Birds in a rock shelter: the Palaeolithic avifauna from the Sesselfelsgrotte (Neuessing, Lower Bavaria)

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1. Introduction

The Sesselfelsgrotte (Neuessing, Lkr. Kelheim/Donau, Germany) is a site in Central Europe with a long Middle and Upper Palaeolithic sequence. The site is located in the lower valley of the river Altmühl, a tributary of the river Danube (Fig. 1). It is a southwest facing rock shelter or abri within the village Neuessing,

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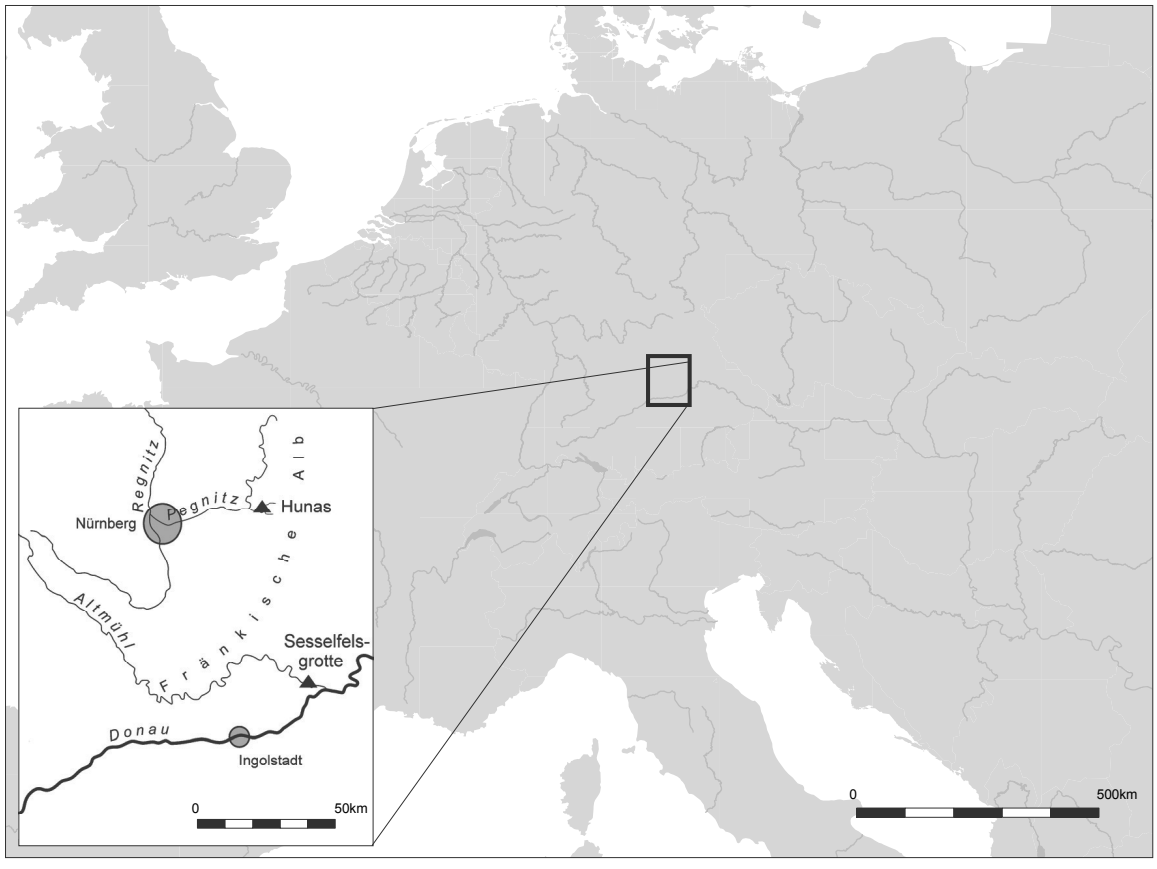

Fig. 1. Geographical location of the Sesselfelsgrotte (after van Kolfschoten 2014).

located 374 m above sea level and about 25 m above the present level of the river Altmühl. The site has been excavated in the frame of the research project "*Das Paläolithikum und Mesolithikum des Unteren Altmühltals II*" and the excavations have been executed under L. Zotz († 1967) and G. Freund in 1964–1977 and in 1981. A detailed description of the excavations and the exposed sedimentological sequence is presented by G. Freund (1998).

The Sesselfelsgrotte with up to nearly 7 m of deposits (mainly rock debris with a matrix of more fine-grained, clay deposits) mainly of Pleistocene age is divided into ca. 35 sedimentological and ca. 25 archaeological (Middle, Upper and Late Palaeolithic) (sub)units (Fig. 2). A layer of loess sediment (D) has been encountered between 1 and 1.50 m from the top of the sequence. The lower part of the sequence (the layers S and 3-West to M1) consists of Early Weichselian, Mousterian deposits (Weißmüller 1995). The unit is correlated with Marine Isotope Stages (MIS) 5d–5a and the beginning of MIS 4 (based on the occurrence of cold indicators in layer M3) (Richter et al. 2000). The overlying L, K and I are archaeologically almost sterile. The layer L and the base of layer K are correlated with the end of MIS 4. The top of layer K and the layer I reflect the transition between MIS 4 and MIS 3 (van Kolfschoten 2014). The layers H to E1–3 have also been referred to MIS 3 (Böhner 2008). Layer G yielded a large number of artefacts indicating several occupations of Mousterian and mostly Micoquian character (Richter 1997). The loess deposits of the archaeologically sterile layer D are correlated with MIS 2. The layers C1 and C2, with Upper and Late Palaeolithic artefacts (Dirian 2003) mark the transition of the Bölling-Allerød complex to the Younger Dryas. Layer A is artificially deposited and has a Holocene, late Medieval age (Freund 1998, 298).

