A BIRD'S EYE VIEW OF THE MIDDLE PALAEOLITHIC: AVIAN FOSSIL REMAINS AND THEIR CONTRIBUTION TO NEANDERTHAL RESEARCH IN EURASIA

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Dedication

As a child, my neighbour took me along on a visit to an archaeological site at the foot of the Eildon Hills in the Scottish Borders. As the adults milled around on the tour, I trailed behind, staring in wonder at the archaeologists in their trenches. One of them looked up and began to chat with me. He showed me his trowel, and some broken bits of pottery. I nodded eagerly, pointed to a smooth shape protruding from his section wall, and asked whether he was going to excavate the entire amphora or not. My neighbour told me many years later that she knew that day that I was destined to be an archaeologist. Thank you, Roslyn. This thesis is dedicated to your memory.

Acknowledgements

I'd like to begin by recording my acknowledgement of the work of two women whose initial investigations feature prominently at two of the sites in this study – Dorothy Garrod and Dorothea Bate. It is an honour to walk in their footsteps.

A heartfelt thank you goes to Richard Jennings, my Director of Studies, for offering me the opportunity to write this thesis. Richard has been an endless source of guidance, encouragement, and motivation from the very beginning of the project, through the ups and downs of planning and data collection, and the challenges of writing up during a global pandemic. I appreciate everything you have done for me. Thank you.

My co-supervisor Clive Finlayson has made a budding ecologist out of this archaeologist. Thank you, Clive, for giving me the opportunity to learn from you. I entered this PhD programme with a well-established love of Neanderthals. I am coming to the end of it with a much greater respect for the importance of birds, not only as remains found in ancient sites, but as members of flourishing ecosystems.

As a co-supervisor, Antonio Sanchez-Marco provided guidance on the complexity of avian taxonomy, and training in the taxonomic identification of avian remains. Thank you for guiding me through the maze of avian classification during our visit to Arturo Morales' comparative collection in Madrid. I would also like to express my gratitude to Joel Irish, who also co-supervised this thesis, for giving me valuable input and advice on the structure of the dissertation.

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Then there are my family and friends who have supported me along the way. Thank you Mum, Egil and the members of Team Amos UK and USA. Thank you Amanda Coburn, Royston Burr, Kerri MacMillan, Tracy and John Bennitt, Petros Dimitriou, Natalie Wilson,

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Abstract

The study of Neanderthal behaviour and ecology has been shaped by the overarching question of Neanderthal cognitive modernity. The debates concerning Neanderthal cultural complexity and subsistence strategies cross paths in the study of birds. Recent research has shed light on the contribution of bird remains as a proxy in interpretations of Middle Palaeolithic diet and behaviour. Additionally, birds function as excellent indicators of past climate and environmental conditions because some species have highly restricted niche requirements.

This thesis contributes new information to our understanding of Neanderthal behaviour and ecology across their geographical and temporal range by employing ecological and taphonomic methods to bird remains recovered from five Neanderthal sites: Gorham's Cave and Devil's Tower rockshelter in Gibraltar, Cova Negra, Spain, Scladina Cave, Belgium, and Tabun Cave, Israel. Intra- and inter-site analyses establish that Neanderthals exploited gamebirds and wetland species for subsistence purposes in all five locations. Ecological results indicate that the Neanderthal bioclimatic and habitat niche did not vary by geographic position.

Within their niche, Neanderthals efficiently exploited birds as a regular addition to their diet, focussing their efforts on specific taxa. This conflicts with earlier research, which proposed that Neanderthals were incapable of conceptualising the complex strategies necessary for hunting birds and small, fast game.

Bird species mentioned in this thesis.

ORDER	SCIENTIFIC NAME		COMMON NAME	AUTHORITY
GALLIFORMES			**GAME BIRDS**	
	Tetrao	*urogallus*	capercaillie	Linnaeus, 1758
	Lyrurus	*tetrix*	black grouse	Linnaeus, 1758
	Lagopus	*muta*	rock ptarmigan	Pontoppidan, 1763
	Lagopus	sp.	ptarmigan	Pontoppidan, 1763
	Alectoris	*chukar*	chukar partridge	Gray, JE, 1830
	Alectoris	*barbara*	barbary partridge	Bonnaterre, 1790
	Alectoris	*rufa*	red-legged partridge	Linnaeus, 1758
	Alectoris	sp.	partridge	Kaup, 1829
	Coturnix	*coturnix*	common quail	Linnaeus, 1758
ANSERIFORMES			**DUCKS AND GEESE**	
	Anser	*albifrons/serrirostris*	white-footed/bean goose	Scopili, 1769/Gould, 1852
	Anser	sp.	goose	Brisson, 1760
	Tadorna	*ferruginea*	ruddy shelduck	Pallas, 1764
	Spatula	*querquedula*	garganey	Linnaeus, 1758
	Mareca	*penelope*	eurasian wigeon	Linnaeus, 1758
	Anas	*platyrhynchos*	mallard	Linnaeus, 1758
	Anas	*acuta*	northern pintail	Linnaeus, 1758
	Anas	*crecca*	eurasian teal	Linnaeus, 1758
	Anas	sp.	dabbling duck	Linnaeus, 1758
	Aythya	*fuligula*	tufted duck	Linnaeus, 1758
	Somateria	sp.	eider duck	Leach, 1819
	Melanitta	*fusca*	velvet scoter	Linnaeus, 1758
	Melanitta	*nigra*	common scoter	Linnaeus, 1758
	Clangula	*hyemalis*	long-tailed duck	Linnaeus, 1758
	Mergus	*merganser*	common merganser	Linnaeus, 1758
	Mergus	*serrator*	red-breasted merganser	Linnaeus, 1758
	Anatidae		duck/goose	
APODIFORMES			**SWIFTS**	
	Tachymarptis	*melba*	alpine swift	Linnaeus, 1758
	Apus	*apus/pallidus*	common/pallid swift	Linnaeus, 1758/Shelley, 1870
COLUMBIFORMES			**PIGEONS AND DOVES**	
	Columba	*livia/oenas*	rock/stock dove	Gmelin, JF, 1789/Linnaeus, 1758
	Columba	*palumbus*	wood pigeon	Linnaeus, 1758
	Streptopelia	*turtur*	turtle dove	Linnaeus, 1758
	Streptopelia	sp.	dove	Bonaparte, 1855
	Spilopelia	*senegalensis*	laughing dove	Linnaeus, 1766
GRUIFORMES			**CRANES AND RAILS**	
	Porzana	*porzana*	spotted crake	Linnaeus, 1766
	Fulica	*atra*	common coot	Linnaeus, 1758
CHARADRIIFORMES			**SHORE BIRDS**	
	Burhinus	*oedicnemus*	eurasian stone-curlew	Linnaeus, 1758
	Haematopus	*ostralegus*	eurasian oystercatcher	Linnaeus, 1758
	Vanellus	*vanellus*	northern lapwing	Linnaeus, 1758
	Numenius	*phaeopus*	eurasian whimbrel	Linnaeus, 1758
	Limosa	sp.	godwit	Brisson, 1760
	Scolopax	*rusticola*	eurasian woodcock	Linnaeus, 1758
	Scolopacidae		sandpiper	
	Larus	*argentatus*	herring gull	Pontoppidan, 1763
	Larus	*cachinnans*	caspian gull	Pallas, 1811
	Larus	*fuscus*	lesser black-headed gull	Linnaeus, 1758

ORDER	SCIENTIFIC NAME		COMMON NAME	AUTHORITY
	Larus	sp.	gull	Linnaeus, 1758
	Uria	*aalge*	common murre	Pontoppidan, 1763
	Alca	*torda*	razorbill	Linnaeus, 1758
	Pinguinus †	*impennis* †	great auk	Linnaeus, 1758
	Fratercula	*arctica*	atlantic puffin	Linnaeus, 1758
GAVIIFORMES			**LOONS**	
	Gavia	*stellata*	red-throated loon	Pontoppidan, 1763
PROCELLARIIFORMES			**SEA BIRDS**	
	Fulmarus	*glacialis*	northern fulmar	Linnaeus, 1761
	Calonectris	*diomedea*	scopoli's shearwater	Scopoli, 1769
	Puffinus	*mauretanicus*	balearic shearwater	Lowe, 1921
SULIFORMES			**DIVING BIRDS**	
	Morus	*bassanus*	northern gannet	Linnaeus, 1758
	Phalacrocorax	*carbo*	great cormorant	Linnaeus, 1758
	Phalacrocorax	*aristotelis*	shag	Linnaeus, 1761
PELICANIFORMES			**WATER BIRDS**	
	Threskiornithidae		ibis, spoonbill	
	Ixobrychus	*minutus*	little bittern	Linnaeus, 1761
	Bubulcus	*ibis*	cattle egret	Linnaeus, 1758
	Ardea	sp.	heron	Linnaeus, 1758
ACCIPITRIFORMES			**DIURNAL RAPTORS**	
	Gyps	*fulvus*	griffon vulture	Hablizl, 1783
	Aegypius	*monachus*	cinereous vulture	Linnaeus, 1766
	Hieraaetus	*pennatus*	booted eagle	Gmelin, JF, 1788
	Aquila	*nipalensis*	steppe eagle	Hodgson, 1833
	Aquila	*fasciata*	bonelli's eagle	Vieillot, 1822
	Accipiter	*nisus*	sparrowhawk	Linnaeus, 1758
	Accipiter	*gentilis*	northern goshawk	Linnaeus, 1758
	Circus	*cyaneus*	hen harrier	Linnaeus, 1766
	Milvus	sp.	kite	Lacépède, 1799
	Haliaeetus	*albicilla*	white-tailed eagle	Linnaeus, 1758
STRIGIFORMES			**OWLS**	
	Tyto	*alba*	barn owl	Scopoli, 1769
	Bubo	*scandiacus*	snowy owl	Linnaeus, 1758
	Bubo	*bubo*	eagle owl	Linnaeus, 1758
	Strix	*aluco*	tawny owl	Linnaeus, 1758
	Athene	*noctua*	litle owl	Scopoli, 1769
	Asio	*otus/flammeus*	long/short-eared owl	Linnaeus, 1758/Pontoppidan, 1763
PICIFORMES			**WOODPECKERS**	
	Picus	*viridis*	green woodpecker	Linnaeus, 1758
FALCONIFORMES			**FALCONS**	
	Falco	*naumanni*	lesser kestrel	Fleischer, JG, 1818
	Falco	*tinnunculus*	common kestrel	Linnaeus, 1758
	Falco	*eleonorae*	eleonora's falcon	Géné, 1839
	Falco	*subbuteo*	hobby	Linnaeus, 1758
	Falco	*peregrinus*	peregrine falcon	Tunstall, 1771
	Falco	sp.	falcon	Linnaeus, 1758
PASSERIFORMES			**PERCHING BIRDS**	
	Lanius	sp.	shrike	Linnaeus, 1758
	Garrulus	*glandarius*	eurasian jay	Linnaeus, 1758
	Cyanopica	*cyanus*	azure-winged magpie	Pallas, 1776
	Pyrrhocorax	*pyrrhocorax*	red-billed chough	Linnaeus, 1758
	Pyrrhocorax	*graculus*	alpine chough	Linnaeus, 1766
	Pyrrhocorax	sp.	chough	Tunstall, 1771
	Coloeus	*monedula*	jackdaw	Linnaeus, 1758

ORDER	SCIENTIFIC NAME		COMMON NAME	AUTHORITY
	Corvus	*corone*	carrion crow	Linnaeus, 1758
	Corvus	*frugilegus*	rook	Linnaeus, 1758
	Corvus	*corax*	raven	Linnaeus, 1758
	Corvus	sp.	crow	Linnaeus, 1758
	Corvidae		corvid	
	Parus	*major*	great tit	Linnaeus, 1758
	Alauda	*arvensis*	eurasian skylark	Linnaeus, 1758
	Alauda	sp.	lark	Linnaeus, 1759
	Melanocorypha	*calandra*	calandra lark	Linnaeus, 1766
	Pycnonotus	*xanthopygos*	white-spectacled bulbul	Hemprich & Ehrenberg, 1833
	Hirundo	*rustica*	barn swallow	Linnaeus, 1758
	Hirundo	sp	swallow	Linnaeus, 1758
	Phylloscopus	*collybita*	commoon chiffchaff	Vieillot, 1817
	Sylvia	*atricapilla*	eurasian blackcap	Linnaeus, 1758
	Curruca	*communis*	common whitethroat	Latham, 1787
	Sturnus	*unicolor*	spotless starling	Temminck, 1820
	Sturnus	sp.	starling	Linnaeus, 1758
	Turdus	*torquatus*	ring ouzel	Linnaeus, 1758
	Turdus	*pilaris*	fieldfare	Linnaeus, 1758
	Turdus	*philomelos*	song thrush	Brehm, CL, 1831
	Turdus	*viscivorus*	mistle thrush	Linnaeus, 1758
	Turdus	sp.	thrush	Linnaeus, 1758
	Erithacus	*rubecula*	european robin	Linnaeus, 1758
	Monticola	*saxatilis*	common rock thrush	Linnaeus, 1766
	Monticola	*solitarius*	blue rock thrush	Linnaeus, 1758
	Oenanthe	*oenanthe*	northern wheatear	Linnaeus, 1758
	Passer	*domesticus*	house sparrow	Linnaeus, 1758
	Passer	sp.	sparrow	Brisson 1760
	Petronia	*petronia*	rock sparrow	Linnaeus, 1766
	Prunella	*modularis*	dunnock	Linnaeus, 1758
	Motacilla	*alba*	white wagtail	Linnaeus, 1758
	Motacilla	sp.	wagtail	Linnaeus, 1758
	Anthus	sp.	pipit	Bechstein, 1805
	Fringilla	*coelebs*	common chiffchaff	Linnaeus, 1758
	Fringilla	*montifringilla*	brambling	Linnaeus, 1758
	Fringilla	sp.	finch	Linnaeus, 1758
	Coccothraustes	*coccothraustes*	hawfinch	Linnaeus, 1758
	Chloris	*chloris*	european greenfinch	Linnaeus, 1758
	Linaria	*cannabina*	common linnet	Linnaeus, 1758
	Carduelis	*carduelis*	european goldfinch	Linnaeus, 1758
	Carduelis	sp.	finch	Linnaeus, 1758
	Emberiza	*calandra*	corn bunting	Linnaeus, 1758
	Emberiza	*citrinella*	Yellowhammer	Linnaeus, 1758
	Emberiza	sp.	bunting	Linnaeus, 1758
	Emberizidae		buntings	Linnaeus, 1758
	Passeriformes		perching birds	Linnaeus, 1758
INDETERMINATE				
	Aves	sp.	bird	

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1 Introduction

In the late 1990s and through the early 2000's, a key element of Palaeolithic research focussed on formulating a definition of modern human behaviour. Researchers compiled a list of traits citing the technological, economical and symbolic markers of cognitive modernity (Klein 1989; McBrearty and Brooks 2000; Stiner 2001; d'Errico 2003; Henshilwood and Marean 2003). The prerequisites for cognitive modernity were focussed on behaviours that were thought to distinguish anatomically modern human (AMH) societies of the European Upper Palaeolithic from the Middle Palaeolithic Neanderthals (Mellars 1991; Henshilwood and Marean 2003). It is now clear that traits of behavioural modernity appear in anatomically modern societies in Africa pre-dating the Middle to Upper Palaeolithic transition (McBrearty and Brooks 2000; d'Errico *et al.* 2005; Henshilwood *et al*. 2009, 2011). Even so, the nature and extent of European Neanderthal behavioural modernity is an unresolved issue.

Although Neanderthals exhibited a wide array of modern behavioural traits, their cultural capacity remains under scrutiny (Taborin 1998; Higham *et al.* 2010; McGill 2015). Finding the subtle differences that define Neanderthal behavioural complexity is problematic and is at the centre of current Middle Palaeolithic studies. It is accepted that Neanderthals produced composite toolsets (Soressi 2005; Moncel *et al.* 2011); developed highly specialized and effective large game hunting methods (de Los Terreros *et al*. 2014); and lived in well-organized living spaces (Vaquero and Pasto 2001; Henry *et al.* 2004). This demanded a degree of social organization and conceptualisation beyond a merely expedient lifestyle. However, generally accepted traits of modernity in anatomically modern humans, such as the use of colourants, are acknowledged but not accepted as symbolic in Neanderthal contexts (Roebroeks *et al.* 2012). These studies all contribute to the mosaic of what comprises known Neanderthal culture, but do not provide decisive content to the debate.

Over the last two decades, studies of bird fossils have contributed to the debate on Neanderthal cultural complexity. Archaeological sites such as Bolomor Cave, Spain have produced taphonomic evidence of Neanderthal utilitarian exploitation of avian resources (Fiore, Gala and Tagliacozzo 2004; Blasco and Peris 2009), while a small number of sites in Gibraltar, Italy, France, and Croatia have produced evidence of Neanderthals harvesting feathers and talons from raptors and birds with dark plumage (Peresani *et al.* 2011;

Finlayson *et al.* 2012; Morin and Laroulandie 2012; Radovcic *et al.* 2015). In itself, the capture of birds for dietary or non-utilitarian purposes demands a capacity for planning, evaluation, and innovation that has, until recently, been considered an exclusively modern behavioural trait (Klein 1989; Stiner 2001; d'Errico 2003; Henshilwood and Marean 2003). The temporal and geographical context of these practises warrants further investigation to determine whether these represent isolated phenomenon in specific ecological niches or represent a widespread focus on birds in both dietary and symbolic contexts.

In addition to providing information about Neanderthal behaviour, birds have also been used as a proxy for past environments, but only sparingly (Finlayson 2006; Sanchez-Marco *et al.* 2016; Finlayson 2019). They are particularly useful because birds have distinct and sometimes narrow environmental requirements. Also, most bird species that were extant in Europe in the Pleistocene are still extant in the present day, meaning that their habitat parameters are well-defined. This allows us to make inferences about the habitats and bioclimatic conditions available around Neanderthal sites (Tyrberg 1998, 2008; Finlayson 2011).

Given that avian fossils have this potential to add to and enrich the debate on Neanderthal behaviour and ecology, this thesis examines avian remains from archaeological sites across the Neanderthal range : Gorham's Cave and Devil's Tower rockshelter (Gibraltar), Cova Negra (Spain), Scladina Cave (Belgium), and Tabun Cave (Mount Carmel, Israel). This study first aims to analyse the taxonomic composition and ecological requirements of avian species contained in these five sites, which are distributed across the Neanderthal range. Secondly, a taphonomic analysis of the bone surfaces is undertaken to improve our understanding of Neanderthal bird exploitation.

In this chapter, I introduce the Neanderthals, defining their range and known cultural and behavioural traits. This is followed by a review of the debates concerning Neanderthal subsistence strategies and hunting aptitude. Next, I present the current evidence of Neanderthal bird exploitation from sites across Eurasia, and the theoretical background that knowledge is based upon. I then highlight some of the problems in this field of research. Finally, I present my research questions and a brief rundown of the thesis structure.

1.1 Neanderthal range

The Neanderthals were a Eurasian branch of the *Homo* genus, present in the Middle to the Late Pleistocene from c. 430,000 years before present (430 ka BP), to soon after 40 ka BP

(Figure 1.1; Figure 1.2; Table 1.1; Stringer and Gamble 1993; Finlayson *et al.* 2006; Dusseldorp 2009; Higham 2011; Meyer *et al*. 2016). They existed during multiple glacial (Saalian and Weichselian) and interglacial (Holstein and Eemian) ice age cycles, corresponding to Marine Isotope Stages (MIS) 11-3 (Table 1.1). Neanderthals were more robust and shorter in stature than contemporary anatomically modern humans (Holliday 1997a; Churchill 1998, 2014; Wood and Collard 1999; Franciscus and Churchill 2002; Steegmann *et al.* 2002; Aeillo and Wheeler 2003; Steudel-Numbers and Tilkens 2004). Their crania displayed heavy brow ridges and large nasal cavities, along with a pronounced occipital bun, sloping foreheads and no protrusion of the chin (Churchill 1998; Depaepe 2014). They had broad torsos, long clavicles, and broad scapulae (Trinkaus 1989; Ruff 1994).

Neanderthals lived widely across Eurasia, with sites known in Finland in the north (Depaepe 2014) and Israel in south (Garrod and Bate 1937; Jelinek *et al.* 1973; Blinkhorn *et al*. 2021), Siberia in the east (Krause *et al.* 2007; Slon *et al.* 2018) and Wales in the west (White and Pettitt 2011; Aldhouse-Green *et al.* 2012). Neanderthal sites have been found in a range of terrain types including mountainous areas such as the Russian Altai (Slon *et al.* 2018), the Zagros Mountains (Marean and Kim 1998), the Caucasus Mountains (Pinhasi *et al.* 2011), the Pyrenees (Morin and Laroulandie 2012), and the Alps (Romandini *et al.* 2014), as well Mediterranean environments that sustained varied and rich habitats such as seen at the Rock of Gibraltar (Finlayson 2015) and Mount Carmel in the Levant (Garrod and Bate 1937; Jelinek *et al.* 1973; Blinkhorn *et al.* 2021). They also appeared at the edge of the ice sheets at Creswell Crags in the UK (White and Pettitt 2011) but were rarely found in the open environments of the Northern European plain (Finlayson 2004).

Neanderthal morphology has been attributed by some as an adaptation to the cold (Stringer and Gamble 1993; Holliday 1997b; Churchill 1998) while others argue that it was an adaptation to the temperate and heterogenous environments of mid-latitude Europe (Finlayson 2004).

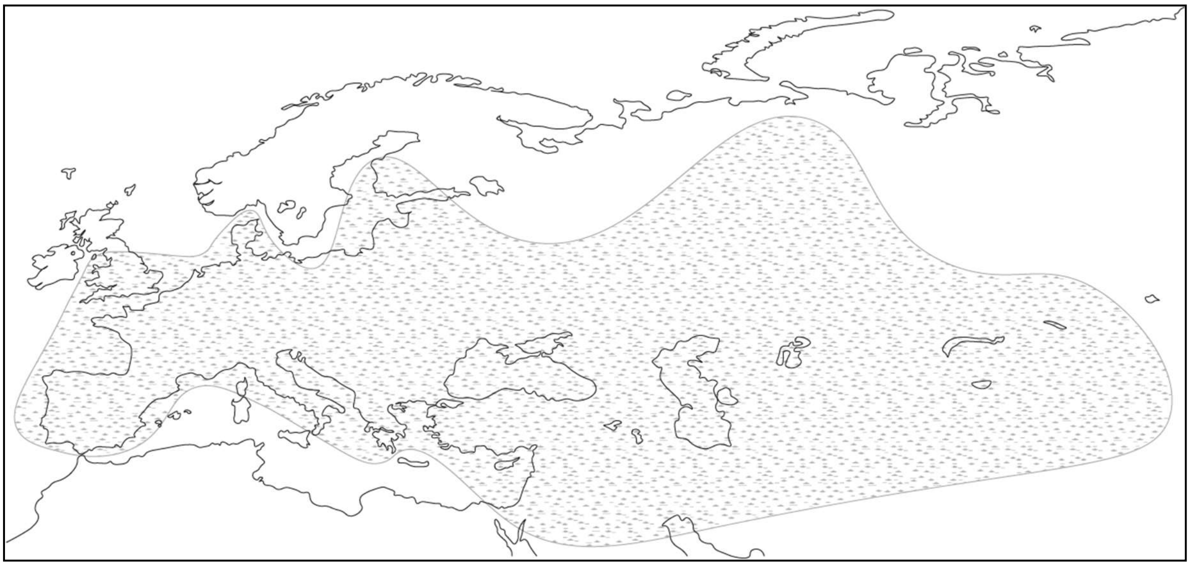


Figure 1.1: The geographical extent of the Neanderthal home range from Wales and the Atlantic coast of Iberia in the west to the Altai mountains in the east. Incursions north towards the arctic circle were likely sporadic. Map: Linda Amos.

Table 1.1: (page 5) Timeline of the appearance of Neanderthals, anatomically modern humans (AMH)l and lithic industries/cultures showing chronological correlations to marine isotope stages (MIS), geological epoch, Glacial/Interglacial (northern European nomenclature). Years are in 100, 000 years (ka) befpre resent (BP). Textured pattern indicates periods of admixture (next page).

Years (ka) BP	MIS		Epoch	Glacial /Interglacial (Northern Europe)		Human type	Cultural period	Cultures
	MIS 1 (11 -)		Holocene (11 -)	Flandrian interglacial		AMH	Mesolithic	
	MIS 2 (24 -)		Late Pleistocene (126 -)		last glacial maximum		Upper Palaeolithic	AMH UP industries
40	MIS 3 (57 -)			Weichselian glacial	Middle Weichselian	Interbreeding with AMH in Middle East and Europe	Transitional industries (38 -30)	Szeletian, Neronien, Chatelperronien, Lincombien-Ranisien -Jerzmanovicien, Streletskian, Zwierzyniecien
							Middle Palaeolithic (300 -) (ends Middle East ~ 48; Europe ~ 40)	Micoquian (60 - 40)
	MIS 4 (71-)							Mousterian of Acheulean, Denticulate Mousterian, Mousterian of Quina, Mousterian of Ferassie, Typical Mousterian
80	MIS 5 (128 -)	MIS5a (82 -)			Odderade interstadial			
		MIS5b (87 -)			Rederstall stadial			
		MIS5c (96 -)			Brørup interstadial			**Mousterian**
120		MIS5d (109 -)			Herning stadial	Neanderthals (400 to 30)		
		MIS5e (128 -)		Eemian interglacial				
160 200	MIS 6 (186 -)		Middle Pleistocene (781 -)	Saalian glacial				
240	MIS 7 (242 -)							
280 320	MIS 8 (301 -)							Transition between Acheulean and Mousterian, aspects of both present
	MIS 9 (334 -)			Holstein interglacial			Lower Palaeolithic (2500 -)	**Acheulean**
360	MIS 10 (364 -)							
400	MIS 11 (427 -)							

1.2 Neanderthal behaviour

Neanderthals manufactured Middle Palaeolithic (Mousterian) stone tools. These were characterised by prepared core technologies, meaning the core was prepared to produce an expected outcome (Bordes 1961; Kuhn 1995; Figure 1.2). This predetermination was employed to produce composite toolsets (Soressi 2005; Moncel *et al.* 2011). Several transitional industries appeared across Eurasia in late MIS 3, which had both Middle and Upper Palaeolithic elements (Table 1.1). These industries have been central to discussions concerning Neanderthal cognition because some authors attribute them to Neanderthal acculturation of AMH behaviours in Europe (Hublin *et al.* 1996, 2012; Allsworth-Jones 2004; Mellars 2005; Zilhão *et al.* 2006; Zilhão 2009; Flas 2014).

Figure 1.2: Statue of a Neanderthal knapping a stone tool inspired by the Neanderthal of La Chapelle –aux-Saints. Displayed at Musee de l'Homme in Paris. Photo: Linda Amos 2018.

Genetic evidence recovered on the remains of 13 Neanderthals from El Sidrón, Spain suggested that Neanderthals there lived in small, family groups and practiced a patrilocal mating behaviour (Lalueza-Fox *et al.* 2011; Rosas *et al.* 2017). At other sites, spatial analyses of lithic and bone remains indicate that Neanderthals lived in well-organised living spaces (Vaquero and Pasto 2001; Henry *et al.* 2004; Jaubert *et al*. 2018). There is also some evidence of housekeeping activities such as sweeping (Currant and Price 2012; Riel-Salvatore *et al.* 2013), and indications of division of labour by sex (Estalrrich and Rosas, 2015). The archaeological record also contains examples of Neanderthals caring for old and infirm group members who could not survive without assistance (Spikins *et al.* 2019). Shanidar 1, a male Neanderthal skeleton found in Shanidar Cave, Iraq, suffered massive crushing injuries to the upper right torso, which would have left him in need of nursing and assistance for the rest of his life, while Shanidar 3 died several weeks after being stabbed by a stone tool. During this time he was nursed and cared for (Trinkaus and Zimmerman 1982). In France, the remains of the 60 – 70-year-old 'Old Man' of La Chapelle aux-Saints indicated osteoarthritic degeneration on several areas of the body as well as Baastrup disease of his spine (Haeusler *et al.* 2019). The cognitive complexity involved in coordinating altruistic care of dependent adults demands a level of social organisation and conceptualisation that goes beyond a purely utilitarian way of life.

