 1758								+		+		
Nyctea scandiaca juv. (LINNAEUS, 1758)				+					+			
Picus virdis LINNAEUS, 1758								+				
Alauda arvensis LINNAEUS, 1758										+		
Sturnus vulgaris LINNAEUS, 1758												+
Turdus sp.				+					+			
Carduelis sp.												+
Not identified birds		+	+	+		+		+	+			

* – 0.8% for 9a and 3.5% for 9b.

the diet of Snowy Owls (USPENSKI & PRIKLONSKI 1961). The dominance of lemmings was also found in Novaya Zemlya, the Yamal Peninsula, Wrangel Island (PORTENKO 1972), as well as in northern Canada in Baffin Island (WATSON 1957), and Greenland (PORTENKO 1972; CRAMP & SIMMONS 1985). Among birds, the most frequent prey are Willow Grouse Ptarmigan *Lagopus lagopus/L. muta*, and in the case of owls nesting close to a coastline, species of sea birds are also included (GROSS 1944; PORTENKO 1972; WILLIAMS & FRANK 1979; CAMPBELL & MAC CALL 1978 in: CRAMP & SIMMONS 1985).

The autumn and winter data coming from non-breeding areas do not provide much insight into the proportion of birds among victims of Snowy Owls. As in the material from the breeding season, avian prey were found to especially include galliforms. At site no. 1 there were only members of *Lagopus* sp., and at site no. 5, exclusively Ptarmigan *Lagopus muta*. In the case of the Svalbard archipelago Common Ptarmigan are the only resident birds there and not away on migration for the winter. Apart from galliforms, anatids also occur in greater numbers. The very high proportion of birds in the diet of Snowy Owls in Öland Island (no. 13) results from their extensive hunting of both Common Partridges *Perdix perdix* and anatids. In sum, at least 36 species of birds were found to occur in the diet of European Snowy Owls (Table IV) (LORENC 2003b, 2004).

Species associated with a 'rock environment'

In the fossil assemblages of birds in Poland there are several species that can nest in various kinds of rock crevices or shelves, including caves. Most of them are recorded sporadically, but some species are found frequently and often in relatively great numbers. This concerns four species: the Kestrel *Falco tinnunculus*, Tawny Owl *Strix aluco*, Swallow *Hirundo rustica*, and Jackdaw *Corvus monedula*. Records of these species among the Vistulian bird remains are presented in Table V. The table also illustrates their occurrence in the diet of modern Eagle Owls (the four species have not been found in the diet of modern Snowy Owls). However, Kestrels, Tawny Owls and Jackdaws are fairly frequent prey to modern Eagle Owls, although Swallows do not seem to be hunted by them.

Table V

Occurrence of the most frequently recorded bird species that can nest in caves, including Eagle Owls and Snowy Owls, in Vistulian bird assemblages and in the diet of contemporary Eagle Owls. [1] – Numbers represent (abbreviations as in Table I): **1.** Raj C.: layers 4-6, **2.** Raj C.: layers 8-10, **3**. Komarowa C.: layer E, **4**. Komarowa C.: layer D, **5**. Komarowa C.: layer C., **6**. Komarowa C.: layer B, **7.** Deszczowa C.: layer VIIa, **8.** Deszczowa C.: layers VIII/VIIIa, **9.** Upper Rs. of the Deszczowa C.: layer VIII, **10.** C. in Dziadowa Skała: layers 8, 7, **11.** Sąspowska Zachodnia C.: layer 3, **12.** Rs. in Krucza Skała: layers 7-8,V, **13.** Rs. in Krucza Skała: layers 4-6, IV, **14.** Rs. in Krucza Skała: layers 3, III , **15.** Rs. in Krucza Skała: layers 2/3, II/III, **16.** Rs. in Krucza Skała: layers 1-2, I, I/II, **17.** Mamutowa C.: layer 2, **18.** Obłazowa C.: layers XIX-XIII, **19.** Obłazowa C.: layers XI-VIII, **20.** Obłazowa C.: layer VII, **21.** Obłazowa C.: layers V-II, **22.** Obłazowa C.: layer I, **23.** Obłazowa 2. [2] – Numbers of sites as in Fig.2. The considered species were not found in sites nos. 2,5,8,13