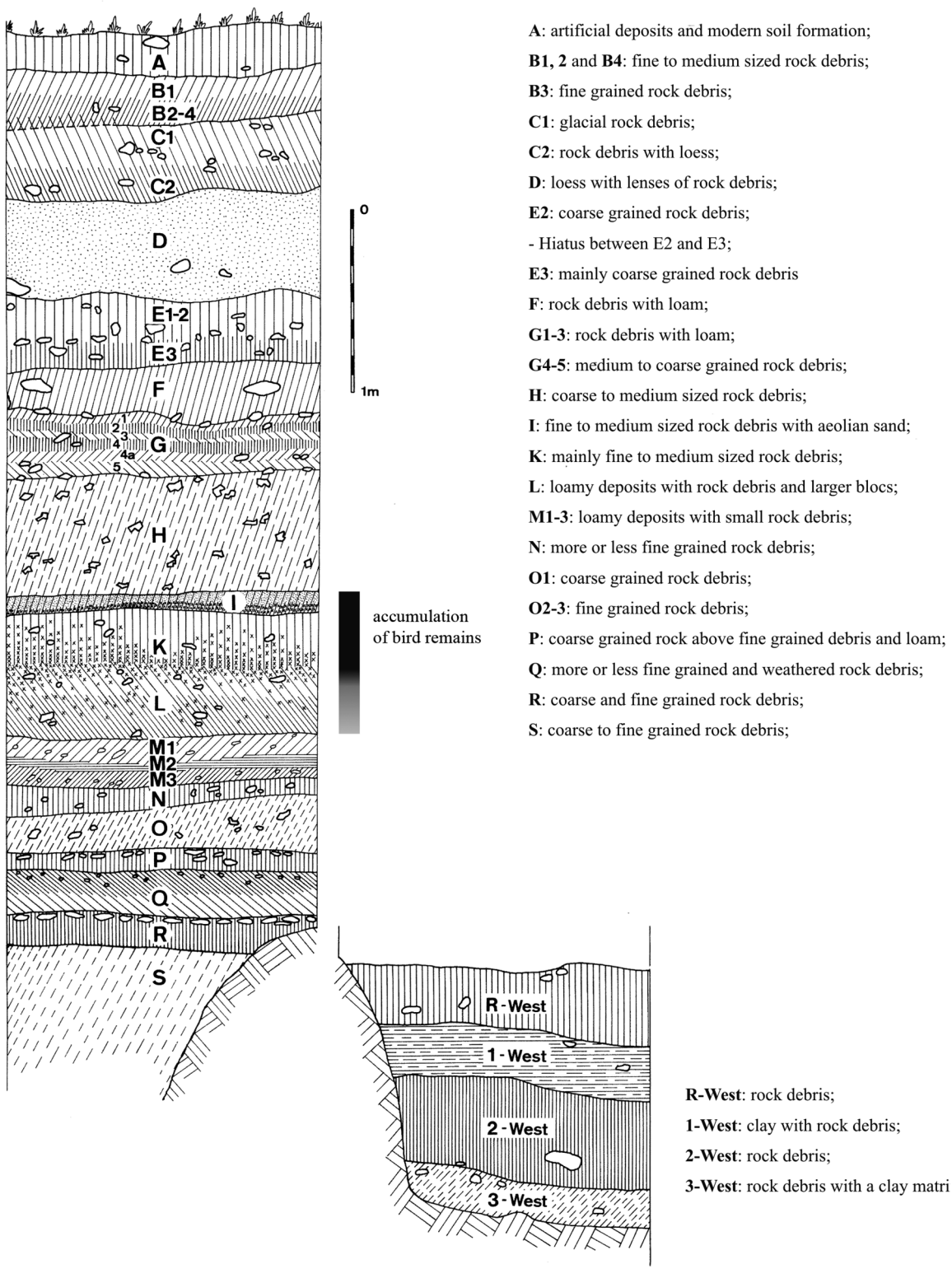

Fig. 2. Schematic profile showing the depositional sequence of the Sesselfelsgrotte infill (modified after Freund 1984, Fig. 34; description by L. Reisch).

Bird remains have been found in almost all strata, be it in (strongly) varying numbers. The layers I and K yielded the largest part: together they account for almost 90 % of the total number of bird bones. As for stratum K, more than half of the remains (56 %) comes from the substrata Kii–iii. These were deposited in cold conditions (though not quite as cold as in layer L), whereas the upper substratum Ki was formed in a period when the climate became warmer.

The analysis of the bird bones and bone fragments was carried out by the late A. von den Driesch, using the reference collection of the Staatssammlung für Anthropologie und Paläoanatomie in Munich (Germany). The preliminary results, based on about 900 "hand-picked" bones, were presented at the 5th Meeting of the ICAZ Bird Working Group in Munich (Germany) in 2004 and published in 2005 (von den Driesch 2005). Since the publication in 2005, more material (c. 3000 bones) mainly from sieving residues became available. This paper presents the results of the analyses of the combined first and second assemblages.