There is evidence that the Neanderthals intentionally buried their dead, though researchers continue to debate whether this was symbolic or merely practical in nature (Gargett *et al.* 1989; Rendu *et al.* 2016; Pomeroy *et al.* 2020). Examples of Neanderthal personal ornaments are known from Neanderthal levels at Grotte du Renne, France (d'Errico *et al.* 1998), Cueva de los Aviones and Cueva Anton in Spain (Zilhão *et al.* 2010), and Krapina in Croatia (Radovcic *et al*. 2015). Duilio Garfoli (2018) considers the cognitive processes behind personal ornamentation a marker for cultural definition and proposes that Neanderthals could conceive the 'coolness' behind personal decoration but were not capable of the mentalistic processes that modern humans employ in the interpretation of symbolically loaded ornamentation.

Other expressions of Neanderthal behaviour can be seen in circular structures constructed by Neanderthals deep inside Bruniquel Cave, France, dated to 176.5 +/- 2.1 ka BP (Jaubert *et al.* 2018), an abstract engraving on the floor of Gorham's Cave, Gibraltar (MIS 3; Rodriguez-Vidal *et al.* 2014), and cave art panels at Ardales, La Pasiega, and Maltravieso caves in Spain (Hoffmann *et al*. 2018). The mask of La Roche-Cotard (Marquet and Lorblanchet 2000, 2003; Marquet *et al.* 2016; Figure 1.3), a face-like stone which was collected and modified by flaking and the insertion of a bone fragment to enhance its humanoid features, illustrates the creative capacity of the Neanderthal who modified it. Despite this evidence, Petru (2017) related a perceived Neanderthal inclination to not care about symbolic representations to the absence of episodic memory, suggesting that they may not have imagined their personal pasts and futures. Meanwhile Coss (2018) linked the ability to create representational art to hunting with spears, postulating that the connection between the overt and covert attention required by the tasks was not part of the Neanderthal cognitive package.

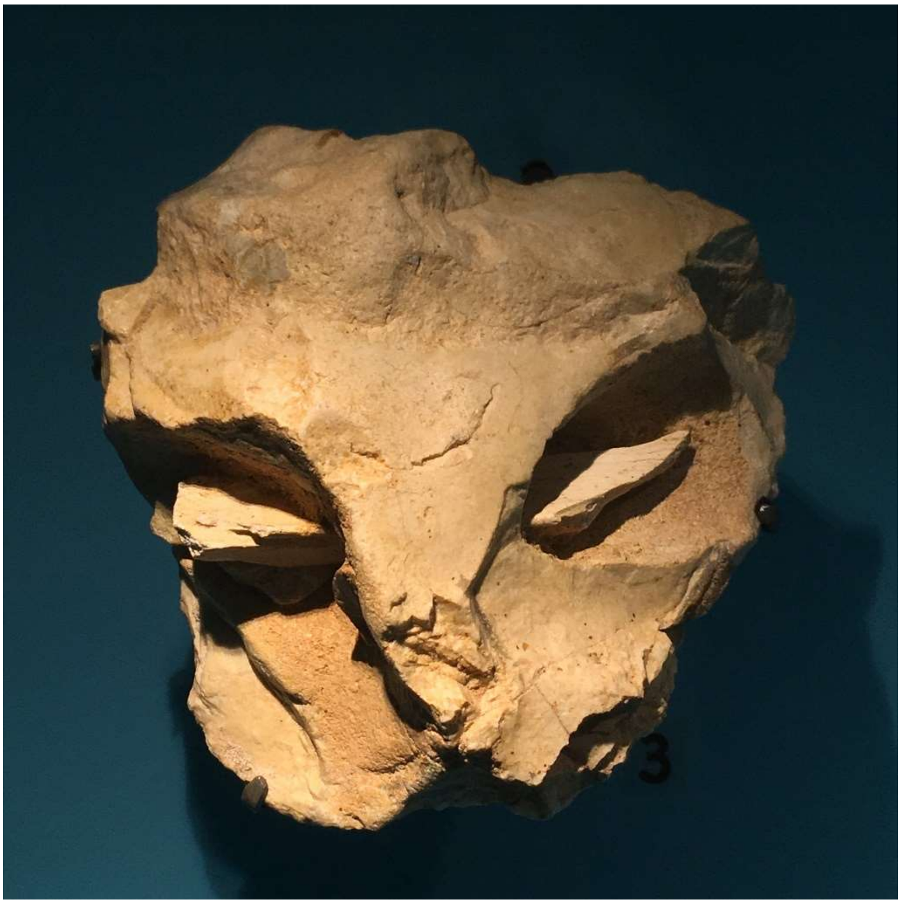


Figure 1.3: The mask of La Roche-Cotard. A face-like object modified by Neanderthals. Displayed at Musee de l'Homme, Paris. Photo: Linda Amos 2018.

The implied need to communicate the complex social organisation evident in Neanderthal sites suggests that Neanderthals must have been capable of composite language and complex behaviour (Dediu and Levinson 2018; Johansson 2015). Recently, morphological studies found that Neanderthals and *Homo sapiens* had similar auditory and speech capacities, confirming the genetic and morphological indications that Neanderthals were capable of perceiving and annunciating complex speech patterns (Arensburg *et al.* 1989; Krause *et al.* 2007; Conde-Valverde 2021). However, Neanderthals have been dubbed the infamous 'Other', a scale against which we *Homo sapiens* could measure our superiority (Shipman 2008). This bias has its roots in the social and cultural climate of the early 20th century when Neanderthals were first described (Sommer 2006) and has persisted in research up to the present day.

Neanderthals and AMHs interbred, leaving a trace of 2-4% of their genetic material in every human outside Africa(Green *et al*. 2010). Consequent studies of ancient DNA discovered that interbreeding events happened several times during their coexistence (Prüfer *et al*.

2013; Fu *et al*. 2015; Kuhlwilm *et al.* 2016; Hajdinjak *et al*. 2018; Villanea and Schaiber 2019; Chen *et al.* 2020). Neanderthals also interbred with the Denisovans (Reich *et al.* 2010, 2011). At Denisova Cave in the Altai Mountains of Siberia, researchers discovered the offspring of a Neanderthal female and a Denisovan male (Slon *et al*. 2018), and an anatomically modern human from Peştera cu Oase, Romania was found to have Neanderthal ancestry (Fu *et al.* 2015, 2016). These interbreeding events restrict the conclusions that can be drawn about differences between human species, as such contact involved not only language capacities, but also the ability to translate and negotiate terms of cohabitation.

There are differing views on what caused Neanderthals to dissapear from the record (Carrión, Lalueza-Fox and Stewart 2019). These include assimilation with AMH (Wakano *et al.* 2018), replacement by anatomically modern humans through direct or indirect competition (Klein 1989; Stringer and Gamble 1993; Mellars 2004, 2005; Benazzi *et al.* 2011; Higham *et al.* 2011; Houldcraft and Underdown 2016), climate change (Finlayson 2004; Finlayson and Carrión 2007; Staubwasser *et al.* 2018), and an intermediate scenario where climate change created conditions which favoured AMH over Neanderthals (Mellars 1998, d'Errico and Sanchez Goni 2003, Banks *et al*. 2008, Barton *et al.* 2011; Jiminez-Espejo *et al.* 2013; Timmermann 2020). The causal contribution of demography is now considered to be the most prominent aspect behind the disappearance of the Neanderthals (Vaesen, Dusseldorp and Brandt 2021).

1.3 Neanderthal diet

1.3.1 Hunters or Scavengers?

With the emergence of Processual Archaeology in the 1960s, researchers started to focus on interpreting the processes that brought animal remains to a site, with a key research question focused on whether they were the product of hunting or scavenging. Debate on Neanderthal subsistence strategies centred on their ability to effectively hunt large game (Binford and Binford 1966; Binford 1985). Based on an analysis by Klein (1976) of the mammalian fauna from Klasies River, South Africa, Binford argued that the predominance of head-and-foot assemblages in Neanderthal sites in Europe was evidence of obligate scavenging (Klein 1976; Binford 1981, 1984, 1985, 1988; Blumenschine *et al.* 1987). Both Binford and Klein also cited a prevalence of bones with carnivore tooth marks and a scarcity of cut-marked bones, where the cut marks were concentrated on elements with low meat yield. Scavenging as a practice was determined to fall outside of the range of modern human behaviour (Henshilwood and Marean 2003), and because assemblages fulfilling the three hallmarks of scavenging were apparently frequent in Neanderthal sites, they were therefore deemed non-modern.

Marean (1998) rejected the scavenging hypotheses completely. He claimed that biased sampling at Combe Grenal (Chase 1986), Grotta Guattari (Stiner 1991a), Grotta dei Moscerini (Stiner and Kuhn 1992), and Grotte Vaufrey (Binford 1988) had shaped the skeletal element and surface modification patterns observed by the original researchers to fit a model of scavenging (1998). By studying the unbiased faunal assemblages of Kobeh Cave, Iran and Layer 10 of Die Kelders Cave, South Africa, Marean proved that discarding long bone shafts and less identifiable fragments led to an abundance of easily identifiable head and feet elements (Marean 1998; Marean and Kim 1998). This bias also limited the usefulness of surface modification data by lowering the frequencies of cut marks because meat-removal traces were generally concentrated along the shafts of meat rich longbones (Marean 1998; Marean and Kim 1998). Although Neanderthals might still have scavenged infrequently, Marean and Kim concluded that they were primarily hunters (1998).

Hunting is knowledge intensive (Kaplan *et al.* 2000). It not only shows the ability to trap prey, but also the conceptual planning and a knowledge of the landscape. Through a series of studies on faunal assemblages from Middle Palaeolithic sites Gaudzinski-Windheuser *et al.* (2018) characterised Neanderthals as capable of selective, controlled, and systematic exploitation of large game. At Salzglitter-Lebenstadt, Germany, they found Neanderthal specialised hunting of reindeer to be comparable to that of Late Glacial AMHs (Gaudzinski 1996, 2006; Gaudzinzki and Roebroeks 2000). Furthermore, a hafted Mousterian point was found embedded in the vertebrae of a wild ass, suggesting Neanderthals were hunting equids at Umm el Tiel in Syria (Boëda *et al*. 1999). Nitrogen and carbon isotope analyses of Neanderthal skeletal remains from Europe also indicated a meat-heavy diet (Bocherens 2009; Richards and Trinkaus 2009; Wiβing *et al*. 2016). Today, Neanderthals are widely regarded as hunters with highly specialised and effective methods of hunting large game (Richards *et al*. 2000; Bocherens and Drucker 2006; Serangeli and Bolus 2008; Rendu *et al*. 2012; Gaudzinski-Windheuser and Kindler 2012a; Germonpré *et al*. 2014; de Los Terreros *et al.* 2014).

1.3.2 Large game or small game?

While the discussion regarding Neanderthal ability to hunt large game was on-going, another debate arose regarding small game. Where Binford (1985) had assumed that

Neanderthals were able to catch small game but not large game, Stiner *et al.* proposed that small game demanded a more complicated approach and therefore demanded a more increased cognitively complexity (Stiner 1991 a, b, c, 1993; 1994; Stiner, Munro, and Surovell 2000, Stiner and Munro 2002; Stiner *et al.* 1999; Stiner 2001). Stiner based her proposal on Flannery's Broad Spectrum Revolution (BSR), a hypothesis that described a shift in subsistence from a focus on large prey in the Palaeolithic towards a more diverse larder leading up to the Neolithic Revolution (Flannery 1969). This resource diversification was linked to demographic density and built on a hypothesis originally forwarded by Binford (1968). Binford argued that late and post-Pleistocene landscapes consisted of a mosaic of favourable 'optimal' environments separated from one another by 'less favourable' habitats. The 'optimal' areas had higher carrying capacities than the 'less favourable' areas and served as regional population growth centres from which small sub-groups would emigrate. Binford proposed that this emigration kept population levels well below the region's carrying capacity. Immigration into more marginal areas, however, disturbed the density equilibrium of resident groups in the 'less favourable' recipient areas and put a strain on the region's lower carrying capacity. According to Flannery, the BSR was reflected as an increasing assortment of small game like tortoises, lagomorphs and birds in the archaeological record. The adoption of small game as a supplementary food source in 'optimal' environments, allowed the area to sustain larger groups, and ease imbalances between population and productivity in less favourable areas (Flannery 1969).

Stiner *et al.* adapted Flannery's hypothesis, pushing the BSR back to the Middle to Upper Palaeolithic transition using results from Mediterranean sites where Upper Palaeolithic AMHs exploited a wider range of food resources than Neanderthals in the region (Stiner 1991 a, b, c, 1993; 1994, 2001; Stiner *et al.* 1999; Stiner, Munro, and Surovell 2000, Stiner and Munro 2002). They sorted small game into two categories: slow, and fast (Stiner, Munro, and Surovell 2000, Stiner *et al.* 1999). Slow species included tortoises and shellfish, which were exploited by Neanderthals at sites in Gibraltar (Stiner *et al*. 1999; Barton 2000; Stringer *et al.* 2008; Fa *et al.* 2016) and Kebara in Israel (Speth and Tchernov 2002). According to Stiner, small, fast moving prey species like rabbits, birds, and fish, were not heavily exploited before the late Middle Palaeolithic when AMH appeared in Europe (Stiner 1991 a, b, c, 1993; 1994;;Stiner *et al.* 1999; Stiner, Munro, and Surovell 2000; Stiner and Munro 2002; Stiner 2001; Richards *et al.* 2001; Kuhn and Stiner 2006; Fa *et al.* 2013).

Stiner proposed that the lack of diversification in food animals was connected to the demise of the Neanderthals through their inability to maintain populations sizes comparable to AMH in the same areas (Flannery 1969; Stiner *et al.* 1999, 2000; Klein, 2001; Richards *et al.* 2001, 2005; Drucker and Bocherens 2004; Klein *et al.* 2004; Balter and Simon 2006; Stiner and Kuhn 2006, 2016; Richards and Trinkaus 2009; Fa *et al.* 2013;). The inferred implication in Stiner's work was that the cognitive prowess necessary to plan and execute the complex hunting strategies necessary to hunt small, fast game was not present in Neanderthals, and that they were unable to compete with the subsistence strategies employed by better-adapted AMH (Klein and Cruz-Uribe 2000; Klein *et al.* 2004).

There are some problems with Stiner's approach to Neanderthal subsistence strategies. Most pressing is that Stiner did not take the collector's bias exhibited at her study sites into account (Marean 1998). Secondly, the division of small game into slow and fast categories was arbitrary. A good example is that of ostrich (*Struthio camelus*) eggs. These were included in the slow category because they are not mobile (Stiner 2001; Stiner *et al.* 1999; Stiner, Munro, and Surovell 2000, Stiner and Munro 2002). However, harvesting the eggs that are protected by a parent bird would be highly dangerous (Dusseldorp 2009). Third, and valid to this thesis especially is that Stiner did not take bird remains into consideration when she examined the fauna (Stiner 1994; Tyrberg 1998, 2008). According to Stiner (1994), birds only become important in the Upper Palaeolithic. Examples of Neanderthals exploiting fast small game like rabbits are recorded in Spain, France, Italy and Gibraltar (Valensi and Guennouni 2004; Stringer *et al.* 2008; Blasco and Fernández Peris 2009, 2012 a,b; Cochard *et al.* 2012; Hardy *et al.* 2013; Morin *et al.* 2019). There is even evidence of them consuming fish (Le Gall 1990, 2000; Muñoz *et al.* 1997; Reselló-Izquierdo and Morales-Muñiz 2005; Hardy and Moncel 2011).

1.3.3 A truly broad spectrum diet

In addition to exploiting large and small game, there is clear evidence that Neanderthals also exploited plants. The presence of charred seeds and phytoliths from edible plants have been found in sediments at Kebara and Tabun Caves in Israel (Albert *et al.* 1999; Lev *et al.* 2005) and Gorham's Cave in Gibraltar (Barton *et al*. 1999). Studies of dental calculus have proven the Neanderthals to have consumed plants as part of their diet (Hardy and Moncel 2011; Henry *et al*. 2011, 2014; Hardy *et al.* 2012; Buck and Stringer 2014), and also for medicinal purposes (Hardy *et al.* 2013b). Plant residues on stone tools point towards the processing of plant material for food and medicinal purposes (Hardy and Moncel 2011; Henry *et al*. 2011; Salazar-García *et al.* 2013). A knowledge of the health and subsistence resources available in the flora highlights the detailed knowledge Neanderthals possessed of the landscapes they inhabited.

1.4 Neanderthal bird exploitation

Birds have been largely overlooked in Palaeolithic research. Recent reinvestigations of avian material from archaeological sites across Eurasia have produced evidence of Neanderthals exploiting avian resources (Finlayson *et al*. 2012; Blasco *et al.* 2014, 2016a, b, 2019). These practices were both utilitarian and non-utilitarian in nature. To date, 46 contexts at 27 sites in the archaeological record show direct evidence of bird exploitation by Neanderthals and pre-Neanderthal Eurasian humans in the form of cut marks (Appendix 1). According to Tyrberg (1998), the number of Middle Palaeolithic sites that contain bird material numbers over 200, and over 500 contexts. The discovery of avian remains from Spain and Turkey dated to 1.2 and 0.9 ma, respectively, extend bird exploitation practices into pre-Neanderthal species (Blasco *et al.* 2019). In general, most of the current evidence of Neanderthal bird exploitation is limited to south-western Europe between MIS 5 and MIS 3 (Figure 1.4).

At Pie Lombard, France, Gorham's Cave, Gibraltar, and Cova Negra, Spain there is a concentration of cutmarks on pigeon bones. These specimens equated to 25.7% of all known cutmarked specimens (n = 311). Blasco *et al.* (2014, 2016) identified pigeons and choughs as favoured food species for the Neanderthals at Gorham's Cave. Choughs were also found in relatively high numbers at Pie Lombard and Cova Negra (Romero *et al.* 2017; Martinez-Valle *et al.* 2016). Neanderthals occupying Bolomor Cave exhibited a broad-spectrum diet, including birds, from MIS 9 - MIS 4 (Blasco *et al*. 2010, 2013; Blasco and Peris 2009, 2012a, b). Tufted duck (*Aythya fuligula*) remains showed cutmarks and tooth marks resulting from human consumption. Other sites produced small numbers of bones with cut marks (Mourer-Chauvire 1989; Roger 2004; Gaudzinski-Windheuser and Niven 2009; Peresani *et al.* 2011; Martinez *et al.* 1993; Blasco *et al*. 2019; Romandini *et al.* 2014, 2016, 2020; Fiore *et al.* 2016; Romero *et al.* 2017). The collections at Abri du Maras and Payre (France) show no taphonomical changes to the bird collections, while feather barbules have been identified in residue analysis on lithics (Hardy and Moncel 2011; Rufa *et al.* 2016a).

Figure 1.4: Map of Eurasia showing the location of sites where cut marks have been identified on avian remains.

At some sites in France, Spain, Italy, Croatia and Gibraltar, Neanderthals not only exploited birds as part of subsistence strategies but also extracted feathers and talons for non-utilitarian purposes (Leroi-Gourhan 1964; Mourer-Chauvire 1989;.d'Errico *et al*. 1998; Soressi *et al.* 2008; Dibble *et al.* 2009; Peresani *et al.* 2011; Finlayson *et al.* 2012; Morin and Laroulandie 2012; Gerbe *et al.* 2014; Romandini *et al*. 2014, 2016; Radovčić *et al.* 2015; Fiore *et al.* 2016; Laroulandie 2016; Laroulandie *et al.* 2016; Rodriguez-Hidalgo *et al.* 2017, 2019; Gomez-Olivencia *et al.* 2018). The scant value of bird feet and wings as food and the rarity of large raptors in ecosystem have been provided by these researchers as plausible reasons for why this behaviour was complex.

The use of bird elements as personal ornamentation is widely known in ethnographic analogies, spanning virtually every studied culture on every continent (Gifford-Gonzalez 1991; Finlayson *et al*. 2012; Serjeantson 2009). There are indications that feather extraction was focussed on corvids and raptors with dark feathers (Finlayson *et al.* 2012, Finlayson and Finlayson 2016; Finlayson 2019). Using Gorham's, Vanguard and Ibex Caves as a case study, Finlayson *et al.* (2012) found that cutmarks on wing elements were clearly related to the extraction of the primary feathers. These are the largest, most durable, and visually impressive elements of a bird's plumage. Extrapolating their finds to the entire western mid latitude belt, and through to the Upper Palaeolithic they further speculated that this continued exploitation of corvids and raptors for feathers indicated a transmission of cultural practice from Neanderthals to AMH (Finlayson and Finlayson 2016), contradicting previous paradigms of acculturation (Mellars 2010).

1.5 Current problems with the study of bird remains from Neanderthal sites

Although the number of studies are increasing, there are still key unresolved issues involved in the use of birds as a proxy in Neanderthal research. Some are connected to the study of birds itself, and others are connected to the extent and ecological parameters of Neanderthal bird exploitation.

1.5.1 Birds are underused as a source of evidence for Neanderthal behaviour

Birds have only systematically formed part of Neanderthal research in the last two decades. This may be due to birds' undeserved reputation for being scarce and uninformative (Morales-Muniz 1993; Tyrberg 1998; Cooper 2005). Ornithologists have complied a large amount of data on the behaviour and biology of many living bird species. When applied to bird remains recovered from archaeological contexts, these modern analogues represent the great potential of birds as ecological markers (Sanchez Marco 2004; Finlayson 2006; Finlayson *et al.* 2006, Finlayson *et al.* 2008; Tyrberg 2010; Finlayson 2011; Finlayson 2019). This is due in part to the highly specific environmental requirements of some species, and in part to the mass of information available about living species, including their environmental tolerances. Nearly all Pleistocene bird species are still present today (Finlayson 2011).

In avian palaeontology, unlike zooarchaeology, the mere presence of a species in an accumulation can be the aim of research (Tyrberg 1998). In palaeontological contexts, the ecological value of avian presence and absence has long been known, because the niche of a target taxon can be accurately defined. The presence or absence of taxa identified to species-level in an assemblage indicates that the surrounding environment is likely to have satisfied the environmental requirements for that species (Finlayson 2011; Finlayson *et al.* 2016). This is important as the highly mobile nature of bird ethology makes them excellent first responders in reacting to changes in climate and environment where other markers, such as micromammals and vegetation have a slower response rate (Baird 1989; Morales-Muniz 1993). Given the high mobility of birds, their presence and diversity can function as a measure of the quality of an ecosystem by informing us about the environmental tolerances that must be fulfilled in the environment for a species to thrive (Finlayson *et al*. 2016). An exception is the presence of vagrants, individuals that appear outside the expected geographical range, which can potentially skew ecological data.

One of the most innovative uses of birds for the reconstruction of environments to date is in Gibraltar (Finlayson 2006; Finlayson *et al.* 2008). Finlayson (2006) used the environmental information provided by bird remains to recreate the ecosystem surrounding the rock of Gibraltar in the Middle to Upper Palaeolithic. A decade later, Finlayson *et al.* (2016) used the avian species diversity of two sites (Gibraltar and Zafarraya) to gauge the quality of the sites, finding that Middle Palaeolithic Gibraltar as a whole reflected a rich and diverse assemblage of bird species, necessarily suggesting that the Neanderthals inhabited a rich environment. On the contrary Zafarraya, despite being close to Gibraltar geographically, had a much lower species diversity. Very recently, it has been suggested that birds present in Neanderthal assemblages suggest that Neanderthals were a temperate species rather than a cold-adapted species as they have traditionally been portrayed (Finlayson 2019).

It is important to note that absence of a species in an assemblage does not exclude it from the surrounding environment (Payne 1975) and that the combined data provided by taxa recovered from an archaeological site will only ever show a partial analogue due to the fragmentary nature of archaeological deposits.

1.5.2 Complexities of avian taxonomy

Morales-Muniz (1993) noted that taxonomic identification of bird bones recovered from archaeological contexts is challenging due to four reasons: First, birds are the most diverse group of terrestrial vertebrates – they comprise 30 orders that are made up of > 180 families, 2,000 genera and 10,000 species (Gill, Donsker and Rasmussen, 2020). Second, the degree of intra- and interspecific skeletal variation between related avian taxa can be minimal or non-existent. Third, the size and fragility of bird bones means they can be prone to physical and chemical alteration due to site formation processes. Fourth, avian remains may be damaged during archaeological excavations.

It is possible to recognise diagnostic elements belonging to certain bird species based on sight alone with the use of comparative collections and illustrated guides (Morales-Muniz 1993; Stewart and Carrasquilla 1997). Of the two, comparative material is preferred because illustrated guides generally concern either a single taxonomical group, or a regional collection of species (Morales-Muniz 1993; Serjeantson 2009). Comparative collections contain examples of known species processed for the purpose of study and are mainly housed in natural history museums and educational institutions. It is imperative that the comparative material used in identification of archaeological remains is from a curated comparative collection and not previously identified archaeological material to limit the propagation of potential mistakes made by primary investigators. Despite these challenges, it is important to note that though birds can be difficult to identify securely, other archaeological proxies also have limitations (Baird 1989).

Even when a comparative collection is easily accessible, it can be challenging to correctly identify a bird species due to the high dregree of intraspecific morphological variations, and the interspecific similarities of some species (Stewart 2005; Bochenski 2008). An excellent example are the *Alectoris* partridges. Though it is not difficult to separate the species in live birds, the skeletal morphology is indistinguishable from species to species. In cases such as these, the geographic position of the find site can be compared to the geographical distribution of the different species (Randi 1996).

1.5.3 The bias concept: bird bone preservation issues

The fossil record is inherently biased in general due to the loss or alteration of information on the ecology and morphology of animals between the time of an organism's death and the time its remains are recovered and studied. This is known as the biased concept and is applicable to all research into the past (Discamps and Faivre 2017). The size and fragility of bird bones means they are prone to physical and chemical alteration due to site formation processes (Morales- Muniz 1993; Discamps and Faivre 2017; Dibble *et al.* 2018; Dirrigl *et al.* 2020). It also means that bird remains are easily damaged during archaeological excavations.

Another bias relevant to the examination of avian remains, especially those from older excavations, is based on the conception that birds are uninformative (Tyrberg 1998; Morales-Muniz 1993; Cooper 2005). Early researchers did not collect smaller, less impressive bones, and focussed instead on the larger, more impressive mammalian specimens. This collection bias has been paired with a lack of care in the curation of some collections, leading to further unnecessary fragmentation, and in insufficient storage containers (Discamps and Faivre 2017). Reitz and Wing (2008, 203) characterise the identifiability of avian remains "*a function of both the number of anatomically similar, and, therefore, potentially misleading species in an assemblage and the degree of breakage or erosion suffered by each specimen.*"

1.5.4 Issues in taphonomy

The main issues in avian taphonomy align with issues that are relevant to the discipline in general. The principles of taphonomy, outlined in Chapter 2, have been criticised on several levels. Firstly, we cannot verify the principle of invariability as we cannot observe the past directly (Hubbert 1967). Secondly, we cannot be certain of our knowledge of natural laws and processes of transformation on the whole (Lyman 1994a, b). In other words, it is possible that some transformation processes no longer work in the present, so we cannot study and understand them and describe their consequences is another objection to the model. These objections combine to the issue of equifinality.