Caves and layers [1]																							Species	Sites with data on the Eagle Owls diet[2]															
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23		1	3	4	6	7	9	10	11	12	14	15	16	17	18	19	20
		+	+			+	+	+	+		+	+	+	+	+		+	+	+	+	+	+	*Falco tinnunculus* LINNAEUS, 1758				+		+	+		+	+	+	+	+	+	+	+
						+			+		+	+			+					+			*Strix aluco* LINNAEUS, 1758						+	+	+		+	+	+	+	+	+	+
+	+	+	+		+					+	+	+		+			+	+		+		+	*Hirundo rustica* LINNAEUS, 1758											+				
		+	+	+	+	+	+	+	+		+	+	+	+	+	+		+	+	+	+	+	*Corvus monedula* LINNAEUS, 1758						+	+			+	+	+	+		
	+*	+							+*									+		+			*Bubo bubo* (LNNAEUS, 1758)	+	+	+		+			+			+			+		
+	+			+																			*Nyctea scandiaca* (LNNAEUS, 1758)															

* – bones identified as cf. *Bubo bubo*.

Table V also gives data on Eagle Owls and Snowy Owls described above. Worth noting is the rare occurrence of Snowy Owl bones in the Vistulian cave deposits in Poland. They were only found in the deposits of Raj Cave (BOCHEŃSKI 1974a, 1993) and Komarowa Cave (TOMEK & BOCHEŃSKI 2005). The absence of their bones from the other caves is somewhat surprising, especially in the light of numerous data documenting the presence of Snowy Owl bones in Vistulian cave deposits in eastern, central, and even southern Europe (BOCHEŃSKI 1992; MOURER-CHAUVIRÉ 1993; BOEV 1998; POTAPOVA 2001). Bones of Eagle Owls were recorded in the deposits of caves Obłazowa and Komarowa, and probably also Raj and the one in Dziadowa Skała. They have often been found in the pellets of modern Eagle Owls as a result of cannibalism (Table V).

IV. DISCUSSION OF THE RESULTS

The results of the analysis of the species composition of Vistulian bird remains as well as those coming from pellets of contemporary Eagle Owls from northern, central and western Europe show there to be many significant similarities between those two types of assemblages (Tables II and III). The following findings were made in both, the fossil material and among victims of modern Eagle Owls:

(a) The occurrence of members of the same systematic groups: Galliformes, Falconiformes, Strigiformes and Passeriformes. Among the last, the biggest passerines regularly occur: Corvidae and *Turdus*. Also present are waterfowl, among which anatids very often stand out.

(b) Similar proportions of members of the above systematic groups occur among all the birds,:

– galliforms tend to predominate, and if not, the dominant group is usually waterfowl. In those cases galliforms come second in terms of numbers. It is only in exceptional situations that other bird groups are more numerous as prey of modern Eagle Owls;

– the proportions of raptors and owls are usually a few per cent;

– the proportion of corvids is usually higher than those of raptors and owls, generally a few per cent, but it can be much higher;

– the proportion of turdids is usually similar to those of raptors and owls;

– other passerines (apart from corvids and the genus *Turdus*) are represented by a variety of species and it is hard to indicate any that occur with exceptional regularity or in a greater numbers of individuals. However, their proportion is higher in the Vistulian assemblages, and this is the greatest difference between the modern and fossil assemblages under study;

– birds from outside the systematic groups listed in Tables II and III constitute only a trace admixture or do not appear at all.

The marked similarities between the fossil and modern bird assemblages from pellets of Eagle Owls indicate that a decided majority of the fossil remains under study are those of Eagle Owl prey. In turn, no significant similarities were established between the assemblages of bird remains from pellets of Snowy Owls (Table IV) and those deriving from cave deposits. That most of the Vistulian bird remains are those of victims of Eagle Owls rather than Snowy Owls is also corroborated by the following facts:

(a) Among the prey of Snowy Owls there are no raptors, owls and the passerine family of corvids, which are regularly found among the Vistulian remains.