2. Species spectrum

The majority of the bird remains (69,2 %) could be identified to species or genus level. At least 72 species are represented, which is considerably more than in the study published by A. von den Driesch in 2005. This is due to the fact that part of the material analyzed after 2005, was collected by sieving, which produced a considerable number of small(er), mainly passerine species. The best represented groups are grouse, thrushes, buntings and finches, corvids, swallows and swifts, woodpeckers, owls, larks and tits. Figure 3 shows the frequencies of the larger species, while in Figure 4 those of the smaller songbirds are shown.

Tab. 1. Number of bird remains per species and layer.

	A–H	H	I	H–I–K	K	K/i	K/ii–iii	K/L	L	M–3–West	R–W	∑
Whooper swan (*Cygnus cygnus*)	1	–	–	–	–	–	–	–	–	–	–	1
Bewick's swan (*Cygnus bewickii*)	1	–	–	–	–	–	–	–	–	–	–	1
Brent goose (*Branta bernicla*)	1	–	–	–	–	–	–	–	–	–	–	1
Goosander (*Mergus merganser*)	–	–	–	–	–	–	–	–	–	1	–	1
Goldeneye/Scaup (*Bucephula clangula*/*Aythya marila*)	1	–	1	–	–	–	–	–	–	–	–	2
Golden eagle (*Aquila chrysaetos*)	1	–	–	–	–	–	–	–	–	2	–	3
White-tailed eagle (*Haliaeetus albicilla*)	1	–	–	1	–	–	–	–	–	–	–	2
Sparrowhawk (*Accipiter nisus*)	–	–	2	–	–	–	–	–	–	–	–	2
Griffon vulture (*Gyps fulvus*)	1	–	–	–	–	–	–	–	–	–	–	1
Peregrine (*Falco peregrinus*)	–	–	–	–	2	–	–	–	–	–	–	2
Kestrel (*Falco tinnunculus*)	–	–	1	–	4	–	–	–	–	1	–	6
Medium-sized falcon (*Falco* sp.)	–	–	–	–	–	–	3	–	–	–	–	3
Merlin (*Falco columbarius*)	–	–	–	–	–	–	–	–	8	–	–	8
Capercaillie (*Tetrao urogallus*)	–	–	1	–	–	–	–	–	–	2	–	3
Black grouse (*Lyrurus tetrix*)	34	9	222	–	19	46	31	4	7	5	–	377
Willow grouse (*Lagopus lagopus*)	2	–	11	–	49	–	–	–	–	–	–	62
Ptarmigan (*Lagopus mutus*)	3	–	3	–	9	–	–	–	–	–	–	15
Lagopus sp.	6	28	372	3	14	107	174	–	14	1	–	719
Grouse (*Lyrurus tetrix*/*Lagopus* sp.)	–	–	206	–	–	36	52	–	–	–	–	294
Hazel hen (*Tetrastes bonasia*)	1	–	58	–	–	–	34	–	4	–	–	97
Grey partridge (*Perdix perdix*)	–	–	1	–	–	1	–	–	–	–	–	2
Spotted crake (*Porzana porzana*)	–	–	1	–	–	–	–	–	–	–	–	1
Redshank (*Tringa totanus*)	–	–	–	–	1	–	–	–	–	–	–	1

	A–H	H	I	H–I–K	K	K/i	K/ii–iii	K/L	L	M–3–West	R–W	Σ
Ruff (*Philomachus pugnax*)	1	–	–	–	–	–	–	–	1	–	–	2
Whimbrel (*Numenius phaeopus*)	–	–	1	–	–	–	–	–	–	–	–	1
Cuckoo (*Cuculus canorus*)	–	–	6	–	–	–	–	–	–	–	–	6
Eagle owl (*Bubo bubo*)	1	–	–	–	–	–	–	–	1	1	–	2
Tengmalm's owl (*Aegolius funereus*)	2	–	9	–	2	2	11	–	2	–	–	28
Tawny owl (*Strix aluco*)	–	–	2	–	–	–	–	–	–	2	–	4
Short-eared owl (*Asio flammeus*)	–	–	–	–	4	–	–	–	–	–	–	4
Long-eared/Short-eared owl *(Asio otus/A. flammeus*)	–	–	51	–	–	–	–	–	–	–	–	51
Pygmy owl (*Glaucidium passerinum*)	–	–	8	–	–	–	–	–	–	–	–	8
Owl, species unknown	1	–	–	–	–	–	–	–	–	–	–	1
Alpine swift (*Apus melba*)	4	–	11	–	1	–	2	–	–	–	–	18
Swift (*Apus apus*)	–	–	5	–	–	–	–	–	–	–	–	5
Black woodpecker (*Dryocopus martius*)	–	–	1	–	–	–	–	–	–	–	–	1
White-backed woodpecker (*Dendrocopus leucotos*)	–	–	4	–	–	1	4	–	–	–	–	6
White-backed/Great spotted woodpecker (*Dendrocopus leucotos/D. major*)	–	–	3	–	–	–	–	–	–	–	–	3
Great spotted woodpecker (*Dendrocopus major*)	–	–	8	–	–	–	–	–	–	1	–	9
Three-toed woodpecker (*Picoides tridactylus*)	–	–	–	–	–	–	–	–	–	2	–	2
Shore lark (*Eremophila alpestris*)	–	1	17	–	–	11	17	–	–	–	–	46
Sky lark (*Alauda arvensis*)	–	–	4	–	1	–	8	–	–	–	–	13
Wood lark (*Lulula arborea*)	–	–	–	–	–	–	2	–	–	–	–	2
Crag martin (*Ptyonoprogne rupestris*)	–	–	1	–	–	–	–	–	–	–	–	1
Barn swallow (*Hirundo rustica*)	3	–	8	3	1	–	–	–	2	1	–	18
Sand/House martin (*Riparia riparia/Delichon urbica*)	–	–	2	–	–	1	–	–	–	–	–	3
Pipit (*Anthus* sp.)	–	–	–	–	–	–	9	–	–	–	–	9
Waxwing (*Bombycilla garrulus*)	1	–	19	–	4	5	41	–	2	–	–	72
Dipper (*Cinclus cinclus*)	–	–	19	–	–	3	10	–	1	3	–	36
Red-backed shrike (*Lanius collurio*)	–	1	2	–	–	–	–	–	–	–	–	3
Great grey shrike (*Lanius excubitor*)	–	–	3	–	–	–	1	–	–	–	–	4
Dunnock (*Prunella modularis*)	–	–	–	–	–	–	3	–	–	–	–	3
Goldcrest (*Regulus regulus*)	–	–	–	–	–	–	1	–	1	–	–	2
Wheatear (*Oenanthe oenanthe*)	–	–	–	–	–	–	11	–	–	–	–	11
Robin (*Erithacus rubecula*)	–	–	1	–	–	–	–	–	–	–	–	1
Robin/Bluethroat (*Erithacus rubecula/Cyanosylvia svecica*)	–	–	19	–	–	7	30	–	–	–	–	56
Mistle trush (*Turdus viscivorus*)	1	1	60	–	4	16	4	–	–	2	–	88
Ring ouzel (*Turdus torquatus*)	1	–	1	–	3	–	–	–	–	–	–	5
Redwing (*Turdus iliacus*)	1	–	10	–	1	–	–	–	–	–	–	12
Ring ouzel/Fieldfare (*Turdus torquatus/T. pilaris*)	8	–	11	6	3	–	–	2	7	1	–	38
Blackbird/Ring ouzel/Fieldfare (*Turdus merula/T. torquatus/T. pilaris*	–	2	101	–	–	44	64	–	–	–	–	211