Equifinality is the concept that several processes can produce the same result (Bonnichsen 1989). Otte (1991) noted that experimental approaches have the potential to become autonomous and deviate too radically from the objectives of prehistory. Lyman (1994a, b) however concludes that no alternatives have been outlined so far. Faced with these limitations, we must acknowledge, "*that knowledge gained from actualistic studies is relevant and applicable to the living systems of the past*" (Binford 1981: 27) knowing that "*the assumption is conditional and may be false*". Recently, Rosell *et al*. (2019) demonstrated the issue through a study of human and bear modifications on ungulate remains, and Bar-Oz and Munro (2004) forwarded a multivariate approach to the issue. Laroulandie (2000) emphasised the importance of considering the whole spectrum of traces present in a collection. Her work showed that only a multifaceted approach could mitigate the issue of equifinality in the interpretation of avian remains and that traces should be interpreted in the context of the entire site. The location on the bone, frequency of modification and intensity of modifications across the site in general adds reliability to an interpretation.

Laroulandie also stressed the importance of a good light source and suitable magnification (*pers. comm*.). Blumenschine *et al.* (1996) ascertained through a series of blind tests, that it was possible to correctly identify taphonomic traces on bone using a magnification of 16x paired with a bright light source. They also concluded that use of a hand lens was more efficient than a microscope as the process of refocussing while turning the specimen in hand during examination is time consuming. Stewart (Stewart and Jacobi 2015) called for the re-examination of cutmarks found on birds using methods employed by Bello (Bello *et al*. 2016) which he deems superior to those used in recent studies on bird material. Although certain micromorphological characteristics demand the use of a high-powered stereomicroscope or scanning electron microscope (SEM) (eg. Bello and Soglio 2008, Bello *et al*. 2016), Blumenschine *et al.* (1996) and other bird taphonomy studies (e.g. Laroulandie *pers. comm.* 2018; Laroulandie 2005; Blasco *et al*. 2014; 2016a) fully support the use of at least 16x paired with a bright light source.

1.6 Research Questions

This thesis investigates the contribution that avian fossils make to our understanding of Neanderthal ecology and behaviour through analysis of the taxonomy and taphonomy of avian assemblages found at five Neanderthal sites across the Eurasia. This thesis will address four specific questions:

1. Based on the avian taxonomic assemblages, how do the ecological parameters of the five Neanderthal sites compare between different geographical regions and through time?
2. How much evidence for human exploitation of birds exists at each site?
3. How does bird exploitation at the five sites inform us about Neanderthal subsistence strategies?
4. What is the temporal depth and geographic range of bird exploitation by Neanderthals?

1.7 Thesis outline

Chapter 2 introduces methodological approaches employed to investigate the avian remains. These methods include the taxonomic, taphonomic and ecological analyses. The chapter also contains the methods applied in the quantification of data and statistical analyses.

Chapters 3 – 7 each concern the examination and interpretation of the taxonomic and taphonomic composition of avian remains from the archaeological sites included in this thesis. Each chapter begins with a summary of the archaeological history of the site, exploring past research and the current status of knowledge. This is followed by a presentation of the taxonomic, environmental, and taphonomic results from each analysis. Each chapter concludes with a site-level interpretation of Neanderthal behaviour and ecology (Research Questions 1 & 2).

- Chapter 3: Gorham's Cave
- Chapter 4: Devil's Tower Rockshelter
- Chapter 5: Cova Negra Cave
- Chapter 6: Scladina Cave
- Chapter 7: Tabun Cave

Chapter 8 begins with a comparative analysis and discussion of ecological results from the five sites aiming to determine whether Neanderthals exhibit specific ecological preferences. This is followed by a discussion of the taphonomic results and their contribution to current knowledge. Finally, the chapter ends with the conclusion of the thesis and remarks on future direction.

2 Methodology

This chapter outlines the methodology used in my analysis of avian remains from archaeological contexts. It is divided into five sections, each describing a step in the analysis of the five avifaunal collections:

- Data acquisition: a list of the collections studied in this thesis, and where the analyses were conducted.
- Taxonomic identification: a description of the methodology involved in the identification of avian remains from archaeological contexts.
- Taphonomic analysis: a description of the methods used to identify traces that allow researchers to interpret the agency behind an accumulation.
- The selection of associated environmental and cultural variables: variables that give context to the avian remains and allow reconstructions of the paleoenvironment they inhabited.
- Application of statistical techniques: methods used to assess the significance of ecological results.

2.1 Data acquisition

The materials studied were obtained from the Middle Palaeolithic layers of five archaeological sites in four locations in Europe and the Middle East (Figure 2.1). Analysis of the individual collections took place at several different locations. The sites examined were:

Gorham's Cave, Gibraltar: This material was repatriated to the Gibraltar National Museum (GNM) in September 2018 from the private collection of Mrs Anne Eastham. Access to study the materials was suggested by Prof. Clive Finlayson, GNM in June 2018, and granted in September 2018. My analysis took place in the laboratory of the GNM, Gibraltar. Specimens were identified to stratigraphic layers assigned by JD Waechter. Provisional specimen ID numbers were assigned in agreement with Prof. Geraldine Finlayson, GNM, using the format LAYERXXX (see: Chapter 3).

Devil's Tower Rock Shelter, Gibraltar: This material is housed in the Natural History Museum (NHM), London. Access was granted by NHM Curator of Palaeontology Dr Sandra

Chapman in August 2018. Analysis took place at NHM over several visits between February and September 2019. Specimens were identified by NHM registration number, format NHMUK A-XXXX (see: Chapter 4).

Cova Negra, Spain: This material is in the private collection of Mrs Anne Eastham. Access was granted in September 2018, and analysis took place in the private workspace of Mrs Eastham in Dwrbach, Wales in May 2019. The specimens were identified by numbers assigned by the original researchers, format XXXX or CNXXXX (see: Chapter 5).

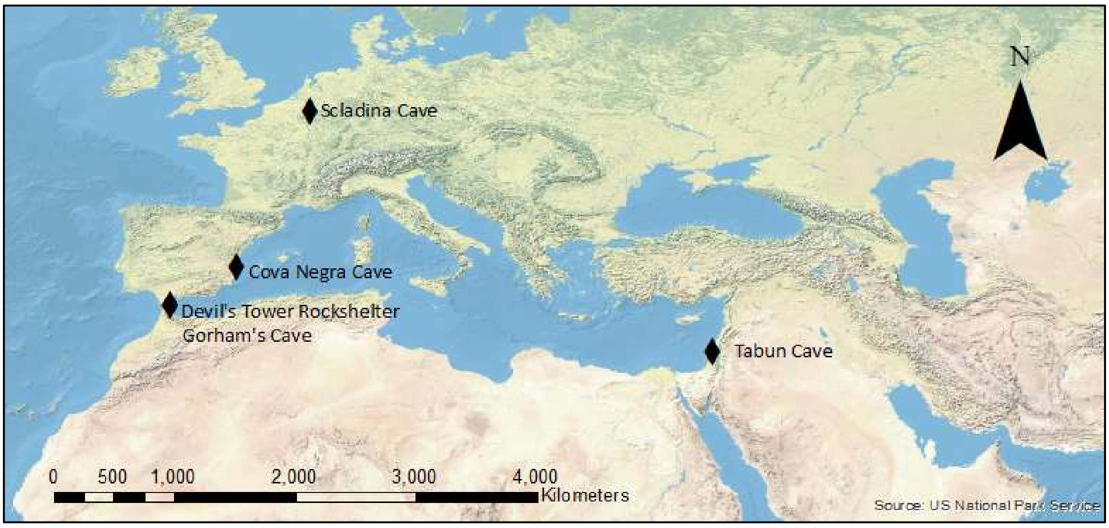


Figure 2.1: Map of Eurasia showing the geographical positions of sites in this thesis.

Scladina Cave, Belgium: This material is housed at Centre Archeologique De La Grotte Scladina, Belgium. Access was granted in May 2018 by Dr Gregory Abrahams and Mr Quentin Goefette of the Royal Belgian Institute of Natural Sciences. Analysis of the material was conducted at the (RBINS), Brussels in May 2018. Specimens were identified using a unique number assigned by Quentin Goefette. This material appears in two different PhD theses. The division of labour was as follows: taxonomic identifications were undertaken by Quentin Goefette and taphonomic analysis by Linda Amos (see: Chapter 6).

Tabun Cave, Israel: This material is split between two institutions. Material from excavations undertaken by Jelinek in the 1960s is kept in the collections of the Hebrew University of Jerusalem (HUJ), Israel. Material from more recent excavations is in the care of the University of Haifa (UOH), Israel. Access to the collections was granted in September 2018 by Professor Mina Weinstein-Evron. Loan of the Jelinek material from HUJ was granted by Prof. Rivka Rabinovich, Academic Curator of Palaeontology and Archaeozoology in November 2019. Analysis was conducted in the Zooarchaeology laboratory, UOH, in

November 2019. Additional comparative material was accessed at the Steinhardt Museum, Tel Aviv University, under the supervision of Dr Amos Belmaker. Specimens were identified using provisional numbers, format LAXXX (see: Chapter 7). A list of specimens and their corresponding provisional numbers was provided to both institutions.

2.2 Taxonomic Identification

My analysis employed taxonomic classifications that were made previously at Devil's Tower (Cooper 1999), Gorham's Cave (Eastham 1968; Cooper 1999), Cova Negra Cave (Eastham 1989), and Scladina Cave (Goefette, unpublished). Minor corrections were made when identification errors were spotted (Table 2.1). For Tabun Cave, I undertook my own classification of the assemblage as it was the first time the material has been examined.

Table 2.1: Analysis of remains from sites included in this study showing the researchers responsible for taxonomic identification, determining the portion of the bone present (Element present), the age and sex of the bird, and the taphonomic study of the bone surfaces. AE = Mrs Anne Eastham, DB = Miss Dorothea Bate, JC = Dr Joanne Cooper (NHM), LA = Linda Amos (author), QG = Quentin Goefette (RBINS). (Garrod et al. 1928; Eastham 1968, 1989; Cooper 2000, 2012).

Site	**Taxonomy**	**Element portion**	**Age and Sex**	**Taphonomy**
Cova Negra Cave	Original researcher: AE Minor corrections: LA	LA	AE	LA
Devil's Tower Rock Shelter	Original researcher: DB Minor Corrections: JC	LA	JC	LA
Gorham's Cave (Waechter)	Original researcher: AE Minor corrections: JC Minor corrections: LA	LA	AE	LA
Scladina Cave	Original researcher: QG	LA	QG	LA
Tabun Cave	Original researcher: LA	LA	LA	LA

I looked at all materials alongside comparative reference collections supplemented by key illustrated guides (Shufeldt 1909; Lambrecht 1933; Bacher 1967; Woelfe 1967; Erbersdobler 1968; Kraft 1972; Fick 1974; von den Driesch 1976; Langer 1980; Otto 1981; Solti 1981, 1996; Schmidt-Burger 1982; Jànossy 1983; Kellner 1986; Moreno 1986; Boev 1988; Cuisin 1989; Baumel *et al*. 1993; Bocheński 1994; Gilbert *et al*. 1996; Tomek and Bocheński 2000; Kessler 2015, 2016) when assigning classifications, and consulted with leading experts including Eastham, Cooper and Sanchez-Marco.

2.2.1 The Avian Skeleton

To work with avian remains it is important to understand the morphology of a bird's skeleton and how it differs from other vertebrates (Figure 2.2). The avian skeleton differs from the mammalian skeleton in several key ways, the most apparent of which are related to flight (Serjeantson 2009; Baumel *et al*. 1993). The structure of the fore and hind limbs are adapted for two distinct kinds of propulsion -flying and walking, respectively (Young 1950). Avian bones have a thinner and lighter bone cortex and retain their strength in the form of trabeculae - thin struts that develop at angles to the bone wall in response to mechanical loading (Serjeantson 2009). Certain elements are pneumatised – another adaptation to flight in which the bone is hollow rather than filled with marrow (Bellairs and Jenkin 1960). The hollow spaces host air sacs that are connected through foramina to the greater pneumatic system which originates in the birds' lungs. Bird bones grow by apposition from shaft to end rather than from a growing point between the epiphysis and diaphysis as in mammals, and have Haversian canals but no osteons, limiting the possibility of separating species by their structure and arrangement as is possible in mammals (Strott 2005; Martiniaková 2006).

	Skeletal element	**abbreviation**
1	Skull	sku
2	Cervical vertebrae	cerv. vert.
3	Furcula	fur
4	Coracoid	cor
5	Uncinate process	-
6	Sternum	stern
7	Patella	pat
8	Tarsometatarsus	tmt
9	Phalanges	phal
10	Tibiotarsus	tbt
11	Tibiotarsus	tbt
12	Femur	fem
13	Ischium	pelvis
14	Pubis	pelvis
15	Ilium	pelvis
16	Caudal vertebrae	caud. vert.
17	Pygostyle	pyg
18	Synsacrum	syns
19	Scapula	scap
20	Lumbar vertebrae	lumb. vert.
21	Humerus	hum
22	Ulna	uln
23	Radius	rad
24	Carpometacarpus	cmc
25	Phalanx	phal
26	Phalanx	phal

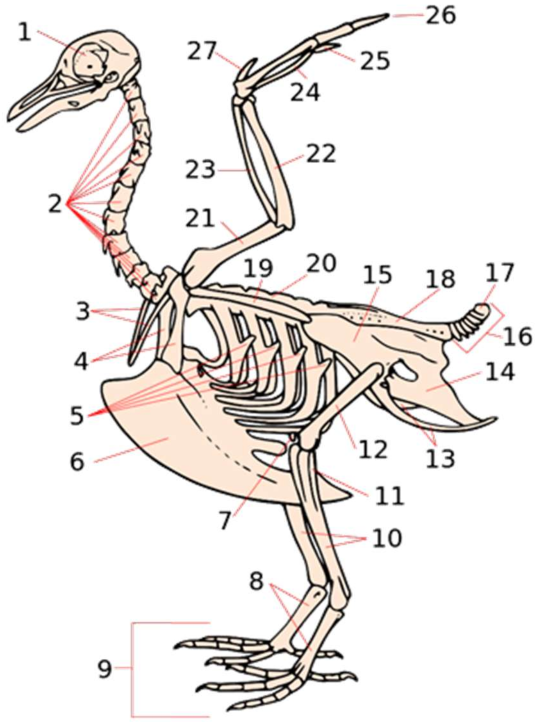


Figure 2.2: Elements of the avian skeleton (Squelette_oiseau.JPG: BIODIDAC derivative work: mario modesto / CC BY)

2.2.1.1 Anatomical elements

The anatomical element, laterality, and portion present were recorded for each specimen. I followed the anatomical nomenclature of Baumel and Witmer (1993) when recording and describing anatomical elements. To record element portion, Blasco and Peris (2009) divided each bone element into five zones (1-5) with 1 being the proximal articular facet and 5 the distal articulation (Figure 2.3). Presence of a zone was noted by number code, with a complete specimen carrying the code '12345'. This approach was preferred to Cohen and Serjeantson (1996), who divided bones into eight zones, because it was considered by Blasco to be more complicated, without significantly improving the accuracy of the analysis (Blasco *pers. comm.*). My own examination of remains confirmed Blasco's view, but I found it productive to deviate from her practice for specific elements due to patterns of preservation I observed in the collections:

- *The carpometacarpal*:
  The minor metacarpal was assigned the number 4, while the numbers 123 and 5 run from the proximal articulation, along the major metacarpal, to the distal articulation. Blasco numbers the carpometacarpal from 1 to 5 along the bone in its entirety, a method which does not consider the presence or absence of the minor metacarpal. I made this change because of the breakage pattern observed during my analysis – very often the more fragile minor metacarpal was completely absent.
- *The furcula:*
  For the furcula the anterior portion is noted as 1, the right side as 2 and 4 and left as 3 and 5. This is because the extremities of the furcula tend to fracture while the anterior portion is more robust.
- *The sternum and the pelvis:*
  Fragments of the sternum and pelvis were recorded as anterior or posterior and by side.

In addition to denoting the portion present in the accumulation, the bone zone was used to record the placement of traces in my taphonomic analyses.

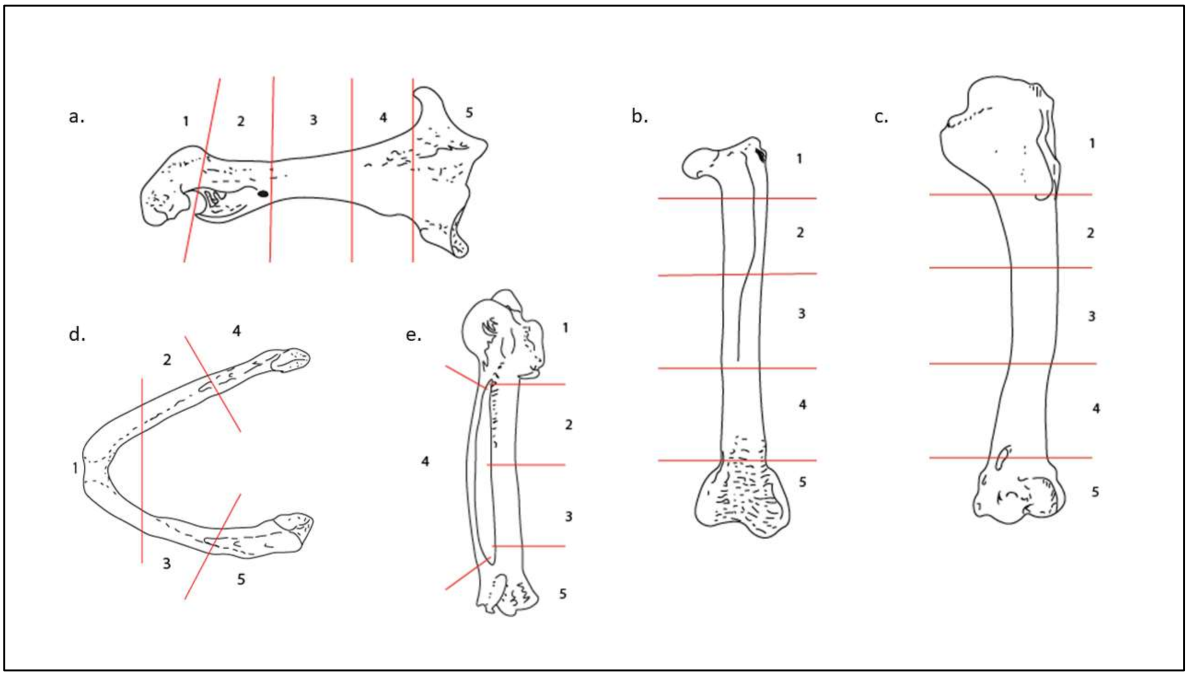


Figure 2.3: Bone zones on five avian skeletal elements: a) herring gull coracoid, b) crow femur, c) red grouse humerus, d) mute swan furcula, e) guillemot carpometacarpal. Drawings made in Adobe Illustrator from templates in Cohen and Serjeantson (1996).

2.2.1.2 Age and sex

When using skeletal morphology as an indicator of age in birds, there is a great discrepancy between the age of skeletal maturation and a bird reaching maturity as reflected in plumage. Studies of avian bone maturation indicate that, in general, a porous long bone equates to an age of <2 months (Lefevre and Pasquet 1994; Hargrave 1970). Specimens marked as juvenile are therefore understood to represent very young individuals while those marked as adult may represent subadults, which are individuals that have reached skeletal maturity, but that are not yet in adult plumage, as well as sexually mature individuals. The sex of each specimen was determined, where possible, by the observation of medullary bone in nesting females (Figure 2.4), and in spurs on the tarsometatarsi in males of some game birds (Serjeantson 2009).

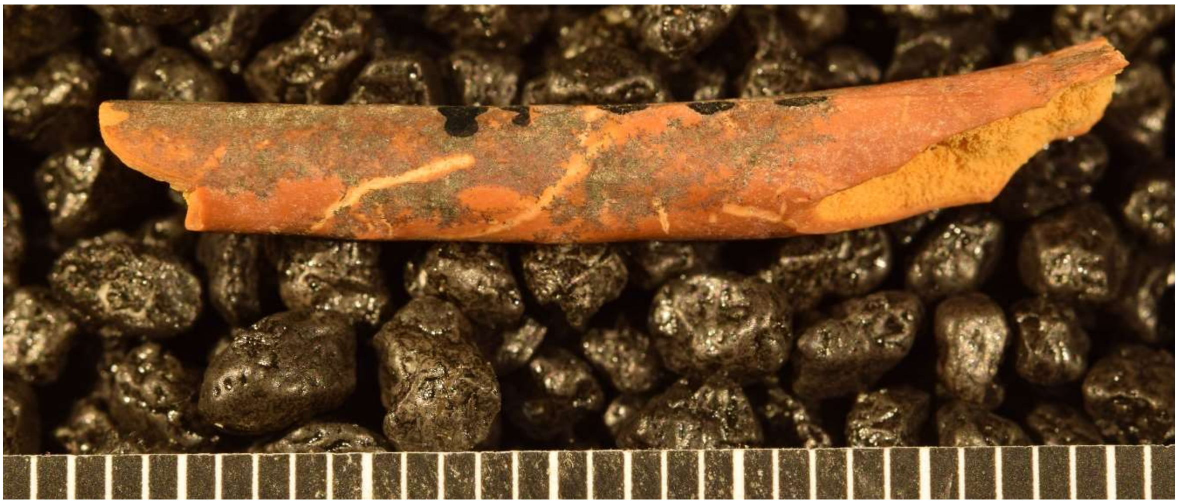


Figure 2.4: A long bone shaft from Cova Negra, Spain with medullary bone visible at the fracture (Spec no. 10891)

2.2.2 Classification

All systematic, and vernacular bird names were derived from the International Ornithological Congress master list as of December 1st, 2020 (Gill, Donsker and Rasmussen 2020). Any outdated names found in previous taxonomic classifications of my study sites were replaced with their current designations. In cases where identification was only possible to genus, the suffix ‘sp.’ was added (Sigovini *et al.* 2016). Order and family were recorded when identification to lower taxonomic categories was not possible.Some elements of the avian skeleton are more reliable than others when identifying material from archaeological sites (Morales-Muniz 1993). This is due to the high degree of intraspecific variation and interspecific similarities of some elements, and the variable robusticity and survivability of each skeletal element (Bellairs and Jenkin 1960; Serjeantson 2009; Ericson and Tyrberg 2004). Following Morales-Muniz (1993), Serjeantson (2009) ranked the skeletal elements of birds into a scale of reliability against robusticity, where reliability reflects how easily a species may be identified by the given element and robusticity reflects the likelihood that the element will survive in an archaeological accumulation (Table 2.2).

Table 2.2: Robusticity vs reliability of skeletal elements (Serjeantson 2009). Though very reliable, the cranium and mandible are not frequently found in archaeological accumulations. Conversely, the synsacra are often recovered, but are less reliable for identification.

	Reliable	**Fairly reliable**	**Least reliable**
Robust	Coracoid Humerus Tibiotarsus Tarsometatarsus	Femur Ulna	Synsacrum
Medium		Radius Carpometacarpus Sternum (articulation) Major wing digit Scapula	Pelvis Foot phalanges Cervical vertrebrae Pygostyle Quadrate
Fragile	Cranium Mandible		Atlas Axis Ribs Tracheal rings Patella

Where species with morphologically indistinguishable bones were identified, the geographical location of the recovery site was taken into consideration. An example of this are the partridges of the genus *Alectoris*. In the Palearctic, the distribution of species within the genus are mutually exclusive with possible sympatry between the rock partridge (*A. graeca*) and the chukar partridge (*A. chukar*) only occurring in Turkey (Watson 1962; Randi 1996). The identification of small birds of the order Passeriformes (perching birds) also warrants special mention (Janossy 1983; Moreno 1986; Cooper 1999). The size and similarity of remains, especially between the smallest species, make it difficult to determine taxa to species-level. Cooper (1999) conducted a blind test to verify the reliability of small passeriform remains. Her results indicated that the most reliable element for identification was the humerus, and then only its proximal articulation. Other researchers (Kessler 2015, Wojcik 2002, Janossy 1983) have published illustrated guides to identification based on the traits of other elements, but in practice, the researchers themselves found these to be unreliable. On balance, I took a conservative approach and limited the identification of small Passeriformes to the traits of the proximal humerus.

2.3 Taphonomic processes

Taphonomy, a term first used by Efremov (1940), is the study of visible extraneous peri- and post-mortem traces on a bone specimen (Binford 1981; O’Connor 2005). It seeks to answer questions that differ in kind or scale from those that are traditionally asked by zooarchaeologists (Lyman 1994). Whereas zooarchaeologists look at the amount of taxa that contribute to diet and the palaeoenvironmental implications of relative abundance of taxa, taphonomists ask how the bones or organisms came to be in the assemblage (Shipman 1981). Taphonomic analysis makes it possible to piece together the order of events that occurred from the moment of death to the study of the remains in a laboratory (O'Connor 2000).

Andrews (1991) highlighted the importance of determining the method of faunal accumulation, which he stated has two possible origins: intervention by a predator (death and consumption), or natural, post-depositional changes (Figure 2.5). He stated that natural death includes individuals that have succumbed to disease, starvation, old age, and to young that have fallen from the nest, and applies to species whose ethology naturally place them within the site environment. He also noted that porous, immature bones may be dead juveniles and a sign of nesting populations (Andrews ibid). The presence of juvenile bones in an accumulation, however, does not rule out predation by an external agent according to Laroulandie (2000, 2010). She noted that an external agent may be a bird of prey, a mammalian carnivore, or a human. Furthermore, species that are the product of predation are not always found naturally within the site environment and may be indicative of an external agent, with each agent leaving distinct taphonomic traces (Laroulandie 2000; Andrews 1990). Taphonomic processes included in this study were grouped into four sets: human agency, non-human predator agency, natural processes, and fragmentation.

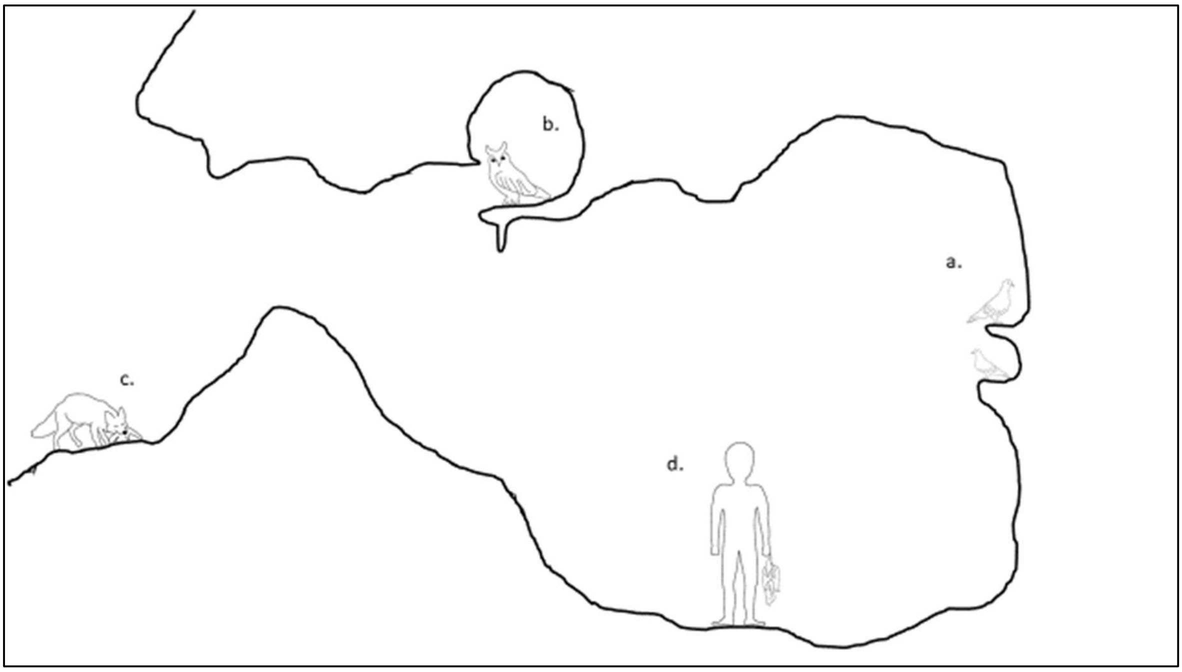


Figure 2.5: A diagram illustrating the various ways bird bones may accumulate in a cave. a) natural death of of species that appear within the site environment; b) bird of prey agency; c) carnivore agency; d) human agency.