(b) If there are rodents (mostly lemmings and voles) in the feeding area of Snowy Owls, they constitute almost the exclusive component of their diet and the percentage of birds in it is negligible, radically smaller than in the diet of Eagle Owls. This is highly significant because rodents (including lemmings and voles) were very abundant in the Polish lands during the Vistulian (e.g. MADEYSKA 1981; NADACHOWSKI 1989). Their remains were recorded in the Vistulian cave deposits under study, usually in large amounts. Hence, even if Snowy Owls appeared near the caves, it was those rodents rather than birds that were hunted by them. It is quite out of the question that Snowy Owls

could have been the suppliers of so many, and so species-rich, bird remains to the cave deposits. It should be added at this point that the abundance of rodent remains in the deposits is no definite proof of the presence of Snowy Owls there. Small mammals are commonly hunted by contemporary Eagle Owls and usually predominate in their diet in terms of individuals caught. Hence, the remains of those animals known from the caves may also have come from Eagle Owl prey.

(c) The presence of Eagle Owls near the caves in the Vistulian is better documented than that of Snowy Owls. The finds of Eagle Owl bones show them to be present there in the Lower Plenivistulian (Raj Cave), Middle Plenivistulian (Obłazowa and Komarowa Caves), and Late Vistulian (Obłazowa and Dziadowa Skała Caves). The bones probably come from birds that nested in or near the caves, because Eagle Owls are not hunted by other birds other than Eagle Owls themselves. The bones of Snowy Owls were only found at two sites, in deposits from the Lower Plenivistulian (Raj Cave) and Upper Plenivistulian (Komarowa Cave) (Table V).

(d) The co-occurrence of Snowy Owls and Eagle Owls in the neighbourhood of the caves, at least during the accumulation of the fossil bird remains under study, should yield more numerous finds of bones of Snowy Owls because Eagle Owls hunt other owls. As they are the biggest and strongest owls, much greater amounts of owls of various species can be found in their diet than in that of other members of this order (MIKKOLA 1976, 1983). That Eagle Owls hunt other owls, often and in great numbers, is also indicated by the data presented in Table III and earlier works (LORENC 2003a, 2004). Scholars account for the presence of Snowy Owl bones in Vistulian cave deposits in eastern and southern Europe by ascribing them to the prey of Eagle Owls (POTAPOVA 2001). In this context, the Snowy Owl bones found in Raj and Komarowa Caves may also be accounted for in this way. This is not impossible, especially in the case of Raj Cave. The bones of a Snowy Owl were recorded there in layer 10, together with a bone of an Eagle Owl. This indicates that both species could have been present in the vicinity of the cave at the same time. However, it is only in this case that such a possibility can be judged highly probable. The occurrence of Snowy Owls near the caves, and especially their habitation there, during the accumulation of the bird material studied, seems doubtful. An alternative interpretation of the above data, that the absence of Snowy Owl bones could have resulted from the absence of Eagle Owls near the caves, seems out of the question in the light of the results presented.

The data collected in the present research also make it possible to indicate other sources of some of the Vistulian bird remains (although this probably concerns a small proportion of the total). Those data include the following:

(a) Among the bird species likely to nest in caves, especially frequent were the finds of remains of the Kestrel *Falco tinnunculus*, Tawny Owl *Strix aluco*, Swallow *Hirundo rustica*, and Jackdaw *Corvus monedula* (Table V). In the light of the results which indicate that the genesis of the Vistulian bird remains is mainly as victims of Eagle Owls, the presence of the remains of the Kestrel, Tawny Owl and Jackdaw is understandable because those species are often observed to fall prey to modern Eagle Owls. Hence their remains can derive from pellets of those owls or from deaths at the nest site. Swallows, however, while not hunted by them, are present in as many as 12 Vistulian bird assemblages, often represented by several individuals in each. This allows one to suppose that a considerable number of Swallow bones come from birds that nested in the caves and rock shelters.