	A–H	H	I	H–I–K	K	K/i	K/ii–iii	K/L	L	M–3–West	R–W	∑
Redwing/Song thrush (*Turdus iliacus*/*T. philomelos*)	–	–	18	–	4	5	8	–	–	–	–	35
Long-tailed tit (*Aegithalos caudatus*)	–	–	6	–	–	–	3	–	–	–	–	9
Great tit (*Parus major*)	–	–	9	–	–	1	–	–	–	–	–	10
Coal/Blue/Crested tit (*Parus ater*/*P. caeruleus*/*P. cristatus*)	–	–	6	–	–	–	1	–	–	–	–	7
Nuthatch (*Sitta europaea*)	–	–	2	–	–	–	3	–	–	–	1	6
Wren (*Troglodytes troglodytes*)	–	–	–	–	1	–	–	–	–	1	–	2
Yellowhammer/Snow bunting (*Emberiza citrinella*/*Plectrophenax nivalis*)	1	–	17	8	17	–	3	4	2	–	–	52
Bunting, unknown species (Emberizidae)	–	–	2	–	10	–	–	3	–	–	–	15
Chaffich/Brambling (*Fringilla coelebs*/*F. montifringilla*)	–	3	44	–	–	24	20	–	2	–	2	95
Goldfinch (*Carduelis carduelis*)	–	–	–	–	–	2	–	–	–	–	–	2
Siskin (*Carduelis spinus*)	–	–	4	–	–	5	3	–	1	–	–	13
Redpoll (*Carduelis flammea*)	1	–	6	–	–	1	–	–	–	–	–	8
Linnet/Twite (*Carduelis cannabina*/*C. flavirostris*)	–	–	1	–	–	–	–	–	–	–	–	1
Bullfinch (*Pyrrhula pyrrhula*)	–	–	20	–	–	7	7	–	–	–	–	34
Hawfinch (*Coccothraustes coccothraustes*)	–	–	–	–	–	–	–	–	2	–	–	2
Crossbill (*Loxia curvirostra*)	–	–	–	–	3	–	–	3	2	–	–	8
Nutcracker (*Nucifraga caryocatactes*)	–	–	–	–	–	–	–	–	–	1	–	1
Jay (*Garrulus glandarius*)	–	–	–	–	–	–	–	–	1	–	–	1
Siberian jay (*Perisoreus infaustus*)	–	–	–	–	1	–	–	–	–	–	–	1
Jay/Siberian jay (*Garrulus glandarius*/*Perisoreus infaustus*)	–	–	–	–	–	–	–	–	–	1	–	1
Jay/Nutcracker (*Garrulus glandarius*/*Nucifraga caryocatactes*)	–	12	7	–	–	2	7	–	–	–	–	28
Jackdaw (*Corvus monedula*)	1	2	–	–	3	2	4	–	3	–	–	15
Chough (*Pyrrhocorax pyrrhocorax*)	3	–	–	–	1	–	4	–	2	–	–	10
Alpine chough (*Pyrrhocorax graculus*)	9	–	1	1	4	4	5	–	1	1	–	26
∑ remains, identified	92	59	1409	22	166	333	580	16	66	29	3	2775
∑ remains, not identified	29	38	589	7	45	153	307	2	37	22	1	1230
∑ remains, total	121	97	1998	29	211	486	887	18	103	51	4	4005