2.3.1 Human agency

Traces left by humans may reflect the hunting, slaughter, butchering and cooking of prey as part of a subsistence strategy (Binford 1981; Brain 1981; Potts and Shipman 1981; Shipman and Rose 1983; Olsen and Shipman 1988; Noe Nygaard 1989; Lyman 2004; Fernández-Jalvo and Andrews 2016; Pedergnana and Blasco 2016). They can also indicate the extraction of raw materials such as bone, tendons, or in the case of birds feathers (Laroulandie 2000; Gala, Raynal and Tagliacozzo 2005; Finlayson *et al.* 2012; Blasco *et al.* 2014, 2016a, b, 2019; Romandini *et al.* 2016). Traces of butchery are rare in bird remains which have accumulated through human agency (Laroulandie 2000; Serjeantson 2009; Brown *et al.* 2011; Finlayson *et al.* 2012; Blasco *et al.* 2014, 2016a), and many well-documented traces found in the butchery of large mammals have no parallel in birds (Laroulandie 2000, Steadman *et al*. 2002).

Signs of human agency appear in the form of striations, peeling, disarticulated depressions and thermal modifications (Laroulandie 2000; Blasco and Peris 2009; O'Connor 2005). For signs of human predation, experimental archaeology is considered crucial (Laroulandie 2000, 2001, 2004, 2005; Laroulandie *et al.* 2008; Blasco *et al*. 2014; Blasco and Pedergnana 2016). This was exemplified in an actualistic study by Blasco and Pedergnana (2016) who demonstrated that feather barbules can become lodged in lithics during skinning and defeathering activities, and that cut marks are individual to the butcher (Blasco and Pedergnana ibid).

2.3.1.1 Striations

Striations are the most widely recognized indicator of human agency (Binford 1981). These are linear traces left by stone and bone tools in the butchery and dismemberment of animals (Binford 1981). They can present as cutmarks or scrapes and can be confused with marks left by natural processes, such as trampling and fine gnawing by carnivores or rodents (Lyman 1994). However, what distinguishes them is their morphology (Potts and Shipman 1981; Shipman and Rose 1983; Table 2.3). Cutmarks are v-shaped in cross-section and are generally asymmetrical with one side presenting a shallower slope than the other. Features known as Hertsian cones appear along the shallow side of a cutmark. These are formed by the stress of the incision as bone material is displaced by the stone tool. Shoulder marks – striations parallel to the main cut – are secondary facets that arise from a lithic or bone implement coming into contact with the bone surface (Fernández-Jalvo and Andrews 2016).

The presence of cutmarks confirms that human agency was at least partly responsible for the formation of the assemblage (Binford 1981; Laroulandie 2000). Scrapes on the other hand are broader than cutmarks and may be u-shaped. They are generally found close to muscle attachments and run parallel or oblique to the long axis of the bone (Binford 1981; Fernández-Jalvo and Andrews 2016). Their number, type, location and orientation were recorded in my analyses (Table 2.6). These are indicative markers of the intended purpose behind the butchery process.

Table 2.3: Terms related to striations in avian taphonomy.

Term	**Definition**	**Reference**
Cut mark	V-shaped linear trace made by a stone tool on the bone surface	Binford 1981; Serjeantson 2009; Fernández-Jalvo and Andrews 2016
Scrape	Striated cuts covering broader areas; oblique or longitudinal to the bone axis when agent is human	Fernández-Jalvo and Andrews 2016
Hertzian cone	Unilateral modification of the edge of a cut mark due to stress	Bromage *et al*. 1991
Skinning	Uncommon in birds; plucking is more common	Serjeantson 2009
Disarticulation	Produced during dismemberment; short cuts, near muscle, tendon, and ligament insertions.	Binford 1981; Laroulandie 2000; Laroulandie 2005
Defleshing	The process of removing flesh from the bone; creates oblique/longitudinal cuts and scrapes	Serjeantson 2009

Table 2.4: Variables used to record striations.

Variable	**Value**	**Type of variable**
n.	Number	Numerical discrete
Type	Cut mark/scrape/cm? (uncertain cutmark)	Categorical nominal
Location	Bone zone 1-5	Categorical Ordinal
Orientation	Longitudinal/oblique/transverse	Categorical Nominal

The signs of three processes can be observed in bird butchery: skinning, disarticulation and defleshing. Skinning is rare in birds as they are more likely to have been plucked than skinned because the layer of fat under bird skin is desirable for nutrition and flavour when cooking (Serjeantson 2009). Disarticulation cuts indicate dismemberment processes and tend to be located close to muscle, tendon and ligament attachments. These cuts are usually short but may be deep (Binford 1981; Fernández-Jalvo and Andrews 2016). Longitudinally orientated marks are generally associated with defleshing activities and can be quite numerous. Cutmarks identified close to the quill knobs on the ulnae and carpometacarpal of birds at several Middle Palaeolithic sites have been interpreted as indicative of an intention to harvest wing feathers (Peresani *et a*l. 2011, Finlayson *et al.* 2012; Blasco *et al.* 2014; 2016a, b; Romandini *et al.* 2014; Finlayson 2019). Talon exploitation is indicated by cutmarks on the pedal phalanges (Fiore *et al*. 2004; Radovcic *et al.* 2015; Laroulandie *et al.* 2016; Finlayson 2019

2.3.1.2 Peeling

Peeling is the result of manual disarticulation on fresh bone (Laroulandie 2005; Blasco *et al*. 2020). A good analogy is the snapping of a fresh twig where the two pieces remain connected by a thin sliver before being peeled apart (White 1992). While peeling is generally accepted as a secure indication of human agency, some studies show peeling to appear in the feeding habits of some diurnal raptors (pers. comm. Bocheński to O'Connor in O'Connor 2005). Peeling is noted as present or absent and by location using the bone zones outlined in Section 2.2.1. Bone peeling is always adjacent to the zone of fragmentation or the articular end, and is most common between the bones of the wing, and the bones of the scapular girdle (Figure 2.4; Laroulandie 2000; Serjeantson 2009).

Figure 2.6: Peeling (small arrows) on the ulnae of Snowy owl (Bubo scandiacus) from Combe Saunière, France (Laroulandie 2000, fig. 112. Photo: Veronique Laroulandie). Scale = 1cm.

2.3.1.3 Disarticulation depressions

Another trait of manual disarticulation is the overextension of the joint between the humerus and ulna causing the olecranon process of the ulna to leave a depression (squash), perforation or notch in the olecranon fossa of the distal humerus (Gourichon 1994, Laroulandie 2000; Figure 2.7). In some cases, the force of this action can result in the complete detachment of the lateral condyle from the humerus (wrench). This tear is then related to a notch. These traces are unique to birds and do not have an equivalent in the disarticulation of large mammals (Laroulandie 2000, 2005). The presence and severity of disarticulations (squash/puncture/wrench) was recorded.

Figure 2.7:The progression of squash (left) through perforation (middle) to notch (right) on the olecranon fossa of ptarmigan (Lagopus mutus) humeri from La Vache. This is the result of overextending the joint while disarticulating the wing (Laroulandie 2005, fig. 3.4. Photo: Veronique Laroulandie). Scale = 1 cm.

2.3.1.4 Thermal modifications

Burning of bone causes brown, black, grey and white discoloration (Buikstra and Swegle 1989; Stiner *et al.* 1995; Cáceres *et al.* 2002; Asmussen 2009; Blasco and Peris 2009; Fernández-Jalvo and Andrews 2016). Though it may be indicative of human agency, burning can also be the result of exposure to natural fire. The colour modification reflects both the heat of the fire that bones were exposed to, and also the length of exposure. Blasco and Peris (2009) use a scale of 0-5 to describe the stages of burning, a standard which was developed by Stiner *et al.* (1995) and adopted for my analysis (Table 2.5).

Table 2.5: Scale of thermal modification after Peris and Blasco (2009) and Stiner et al. (1995).

Degree of thermal modification	**Definition**
0	Unburnt bones
1	The bone surface presents small dots, scattered brown
2	Brown stain more or less across the bone surface
3	The bone is charred, colour is black
4	Grey stain. Occasionally veins appear with blueish tones
5	The fossil appears calcined. Colour is white

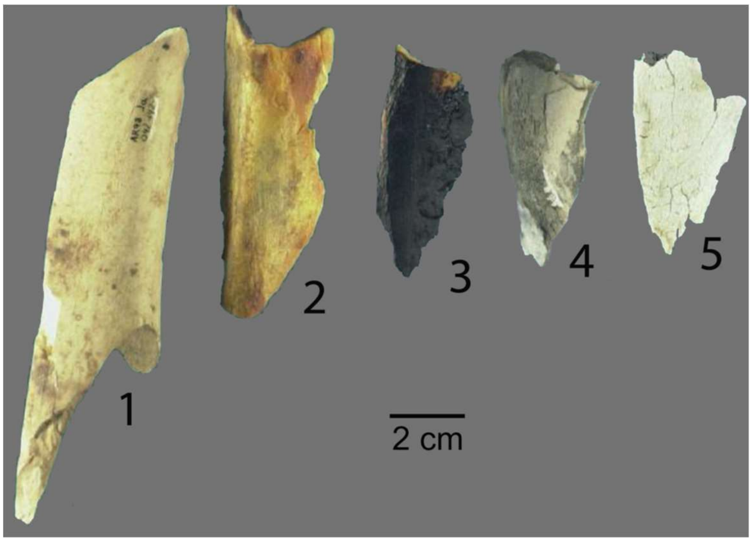


Figure 2.8: The stages of thermal modification. 1 = brown staining, 2 = brownish discolouration, 3 = charring and a dull black colour, 4 = dark grey in colour and cracked, 5 = white in colour; calcinated (Fernández-Jalvo and Andrews 2016, fig 5.2. Photo: Cáceres et al. 2002).

The location of burning on the bone can indicate the origin of the accumulation. At Tromelin Island, Madagascar, Laroulandie and Lefevre (2014) identified a recurrent pattern of burning on the fractured distal ends of tern (Sternidae) humeri. This was interpreted as a reflection of butchery and cooking practices of African slaves stranded on the island in the 1700s. This type of localised burning only appears on one area of the bone and is interpreted as the result of flesh covering parts of the bone during cooking (Laroulandie 2000; Blasco and Peris 2009; Blasco *et al*. 2014, 2016a; Laroulandie and Lefevre 2014.). Thus, for recording burning modification, when more than one stage was evident on the same bone, both zones were recorded, and the record marked as 'double' for double colouration.

2.3.2 Non-human predator agency

Differentiation between taphonomic traces left by human and non-human predators has been recognized for some time. Milne-Edwards (1875) commented that willow grouse (*Lagopus lagopus*) bones from Palaeolithic caves of the Perigord in south-west France must accumulated as a result of human agency because they lacked the fractures patterns and gnawing traces traditionally assigned to birds of prey and mammalian carnivores. Since these early observations, considerable research has dedicated to the taphonomic markers left by non-human predators (Mayhew 1977; Binford 1981; Haynes 1980, 1983; Mourer-Chauviré 1975; Bickart 1984; Shipman *et al*. 1984; Ericsson 1987; Andrews 1990; Serjeantson 1997; Stiner 1994; Blumenschine 1995; Laroulandie 2000; Rufa *et al.* 2016; Pedergnana and Blasco 2016; Bocheński, Wertz and Tomek 2018).

Mammalian carnivores (large and small), nocturnal and diurnal birds of prey, and other birds like shrikes and corvids have all been identified as contributors to avian bone accumulations. In relation to birds of prey, extensive literature is available on the traces left by nocturnal and diurnal avian predators including the eagle owl, snowy owl, tawny owl, long-eared owl, peregrine falcon, gyrfalcon, golden eagle, imperial eagle, and white-tailed eagle (Andrews 1990; Bochenski *et al.* 1993, 1997, 1998, 1999, 2009, 2018; Bochenski 1997, 2005; Bochenski and Tomek 1994, 1997; Laroulandie 2000, 2002; Bochenski and Nekrasov 2001; Bochenski and Tornberg 2003; Lloveras *et al.* 2008, 2009; Rufa and Laroulandie 2019; Alonso *et al*. 2020).

For mammalian carnivores, studies of bird predation by foxes, badgers, dogs, coyotes, and felids (Laroulandie 2000; Rodriguez-Hidalgo *et al.* 2016) are complemented by studies on leporid remains (Payne and Munson 1985; Schmitt and Juell 1994; Hockett 1999; Sanchis 1999, 2000, 2012; Hockett and Haws 2002; Cochard 2004, Lloveras *et al.* 2008, 2010, 2011, 2012, 2014, 2018; Mallye *et al.* 2008; Rodriguez-Hidalgo *et al.* 2013; Young *et al.* 2015; Marin-Monfort *et al*. 2019; Arilla *et al.* 2019, 2020a, 2020b).

Based on these analyses, traces that indicate non-human predators as the agent responsible for an assemblage are divided into two groups: mechanical modifications and biochemical modifications.

2.3.2.1 Mechanical modifications (manducation)

Mammalian carnivores modify bones through the processes of predation, defleshing and disarticulation (Table 2.6). Additionally, some carnivores and rodents gnaw on the bones remaining after primary consumption. Mechanical processes of non-human predators were interpreted through the recording of the number, type, and location of the modifications found on specimens Tables 2.8 and 2.9. These present as varying degrees of punctures, scores and crenulated edges (Haynes 1980, 1983; Binford 1981).

Punctures range from a pit or shallow depression in the bone cortex to a complete perforation of the bone. These perforations often have inverted bone flakes attached and associated cracks as a result of bite pressure (Fernández-Jalvo and Andrews 2016). A notch is the collapse of pitted bone tissue close to a fracture edge (Fernández-Jalvo and Andrews 2016; Rufa *et al.* 2018). Crenulated edges are a product of gnawing on the articular ends of bones where a series of punctures to access marrow has resulted in the detachment of the epiphysis. Continued gnawing of this region of a bone creates a rough edge (Lyman 1994, Binford 1981, Laroulandie 2000, Serjeantson 2009, Capaldi and Blumenschine 2011). Scores are dentition marks that are produced by the scraping of a predator's tooth across the surface of the bone. They are generally u-shaped and wider than cutmarks and marks resulting from human ingestion. They also present with cracking in the score (Blumenschine *et al.* 1996).

Large carnivores tend not to leave traces of manducation on avian material, as the entire carcass is generally ingested (Andrews 1990). The size of a tooth or beak puncture can also indicate the predator responsible for the bone accumulation (Laroulandie 2000). Smaller animals such as rodents leave gnawing marks that present as paired, flat-bottomed scrapes created by the repeated motion of rodent incisors against the bone surface. The rodent is not necessarily the predator, but these traces can obscure the true accumulator (Fernández-Jalvo and Andrews 2016). Herbivores are also known to gnaw on dry bone, leaving rough bottomed scrapes that may obscure the original traces (Fernández-Jalvo and Andrews 2016).

Birds of prey leave distinctive patterns of modification depending on their behaviour (Andrews 1990). Diurnal raptors may retire to the roost with their prey where they hold the carcass in their talons and tear small pieces of flesh from the bone with hooked beaks (Laroulandie 2000; Bocheński 2005; Serjeantson 2009). They generally only consume the parts of bone that tear away with the flesh, and discard the remaining bones to accumulate beneath the roost (Bocheński *et* al. 1997, 1999; Bocheński 2005; Serjeantson 2009). This defleshing process leaves traces where the beak inadvertently punctures the bone (Laroulandie 2002; Bocheński *et al*. 2009). These are generally irregular or triangular in shape. Beaks may also leave a diagnostic score with tapered edges and a curvilinear body that is thicker in the centre (Blumenschine *et al.* 1996). Owls, on the other hand, swallow their prey whole and usually head first. It is possible that an owl may leave beak punctures on prey but the traces left behind are generally from the digestive process (Andrews 1990; Bocheński *et al.* 1998).

Table 2.6: Terminology used in the description of manducation modifications.

Term	**Definition**	**Potential agent**	**Reference**
Puncture	Perforation of the bone cortex	Carnivore, bird of prey	Haynes 1980, 1983; Binford 1981
Pitting	Incomplete perforation of the bone cortex	Carnivore, bird of prey	Haynes 1980, 1983; Binford 1981
Notch	Collapse of pitted cortical tissue close to an edge: rounded morphology	Carnivore, bird of prey	Rufa *et al.* 2018; Fernández-Jalvo and Andrews 2016
Score	Epiphenomenal striation on the bone surface caused by beak or tooth	Carnivore, bird of prey	Haynes 1980, 1983; Blumenschine *et al.* 1996.; Serjeantson 2009
Crenulated edges	The scalloped edges of a fracture which is made by chewing	Carnivore	Haynes 1980, 1983; Binford 1981; Lyman 1994
Gnaw	Repeated chewing of a bone surface resulting in gouges into the cortex	Carnivore/rodent	Serjeantson 2009; Fernández-Jalvo and Andrews 2016.

Table 2.7: Variables collected to describe manducation modifications.

Variable	**Value**	**Type of variable**
n.	Number	Numerical discrete
Type	Puncture/Gnaw/Score/Crenulated edges	Categorical nominal
Location	1-5 (bone zone)	Categorical ordinal
Predator	Carnivore/Bird of Prey/Rodent/Human	Categorical nominal

Mechanical modifications can be categorized as conspicuous or inconspicuous. Inconspicuous traces are thought to be made when there is flesh present on the bone. Such traces are not easily identified at magnifications lower than 16x (Blumenschine *et al.* 1996). Conspicuous traces can, however, be easily identified at low magnifications. These are the product of consumption of partially, or wholly defleshed bones (Laroulandie 2000; O'Connor 2005). My use of a magnification of 20-45x was suitable to identify both conspicuous and inconspicuous traces (Blumenschine *et al.* 1996). No division was made between them as both are evidence of modification.

2.3.2.2 Biochemical modifications

Digestion leads to corrosion of the bone material through acid etching of the bone surface by digestive juices in the stomach. These digestive enzymes also break down the organic constituents of the bone (Andrews 1990; Bocheński *et al.* 1998; Bocheński 2005; Serjeantson 2009; Fernández-Jalvo and Andrews 2016). Digested bone has a polished surface, thin fracture edges, and has the appearance of “plastic that has begun to melt” (Bocheński and Tomek 1997), but may also show rounding, cracking and breakage in addition to corrosion (Laroulandie 2000, 2002). Breakage before ingestion increases effects of digestion, allowing the digestive juices to attack the inner surface of the bone, as well as the outside. Bones that have been broken before ingestion present a thinning and rounding of the fracture edges (Bocheński and Tomek 1997, Andrews 1990, Andrews and Fernández Jalvo 2016). Digestion was recorded on a scale of 0-3. The presence of a polished surface on digested bone was noted with presence/absence. Evidence of digestion traces on fracture margins was also recorded when examining bone fragmentation as a rounding of the fracture surface and thinning of the cortical bone (Bocheński and Tomek 1997).

Table 2.8: Degree of digestion evident on the bone surface after Bocheński et al. (1998). Potential agency is taken from references in the text.

Digestion rank	**Definition**	**Potential agent**
0	No digestion evident.	Unknown
1	Lightly modified bone (damage beginning on specific areas)	Snowy owl; long-eared owl; wild cat
2	Moderately modified bone (damage on cortical surface and edges)	Tawny owl; eagle owl; wild cat
3	Highly modified bone (severe or extreme damage)	Diurnal raptors; fox; lynx

Digestion perforates the articular ends of bones, particularly in predated birds (Bocheński and Tomek 1997; Laroulandie 2000). These perforations are circular with polished edges and can become anastomised, forming a meandering surface. Exposed spongey bone also shows rounded edges, in contrast to puncture marks where the break pattern is sharp. The intensity of digestion can be diagnostic of the predator responsible for the accumulation (Andrews 1990; Laroulandie 2000; Bocheński 2005).

Accumulations assigned to avian predators exhibited varying degrees of corrosion depending on the agent (Bocheński 2005). This is partially due to the method in which raptors ingest their prey, and partially due to the acidity of their digestive juices (Andrews 1990). Owls generally swallow their prey whole. This allows the bones of the prey animal to be protected by its skin and pelt or feathers during digestion of the flesh. Owls eject undigested remains as pellets. Diurnal raptors also eject pellets that contain digested remains, but these are usually only fragments consumed incidentally with pieces of flesh (Serjeantson 2009). Diurnal raptors have more acidic digestive juices, which dissolve more of the bone material (Bocheński 2005). Carnivores have digestive juices capable of dissolving bone completely (Rufa *et al*. 2018). Studies of carnivore digestion patterns of birds remains are rare, but comparisons can be made with studies of leporid and micromammal remains modified by fox (Laroulandie 2000; Lloveras *et al.* 2012), lynx (Lloveras *et al*. 2008), wolf (Lloveras *et al.* 2020), and wild cat (Lloveras *et al.* 2018b; Marin-Monfort *et al*. 2019). Humans may digest bone, but like the diurnal raptors, only fragments rather than whole bones. Where there is a prey species overlap with humans, the absence of cut marks and breakage patterns typical of human consumption paired with the presence of raptor modifications, indicate non-human origin (Serjeantson 2009).

2.3.3 Natural processes

Natural processes may affect any bone regardless of the primary agency. Taphonomic marks or traces left by natural processes are the result of bone decomposition in the depositional environment (Fernández-Jalvo and Andrews 2016). This can affect each specimen differently due to the circumstances of deposition (Lyman 1994, O'Connor 2000, 2005; Serjeantson 2009). A half-buried specimen may even show differential exposure to natural processes on its buried surface compared to the surface exposed to air. Natural processes can leave traces that may obscure or remove diagnostic features of other modifications (Lyman 1994). The effects of natural taphonomic processes can be studied through carcass monitoring, though few such studies have been done on bird remains (Behrensmeyer et al. 2003; Bochenski, Wertz and Tomek 2017).

The sum of these agents is relevant to the overall readability (lisibility) of the bone. Lisibility bears a rank of 1-4 reflecting the ease with which traces could be identified (Table 2.9).

Table 2.9: Ranks for the recording of lisibility, degree of concretions, degree of manganese staining, presence or absence of trampling, and degree of acid etch from rooting.

	Variable				
Rank	**Lisibility**	**Concretions**	**Manganese staining**	**Trampling**	**Rooting**
0	-	No concretion	No manganese	No trample	No rooting evident
1	Clear	1- 25% coverage	1- 25% coverage	Trample	Lightly modified bone (damage beginning on specific areas)
2	Some difficulties	26-50% coverage	26-50% coverage	-	Moderately modified bone (damage on cortical surface and edges)
3	Difficult	51-75% coverage	51-75% coverage	-	Highly modified bone (severe or extreme damage)
4	Very compromised/ unreadable	76 – 100% coverage	76 – 100% coverage	-	-

2.3.3.1 Concretions/Calcite coating

Concretions are bodies of sediment that form through the precipitation of mineral cement within the spaces between particles (Fernández-Jalvo and Andrews 2016, Lyman 1994). In archaeological assemblages, concretions attach to artefacts due to the movement of mineralised water through the depositional environment. This causes the sediment to attach to itself and to any remains contained within it, forming hard and compacted units. Calcite coatings are mineral deposits on the surface of an artefact or specimen (Fernández-Jalvo and Andrews 2016). Concretions and calcite coatings may obscure traces on the bone surfaces and limit analysis of any underlying taphonomy (Lyman 1994). The presence of concretions and/or calcite coating on specimens was recorded on a scale from 0-4 (Table 2.9).

2.3.3.2 Manganese-dioxide staining

Manganese is a trace mineral that is abundant in calcareous rocks (López-González *et al.* 2006). It can be is transported in water percolating through sediments. Soluble manganese can precipitate on the surface of bones within sediments in the form of insoluble manganese oxide compounds. The mineral deposition of manganese dioxide crystals reflects wet, mildly alkaline environments such as caves (López-González *et al.* 2006). Microorganisms may also play a role in the deposition of manganese oxides by releasing the manganese ion when breaking down organic matter (Hill 1982; Palmer *et al.* 1986). Manganese oxide staining may affect the entire specimen, or only the portions in contact with the substrate. It presents in a sprawling pattern of crystal growth which is easily identified under magnification (Lyman 1994; Andrews and Fernández-Jalvo 2016). Documentation of the presence and degree of manganese coverage is important because it may obscure other taphonomic traces. Manganese can be removed with hydrogen peroxide, but on a large collection this is time consuming and can be detrimental to the bone surface (Andrews and Fernández-Jalvo 2016). The presence of manganese dioxide deposits on the bone surface was ranked on a scale from 0 (no manganese) to 4 (full coverage) (Table 2.9).

2.3.3.3 Trampling modifications

Trampling is the product of movement against the substrate, resulting from the specimen being trodden on by larger animals, including humans. The process removes specimens from their depositional context, fragments them, and leaves marks on the surviving specimens in the form of grooves, scratches and abrasion (Lyman 1994). These pseudo-cuts are generally less deep and shorter than traces left by predatory agents, occurring much more frequently and showing little or no purpose in placement (Fernández-Jalvo and Andrews 2016, Olsen and Shipman 1988; Rufa *et al.* 2018). Actualistic studies have been conducted to examine the properties of trampling (Brain 1981; Behrensmeyer *et al.* 1986; Olsen and Shipman 1988; Blasco *et al*. 2008; Dominguez-Rodrigo *et al.* 2009). The shape, depth and frequency depend on the depositional substrate, the size and weight of the agent, and the condition of the bone when trampled (Lev *et al.* 2020). Trampling is recorded as the presence/absence of pseudo-cuts on the bone surface (Table 2.9). Trampling also leads to fracture of the bone, but there is no particular pattern that is diagnostic of trampling. Fracture is discussed further in Section 2.3.4.

2.3.3.4 Rooting

A type of bioerosion, rooting is the acidic etching of macaroni type motifs into the cortex of the bone as the result of vegetation growing in the sediment. Chemicals produced at the growing tips of plants result in the solution of bone material. The branched, organic pattern of u-shaped grooves in the cortex may also be stained lighter or darker by the process (Fernández-Jalvo and Andrews 2016). Rooting is unsystematic in that it may affect the entire surface of the bone or appear only on some surfaces. The extent of rooting damage on a specimen is ranked from 0 - 3 (Table 2.9; Fernández-Jalvo and Andrews 2016).

2.3.3.5 Weathering

Weathering is the process of *in situ* destruction of the original organic and inorganic components of a bone by physical and chemical agents, which can happen on the surface or within the substrate (Behrensmeyer 1978; Andrews 1990; Serjeantson 2009; Fernández-Jalvo and Andrews 2016). In open-air environments, weathering takes the form of bioerosion and/or damage from sunlight. Once buried, damage results from acid etching by organic acids in the soil. As such, weathering is part of the natural recycling of nutrients and can reflect climatic variations (Behrensmeyer 1978; Andrews 1990; Serjeantson 2009; Fernández-Jalvo and Andrews 2016). It has been suggested that bones from human accumulation are often more weathered than natural accumulations as the bones are de-fleshed before deposition, while a uniform degree of weathering in an assemblage indicates the simultaneous burial of the material (Bocheński, Wertz and Tomek 2018). Over time, bones present in various stages of demineralisation and display a progressive mosaic pattern of cracked and flaking bone (Behrensmeyer 1978; Andrews 1990; Bocheński, Wertz and Tomek 2018). Behrensmeyer (1978) developed a scale describing six degrees (0 - 5) of weathering based on field observations of recent mammal bones in the Amboseli Basin, Kenya. The six degrees reflect the progression of decay in modern animals and have since been used to describe weathering apparent in archaeological materials.