(b) The relatively frequently found bones of the Tawny Owl *Strix aluco* in the Vistulian bird assemblages (present in six of them) is incontrovertible proof that those owls lived near the caves. One cannot rule out their nesting in the caves. Thus, it can be assumed that some bird bones from the cave deposits may derive from victims of Tawny Owls. This, however, concerns exclusively small birds, largely passerines, because other birds do not appear in the diet of those owls (GLUTZ & BAUER 1980; MIKKOLA 1983; CRAMP & SIMMONS 1985; BOCHEŃSKI jun. 1990a). That some remains of small birds may be victims of Tawny Owls is also suggested by the fact that their proportion in the fossil material is much greater than in pellets of modern Eagle Owls. As has been mentioned, this is the biggest difference between those two assemblages of remains (Tables II and III). The Eagle Owl, being a large predator, hunts small prey only rarely and focuses on animals

whose weight usually exceeds 100 grams (HIRALDO et al. 1976; JAKSIC & MARTI 1984; KORPIMAKI & MARTI 1995). Because Eagle Owls hunt other owls (MIKKOLA 1976, 1983), which may result from similar rhythms of activity of those birds, the bones of Tawny Owls known from the Vistulian cave deposits may come from individuals caught by Eagle Owls.

The similarities that were shown to occur between fossil assemblages of birds and remains from pellets of modern Eagle Owls are especially striking with reference to Eagle Owls from northern Europe. This indicates that the environment and climate (hence also the food base) in the area of the caves under study, in the Vistulian, were closer to the conditions today in the Scandinavian Mountains (where sites nos. 1 to 6 are located) than in central Europe. The main similarities between those assemblages include the following:

(a) The numerical dominance of birds of the same systematic groups: either galliforms or waterfowl. The proportion of members of other groups is very low, rarely more than a few per cent. Among the avian prey of Eagle Owls in central and western Europe the proportion is usually markedly higher. Also other systematic groups may happen to predominate (pigeons, owls, corvids).

(b) The dominance of the genus *Lagopus* and *Tetrao* among the galliforms. In central and western Europe the predominant species is usually the Common Partridge *Perdix perdix*.

(c) A frequent dominance of anatids among waterfowl. In central and western Europe this happens much less often and is usually accompanied by a substantial proportion of the *Rallidae*.

(d) A lack, or at most a minimum percentage, of pigeons. Today the geographical range of pigeons do not cover a considerable area of Scandinavia, especially its northern part (VOOUS 1962). As has been shown, Eagle Owls hunt pigeons only if they occur in their hunting territories (data from central and western Europe). It follows that pigeons did not occur, or were scarce, in the vicinity of most of the caves under study at the time of accumulation of the bird remains. This leads to the supposition that at that time southern Poland lay outside the geographical range of pigeons or near its northern limit.

V. CONCLUSIONS

1. Bird remains from the Vistulian cave deposits in Poland come mainly from victims of Eagle Owls *Bubo bubo* nesting in caves and rock shelters or in their vicinity.

2. Some of the remains of small birds, largely passerines, are probably victims of Tawny Owls *Strix aluco* that used the caves in the absence of Eagle Owls. Evidence of competition between the two species of owls may exist in the frequent presence of Tawny Owls in the Vistulian cave deposits.

3. A substantial proportion of bones of Common Swallows *Hirundo rustica* that are frequently found in the Vistulian cave deposits comes from birds that nested in the individual caves and rock shelters.

4. There is no irrefutable proof (remains) of Snowy Owls occurring in Poland in the Early Vistulian, Middle Plenivistulian and Late Vistulian, i.e. the entire Vistulian except the Lower and Upper Plenivistulian. The presence of Eagle Owls in Poland is better documented by fossil material.

5. In the period of accumulation of bird bones in the cave deposits under study, pigeons did not occur, or occurred in very small numbers, in the vicinity of most of the caves. This suggests that Poland lay outside the geographical range of pigeons or near its northern limit.

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