As can be seen in Table 1 and Figs. 3 and 4, grouse – mostly black grouse (*Lyrurus tetrix*), willow grouse (*Lagopus lagopus*) and ptarmigan (*Lagopus mutus*) – is the best represented group, followed by thrushes. Of these, at least three species could be identified: mistle thrush (*Turdus viscivorus*), ring ouzel (*Turdus torquatus*) and redwing (*Turdus iliacus*). Buntings and finches come third, with at least nine different species: yellowhammer or snow bunting (*Emberiza citrinella*/*Plectrophenax nivalis*), chaffinch or brambling (*Fringilla coelebs*/*F. montifringilla*), goldfinch (*Carduelis carduelis*), siskin (*Carduelis spinus*), redpoll (*Carduelis flammea*), linnet or twite (*Carduelis cannabina*/*C. flavirostris*), bullfinch (*Pyrrhula pyrrhula*), hawfinch (*Coccothraustes coccothraustes*) and crossbill (*Loxia curvirostra*). The other small passerine birds, like swallows, larks and tits are represented in lower numbers. These include, among others, crag martin (*Ptyonoprogne rupestris*), barn swallow (*Hirundo rustica*), sand or house martin (*Riparia riparia*/*Delichon urbicum*), shore lark (*Eremophila*

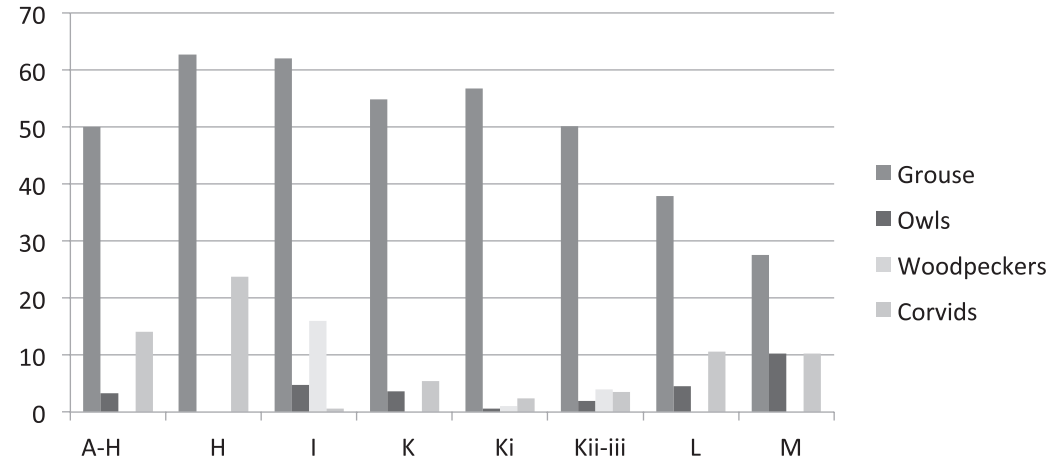

Fig. 3. Proportion of grouse, owls, woodpeckers and corvids (% of identified remains) per stratum (only strata with > 25 identified remains).

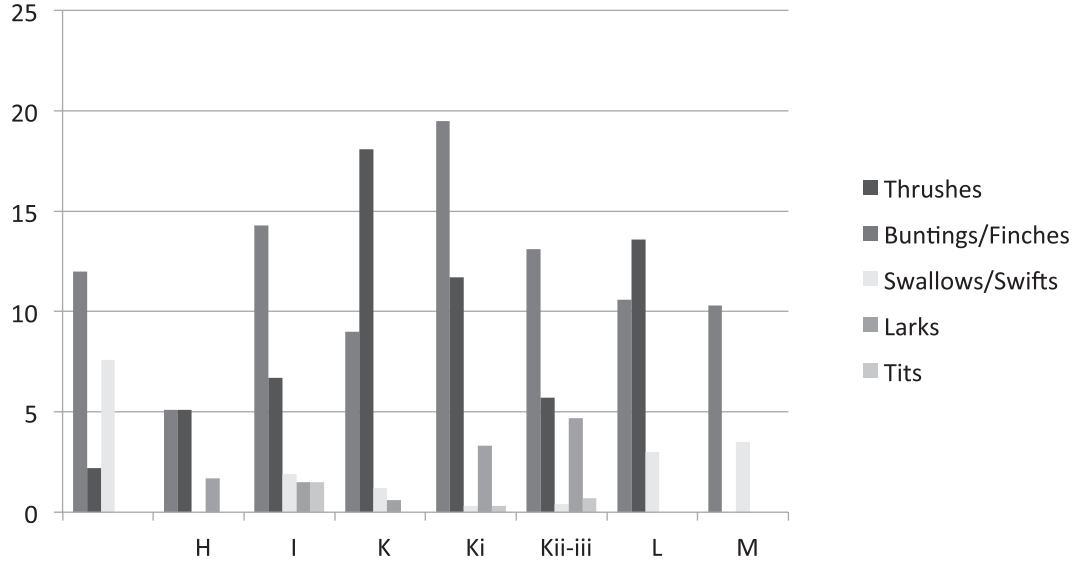

Fig. 4. Proportion of thrushes, buntings/finches, swallows/swifts, larks and tits (% of identified remains) per stratum (only strata with > 25 identified remains).

alpestris), sky lark (*Alauda arvensis*), wood lark (*Lulula arborea*) and long-tailed tit (*Aegithalos caudatus*). The smallest bird species represented are wren (*Troglodytes troglodytes*) and goldcrest (*Regulus regulus*).