To some degree, avian remains show the same progression of weathering as other classes of bone. In an actualistic study of avian remains monitored over a number of years at Ciemna Cave, Poland, Bocheński and Tomek (1997) were unable to see changes beyond Stage 2 on Behrensmeyer's mammal scale. A 2003 study of bird material from the surface of the Amboseli Basin (Behrensmeyer *et al*. 2003) supported their observations, concluding that avian remains weather faster than mammal remains, quickly disintegrating after Stage 2. This was interpreted as a consequence of the internal structure of avian bones, which lack the thick cortical bone of mammals. In 2018, Bocheński, Wertz and Tomek published the results of a 25-year monitoring of the same material in Ciemna Cave. This time they found evidence of all five stages of weathering defined by Behrensmeyer (1978). Their results indicated that avian bones weather at a different pace from mammal bones, and that de-fleshed avian bones have a greater chance to survive and fossilise than bones deposited as complete carcasses in a cave.

Table 2.10: Behrensmeyer's scale to record weathering (1978) with reference to Bocheński and Tomek's 1997 which emphasizes the different progression of weathering in bird bones.

	Behrensmeyer (1978)	**Bocheński and Tomek (1997)**	**Bochenski *et al.* 2018**
0	No cracking on surface.	No cracking on surface.	-
1	Cracking, usually parallel to the orientation of collagen fibres Articular surfaces may show cracking in a mosaic pattern.	Articular ends: one or more small holes with rough edges Shaft: no modification or small, singular holes with rough edges or merely depressions with rough bases Breakage: may be sharp and rounded, or semi-rounded	Modifications on up to 10% of the bone, typically in the form of one or several pits/perforations. Edges of broken bones show initial delamination.
2	Bone surfaces show flaking, usually along the edges of cracks Crack edges are angular, with no rounding	Articular ends: holes with sharp and rough edges Shaft: many large and small holes with rough edges and depressions with rough bases Concentric flaking; Breakage: sharp and rough Very fragile	Modifications on 10 – 75% of the bone. Bone surface is wrinkled and/or dotted by pits and perforations. Bone surface collapse due to delamination is visible along broken edges, perforations, and cracks. Interior bone corrosion.
3	Bone surfaces show roughened patches resulting from flaking of surface bone, but only to a depth of 1.0-1.5 mm Crack edges are typically rounded		Modifications on >75% of the bone. Heavy wrinkling of the bone surface and bending of complete bone fragments. Inner layer of bone corrodes/dissolves, and the outer layer becomes brittle and delicate.
4	Bone surfaces are rough, with loose splinters Cracks are wide, with rounded or actively splintering edges		
5	The bone is disintegrating into splinters The original shape may no longer be apparent		

2.3.4 Fragmentation

Bone fragmentation is a function of the taphonomic processes applied at a number of stages in a bone assemblage's history (Marean, Domínguez-Rodrigo & Pickering 2004). It is an ongoing process that may occur at any point in time between the death of an individual up to the moment that it is examined during analysis (Lyman 1994; O'Connor 2005). Recording fragmentation is not a secure way to identify the predator responsible for an accumulation (Laroulandie 2000). Though breakage proportion differs between some agents, e.g. diurnal and nocturnal birds of prey, some breakage patterns may be the result of several agents, both natural and non-natural, working on an accumulation (Bocheński *et al.* 1998, 2009); Laroulandie 2000; Bocheński 2005).

Fracture outline, fracture angle and morphology of the fracture edge were recorded during analysis according to the standards described by Villa and Mahieu (1991). These variables can collectively indicate whether breakage was the product of human or non-human predator agency or was due to natural post-depositional causes (Villa and Mahieu 1991, Fernández-Jalvo and Andrews 2016). Tomek and Bocheński (1997) noted the difference in fragmentation patterns in bones that had naturally eroded in contrast to remains from owl pellets. The remains from owl pellets had rounded and thinned edges, while the weathered bones and control specimens all presented fractures at right angles to the shaft axis.

2.3.4.1 Fracture outline

Fracture outline can indicate the method of fracture and the condition of the bone at the time of fracture (Villa and Mahieu 1991). Curved or pointed fractures are described as spiral fractures. Curved/spiral fractures appear on fresh bone and are often attributed to human action. Laroulandie (2000) labels recurrent spiral fractures on bird bones as indicative of human agency, reflecting the twisting motion employed during manual wing disarticulation. Transverse fractures are perpendicular to the long axis of the bone and are made on mineralised bone. They are more likely to be the result of post-depositional factors such as sediment movement and compaction (Fernández-Jalvo and Andrews 2016). Irregular fractures include fractures that have a straight morphology, but are diagonal, and fractures with a stepped outline (Villa and Mahieu 1991). Fracture outline was recorded as spiral (sp), transverse (tr) or mixed (mix).

2.3.4.2 Fracture angle

Fracture angle is the angle between the fracture surface and the bone cortical surface (Villa and Mahieu 1991). This angle can be oblique (acute/obtuse), perpendicular (right), or intermediate (mixed). Each reflect a different state of bone preservation when the fracture occurred. Oblique angles are generally associated with fresh bone fractures, while right angles are associated with dry bone. A fracture presenting more than one angle is associated with dry bone fracture (Fernández-Jalvo and Andrews 2016). Fracture angle was recorded as oblique (obl), right (r), or mixed (mix).

2.3.4.3 Fracture edge

The texture or aspect of the fracture margin may be smooth or rough (Villa and Mahieu 1991). Smooth margins are characteristic of fresh bone breakage, while jagged edges are attributed to dry bone fractures (Fernández-Jalvo and Andrews 2016). Fracture edges were recorded as smooth (sm) or rough (r).

2.4 Equipment and repeat testing

Specimens were first examined with a lupe at 20x magnification. This was higher than the 16x recommended by Blumenschine *et al.* (1996) so I am confident that the equipment used was suitable for this work. I then used a microscope at a magnification of 20-45x to study the material in greater detail. There was variation in the maximum magnification of microscopes available at the five institutions I visited to access the collections (Table 2.4). Potential candidates for human modification were examined further under more powerful magnification and photographed.

Table 2.11: Equipment used during taxonomic and taphonomic analysis.

Site	**Microscope**	**Camera**
Gorham's Cave	Nikon SMZ 1500	Nikon D3x (Nikkor 105 mm macro lens)
Devil's Tower Rockshelter	Table microscope (NHM) 7x – 45x Digital USB Microscope HD 640x480P	Nikon D5300 (Nikkor 60 mm macro lens)
Cova Negra Cave	Generic Stereozoom 7x-45x	Nikon D5300 (Nikkor 60 mm macro lens)
Tabun Cave	Generic Stereozoom 7x-45x Zeiss Discovery V8 Stereomicroscope	Nikon D5300 (Nikkor 60 mm macro lens) ZEISS Axiocam 208 color
Scladina Cave	Generic Stereozoom 7x-45x and SEM	Nikon D5300 (Nikkor 60 mm macro lens)

An important aspect when classifying assemblages and identifying taphonomic traces is consistency. I undertook repeat testing to test my recording of taphonomic traces. I analysed avian material from Waechter's Layer A in February 2019, repeated the analysis in July 2019, and compared my results. I also performed a repeat analyses of the Corvidae remains from Devil's Tower in February 2019 and again in April 2019. In both tests, the results of the second examination matched the initial observations made.

2.5 Ecological Variables

Raw taxonomic data for each site was prepared for ecological analysis using the following steps:

1. Each identified species was assigned ecological tolerance variables following Finlayson (2011). Finlayson (ibid) assigned ranks to 860 Palearctic bird species describing variables relevant to bioclimatic tolerance, latitude range, temperature tolerance, humidity tolerance, and habitat exploitation.
2. The frequency of each variable was counted following the principle of presence and absence (Hernández-Fernández 2001, Finlayson *et al*. 2016). Multiple species presenting with the same ecological variable in any single context only counted as one presence when calculating the frequency of ecological variables at site level.
3. The relative frequency of each variable per site was calculated by dividing the frequency by the total number of stratigraphic contexts in the site.
4. The results were tested for statistical significance (see section 2.7.2**Error! Reference source not found.**) using chi2-testing against the expected frequencies for a general Palearctic population (EPal in tables below) calculated from Finlayson's database (2011).

This data was discussed in chapters 3-7 to describe the climatic and environmental opportunities available at each site. In Chapter 8, the results were used to define the Neanderthal bioclimatic and habitat niches.

2.5.1 Bioclimatic Tolerance

A bioclimate is an ecological term describing an environment which is modulated by its climatic conditions, foremostly rainfall and temperature (Finlayson 2011). Bioclimate models are used in the study of how species react to changes in their habitats due to climate change (Heikinnen *et al.* 2006; Caddy-Retalic *et al.* 2017). Finlayson (2011) defined bioclimatic tolerance as the adaptive potential of a species by measuring how many zones it occupies on a bioclimatic map (Figure 2.9). Palearctic bird species were ranked into five categories based on their present-day breeding distributions (Table 2.12).

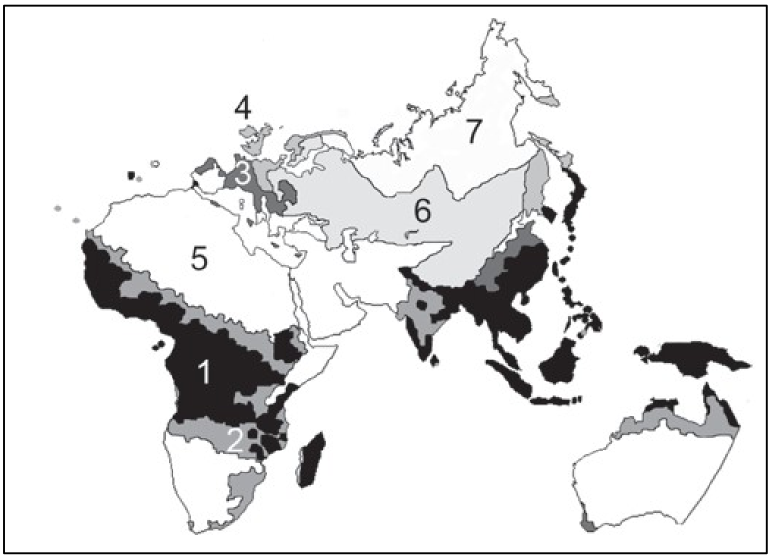


Figure 2.9: Map of present day bioclimates in the Old World. Key: 1 warm/wet (annual temperature T > 20°C, annual rainfall R > 1200mm); 2 warm/humid (T > 20°C, R 600-1200mm); 3 temperate/wet-humid (T 10–20°C, R > 600mm); 4 cool/wet-humid (T 0–10°C; R > 600mm); 5 warm/dry (T > 20°C; R < 600mm); 6 temperate/dry (T 10–20°C; R < 600mm); 7 cold/dry (T < 0°C; R < 600mm) (Image source: Finlayson 2011, page 19).

Table 2.12: The categories of bioclimatic tolerance showing the number of Palearctic species belonging to each category and the relative frequencies (Finlayson 2011).

	Category	**Definition**	**Bioclimates occupied**	**n. Palearctic species**	**% of Palearctic species (EPal)**
Bioclimatic tolerance	A	Specialist	1-20%	271	31.5
	B	Semi-specialist	21-40%	233	27.1
	C	Moderate	41-60%	241	28.0
	D	Semi-generalist	61-80%	64	7.4
	E	Generalist	81-100%	51	5.9
	PALEARCTIC TOTAL			860	

2.5.2 Latitude Range

Latitude range reflects the latitude band on which a species' geographical range is centred (Finlayson 2011; Figure 2.10). 852 of the 860 species Finlayson ranked belong to the categories which are present at sites in this thesis (Table 2.13). Finlayson assigned each of the remaining 8 species to two distinct groups based on their distribution across two latitude bands– 1 = A/C (70°N/50°N), 4 = A/D (70°N/40°N), and 3 = C/D (50°N/40°N). These are included in the calculation of the relative frequencies of each category but are not otherwise discussed in this thesis because the corresponding species do not appear at the sites in this thesis.

Table 2.13: The categories of latitude range showing the number of Palearctic species belonging to each category and the relative frequencies (Finlayson 2011).

	Category	**Definition**	**Centred on latitude band**	**n. Palearctic species**	**% of Palearctic species (EPal)**
Latitude range	A	Arctic	70°N	73	8.5
	B	Boreal	60°N	99	11.5
	C	Temperate	50°N	115	13.4
	D	Mid-latitude belt, warm	40°N	303	35.2
	E	Subtropical	30°N	114	13.3
	F	Multi-latitude	several bands	125	14.5
	B/D	Boreal/montane relict	60°N/40°N	23	2.7
	PALEARCTIC TOTAL			852	

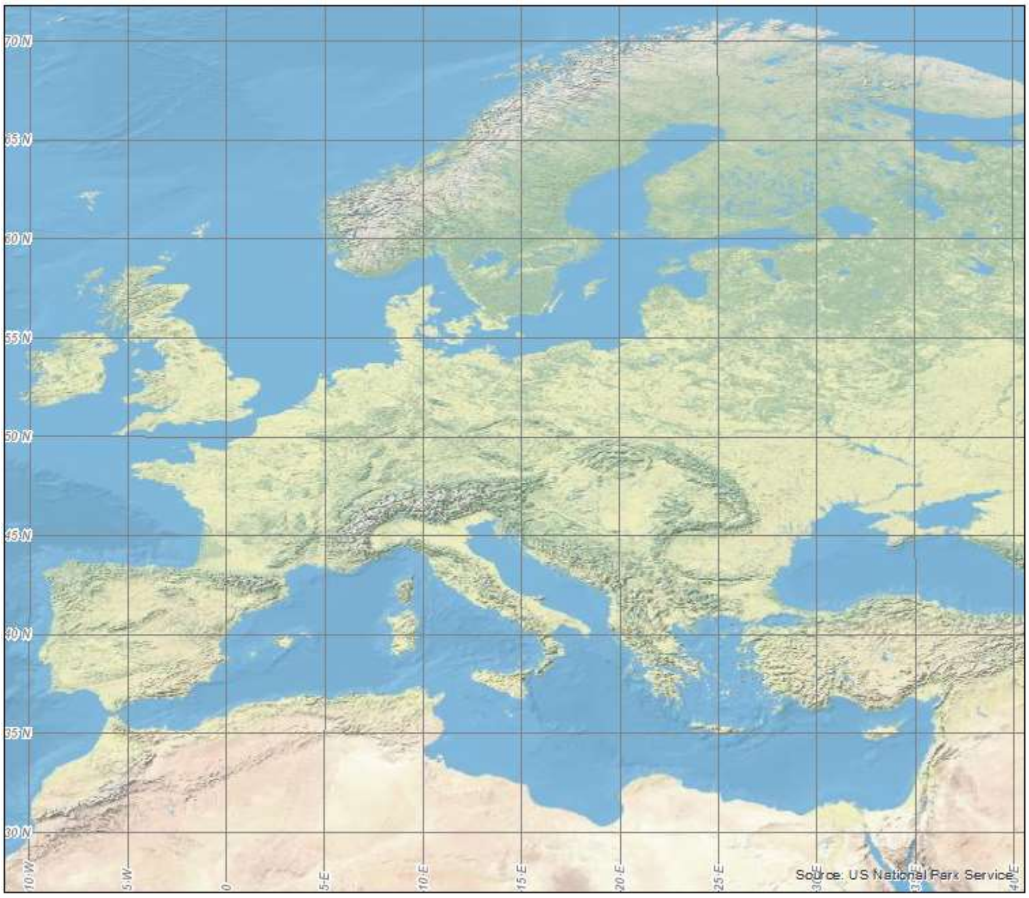


Figure 2.10 Map of western Eurasia and north Africa showing the latitude bands discussed in this thesis.

2.5.3 Temperature and Humidity Tolerance

Finlayson (2011) assigned ranks of temperature and humidity tolerance to 817 of 860 species (Table 2.14; Table 2.15). Both variables were a ranked on a gradient scale from 0%-

100% (cold/arid-hot/humid) and reflected the climatic tolerances of the species based on global maps used to calculate tolerance (Finlayson 2011).

Table 2.14: The categories of temperature tolerance showing the number of Palearctic species belonging to each category and the relative frequencies (Finlayson 2011).

	Category	**Definition**	**Temperature gradient**	**n. Palearctic species**	**% of Palearctic species (EPal)**
Temperature tolerance	A	Cold	1-20%	119	14.6
	B	Semi-cold	21-40%	221	27.1
	C	Moderate	41-60%	172	21.1
	D	Semi-hot	61-80%	117	14.3
	E	Hot	81-100%	188	23.0
	PALEARCTIC TOTAL			817	

Table 2.15: The categories of humidity tolerance showing the number of Palearctic species belonging to each category and the relative frequencies (Finlayson 2011).

	Category	**Definition**	**Humidity gradient**	**n. Palearctic species**	**% of Palearctic species (EPal)**
Humidity tolerance	A	Arid	1-20%	261	31.9
	B	Semi-arid	21-40%	177	21.7
	C	Moderate	41-60%	191	23.4
	D	Semi-humid	61-80%	93	11.4
	E	Humid	81-100%	95	11.6
	PALEARCTIC TOTAL			817	

2.5.4 Foraging and Nesting habitats

The foraging and nesting requirements of birds are not always the same (Cramp *et al.* 1977-1994; Finlayson 2011). For this reason, each variable was assessed individually, though the categories used to describe them were the same. These habitats inform us about the environment which the birds live in and can therefore indicate the presence and absence of these habitats when the bird bones accumulated in the examined sites. The categories reflect the broad habitat inhabited by each species, but do not discriminate between the climatic conditions the habitat occurs in. For example, ‘Forest’ may indicate temperate broad-leaf forest, as well as boreal coniferous forest. Likewise, ‘Open’ reflects all types of open habitat, tundra and plains alike. ‘Mixed’ habitats show traits of both forest and open habitats, while ‘Rocky’ habitats are vertically inclined open habitats. The category ‘Wetland’ includes all water habitats (fluvial, lacustrine, estuarine, and coastal – except marine). ‘Marine’ and ‘Aerial’ only relate to foraging habitat (Finlayson *et al*. 2006; Finlayson 2006; Finlayson *et al*. 2008; Finlayson 2011; Finlayson *et al.* 2016).

Table 2.16: The categories of foraging habitat showing the number of Palearctic species belonging to each category and the relative frequencies (Finlayson 2011).

	Category	Definition	Description	n. Palearctic species	% of Palearctic species (EPal)
Foraging habitat	F	Forest	High tree density	176	20.5
	O	Open	No trees	210	24.4
	M	Mixed	Savannah, shrubland, mosaics	146	17.0
	R	Rocky	Cliffs, rocky landscapes	19	2.2
	W	Wetland	All water habitats, including coastal	223	25.9
	Ma	Marine	Marine	51	5.9
	A	Aerial	Aerial	35	4.1
	PALEARCTIC TOTAL			860	

Table 2.17: The categories of nesting habitat showing the number of Palearctic species belonging to each category and the relative frequencies (Finlayson 2011).

	Category	Definition	Description	n. Palearctic species	% of Palearctic species (EPal)
Nesting habitat	F	Forest	High tree density	184	21.4
	O	Open	No trees	205	23.8
	M	Mixed	Savannah, shrubland, mosaics	148	17.2
	R	Rocky	Cliffs, rocky landscapes	116	13.5
	W	Wetland	All water habitats, including coastal	207	24.1
	PALEARCTIC TOTAL			860	

2.6 Archaeological site information

The following archaeological information was recorded for each of my five study sites in order to provide context to the avian remains recovered: geographic location, human remains, material culture, excavation history, associated stratigraphic unit, site / unit age, associated palaeoenvironmental evidence, cultural evidence, and the presence of human remains.

2.6.1 Geographic location

GPS locations were collected to provide a greater geographical and topographical context for the studied sites. This also allowed the placement of the sites within the latitude ranges of bird species, indicating which bird species naturally appear there in the present day.

2.6.2 Human remains

The presence of human remains in an archaeological site context can inform us about the human taxa contributing to an avian assemblage. Furthermore, Neanderthals are known to have buried their dead, a practice which involves a cognitive capacity which is beyond the purely utilitarian (Tabun – Garrod and Bate 1937; La Ferassie - Peyrony 1934, Defleur 1993; Kebara – Valladas *et al.* 1987; Shanidar – Pomeroy *et al.* 2020; Spy – Maureille, Toussaint and Semal 2013; La Chapelle aux Saints – Rendu *et al.* 2014).

2.6.3 Material culture

When human remains are absent at an archaeological site, material culture becomes key to demonstrating a human presence (Andrefsky 2005). Middle Palaeolithic or Mousterian stone tool industries are the types of material culture associated with Neanderthals in Europe. In the Middle East, these industries may also be attributed to *Homo sapiens* (Mellars 1996; Richter *et al*. 2010; Eixea 2018). The implication of this is that for my four study sites in Europe, I equate Middle Palaeolithic to Neanderthals, and at Tabun Cave in the Middle East, the stone tools there may have been made by Neanderthals or *Homo sapiens.*

The four defining traits of the Middle Palaeolithic technology are centripetal reduction (including the Levallois and discoidal techniques), flake production, an overrepresentation of side scrapers which is the implement of reference, and the long-lasting homogeneity of the technocomplex (Bordes, F.& M. Bourgon. 1951; Bordes 1953; Binford & Binford 1966). Eixea (2018) challenged this homogeneity in a review of lithic assemblages in the western Mediterranean between MIS 5 and MIS 3. Instead, he found a high degree of technical variations and proposed that Neanderthal populations had diverse cultural traditions.

At Abrigo de la Quebrada and Cova Negra, some of the lithic materials were sourced over long distances (>100 km and 30 – 50 km, respectively; Eixea *et al.* 2011, Eixea *et al.* 2014). This speaks to the catchment range of the Neanderthals and their knowledge of which resources were available to them in the landscape surrounding their camp sites (Turq *et al.* 2013). Furthermore, residue analysis on the surfaces of stone tools can indicate exploitation (Hardy *et al.* 2001; Robertson *et al.* 2009; Pedergnana and Olle 2018). The presence of feather barbules on lithics from the sites of Payre and Abri du Maras (France) have been interpreted as evidence of bird exploitation at the site despite no direct evidence being found on the avian remains (Hardy and Moncel 2011; Hardy *et al*. 2013).

Some lithics can point towards a cognitive or cultural capacity in the humans who made them (Andrefsky 2005). These are artefacts that have a purpose beyond the strictly utilitarian and point towards a capacity for complex cognitive abilities in their creators. They may be hunting weapons or tools which require complex manufacturing methods (Koller *et al.* 2001; Mazza *et al.* 2006; Degano *et al*. 2019).

Other artefacts can also convey a symbolic capacity (Henshilwood and Marean 2003; Caron *et al*. 2011; Zilhao 2012). Some carry a clear symbolic content like objects of personal ornamentation (d'Errico *et al.* 1998; Bar-Yosef *et al.* 2009; Zilhao *et al.* 2010; Hoffmann *et al.* 2018b), pigments (d'Errico 2003; Soressi and d'Errico 2007; Zilhao *et al.* 2010; Bonjean *et al.* 2015), engraved images (Rodriguez-Vidal *et al*. 2014), or painted on surfaces (Henshilwood and Marean 2003, d'Errico 2003, Henshilwood *et al*. 2011; Rodriguez-Vidal *et al*. 2014). These artefacts represent a fundamental step away from the solely utilitarian needs pertaining to survival. When artefacts of this type appear in contexts where there is exploitation of birds, they can shed light on the cultural practices of the humans who occupied the site.

2.6.4 Excavation history

The excavation history of a site can reveal information about the methodology employed. The means of collection can and does influence what is recovered (Lyman 2008). Whereas modern excavations seek to answer targeted research questions and implement strict screening and collection procedures, early excavations were generally less thorough. A focus on larger, more impressive objects in early archaeological investigations often lead to smaller remains like birds ending up on spoil heaps (Discamps and Faivre 2017). It is important to recognise this bias, as it can greatly affect the proportion of small remains recovered from a site, which again reflects the reliability of the sample. Absolute dates help us pinpoint where in the past a context is placed chronologically. The dates recorded in this thesis are relative to the bird material examined in the sense that they belong to objects within the same or adjacent stratigraphic contexts to the recovered material. Dates are vital in an effort to investigate the genesis of bird exploitation in Eurasia by providing a chronological framework for evidence of the behaviour on both intra- and intersite-levels. Available dates are recorded along with the method through which they were attained and margins of error.

2.6.5 Spatial position

The spatial distribution of remains can indicate the agency behind an accumulation. Bird bones recovered close to a cave wall are more likely to be the remains of raptor pellets dropped by roosting birds, while remains excavated mid-cave are more likely there due to carnivore or human agency (Serjeantson 1997, Laroulandie 2000). Spatial distribution within a site occupied by humans can also indicate behaviours exhibited by the inhabitants (Wadley 2001; Currant and Price 2012; Jaubert *et al.* 2016). Maps of the density and distribution of human debitage and faunal remains in archaeological sites is a common method for understanding how humans and non-humans used the space (DiModica 2010; Discamps *et al.* 2012; Blasco *et al.* 2016b; Sánchez-Romero *et al.* 2020). Where noted by the principal researchers, the spatial context of the remains was recorded.

2.6.6 Environmental evidence

Biological evidence recovered from archaeological excavations is used to reconstruct past environments (Finlayson 2006; Finlayson *et al.* 2016; Sanchez-Marco *et al.* 2016; Carrion, Lalueza-Fox and Stewart 2019). In this section I report on three main types of evidence that have been recovered and studied to varying degrees at all of my study sites: macrofauna, microfauna, and flora. There are many other proxies that can be used for environmental reconstructions, but this information was not readily available for my sites.

2.6.6.1 Macrofauna

Large vertebrate remains recovered from archaeological contexts provide useful information in terms of human dietary preferences, but these have less value for environmental reconstruction. This is because prey animals may be over-represented in an assemblage and therefore do not represent the full range of fauna present in an ecosystem (Renfrew and Bahn 1993). However, the presence and absence of macrofauna are valuable to this thesis both as an aspect of Neanderthal behaviour, and as representatives of the habitats available close to the site. This information was compared to the results of the avian ecological analysis at each site.

2.6.6.2 *Microfauna*

Microfauna remains are the remains of small mammals such as rodents, insectivores, and bats. They are more informative of past environments than macrofauna. This is because they have smaller home ranges and, like birds, certain species of microfauna have highly specific environmental requirements (Reitz and Wing 2008; Finlayson 2011). In this sense they are more sensitive to climatic oscillations and react relatively quickly to climatic and environmental changes (Renfrew and Bahn 1993; Connolly *et al*. 2019). Microfauna remains tend to accumulate naturally on a site and therefore give a more reliable representation of the species present in the ecosystem. Microfauna may also represent prey animals for predatory birds (Andrews 1990), and may add to the interpretation of the avian sample by identifying the presence of raptors where no skeletal remains are found. The recovery of microfauna remains relies heavily on a thorough screening strategy, so may be less reliable in older assemblages where screening was not well executed (Lyman 1994; Reitz and Wing 2008; Serjeantson 2009).