Corvids are best represented in strata A–H, H, L and M. The Siberian jay (*Perisoreus infaustus*), jay (*Garrulus glandarius*) and nutcracker (*Nucifraga caryocatactes*) are poorly represented; only a single bone of every species could be identified with certainty. However, jay and nutcracker have been more common, as appears from 28 remains that belong to either one of the species. Of the other two corvids, Alpine chough (*Pyrrhocorax graculus*) is present in more strata and in higher numbers than the red-billed chough (*Pyrrhocorax pyrrhocorax*).

Remains of woodpeckers and owls are most numerous in layer I. Of the first, four species were identified: black, white-backed, great spotted and three-toed woodpecker (*Dryocopus martius* / *Dendrocopus leucotos* / *D.*

major / *Picoides tridactylus*). As for the owls, the remains represent at least five species: eagle owl (*Bubo bubo*), Tengmalm's owl (*Aegolius funereus*), tawny owl (*Strix aluco*), short-eared owl (*Asio flammeus*) and pygmy owl (*Glaucidium passerinum*).

Diurnal birds of prey are relatively rare and appear in low numbers, although seven different species have been identified: golden eagle (*Aquila chrysaetos*), white-tailed eagle (*Haliaeetus albicilla*), sparrowhawk (*Accipiter nisus*), griffon vulture (*Gyps fulvus*), peregrine (*Falco peregrinus*), kestrel (*Falco tinnunculus*) and merlin (*Falco columbarius*).

In terms of biotope, the bird species represent both open and more wooded areas. For instance, willow grouse breed in birch and other forests as well as in moorlands and the tundra of Scandinavia, while the hazel hen is a bird of mixed woodland. Other typical forest species are woodpeckers and owls (except for the short-eared owl which is a bird of open areas). Part of the small songbirds, such as thrushes, finches and tits, as well as corvids (especially jay, Siberian jay and nutcracker) depend on the presence of trees and/or shrubs. Sky lark, shore lark, pipit, wheatear, swallows, martins and swifts are typical birds of open landscapes.

It is striking that remains of waterfowl (swans, geese and ducks) and waders are very rare, and found almost exclusively in strata A–H. They include whooper swan (*Cygnus cygnus*), Bewick's swan (*Cygnus bewickii*), brent goose (*Branta bernicla*), goosander (*Mergus merganser*), redshank (*Tringa totanus*), ruff (*Philomachus pugnax*) and whimbrel (*Numenius phaeopus*). Except for the merganser, all waterfowl species nowadays are migratory. Goldeneyes breed in the boreal forests of northern and eastern Europe. Bewick's swan and brent goose are arctic species; the breeding grounds of the whooper swan lie in subarctic Eurasia, further south than those of Bewick's in the taiga zone. Scaups breed in the northernmost reaches of Europe.

3. Taphonomical analyses

Detailed conclusions about the palaeoenvironmental conditions during the deposition of the different levels and the conditions during human occupation can only be drawn if one knows the taphonomical history of the fossil remains. It is important to know if there is a taphonomical bias in the accumulated assemblage. The main question to be answered first of all, is: who is responsible for the accumulation? Birds of prey are the most obvious candidates, but carnivores and, of the larger animals, hominins should not be excluded. It is important to stress that the majority of the bird remains has been collected from the archaeologically (almost) sterile layers L–H, whereas the archaeologically rich layers P–M1 and G yielded only a small amount of bird remains. Layer G for example, is very rich in archaeological finds; it also yielded the majority of the larger mammal fossils (Rathgeber 2014) as well as the majority of the Leporid remains (referred to *Lepus timidus*) that show cut marks (Maul 2014). Remarkable are the hominin remains from Layer G which include one worn milk molar and 12 bones of a foetal skeleton (Rathgeber 2006). The presence of cut marks as well as the spatial distribution indicate hominin interference in the accumulation of the larger mammal and Leporid remains.

The Sesselfelsgrotte bird remains do not show any sign of hominin interaction: no cut marks, or hominin/human tooth marks. Although these signs of human activities are relatively seldom found on bird bones, their complete absence among the large amount of bird bones from the Sesselfelsgrotte is indeed striking. On the other hand, as is noted by Bochenski (2005), signs of activities by birds of prey (such as beak impacts) are equally rare. This suggests that the Sesselfelsgrotte bird remains including those from the archaeologically rich layers G and M must have been the result of natural accumulations, most certainly deposited through pellets of owls and birds of prey, species that are also represented in the fossil record of the Sesselfelsgrotte.

3.1 Spatial distribution of the bird remains

The fossil bird remains show no random spatial distribution; most of them are concentrated in a limited number of squares (Fig. 5). A. von den Driesch demonstrated, based on the remains she analysed up to that

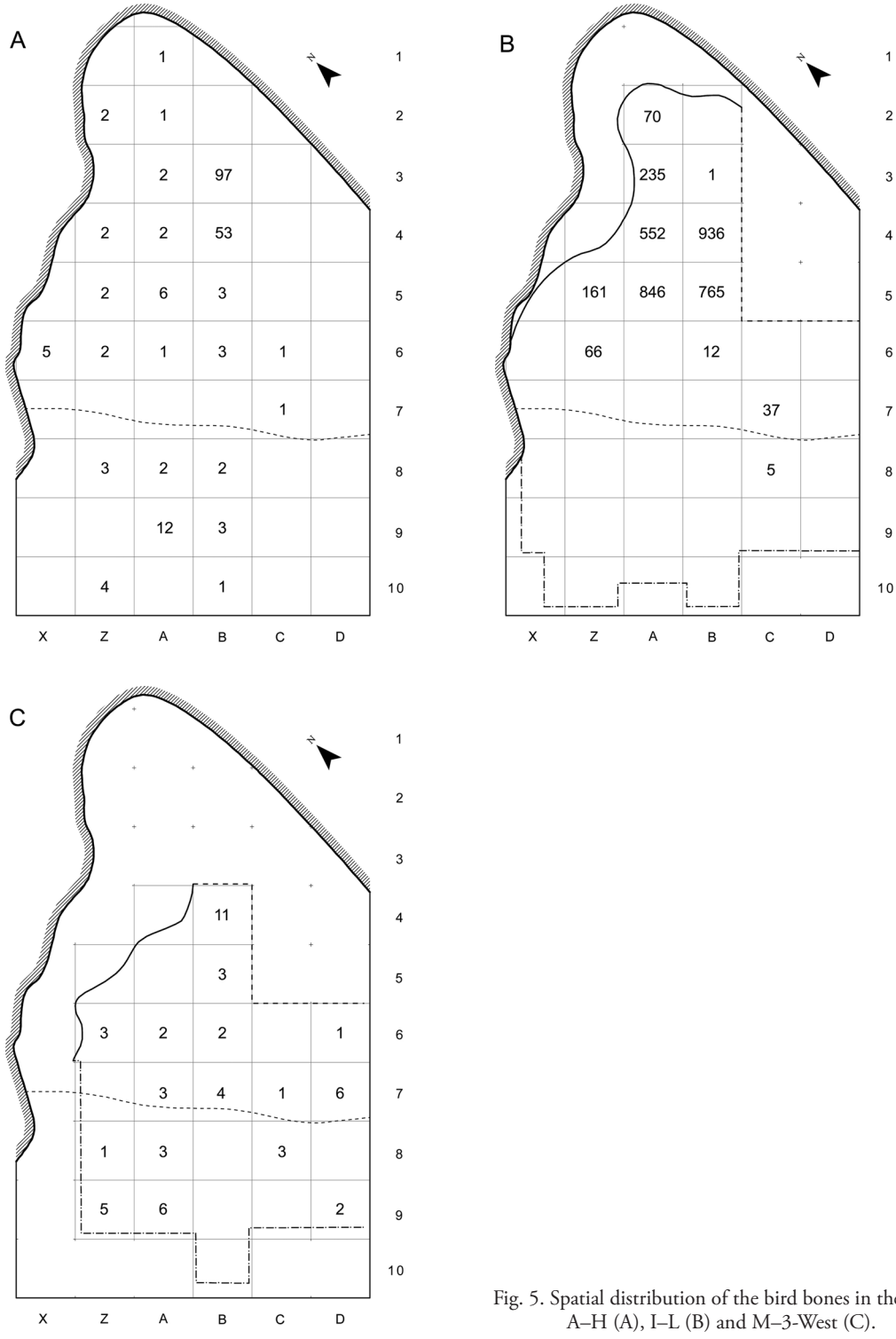

Fig. 5. Spatial distribution of the bird bones in the levels A–H (A), I–L (B) and M–3-West (C).

Tab. 2. Distribution of bones of grouse (Tetraonidae), diurnal and nocturnal raptors (Accipitridae/Strigidae) and crows (Corvidae) per square (after Von den Driesch 2005).

Taxa	Square	X	Z	A	B	C	D
Tetraonidae	2	–	–	3	–	–	–
Accipitridae/Strigidae	2	–	–	1	–	–	–
Corvidae	2	–	–	1	–	–	–
Tetraonidae	3	–	–	23	–	–	–
Accipitridae/Strigidae	3	–	–	1	–	–	–
Corvidae	3	–	–	–	–	–	–
Tetraonidae	4	–	–	57	58	–	–
Accipitridae/Strigidae	4	–	1	–	12	–	–
Corvidae	4	–	–	3	2	–	–
Tetraonidae	5	–	4	148	31	–	–
Accipitridae/Strigidae	5	–	7	7	1	–	–
Corvidae	5	–	1	–	1	–	–
Tetraonidae	6	1	2	1	1	1	–
Accipitridae/Strigidae	6	1	–	1	–	–	1
Corvidae	6	3	1	3	1	–	–
Tetraonidae	7	–	–	–	–	6	1
Accipitridae/Strigidae	7	–	–	–	1	2	2
Corvidae	7	–	–	–	–	8	–
Tetraonidae	8	–	–	1	2	–	–
Accipitridae/Strigidae	8	–	–	–	–	–	–
Corvidae	8	–	–	–	–	1	–
Tetraonidae	9	–	–	5	–	–	3
Accipitridae/Strigidae	9	–	–	1	–	–	–
Corvidae	9	–	1	7	–	–	–
Tetraonidae	10	–	3	–	–	–	–
Accipitridae/Strigidae	10	–	–	–	–	–	–
Corvidae	10	–	–	–	–	–	–

point, that the bones of three of the best represented groups (grouse, diurnal and nocturnal raptors and corvids) were mainly found in squares A4, A5, B4 and B5 (Table 2) and she concluded that we are dealing with remnants of pellets dropped at a covered place in the cave; a location preferred by most birds of prey (von den Driesch 2005). The distribution of the "new" material that has been analysed more recently shows the same pattern (Table 3).

The spatial concentration of birds remains overlaps significantly with the distribution area of the small mammal remains. The spatial distribution of the small mammal remains in the layers L, K and I is also mainly restricted to the squares A4, A5, B4 and B5 (Van Kolfschoten 2014). The distribution of other small vertebrate remains (fish, reptiles and amphibians) (Böttcher 2014) is also strikingly similar. This indicates that their accumulation is probably caused by the same actors, birds of prey.