2.6.6.3 Flora

Palaeobotanical studies such as palynology (Bryant and Holloway 1983; Mercuri 2015; Carrión *et al.* 2003, 2008, 2018, 2019) and anthracology (Chabal 1997; Chabal *et al*. 1999) contribute to archaeology through the identification of plants which existed in the environment close to a site. Identification of past floras can produce an image of the past landscape and inform us about which habitats were available at the time of deposition. This is a useful proxy in this thesis for comparison against the ecological data collected through the presence of avian species (Finlayson 2006; Finlayson and Carrion 2007; Finlayson 2011).

Palynology is the study of palynomorphs (Halbritter *et al.* 2018). These pollen, spores, cysts, and diatoms. Pollen preserved in the sediments of archaeological sites provide important information pertaining to fluctuations in the vegetation present in the surrounding landscape (Bryant and Holloway 1983; Mercuri 2015; Carrion *et al.* 2003, 2008, 2018, 2019). In this sense, pollen is an excellent proxy in environmental and climate reconstructions, as vegetation will change in response to changes in temperature and rainfall (Finlayson 2006). The results of palynological studies can be used to date sediments by comparison to known core samples taken at strategic locations worldwide (Davis 1976; Brewer *et al.* 2017).

Anthracology, the study of charcoal remains, has its origins in the 19th century. It is useful in the study of long-term vegetation reconstruction as it can be applied on to stratified occupation layers across several sites. In north-eastern Iberia Allue *et al.* (2017) summarized the anthracological sequence of five sites spanning the Paleolithic to the Holocene. The analysis of wood charcoals from caves, settlements, camp-fires and graves can also inform us about human use of fuel and timber (Chabal 1997; Ludemann and Nelle 2017ab).

2.7 Data Analysis

The taxonomic, and taphonomic variables described in the above sections 2.2 and 2.3 were quantified using three abundance calculations. These and the ecological variables in section 2.4 were analysed using chi-square tests and Categorical Principal Component Analyses (CATPCA). These are defined in this section.

2.7.1 Faunal abundance

Three ways are commonly used to calculate abundance of either a specimen, species, element, or a taphonomic modification. These are: number of identifiable specimens (NISP), minimum number of individuals (MNI) and number of identified taxa (NTAXA). I use all three in my thesis although there are advantages and disadvantages to each method (Figure 2.11).

NISP is a quantitative, observational unit of the number of identified specimens in the sample, including whole bones and bone fragments (Grayson 1984). It is the simplest, and oldest, method of quantifying faunal data and it is the first step taken by researchers when calculating the taxonomic abundances of an assemblage (Chaplin 1971: 64-67; Payne 1975; Grayson, 1978). NISP can be affected by butchering processes, differential preservation, and collection biases. This has led to debate on the usefulness of the unit when describing the relative abundance of species in a collection (White 1952, 1953; Payne 1972; Grayson 1973, 1979, 1984; Lyman 1979, 1994, 2008; Bobrowsky 1982; Ringrose 1993; Driver 1993; O'Connor 2000).

MNI is a calculation of the smallest number of animals necessary to account for the specimens of a certain taxon in a sample (White 1953; Shotwell 1955). It was first forwarded by White (1953) as a method of translating NISP into diet by counting the number of prey animals represented in the accumulation. MNI is calculated for each element of a species in the sample, then the maximum count is the MNI for the species (Ringrose 1993). MNI is limited by aggregation -the contextual units to which the bones are allocated for study- and by sample size (Grayson 1973, 1978. 1979, 1984; Klein and Cruz-Uribe 1984; O'Connor 2000; Lyman 2008).

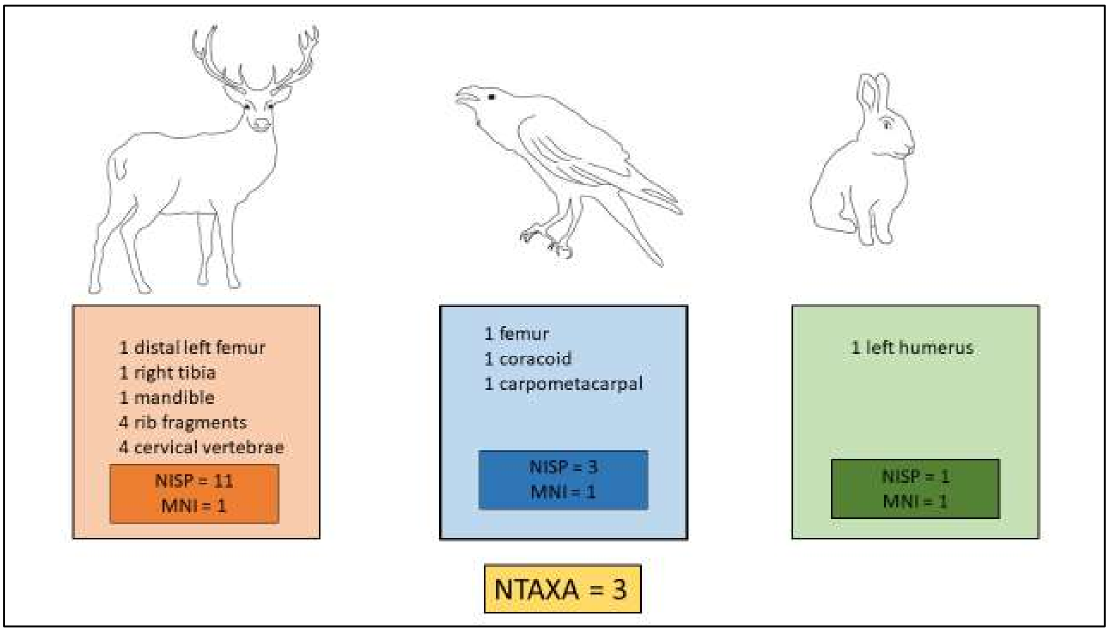


Figure 2.11: Illustration showing quantification of faunal remains. NISP = number of identified specimen, MNI = minimum number of individuals, NTAXA = species richness.

NISP and MNI generally produce equivalent results when analysing taxonomic abundance, unless levels of fragmentation in the sample are very high (Grayson 1984; Klein and Cruz-Uribe 1984). Fragmentation affects NISP and MNI differently. The NISP is increased by low to moderate levels of fragmentation but falls at higher levels because fewer specimens are identifiable, while MNI is reduced by fragmentation at all levels because of the decreased number of fragments which can be counted (Marshall and Pilgrim 1993). Fragmentation causes a higher inflation of the NISP in mammals than in birds and is more likely to decrease the NISP of birds as the bones quickly become too fragmented to be identified (Serjeantson 2009). Therefore, a rise in NISP paired with a rise in MNI can be interpreted as evidence of more individuals being introduced to a site rather than as the product of a higher rate of fragmentation or differential preservation (Marshall and Pilgrim 1993).

NTAXA is a tally of the unique taxa in a collection (Grayson 1991). Also known as species richness, it can reflect a broad-spectrum subsistence strategy when human traces are found on a bone, but also counts towards the richness of the ecosystem of a given site (Faith 2011; Grayson and Delpeche 1998; Lyman 2012, 2014). If a significantly positive relationship between NISP and NTAXA occurs, it can represent changes in human diet breadth. Humans accelerate the skeletal part input through hunting and introduce a wider range of species to the accumulation (Grayson and Delpeche 1998).

Though the NISP of some of the collections under study in this thesis contained several hundred specimens, many species were represented by single specimens. In these circumstances, it was better to rely on presence and absence of a species and the frequency in presence in different contexts of a given site to assess the ecological significance of the birds in the accumulation. It follows that a single specimen always represents at least one individual (Payne and Munson 1985). However, absence of a species does not imply absence in the ecosystem.

2.7.2 Statistical analyses

Chi-square tests are non-parametric tests designed for use with frequency data (Pearson 1900). They are the most widely used test of frequencies and are applicable to almost all datasets which concern unrelated data (Drennan 2010; Hawkins 2019). This means that each object must only contribute to a single category, or combination of categories, depending on which type of chi-square test is used. A one-way chi-square test (also called a goodness-of-fit chi-square test) was used to compare observed with expected ecological tolerances for the Palearctic in Chapters 3-7.

For comparison between the study sites in Chapter 8, low frequency counts at Tabun and Scladina required an alternative approach. Contrary to the Pearson's Chi^2- test, the Fisher-Freeman-Halton exact test allows calculation of a p-value when more than 20% of the expected values are less than 5. The test is conventionally reserved for 2x2 contingency tables, but it can be applied to larger tables. In this thesis, running exact tests on 5x5 and 5x7 tables was too computationally demanding to test every possible permutation in SPSS, so I applied the Monte Carlo method to calculate the p-value from a sample of 10,000 permutations (Mehta and Patel 2011).

Categorical Principal Component Analyses (CATPCA) were performed using SPSS v. 27 software with a variable principal normalisation discretization method in order to identify the most important ecological variables at the study sites. Final scores were obtained by a Varimax rotation with Kaizer normalisation of the CATPCA and displayed as biplots where those objects variables which were most closely related appear closer on the plot (IBM SPSS V27 2020).

Linear regression was used to examine the relationship between NISP and MNI, and the results were tested for significance using Spearman's rank coefficient (Spearman 1904) and t-statistic to calculate the p-value (Spearman 1904, Corder and Foreman 2014).

2.7.3 Additional software

I used the following software programs to create the figures presented in this thesis.

- ArcGIS 10: GIS software is frequently employed in archaeological research to study spatial distribution (Conolly, James and Lake 2006). In this thesis I used AcrGIS 10 to create key maps illustrating the distribution of sites across the Neanderthal range
- Adobe Illustrator: I used this software to create intrasite spatial distribution maps for Scladina and Tabun caves, and to create diagrams.

3 Gorham's Cave

In this chapter, I examine the surviving avian remains of the Waechter collection (Waechter 1951, 1964; Eastham 1968) from Gorham's Cave, Gibraltar. Gibraltar is a peninsula on the southernmost part of the Iberian Peninsula, 21 km from North Africa (Rodríguez-Vidal *et al.* 2004, 2007; Finlayson *et al*. 2006, 2008, Finlayson *et al.* 2008). Gibraltar is a unique site for the study of Middle Palaeolithic bird species as it not only lies in the path of the East Atlantic bird migration flyway between Africa and the western Palearctic (Boere and Straud 2006; Finlayson 2010), but it was also part of a southern Iberian glacial refugium during the Last Glaciation (MIS 5 - MIS 3) (Carrión *et al.* 2003, 2008, 2018; Gomez and Lunt 2007; Rodríguez-Sanchez *et al*. 2008; Cortes-Sánchez *et al*. 2008; Finlayson *et al*. 2008). The avifaunal remains from Waechter's excavations have not been studied beyond the classification of the specimens conducted by Mrs Anne Eastham (1968). Consisting of 209 Middle Palaeolithic specimens, I suggest the collection can add to our understanding of Neanderthal behaviour and ecology in Gibraltar by providing information about the agency behind the accumulation and the habitats which are reflected in the composition of species present. This new data will complement the results of more recent excavations (Stringer, Barton, and Finlayson 2000; Barton, Stringer, and Finlayson 2012; Finlayson *et al.* 2012; Blasco *et al.* 2014, 2016a).

The chapter begins with an overview of archaeological results from Gorham's Cave. Followed by a run down of the distribution of taxonomical identifications. This is followed by a presentation of my ecological and taphonomic results, which are subsequently discussed in the context of Neanderthal-bird interactions and the Middle Palaeolithic envoironmental conditions in Gibraltar during the Last Glaciation (MIS 5 – MIS 3).

3.1 Site Background

Gorham's Cave (36°7'13.43"N, 5°20'31.47"W; Figure 3.1) is located on the south-east side of the Rock of Gibraltar, facing east into the Mediterranean Sea and flanked by the Middle Palaeolithic sites of Bennett, Vanguard, and Hyaena Caves. Together they are the principal sites of the Gorham's Cave Complex, a UNESCO World Heritage site since 2016 (Finlayson 2015).

The Rock of Gibraltar lies on the northern shore of the Strait of Gibraltar, joined to the rest of the Iberian Peninsula by a sandy isthmus (Rose and Rosenbaum 1990, 1991; Rose 2000). A promontory of Jurassic limestone, it rose from the ancient seabed through a series of tectonic events by 15-20 million years ago (Rose and Rosenbaum 1991; Rodríguez-Vidal *et al.* 2004). The same tectonic forces responsible for the rise of the Rock of Gibraltar also created fissures within it (Rose and Hardmann 1996). External erosional forces such as the dissolution of limestone from rainfall also contributed to speleogenesis through the formation of karstic cave systems (Rose and Hardmann 1996). At sea level, erosion through wave action gradually created sea caves like Gorham's Cave, some of which came to provide perfect shelter for a variety of species, hominins included (Rodríguez-Vidal and Gracia 2000; Rodríguez-Vidal *et al.* 2004). Continuing uplift throughout the Quaternary has lifted several sea caves up to the higher terraces (Rodríguez-Vidal *et al.* 2004). To date, 214 caves have been discovered on the Rock of Gibraltar (Gibraltar National Museum Caving Unit, 2019).

Figure 3.1: Gorham's Cave sits between Vanguard and Bennet's Caves in what is known as the Gorham's Cave Complex. The cave faces east onto the Mediterranean coast. Remnants of raised beaches representing the MIS 5 high stands can be seen attached to the cave/cliff face in the lower right quadrant of the image. Photo: Linda Amos 2015

Gorham's Cave extends c. 100 metres from the cliff face into the rock where it narrows to bedrock. It contains ~18 m of stratigraphy made of environmental and cultural evidence pertaining to the last 125,000 years (Stringer *et al.* 2000; Finlayson *et al.* 2006). At different times, the cave has served as a shelter for Middle Palaeolithic Neanderthals, Upper Palaeolithic Magdalenian and Solutrean anatomically modern humans, Neolithic fishermen, and as a shrine in the Punic period when sailors would leave offerings to their deity before embarking on voyages beyond the Pillars of Herakles, the marker of the end of the world in Classical times (Waechter 1951; Stringer *et al.* 2000; Barton *et al.* 2012; Stringer 2012; Finlayson *et al.* 2006, 2008, 2014, 2021). Gorham's Cave is one of eight caves on the Rock known to contain evidence of Middle Palaeolithic occupation, the others being: Beefsteak Cave, Bennett's Cave, Devil's Tower Rock Shelter, Europa Point 1, Forbes's Quarry, Hyaena Cave, Ibex Cave, and Vanguard Cave (Finlayson 2015).

During the Late Pleistocene, periods of low sea level exposed a coastal plain and a dune-type environment on the eastern side of the Rock that extended in front of Gorham's Cave (Finlayson and Giles-Pacheco 2000; Siddall *et al.* 2003; Rodríguez-Vidal *et al.* 2013). Fresh water springs, still active on the seabed today, created lakes and allowed for vegetation and a variety of animals to thrive (Faure *et al.* 2002; Finlayson *et al.* 2006, 2008; Finlayson and Carrión 2007; Carrión *et al.* 2008, 2018; Rodríguez-Vidal *et al.* 2013). In addition to mammal, reptile, and amphibian populations a great variety of birds exploited the habitats around the Rock of Gibraltar (Currant 2000; Currant, Fernandez-Jalvo and Price 2012; Currant and Price 2012; Price 2012; Blain *et al.* 2013; Gleed-Owen and Price 2012; Finlayson 2006; Finlayson *et al.* 2008; Finlayson *et al.* 2016). Remarkably, 151 species of birds have been found in Middle Palaeolithic contexts in Gibraltar, representing 29% of species still breeding in Europe today (Finlayson 2011). 142 species have been identified in the archaeological levels of Gorham's Cave (Finlayson *et al.* 2016)

3.2 Archaeological Investigations

Gorham's Cave was discovered in 1907 by Captain A. Gorham of the 2nd Battalion Munster Fusiliers, who inscribed his name and the date of discovery on the wall of the cave (Waechter 1951,1964). The first archaeological investigations were conducted on the uppermost levels by Lt. George Baker Alexander between 1945 and 1948 (Stringer 2012). There are no preserved materials describing these excavations (Finlayson 2010).

3.2.1 Waechter’s excavation 1948-1954

The next phase of excavation spanned several seasons between 1948 and 1954 under the direction of John D’Arcy Waechter of the British Institute of Archaeology in Ankara (Table 3.1; Table 3.2). He excavated a major portion of the sediments and published his discoveries in two publications, describing an 18-metre sequence of layers named A-U, of which G-T corresponded to the Middle Palaeolithic (Waechter 1951, 1964).

Waechter concluded that the Gorham’s Middle Palaeolithic belonged to an Upper Mousterian lithic tradition similar to the nearby Devil’s Tower Rock Shelter. This equates to the Typical Mousterian in today’s terminology (Bernal 2017). He identified twenty-one layers (A-U) which were interpreted as spanning the Epi-Monastirian to the Punic Era (Waechter 1951, 1964, Zeuner 1953). Within these he located five Mousterian levels of occupation (Layers G, K, M, P and R) separated by sterile sands and stalagmitic floors. Zeuner (1953) suggested that these sterile layers were deposited during high-sea level phases when the cave was less accessible. During the purported low-sea-level phases, Waechter (1964) proposed that the faunal remains recovered pointed towards a generally stable environment despite Layer G exhibiting a higher frequency of red deer to ibex than the underlying layers and an abundance of carnivores in Layer K. In Layer G he also discovered charcoals and cone fragments identified by C. R. Metcalf of the Royal Botanic Gardens at Kew as stone pine (*Pinus pinea*). Radiocarbon dates placed the occupations in Layer G between 47,000 and 49,200+/-3200 years BP (Waechter 1964; Vogel and Waterbolk 1964).

Table 3.1: NISP of mammal species by stratigraphic context at Gorham's Cave, after Waechter (1964).

		Layer (NISP)													
Taxonomic ID	**Common name**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N/O**	**P**	**Q**	**R**	**S**	**T**	**U**
Bos cf. *primigenius*	aurochs	5				5		11		1	1				
Cervus elaphus	red deer	52				29	1	53	4	10	1	9		3	1
Capra cf. *ibex*	ibex	11				162		132	6	30	2	1		1	1
Sus scrofa	wild boar						2		4			1		1	
Equus caballus	horse	2						8				1			
Dicerorhinus sp.	rhinoceros sp.		1		1	2		1							
Canis lupus	wolf					2		1		1					
Ursus arctos	brown bear					3	1	1							
Crocuta crocuta	spotted hyena	5				5		4		1	1			1	
?Crocuta crocuta	spotted hyena coprolites	2		1		21	1	2	1	1		3			
Felix sylvestris	wild cat	1						1	1						
Felis lynx	lynx	5				2		2		1	1	1			
Panthera pardus	leopard	1				6		2			2				
?Panthera cf. *leo*	lion	?				?									
Halichoerus grypus	atlantic grey seal									?					
Erinaceus sp.	hedgehog sp.	1													
Talpa sp.	mole sp.														1
Oryctolagus cunniculus	rabbit	94	5		5	187	21	178	30	52	17	56		3	1
Total		**179**	**6**	**1**	**6**	**424**	**26**	**396**	**46**	**97**	**25**	**72**	**0**	**9**	**4**

3.2.2 Recent excavations 1989 – present

The Gibraltar Caves Project initiated new investigations in 1989 that are still in progress today (Table 3.2). This collaboration between the Gibraltar Museum, the British Museum, and the Natural History Museum surveyed what remained after the Waechter excavations and attempted to correlate the standing sections with Waechter's documentary records (Stringer, Barton and Finlayson 2000; Barton, Stringer, and Finlayson 2012; Finlayson 2015). In addition, they investigated neighbouring Vanguard and Hyaena Caves, and Ibex Cave near the summit of the Rock of Gibraltar (Stringer, Barton and Finlayson 2000; Barton, Stringer, and Finlayson 2012). At Gorham's Cave they were unable to find any secure correspondence between Waechter's levels and the stratigraphy they examined (Stringer 2000, 2012; Collcutt 2012; Colcutt and Currant 2012). However, the excavations did spur a sequence of publications describing the nature of the site, the landscape surrounding it and the humans who inhabited it (Stringer, Barton and Finlayson 2000; Rodríguez-Vidal *et al.* 2004, 2007, 2010, 2013, 2014; Finlayson 2006; Finlayson *et al.* 2006, 2008, 2014; Barton, Stringer, and Finlayson 2012; Jennings 2007; Jennings *et al.* 2011; Carrión *et al.* 2003, 2008, 2018; Muniz *et al.* 2019; Finlayson 2019).

Sediment studies conducted by Rodríguez-Vidal *et al.* disproved the three-phase sea-level theory forwarded by Waechter and Zeuner (2004, 2007). In fossilized marine beaches inside and around the cave, they found evidence of several sea-level fluctuations during the MIS 5 interglacial aligning with more widespread data for the Mediterranean collected by Zazo *et al*. (2000). Highstands in MIS5c and 5a reached 5 metres and 2-1.5 metres above present sea-levels (Hoyos *et al.* 1994, Zazo *et al.* 1994, 1999). No emerged marine terraces were representative of MIS3 (Jimenez-Espejo *et al.* 2013). During this period, the average sea-level in Gibraltar was ~80 m below the present (Siddall *et al*. 2003). At this point the shoreline would have been around 4.5 km from the mouth of Gorham's Cave (Finlayson 2006; Finlayson *et al.* 2008; Rodríguez-Vidal *et al.* 2013; Jimenez-Espejo *et al.* 2013).

The coastal plains that were exposed supported a highly varied mosaic-type ecosystem that was reflected in the faunal and floral record of the site (Finlayson 2006; Finlayson *et al.* 2008, 2016; Bernal 2017, Table 3.3). Palynological and anthracological studies revealed a varied Mediterranean landscape in the Middle Palaeolithic (Carrión *et al.* 2005, 2008, 2018; Ward, Gale and Carruthers 2012), with vegetation including oaks (*Quercus* sp.), pistachios (Pistaceae) and junipers (*Juniperus* sp.) in addition to a dominance of pine (*Pinus* sp.). In addition to woodlands, species indicating savannah, grassland with heaths, scrubs, wetlands, and Mediterranean coastal scrubland were present in the pollen count (Carrión *et al.* 2003, 2005, 2008, 2018; Ward, Gale, and Carruthers 2012). Zooarchaeological studies of the recovered macro- and microfauna (Currant 2000; Currant & Price 2012; Price 2012; López-García *et al.* 2011), herpetofauna (Gleed-Owen and Price 2012; Blain *et al.* 2013), and avifauna (Cooper 1999, 2000, 2012; Finlayson 2006, Finlayson *et al.* 2006, 2008, 2012) suggested a stable climate persisting throughout the Late Pleistocene record with summer temperatures equal to the present day and slightly cooler winters. These results led to an interpretation of Gibraltar as part of a southern Iberian glacial refugium - an environment unaffected by the climatic changes caused by advancing ice sheets in northern Europe where displaced northern species lived alongside species indigenous to the latitude band (Finlayson and Carrión 2007; Finlayson 2007; Carrión *et al.* 2008; Cooper 1999; Cortes-Sanchez *et al.* 2008).

Since 1999, ongoing excavations have been under the sole direction of the Gibraltar National Museum. In 2014, the discovery of a Middle Palaeolithic abstract engraving on the cave wall was announced (Rodríguez-Vidal *et al.* 2014). Dated to >39,000 BP, the engraving represents a purposeful, non-utilitarian abstract pattern and is evidence of complexity in Neanderthal behaviour. Support for the complex cognitive abilities of Neanderthals is also visible in avian remains recovered since 1989 (Finlayson *et al.* 2012; Blasco *et al.* 2014, 2016a). Detailed investigations indicated human exploitation was found on chough, pigeon and raptor bones. Striations created by stone tools through human agency were identified not only on meat-heavy elements, but also along wing bones close to the quill knobs and on the distal limb bones. This has been interpreted as evidence of feather and talon harvesting, a deliberate and non-functional practice (Finlayson *et al.* 2012; Blasco *et al.* 2014, 2016a).

Table 3.2 Summary of 1990s-present investigations compared with earlier stratigraphic interpretations. Compiled from Barton et al. (2012).

Stratigraphy				**Dates (AMS)**	**Dates (OSL)**	**Micromammals**	**Lithics**	**Vegetation**	**Herpetofauna**
Waechter (1964)	**Zeuner (1953)**	**Colcutt and Currant (2012)**	**Notes (author's own)**	**(Higham *et al.* 2012)**	**(Rhodes 2012)**	**(Price 2012)**	**(Barton and Jennings 2012)**	**(Ward, Gale, Carruthers 2012)**	**(Gleed-Owen and Price 2012)**
A						Temperate climate without extreme cold or aridity. Terrain offers a variety of ecological niches. Remarkably stable.		Environmental stability throughout the Last Glacial period. Charred seeds indicate that Pinus pinea nuts formed a major constituent of diet in the Upper Pleistocene.	Wide range of haibtats available in the area surrounding the cave. No evidence for extended periods of cold conditions.
	Stal 4	USFm(base)							
B,D,E		CHm							
	Stal 3	UBSm.1							
F		UBSm.2-4	Exact correlation not possible	**UBSm** = 23800+/- 600 - 42200+/-1100 BP			Upper limit of Mousterian		
G		UBSm.5-7			**UBSm.5** = 39.2+/-6.6ka BP		Exploitation of highly localised raw material resources. Many available right outside the cave mouth. At most moveement of 20km to procure material. Episodic, ephemral activities within the area of the cave dripline.		
H	Stal 2	BeSm	Loose correlation, probably only OSSm	**BeSm.1**= 31900+/- 1400 - 46700+/- 1900 BP	**BeSm PLsm.3** = 49.4+/- 4.4ka BP				
J-M		LBSm							
J,K	Stal 1	Fine facies	Brightly coloured/banded (Waechter)						
L, M		Coarse facies	Laminated sands (Waechter) **Layer M:** Possibly equates to LBSmcf.11 (Cooper 1999)	**LBSmcf.4**= 45300+/-1700 - 51700+/-3300 BP	**SSLm Usm.2** = 54.2+/- 9.0ka BP, **SSLm Usm.5** = 67.2+/-5.6ka BP				
N/O		SSLm(Usm)	"scree-like"						
P,Q,R		SSLm(Lsm)	Sands, limestone clasts, distributed stalagmites		**SSLm Lsm.10** = 90.0+/- 8.2ka BP				
S I, II, III		VSSm&RSSm							
T		CSSm (top)			**CSm** = 119+/-16ka BP				
U			Mousterian core found in this level, raised beach is further down.						

Table 3.3: Habitats reflected by the ungulate species in Waechter's layers, as presented by Bernal in his PhD thesis (2017). Values reflect NISP.

		Layer (Waechter)												
Habitat	**Taxa**	**G**	**H**	**J**	**K**	**L**	**M**	**N**	**P**	**Q**	**R**	**T**	**U**	**Total**
rocky	caprids	11			162		132	6	30	2	1	1	1	**346**
woodland	cervids/suids	52			29	3	53	8	10	1	10	4	1	**171**
plains	equids/bovids/rhinos	7	1	1	7		20		1	1	1			**39**
Total ungulates		**70**	**1**	**1**	**198**	**3**	**205**	**14**	**41**	**4**	**12**	**5**	**2**	**556**

3.3 The Waechter Avifauna

The avifaunal remains collected by Waechter were held in the private collection of archaeologist Mrs Anne Eastham for more than half-a-century. Mrs Eastham published her analysis of the material in 1968 (Eastham 1968). Mrs. Eastham agreed to donate the collection to the Gibraltar National Museum in September 2018, after I visited her at her home in Pembrokeshire, Wales.

The material required a period of curation before analysis could take place. The specimens were stored in bulk bags according to species identification. Before analysis, I divided them into layer and species following Waechter's original stratigraphy and bagged them individually. Some specimens were marked with numbers in addition to level. No explanation of those numbers appeared in any published material, and they were therefore disregarded in the analysis. Each specimen was assigned a unique provisional number in the format LAYER000. Of concern was the presence of individual elements in some of the bulk specimen bags that clearly did not belong to the species indicated on the bag. These specimens were re-bagged, and their classification revised.