Tab. 3. Distribution of the bird bones (incl. not identified remains) per square and stratum (excl. H–I–K and K/L).

	A–H	H	I	K	L	M–3-West	R–W	∑
A1	1							1
A2	1		70					71
A3	2		235					237
A4	2		168	365	19			554
A5	6		576	270				852
A6	1					2		3
A7						3		3
A8	2					1	2	5
A9	12					4	2	18
B3		97	1					98
B4	53		337	529	70	11		1000
B5	3		393	362	10	3		771
B6	3		4	8		2		17
B7						4		4
B8	2							2
B10	1							1
C6	1							1
C7	1		2	35		1		39
C8			5			3		8
D6						1		1
D7						6		6
D9						2		2
H9	3							3
X6	5							5
Z2	2							2
Z4	2							2
Z5	2		142	19				163
Z6	2		60	2	4	3		71
Z8	3					1		4
Z9						5		5
Z10	4							4
∑	114	97	1993	1590	103	52	4	3953

3.2 Accumulation by raptors

The variation in the representation of specific skeletal elements (Table 4) points to accumulation by raptors. Parts of the head and the pectoral girdle (furcula, scapula and coracoid) are well represented, as are the vertebra. The long bones of the wings and the legs are about equally represented, but the femora are relatively scarce. Also sternum and pelvosacrum are represented in low numbers. As stated by von den Driesch (2005), sternum, pelvosacrum and femur (as well as the proximal part of the tibiotarsus) are from that part of the bird that is rich in meat. This makes these bones far more subject to damage than the pectoral girdle and the wings that often are not digested but dropped just as the vertebra and the lower leg bones (distal part of the tibiotarsus, tarsometatarsus, tarsalia and phalanges).

According to Bochenski (2005) the ratio of wing to leg elements in pellets and uneaten food remains of owls and gyrfalcons is either 1:1 (as it is in the Sesselfelsgrotte) or the wing elements predominate, be it with a predominance that is not high in terms of percentages. Furthermore, in pellets of owls and diurnal preda-

Tab. 4. Spatial distribution of bird remains: skeletal elements of body parts (numbers) per layers and square meters.

	head	sternum	pectoral girdle*	vertebra	wings			legs			phalanges div.	totals
					long bones	phalanges	pelvo-sacrum	long bones (-femur)	femur	phalanges		
I - A2	4	0	4	18	13	0	1	5	0	7	40	92
I - A4	6	0	7	11	7	5	0	5	2	0	19	62
K - A4	18	3	28	56	43	3	1	43	8	14	116	333
I - A5	18	1	15	48	36	9	1	30	3	9	125	295
K - A5	13	2	15	12	25	7	1	20	4	12	89	200
I - B4	17	2	16	59	40	6	0	27	14	12	116	309
K - B4	32	5	37	33	55	4	2	52	5	13	138	376
I - B5	20	1	13	63	17	6	1	23	5	7	91	247
K - B5	16	1	39	14	42	23	2	32	5	7	96	277
I - Z5	5	0	3	33	15	3	1	9	1	10	61	141
	149	15	177	347	293	66	10	246	47	91	891	

* pectoral girdle = furcula, coracoid, scapula

tors limb elements (wing and leg bones) greatly predominate over core elements (sternum, coracoid, scapula and pelvis). In uneaten food remains, they predominate to a lesser degree and even are in the minority. In the material from the Sesselfels cave, there is a general predominance of limb elements, which could mean that at least a considerable part of the remains come from pellets. A third criterion mentioned by Bochenski (2005) is the ratio of proximal (upper) elements (scapula, coracoid, humerus, femur and tibiotarsus) to distal (lower) elements (ulna, radius, carpometacarpus and tarsometatarsus). Using this ratio, three groups of avian predators can be distinguished:

Tab. 5. Spatial distribution of bird remains: numbers of proximal elements (scapula, coracoid, humerus, femur, tibiotarsus) vs. distal elements (ulna, radius, carpometacarpus, tarsometatarsus) per layers and square meters.

	total number of remains	proximal elements	distal elements	ratio prox:dist
I – A2	92	10	11	1:1,1
I – A4	62	11	9	1:0,8
K – A4	333	53	60	1:1,1
I – A5	295	33	48	1:1,5
K – A5	200	25	37	1:1,5
I – B4	309	44	50	1:1,1
K – B4	376	62	78	1:1,3
I – B5	247	31	22	1:0,7
K – B5	277	55	56	1:1,0
I – Z5	141	10	18	1:1,8

– diurnal birds of prey (only pellets), with a ratio of 1:1
– owls (pellets) and uneaten food remains of some diurnal birds of prey (gyrfalcon, peregrine falcon, imperial eagle and white-tailed eagle), with a clear but not very great predominance of proximal elements
– golden eagles (uneaten food remains), with a great predominance of proximal elements

Following Bochenski's criteria, we can see that in the Sesselfelsgrotte limb elements greatly predominate over core elements, and in most cases there is only a slight predominance of proximal elements over distal elements (Table 5). These are strong indications that most of the material comes from pellets. Also the fact that remains of both birds and fish, reptiles, amphibians and small mammals (e. g. rodents) are concentrated in the same squares of layers L, K and I, is a strong indication that at least a considerable part of the remains come from pellets, most probably of owls as the digestion of bones by diurnal raptors is stronger (see e. g. Andrews 1990).