In preparation for her doctoral thesis, Dr. Joanne Cooper visited Mrs Eastham at her home and reviewed the material. She found some of the taxonomic identifications to be unreliable (Cooper 1999). Cooper justified the re-identification of several species from Eastham's collection in her thesis, including the reclassification of snowy owl (*Bubo scandiacus)* and demoiselle crane (*Anthropoides virgo)* specimens to eagle owl (*Bubo bubo)*, and the assignation of several specimens labelled as white stork (*Ciconia ciconia*) to the order Accipitriformes. Due to this, and to the uncertain nature of Waechter's stratigraphy, Cooper did not include the Waechter avifauna in her analysis of Gibraltarian Middle Palaeolithic avifauna (Cooper ibid). After reading Cooper's justification and examining the specimens myself, I agree with her revised identifications and use them in this thesis. Mrs Eastham herself admitted that this collection was her first archaeornithological project and that those taxonomic revisions were merited (Eastham, *pers. comm.*).

3.4 Taxonomic Results

The collection consisted of 196 remains (NISP), 190 of which could be identified beyond class (Aves sp.). Of these, 177 were identified to species-level, four to genus, one to family, and eight to order (Table 3.4). Three layers (H, J, T) were represented by a single element identified to species, and 14 taxa were represented by a single element. The species richness (NTAXA) was 27.

181 remains (92.3%) originated from five layers (G, K, M, P and R) which Waechter identified as Middle Palaeolithic occupations (Waechter 1951, 1964). The lower NISPs in layers P and R in comparison to layers G, K and M were likely due to the thin nature of level P, and the sparse occupation evidence in the south side of the cave where Layer R was excavated (Waechter ibid). Additionally, at this depth, Waechter only excavated a small area of each layer whereas layers G, K and M were much more extensively investigated (Waechter 1964).

Eighty of the remains (40.8%) were of rock dove (*C. livia*), whose descendant, the feral dove, is resident in Gorham's Cave to the present day (Finlayson 2010). Two species of chough (*P. pyrrhocorax*, *P. graculus*) constituted a further 33 specimens (16.8%), with the red-legged partridge (*A. rufa*) ranking as the third most prolific taxon (n=18, 9.2%). Fourteen classifications were represented by a single element. Six (3.1%) specimens were not identifiable beyond Class and were recorded as *Aves sp*. Only specimens identified to species level were considered in the ecological analyses.

Other than a single specimen of mistle thrush (*T. viscivorous*) and two remains of spotless starling (*S. unicolor*) in level G, there were no non-corvid passerines in the sample. Non-corvid passerines are by far more speciose than non-passerines, constituting 41.6% of the present European avifauna (Lepage 2020). Their scarcity in the sample may be due to a collector's bias towards larger specimens paired with not using sieves during excavation, or to post-depositional processes, which could have resulted in the degradation of small, fragile passerine remains (Serjeantson 2009).

Eastham's identification of a rock ptarmigan (*L. muta*) in layer G is likely a misidentification. Gorham's Cave is outside the range of this species both in the present and in the Middle Palaeolithic (Birdlife Data Zone 2021; Tyrberg 1998, 2008; Finlayson 2011).

The MNI present in the collection is 107, of which 91 are from the levels identified as containing Neanderthal occupations (G, K, M, P and R). An investigation of the relationship between NISP and MNI showed that more individuals were preserved in Layers G, K, and M than in other, less numerically rich layers (P, R) in the cave during periods of human occupation (Figure 3.2). During periods without human occupation, few individuals were introduced into the cave. These layers are also those with the highest NTAXA. Results of Spearman correlation tests indicated that there was a significant positive association between both the NISP and MNI (rs[11] = .9884, p = 0.001) and the NISP and the NTAXA (rs[11] = . 9579, p = 0.001).

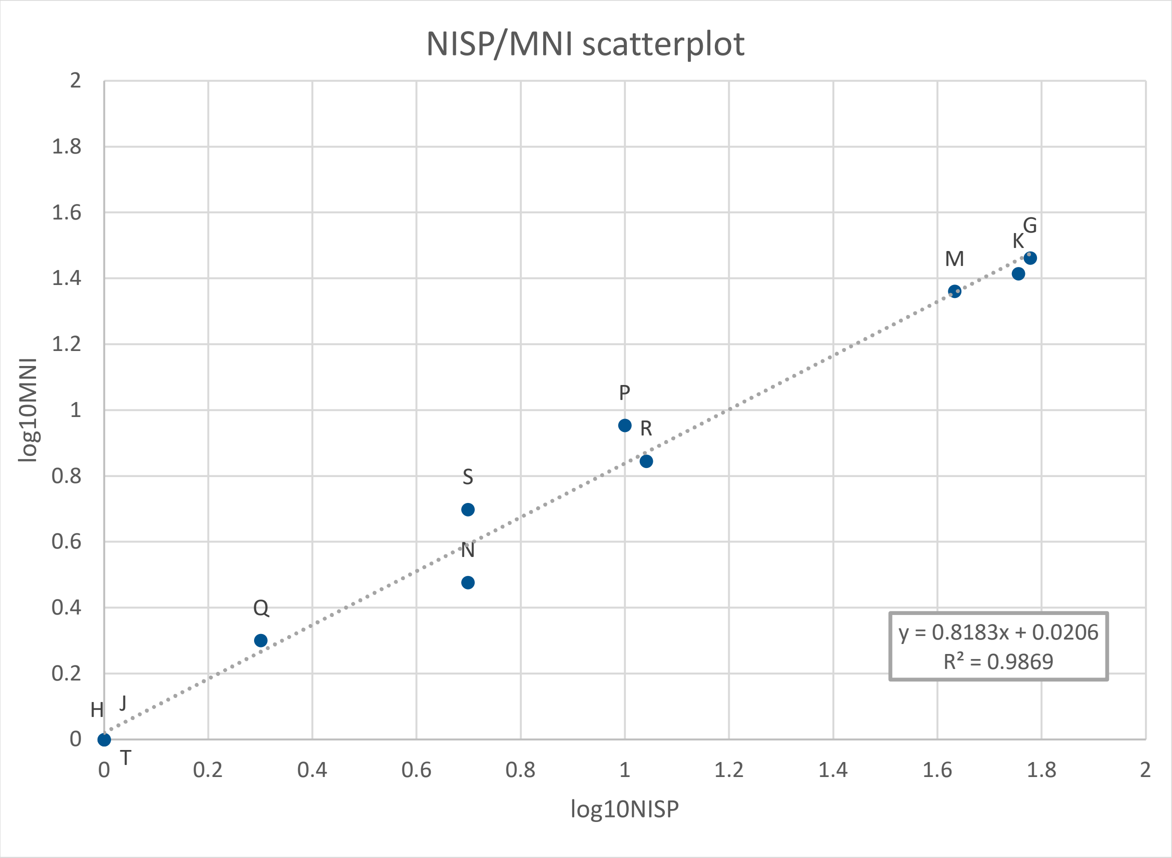


Figure 3.2: Scatterplot illustrating the relationship between NISP and MNI. More remains per individual were preserved in the most well-explored occupation layers (Layers G, K, M), but the R^2-value indicated that this increase fell within the expectations of the model.

Table 3.4: Taxonomic representation of Waechter Avifauna, including NISP, NTAXA, and MNI. † indicates species that are not extant in the present day.

			LAYER											TOTAL
Order	**Genus**	**Species**	**G**	**H**	**J**	**K**	**M**	**N**	**P**	**Q**	**R**	**S**	**T**	
GALLIFORMES														
	Lagopus	*muta*	1											1
	Alectoris	*rufa*	8			3	2			1	3	1		18
ANSERIFORMES														
	Tadorna	*ferruginea*							1					1
	Aythya	*fuligula*					1							1
	Clangula	*hyemalis*					1							1
	Anatidae?						1							1
COLUMBIFORMES														
	Columba	*livia/oenas*	30			23	15	4	5	1	2			80
	Columba	*palumbus*				1								1
	Columba	sp.	1											1
GRUIFORMES														
	Fulica	*atra*	1				1		1					3
CHARADRIIFORMES														
	Haematopus	*ostralegus*				1	1							2
	Larus	*argentatus*				1								1
	Pinguinus †	*impennis* †				2								2
GAVIIFORMES														
	Gavia	*stellata*				1					1			2
SULIFORMES														
	Phalacrocorax	*aristotelis*	2			1	1				1	1		6
PELECANIFORMES														
	Ardea	sp.				1								1
ACCIPITRIFORMES														
	Aquila	*fasciata*										1		1
	Accipiter	*gentilis*									1			1
	Haliaeetus	*albicilla*	1			2								3
	Accipitriformes		2	1		3	1	1						8
STRIGIFORMES														
	Bubo	*bubo*					1							1
	Strix	*aluco*				1						1		2
FALCONIFORMES														
	Falco	*tinnunculus*				1	1							2
	Falco	*peregrinus*	1											1
	Falco	sp				2								2
PASSERIFORMES														
	Pyrrhocorax	*pyrrhocorax*	6			8	8		1		1			24
	Pyrrhocorax	*graculus*	2			4	3							9
	Corvus	*corone*					3		1			1		5
	Corvus	*corax*	1		1		1				2		1	6
	Sturnus	*unicolor*	2											2
	Turdus	sp. *viscivorus*	1											1
INDETERMINATE														
	Aves	sp.	1			2	2		1					6
		NISP	**60**	**1**	**1**	**57**	**43**	**5**	**10**	**2**	**11**	**5**	**1**	**196**
		NTAXA	**12**	**1**	**1**	**14**	**14**	**2**	**5**	**2**	**7**	**5**	**1**	**27**
		MNI	**29**	**1**	**1**	**26**	**23**	**3**	**9**	**2**	**7**	**5**	**1**	**107**

3.5 Environmental Results

In this section, I present the results of my ecological analysis of the Waechter avifauna using variables presented in Finlayson 2011 (Table 3.7). Due to small samples sizes, some variables had to be lumped to produce workable data for significance testing.

3.5.1 Bioclimatic tolerance

No species with specialist tolerances (A) were present in the sample, while species with moderate to generalist bioclimatic tolerance appear most frequently in the sequence (Table 3.5). A chi^2-test was performed to test for differences between the observed frequencies in the sequence and the expected frequencies calculated from the present occurrence of each category in Palearctic species today (Finlayson 2011; **Error! Reference source not found.**). Moderate to generalist species (CDE) were lumped to produce workable data. The result was highly significant (χ^2 (2, n = 27) = 22.518, p = <0.001). The absence of category A species in the sample was different to the expected (n = 9), while the observed value of categories CDE (n = 23) was more than twice what was expected (n = 11). Semi-specialist species were also observed (n = 4) at a lower frequency than expected (n = 7).

Table 3.5: Bioclimatic tolerances by layer. A – Specialist, B – Semi-specialist, C – Moderate, D – Semi-generalist, E – Generalist. After Finlayson 2011. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). There was a numerical tendency towards moderate to generalist species.

	Layer (NTAXA)												
TOL	**G**	**H**	**J**	**K**	**M**	**N**	**P**	**Q**	**R**	**S**	**T**	**FREQ**	**FREQ%**
A												0	-
B	1			2	2				1			4	36
C	3			3	1			1	1	1		7	64
D	4			5	5	1	3	1	2	3		8	73
E	3		1	3	4		1		2	1	1	8	73

Table 3.6: Observed and expected frequencies of bioclimatic tolerances. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see Section 2.5).

TOL	Observed	EPal	Expected
A	0.00	0.315	8.51
B	4.00	0.271	7.32
CDE	23.00	0.414	11.18
sum	27		27

Table 3.7: Ecological variables by species after Finlayson, 2011. TOL: bioclimatic tolerance (A= specialist, B= semi-specialist, C= moderate, D= semi-generalist, E= general.ist), LAT: latitude range (A= arctic 70°N, B= boreal 60°N, C= temperate 50°N, D= mid-latitude belt (warm species) 40°N, E= subtropical 30°N, F= multilatitude – species occupies several latitude bands), TEM: temperature tolerance (A-E from cold to hot), HUM: humidity tolerance (A-E from arid to wet), Foraging and Nesting habitats (F= forest, O= open, M= mixed F/O, W= wetland, R= rocky, Ma= marine, A= aerial.) , diet (E= endotherm, O= omnivore, I= insectivore, H= herbivore, N= necrophyte, M= mixed strategy carnivore, F= fish eater), and Migration behaviours (M= migratory, S= sedentary, P = partially migratory).

			Ecological variables							
Common name	**Taxon**	**Order**	**TOL**	**LAT**	**TEM**	**HUM**	**Foraging**	**Nesting**	**Diet**	**Migration**
Rock ptarmigan	*Lagopus mutus*	Galliformes	C	B/D	B	B	O	O	O	S
Red-legged partridge	*Alectoris rufa*	Galliformes	C	D	D	C	O	O	O	S
Ruddy shelduck	*Tadorna ferruginea*	Anseriformes	C	D	C	E	W	W	O	P
Tufted duck	*Aythya fuligula*	Anseriformes	C	B	B	B	W	W	O	P
Long-tailed duck	*Clangula hyemalis*	Anseriformes	B	A	A	C	W	W	O	M
Rock dove	*Columba livia*	Columbiformes	D	F	D	D	M	R	O	S
Wood pigeon	*Columba palumbus*	Columbiformes	D	F	C	C	F	F	O	P
Common coot	*Fulica atra*	Gruiformes	D	F	C	D	W	W	O	P
Oystercatcher	*Haematopus ostralegus*	Charadriiformes	D	F	B	C	W	W	M	P
Herring gull	*Larus argentatus*	Charadriiformes	C	B	B	D	W	R	M	P
Great auk	*Pinguinus impennis*	Charadriiformes	C	B	B	D	Ma	R	M	P
Red-throated diver	*Gavia stellata*	Gaviiformes	B	A	A	C	W	W	M	M
European shag	*Phalacrocorax aristotelis*	Suliformes	D	F	B	B	Ma	R	F	S
Heron	*Ardea sp.*	Pelecaniformes	D	F	D	D	W	W	M	P
Northern goshawk	*Accipiter gentilis*	Accipitriformes	E	C	B	B	F	F	E	S

			Ecological variables							
Common name	**Taxon**	**Order**	**TOL**	**LAT**	**TEM**	**HUM**	**Foraging**	**Nesting**	**Diet**	**Migration**
Bonelli's eagle	*Aquila fasciata*	Accipitriformes	D	D	D	C	M	R	E	S
White-tailed aagle	*Haliaeetus albicilla*	Accipitriformes	D	F	B	B	W	W	M	M
Eagle owl	*Bubo bubo*	Strigiformes	E	F	B	D	M	R	E	S
Tawny owl	*Strix aluco*	Strigiformes	E	F	C	D	F	F	M	S
Peregrine falcon	*Falco peregrinus*	Falconiformes	E	F	D	C	A	R	E	P
Common kestrel	*Falco tinnunculus*	Falconiformes	E	F	C	D	M	R	M	P
Red-billed chough	*Pyrrhocorax pyrrhocorax*	Passeriformes	E	D	C	D	O	R	O	S
Alpine chough	*Pyrrhocorax graculus*	Passeriformes	B	D	C	E	O	R	O	S
Carrion/hooded crow	*Corvus corone/cornix*	Passeriformes	D	F	B	C	O	O	M	P
Raven	*Corvus corax*	Passeriformes	E	F	B	B	M	R	M	S
Common starling	*Sturnus vulgaris*	Passeriformes	C	F	B	C	O	O	O	P
Mistle thrush	*Turdus sp. viscivorus*	Passeriformes	D	F	C	C	F	F	O	P

3.5.2 Latitude range, temperature tolerance, and humidity tolerance.

Multi-latitude (F) and Category D (mid-latitude belt, warm) species were most frequently observed in the sequence (n = 7 and n = 10, respectively) (Table 3.8). Categories A and B (Arctic and Boreal) appeared in 2 and 3 layers, respectively (layers R, K and M). A single temperate species (*A. gentilis*) only featured in level R. This species has been identified in other Middle Palaeolithic contexts in Gibraltar (Cooper 1999, Eastham 1968).

A chi^2-test was used to test for differences between the observed values and expected values for the Palearctic and produced no significant result (Table 3.9; χ^2 (2, n = 24) = 4.709, p = 0.095). Northern (A and B), southern (D and E), and temperate and multi-latitude (C, B/D, F) species were lumped to produce workable data. The non-significant result was interesting given the geographical position of Gibraltar, as cold species which are expected in a general Palearctic population do not regularly appear in the area at present (Finlayson 2010, 2011). The appearance of a population that does not differ significantly from what is expected for the general Palearctic population suggests that the avian community in Gibraltar between MIS5 and MIS3 included species that do not frequent that latitude in the present day.

Table 3.8: Latitude range by layer. A – Arctic 70°N, B – Boreal 60°N, C – Temperate 50°N, D - Mid-latitude belt, warm, 40°N, E – Subtropical 30°N, F - Multi-latitude (occupies several. bands). Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Mid- and multi-latitude (categories D and F) were most frequently observed.

	Layer (NTAXA)												
LAT	**G**	**H**	**J**	**K**	**M**	**N**	**P**	**Q**	**R**	**S**	**T**	**FREQ**	**FREQ%**
A				1	1				1			3	27
B				2	1							2	18
B/D	1											1	9
C									1			1	9
D	3			3	3		2	1	2	2		7	64
E												0	-
F	7		1	7	8	1	3	1	3	3	1	10	91

Table 3.9: Observed and expected frequencies of Latitude ranges. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see Section 2.5).

LAT	Observed	EPal	Expected
AB	5.00	0.200	4.80
CF-B/D	12.00	0.306	7.34
DE	7.00	0.478	11.47
sum	24		24

Moderate temperature tolerances (B, C, D) were most frequent in the sequence (Table 3.10). The relationship between the observed frequencies and those expected in a Palearctic population was examined using a chi^2-test (Table 3.11). Cold species (A,B) and hot (D,E) species were lumped to produce workable data. The results were not significant (χ^2 (2, n = 25) = 0.328, p = 0.849). However, no species with high temperature tolerances were present in the sequence.

Table 3.10: Temperature tolerances by layer Scale from cold to hot, A – 1-20%, B – 21-40%, C – 41-60%, D – 61-80%, E – 81-100%. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Moderate temperature tolerances are most frequently observed.

	Layer (NTAXA)												
TEM	**G**	**H**	**J**	**K**	**M**	**N**	**P**	**Q**	**R**	**S**	**T**	**FREQ**	**FREQ%**
A				1	1				1			3	27
B	5		1	5	6		1		3	2	1	8	73
C	3			5	4		3		1	1		6	55
D	3			2	2	1	1	2	2	2		8	73
E												0	-

Table 3.11: Observed and expected frequencies of Temperature tolerances. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see Section 2.5).

TEM	Observed	EPal	Expected
AB	11.00	0.416	10.40
C	6.00	0.211	5.26
DE	8.00	0.373	9.33
sum	25		25

Species with moderate humidity tolerances (B, C, D) were most frequent in the sequence, while species with a high humidity tolerance (E) were present in 4 layers (Table 3.12). A chi^2-test was performed to investigate the differences between the observed values and expected values calculated from current Palearctic data (Finlayson 2011). High humidity tolerant species (D, E) were grouped to produce workable data (Table 3.13). There were significant differences (χ^2 (3, n = 26) = 14.830, p = 0.002). While arid species were under-represented (n = 0) relative to the expected value (n = 8), humidity tolerant species (DE; n = 12) were observed at twice the expected frequency (n = 6). Only two species with high humidity tolerance (E) were identified in the Waechter avifauna – the ruddy shelduck (*T. ferruginea*) and the alpine chough (*P. graculus*).

Table 3.12: Humidity tolerances by layer. Scale from arid to humid, A – 1-20%, B – 21-40%, C – 41-60%, D – 61-80%, E – 81-100%. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Moderate humidity tolerances are most frequent.

	Layer (NTAXA)												
HUM	**G**	**H**	**J**	**K**	**M**	**N**	**P**	**Q**	**R**	**S**	**T**	**FREQ**	**FREQ%**
A												0	0
B	4		1	2	3				3	1	1	7	64
C	3			4	4		1	1	2	3		7	64
D	3			6	5	1	3	1	2	1		8	73
E	1			1	1		1					4	36

Table 3.13: Observed and expected frequencies of humidity tolerances. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see Section 2.5).

HUM	**Observed**	**EPal**	**Expected**
A	0.00	0.319	8.31
B	7.00	0.217	5.63
C	7.00	0.234	6.08
DE	12.00	0.230	5.98
sum	26		26

Though no species with hot (TEM-E) or arid (HUM-A) tolerances were present in the Waechter avifauna, species endemic to these environments do feature in other contemporary contexts from Gibraltar (Finlayson 2006; Finlayson *et al.* 2016).

3.5.3 Foraging and Nesting habitats.

Species that favour mixed foraging habitats (category M) appeared most frequently in the sequence, followed by those that favour open landscapes (n = 7) and wetland foragers (n = 5) (Table 3.14). On an intra-site level, layers G, K, M, and R showed a greater diversity of foraging habitat (n > 4) than other layers. This was an artefact of low NISP in these layers rather than a reflection of a change in habitat availability.

A chi^2-test was performed to test for differences between the observed values and expected values for the general Palearctic population (Table 3.15). Mixed and forest (M, F); open, aerial, and rocky (O, A, R); and wetland and marine (W, Ma) foragers were grouped to produce workable data. The results were not significant (χ^2 (2, n = 28) = 1.169, p = 0.557). Forest and mixed foragers featured at a slightly higher frequency than expected while both wetland and marine, and open, rocky, aerial foragers were slightly under-represented. The presence of foragers displaying a suite of foraging preferences points to a varied landscape with diverse foraging opportunities as indicated in other environmental reconstructions (Finlayson 2006; Rodriguez-Vidal *et al.* 2013).

Table 3.14: Foraging habitats by layer. A= aerial, F = forest, M = mixed open and forest, Ma = marine, O = open, R = rocky, W = wetland. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Mixed and open foragers were most frequently observed.

	Layer (NTAXA)												
HF	**G**	**H**	**J**	**K**	**M**	**N**	**P**	**Q**	**R**	**S**	**T**	**FREQ**	**FREQ%**
A	1											1	9
F				2					1	1		3	27
M	2		1	2	4	1	1	1	2	1	1	10	91
Ma				1				1				2	18
O	5			3	4		2	1	2	2		7	64
R												0	-
W	2			4	4		2		1			5	45

Table 3.15: Observed and expected frequencies of foraging habitats. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see Section 2.5).

HF	**Observed**	**Eprop**	**Expected**
MF	13.00	0.374	10.48
ORA	8.00	0.307	8.60
WMa	7.00	0.319	8.92
sum	28		28

Rocky nesters appeared in 10 of 11 layers at Gorham's Cave (Table 3.16). Open and wetland nesters, equating to the foragers in the same habitats, were the next most frequent groups. A chi^2-test was performed to examine the relationship between the observed values and the expected frequencies for general Palearctic populations (Table 3.17). Forest and mixed (F, M) and open and rocky (O, R) nesters were lumped to produce workable data. The results were very significant (χ^2 (2, n = 25) = 11.058, p = 0.004). Forest and mixed habitat nesters (n = 3) were under-represented relative to the expected values (n = 10) while open and rocky nesting habitats (n = 17) featured at a much higher frequency than expected (n = 9). This reflected the ample rocky nesting opportunities offered by the cliffs close to Gorham's cave (Rodríguez-Vidal *et al*. 2004, 2007; Finlayson *et al*. 2008, 2016).

Table 3.16: Nesting habitats represented by the presence of species per layer. F = forest, M = mixed open and forest, O = open, R = rocky, W = wetland. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Rocky nesters are most frequent, followed by Wetland nesters.

	Layer (NTAXA)												
HN	**G**	**H**	**J**	**K**	**M**	**N**	**P**	**Q**	**R**	**S**	**T**	**FREQ**	**FREQ%**
F				2					1	1		3	27.3
M												0	0
O	3			1	2		1	1	1	2		7	63.6
R	6		1	7	7	1	2	1	4	2	1	10	91
W	2			3	4		2		1			5	45.5

Table 3.17: Observed and expected frequencies of nesting habitats. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see Section 2.5).

HN	**Observed**	**EPal**	**Expected**
FM	3.00	0.386	9.65
OR	17.00	0.373	9.33
W	5.00	0.241	6.02
sum	25		25

3.5.4 Higher Taxa Groups

Diurnal raptors appeared in seven layers at Gorham's Cave (Table 3.18; Figure 3.3). Their remains were spread throughout both occupied (G, K, M, R) and unoccupied (H, N, S) deposits. Identified species (*H. albicilla, A. gentilis, A. fasciata*) only accounted for 5 remains in 4 contexts (36.4%). The inclusion of 8 accipitriform remains not identified beyond order boosted the frequency to three extra layers, indicating a much more widespread presence in the sequence (n = 7, 63.6%). Strigiformes also appeared in both occupied and unoccupied layers, albeit only three layers in total (K, M, S).

Corvids were the most frequent taxa group, appearing in 8 layers (73%). They were present in occupation layers G, K, M, P, R (n = 41), but were also found in layers S, T, and J (n = 3). This persistence indicates their continuous presence in the ecosystem and does not confine their presence in the cave to periods of Neanderthal occupation. Choughs (*Pyrrhocorax* spp.) are rocky nesters and would breed on the cliffs surrounding the cave (Cramp *et al.* 1977 - 1994; Finlayson 2011). Another rocky nester is the rock dove (*C. livia*) which was present in 7 layers of the sequence. Along with the choughs, rock doves were available close to the cave, and are known to have been exploited by Neanderthals at Gorham's Cave (Finlayson *et al*. 2012; Blasco *et al*. 2014, 2016).

Other food species such as game birds and ducks were identified in 6 and 2 layers, respectively. While ducks were only present in occupation layers M and P, game birds were also found in occupationally sterile layers (Q, S). Like doves and corvids, open-foraging game birds such as red-legged partridges (*A. rufa*) would have been present in the landscape close to the cave. Ducks, however, would not have been as readily available, frequenting wetland and coastal areas 1-4.5 km from the site (Finlayson 2010; Finlayson 2011; Rodríguez-Vidal *et al.* 2013). The heron (*Ardea sp.*) from K was another wetland taxon that might have occupied suitable habitats along the coastline and freshwater springs nearby (Birdlife Data Zone 2021; Rodríguez-Vidal ibid.).

It is tempting to allot the presence of non-cave-native wetland species and higher frequencies of known food species in Waechter's defined occupation layers as the result of human exploitation. However, such a conclusion would only be speculative at best. An examination of bone surface is necessary to confirm any human agency behind the accumulation.

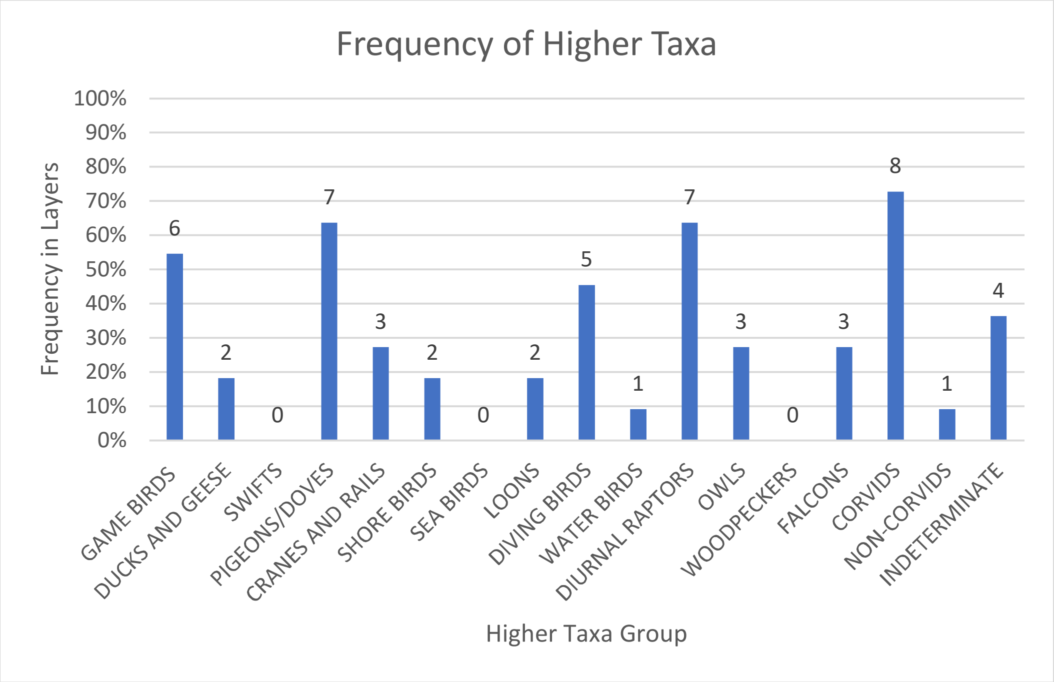


Figure 3.3: Frequency of higher taxa groups in Waechter's Middle Palaeolithic layers of Gorham's Cave.

Table 3.18: Distribution of avifaunal remains sorted at higher taxa level.

			LAYER											
Common name	**Order**	**Family**	**G**	**H**	**J**	**K**	**M**	**N**	**P**	**Q**	**R**	**S**	**T**	**TOTAL**
GAME BIRDS	GALLIFORMES	ALL	9			3	2			1	3	1		19
DUCKS AND GEESE	ANSERIFORMES	ALL					3		1					4
SWIFTS	APODIFORMES	ALL												
PIGEONS/DOVES	COLUMBIFORMES	ALL	31			24	15	4	5	1	2			82
CRANES AND RAILS	GRUIFORMES	ALL	1				1		1					3
SHORE BIRDS	CHARADRIIFORMES	ALL				4	1							5
SEA BIRDS	PROCELLARIIFORMES	ALL												
LOONS	GAVIIFORMES	ALL				1					1			2
DIVING BIRDS	SULIFORMES	ALL	2			1	1				1	1		6
WATER BIRDS	PELICANIFORMES	ALL				1								1
DIURNAL RAPTORS	ACCIPITRIFORMES	ALL	3	1		5	1	1			1	1		13
OWLS	STRIGIFORMES	ALL				1	1					1		3
WOODPECKERS	PICIFORMES	ALL												
FALCONS	FALCONIFORMES	ALL	1			3	1							5
CORVIDS	PASSERIFORMES	CORVIDAE	9		1	12	15		2		3	1	1	44
NON-CORVIDS	PASSERIFORMES	NON-CORVIDS	3											3
	INDETERMINATE	ALL	1			2	2		1					6
		NISP	**60**	**1**	**1**	**57**	**43**	**5**	**10**	**2**	**11**	**5**	**1**	**196**
		NTAXA	**12**	**1**	**1**	**14**	**14**	**2**	**5**	**2**	**7**	**5**	**1**	**27**

3.6 Taphonomic results

This section presents the results of taphonomic analysis of Waechter's Avifauna (Table 3.19). I begin with a survey of the traces that were attributed to natural processes, followed by evidence of carnivore and bird of prey agency. Finally, I present observations of traces, which were connected to Neanderthal activities.

196 specimens were included in the analysis. The lisibility of the sample was generally clear (Figure 3.4). Some level of obstruction was visible on 27.6% of the sample (n = 54). Few specimens (n = 8) were too obscured by natural processes to further examine. In most cases, the lisibility was impaired by concretions, manganese-oxide staining, or rooting as reported below.

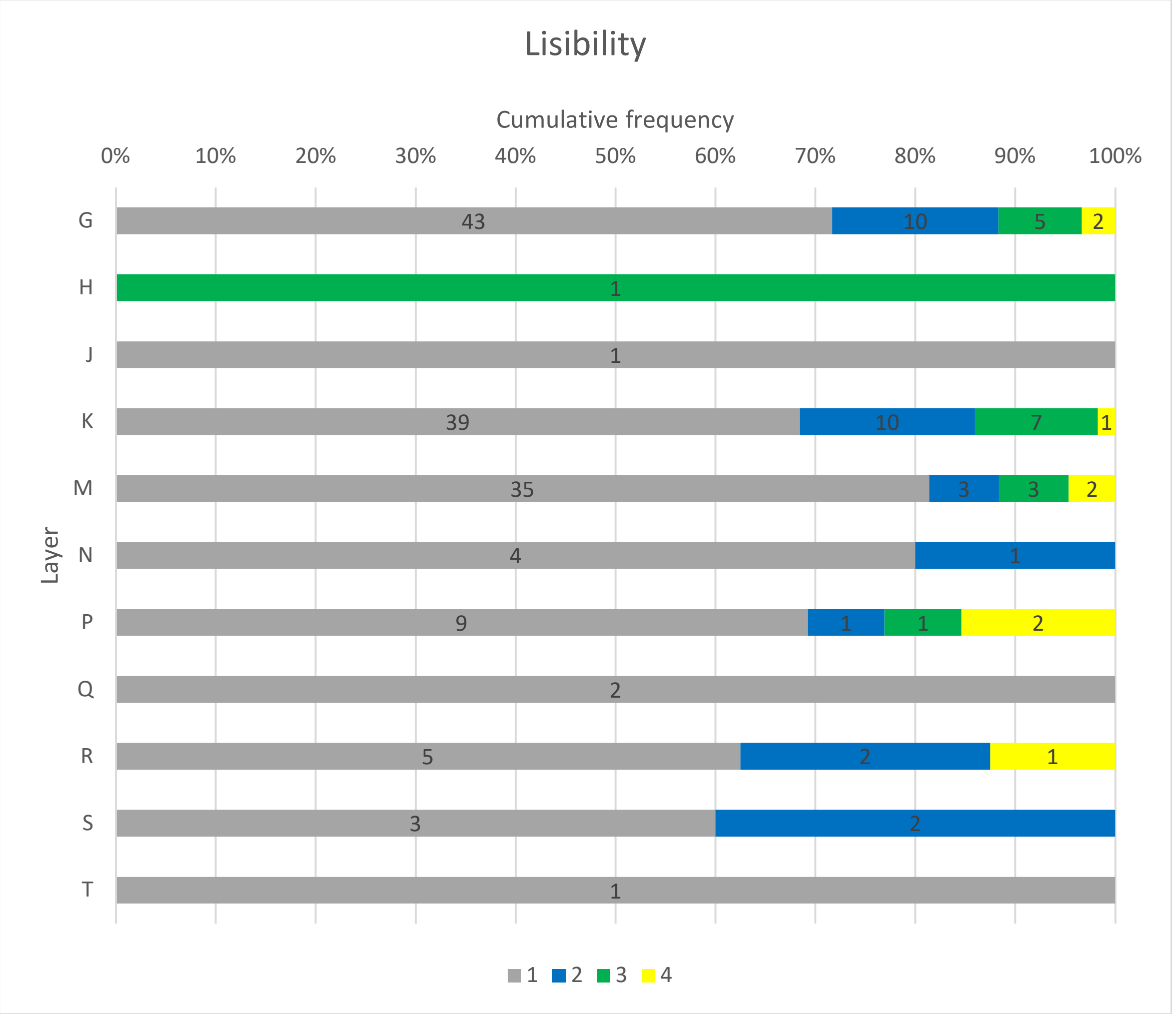


Figure 3.4: Cumulative frequency of Lisibility rankings by layer. Labels reflect the number of specimens in each layer that displayed the indicated rank. 1= clear, 2= some difficulty, 3= difficulties, 4= severe difficulties/unreadable.

Table 3.19: Taphonomic results by level showing count of modifications by unit and percentage of modified specimens per layer.

Modification	**G**		**H**		**J**		**K**		**M**		**N**		**P**		**Q**		**R**		**S**		**T**	
Concretions	27	45.0%	1	100.0%	1	100.0%	41	71.9%	29	67.4%	3	60.0%	8	80.0%	2	100.0%	10	90.9%	1	20.0%		
Manganese staining	56	93.3%	1	100.0%	1	100.0%	52	91.2%	39	90.7%	4	80.0%	6	60.0%	2	100.0%	10	90.9%	5	100.0%	1	100.0%
Trample	25	41.7%					19	33.3%	15	34.9%			5	50.0%	1	50.0%	2	18.2%	3	60.0%	1	100.0%
Root etching	18	30.0%	1	100.0%	1	100.0%	7	12.3%	8	18.6%	2	40.0%					6	54.5%	1	20.0%		
Weathering	52	86.7%	1	100.0%	1	100.0%	51	89.5%	35	81.4%	3	60.0%	8	80.0%	2	100.0%	11	100.0%	5	100.0%	1	100.0%
Human? Toothmark													1	10.0%								
Carnivore toothmark	10	16.7%			1	100.0%	18	31.6%	10	23.3%	1	20.0%	2	20.0%	1	50.0%	3	27.3%	4	80.0%	1	100.0%
Rodent gnaw	2	3.3%					1	1.8%	2	4.7%												
Bird of prey beakmark	6	10.0%					5	8.8%	6	14.0%	1	20.0%	1	10.0%	1	50.0%						
Indeterminate toothmark	2	3.3%																				
Digestion	38	63.3%					28	49.1%	24	55.8%	3	60.0%	2	20.0%	2	100.0%	11	100.0%	4	80.0%	1	100.0%
Cutmark	2	3.3%					4	7.0%	1	2.3%			2	20.0%								
Thermal modification	14	23.3%					7	12.3%	8	18.6%	3	60.0%	5	50.0%	1	50.0%			1	20.0%		
Peeling	1	1.7%					1	1.8%	2	4.7%			1	10.0%								

There was a high frequency of peri- and post-excavation damage (Figure 3.5). Over 75% (n = 46) of specimens in Layer G exhibited some degree of recent damage. These traces were the result of excavation practices and post-excavation processing, including cleaning efforts and inadequate storage conditions. They appeared as fractures, flaking of fracture surfaces, and striations on the bone surface. These damages may have obscured original modifications to the bone surface.

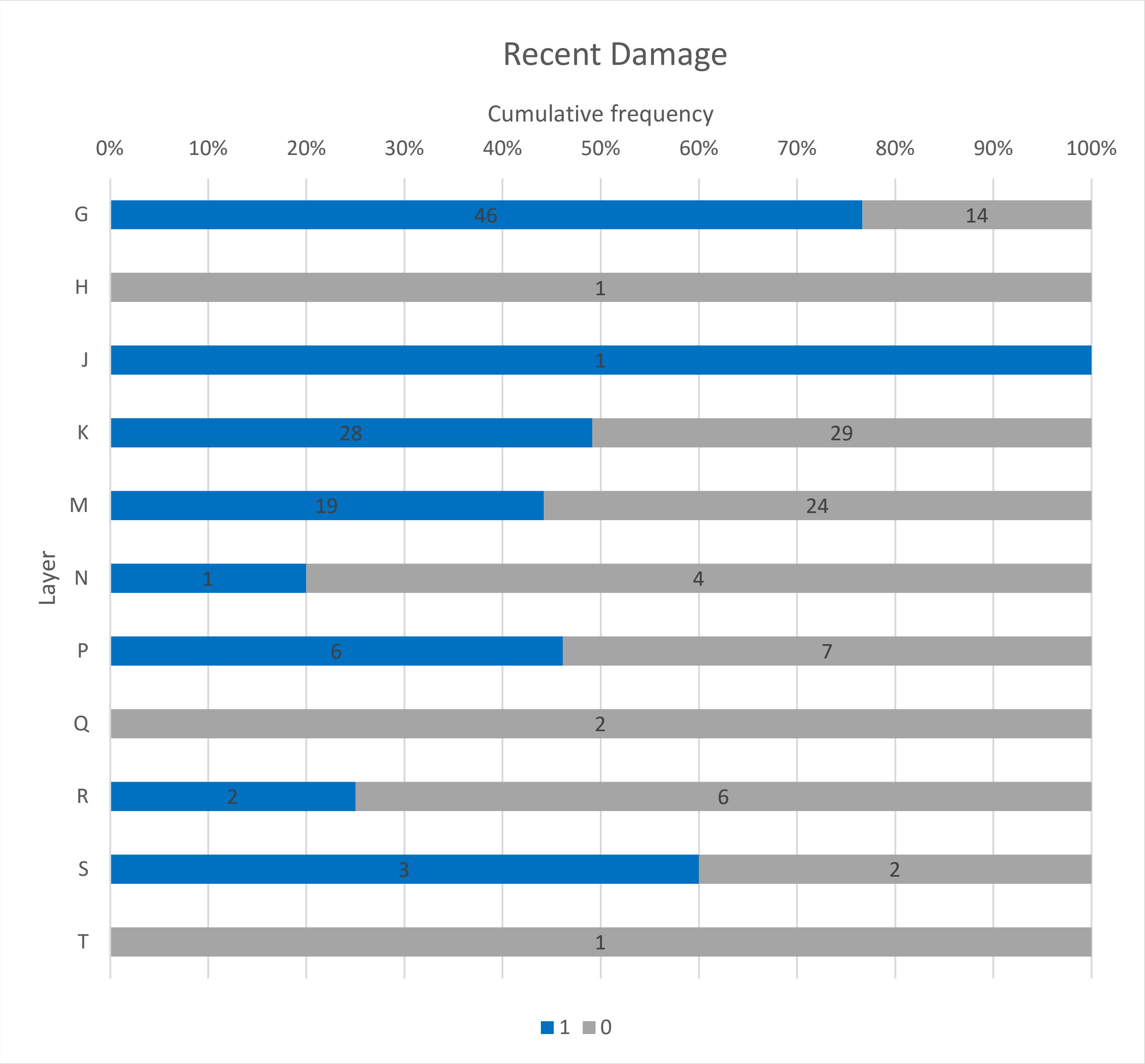


Figure 3.5: Presence (1) and absence (0) of recent damage on remains by layer. Labels show NISP.

3.6.1 Natural modifications

3.6.1.1 Concretions, Manganese staining and Root etching.

Most specimens exhibited some degree of concretion (n = 123) (

Figure *3.6*). The deposition of mineral residues on the bone surface was the result of water permeating through the sediment (Fernandez-Jalvo and Andrews 2016). Higher ratios of concretions in layers K and M may correspond to the wetter, ponding events suggested in the LBSm sequences identified in the 1990's excavations (Currant and Collcutt 2012).

The presence of manganese oxide deposits on the bulk of the sample (n = 177) was typical of a cave environment (Figure 3.7). Water moving through the limestone carried manganese that oxidised in the cave environment and formed stains on bone surfaces (Hill 1982; Fernandez-Jalvo and Andrews 2016). Water continuously permeates through the limestone walls of Gorham's Cave to the present day.

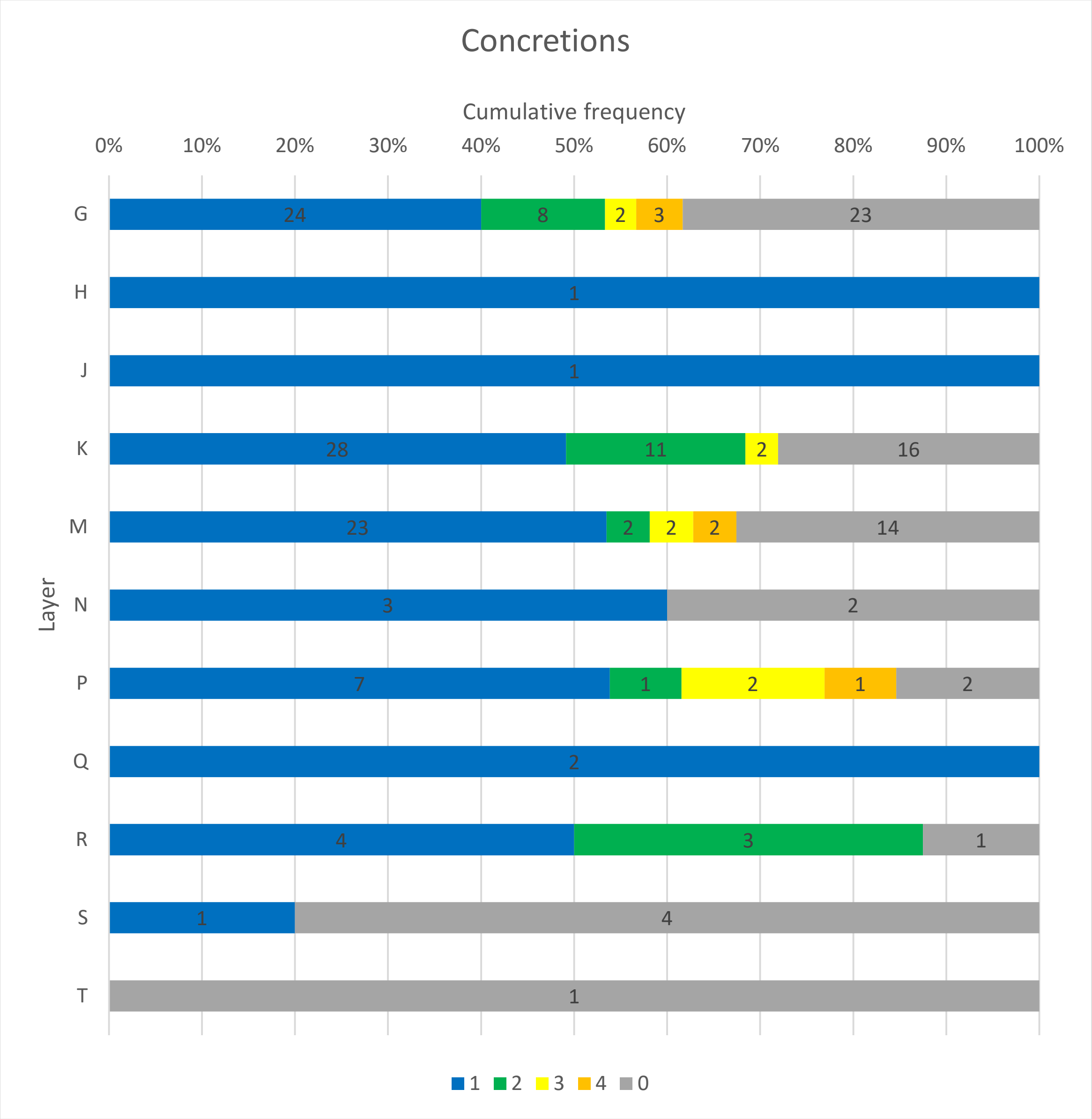


Figure 3.6: Degree of concretions present by level. 1= 1-25% coverage, 2= 26-50% coverage, 3= 51-75% coverage, 4= 76-100% coverage, 0 = no concretions. Labels show NISP.

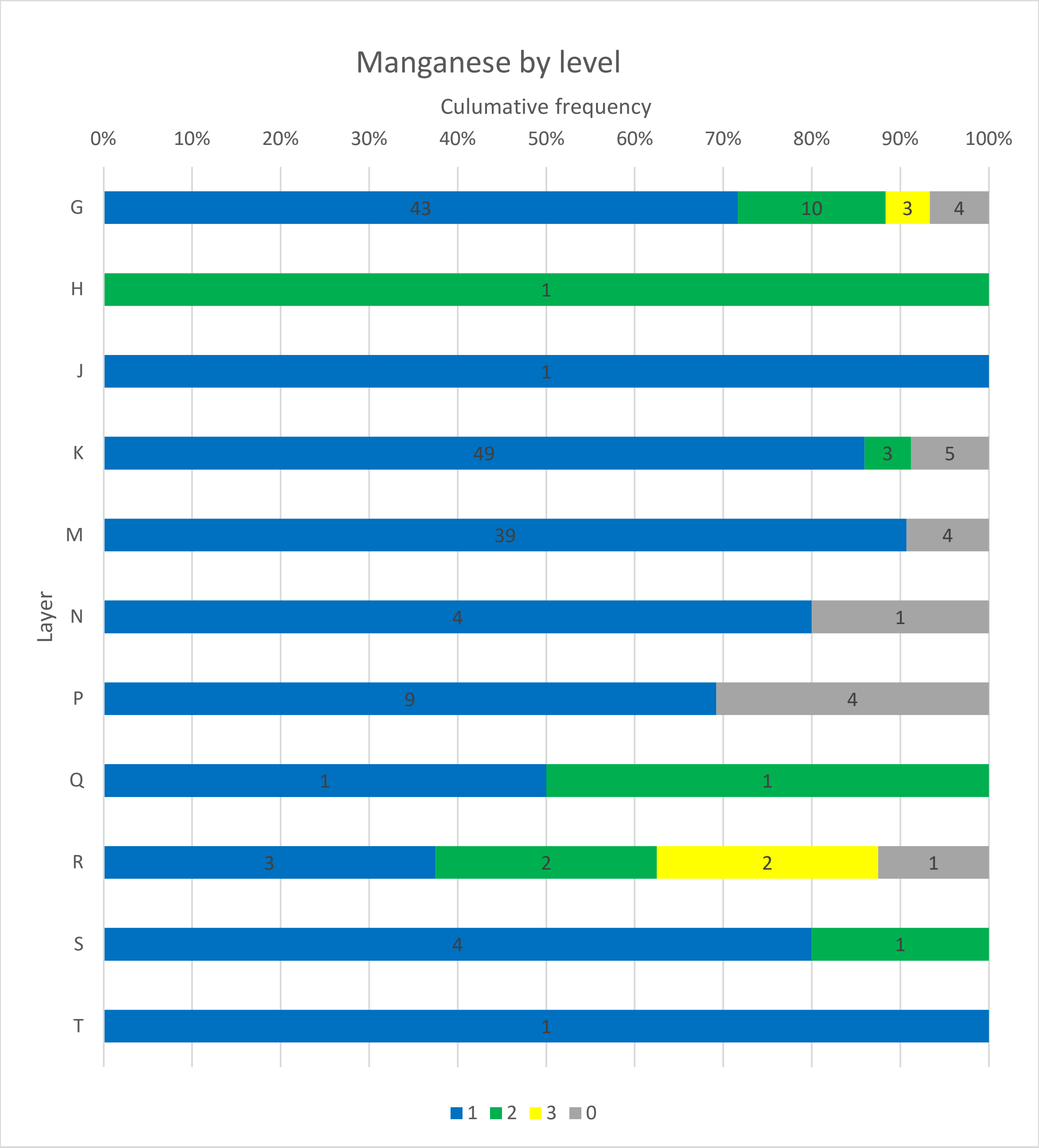


Figure 3.7: Degree of manganese oxide staining by level. 1= 1-25% coverage, 2= 26-50% coverage, 3= 51-75% coverage, 0 = no staining. Labels are NISP.

Only 42 0f 197 specimens showed evidence of root etching (Figure 3.8). Root etching was not observed to cover the entire surface of any bone, indicating a differential preservation where only one part of the bone was covered by root-bearing sediment. These results suggested that plants did not cover the entire surface of the deposit (Fernandez Jalvo and Andrews 2016). In a cave environment, plant growth is limited to areas where enough light is available to drive photosynthesis.

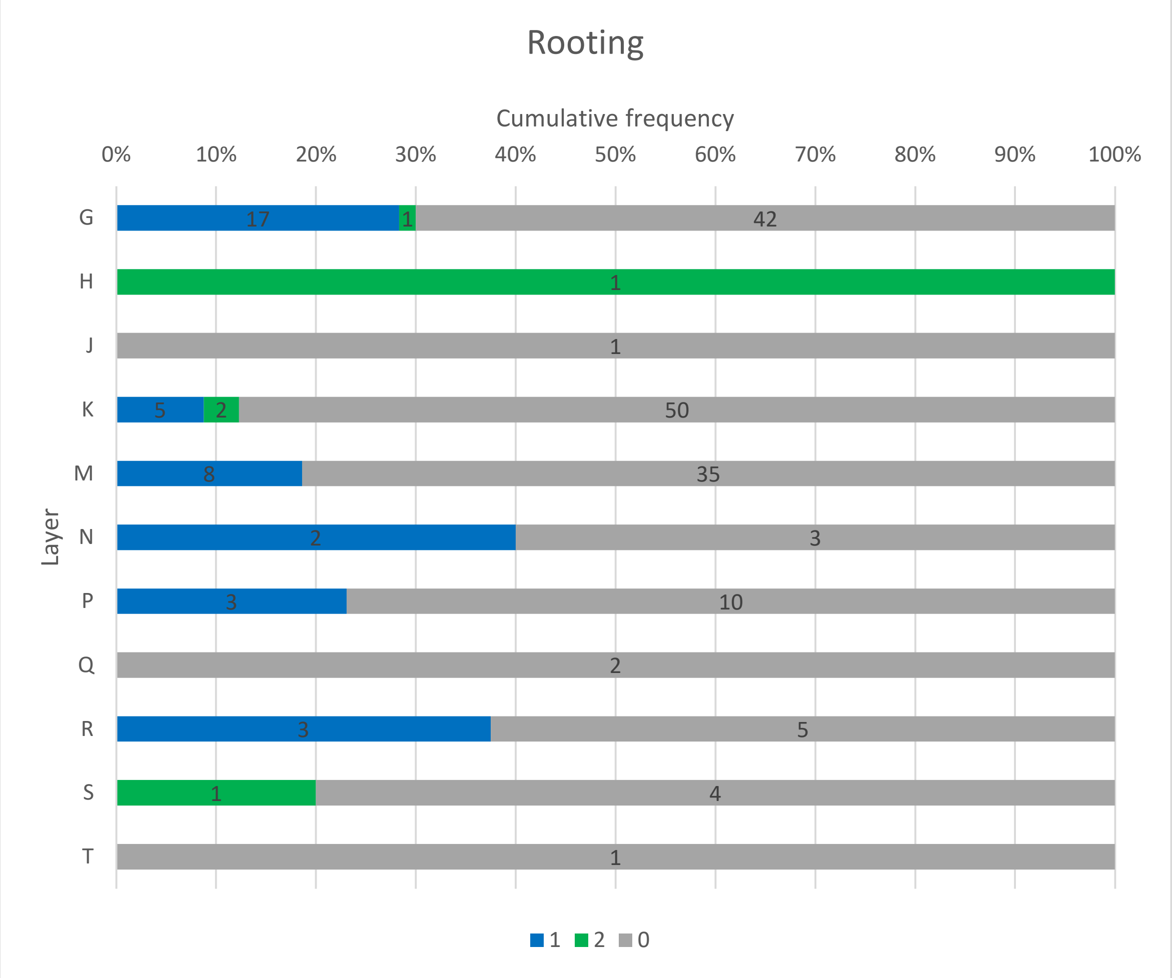


Figure 3.8: Presence of acid etch from rooting by level. 1= low level of root etch, 2= moderate level of root etch, 0 = no rooting. Labels are NISP.

3.6.1.2 Weathering and trampling

Weathering was evident on all but 26 remains (Figure 3.9), with 99 (50.5%) showing a weathering of degree 2 or higher. This was not unexpected in a cave environment where humidity levels were high. Weathering in such conditions is dubbed ‘cave corrosion’, but the exact processes behind the modification are unknown (Behrensmeyer 1978; Fernandez-Jalvo and Andrews 2016).

Trampling was identified in 8 of 11 layers (Figure 3.10) indicating a degree of post-depositional movement in the sediment. The agent may be predators, scavengers, and humans moving through the site (Behrensmeyer *et al.* 1986; Fernandez-Jalvo and Andrews 2016).

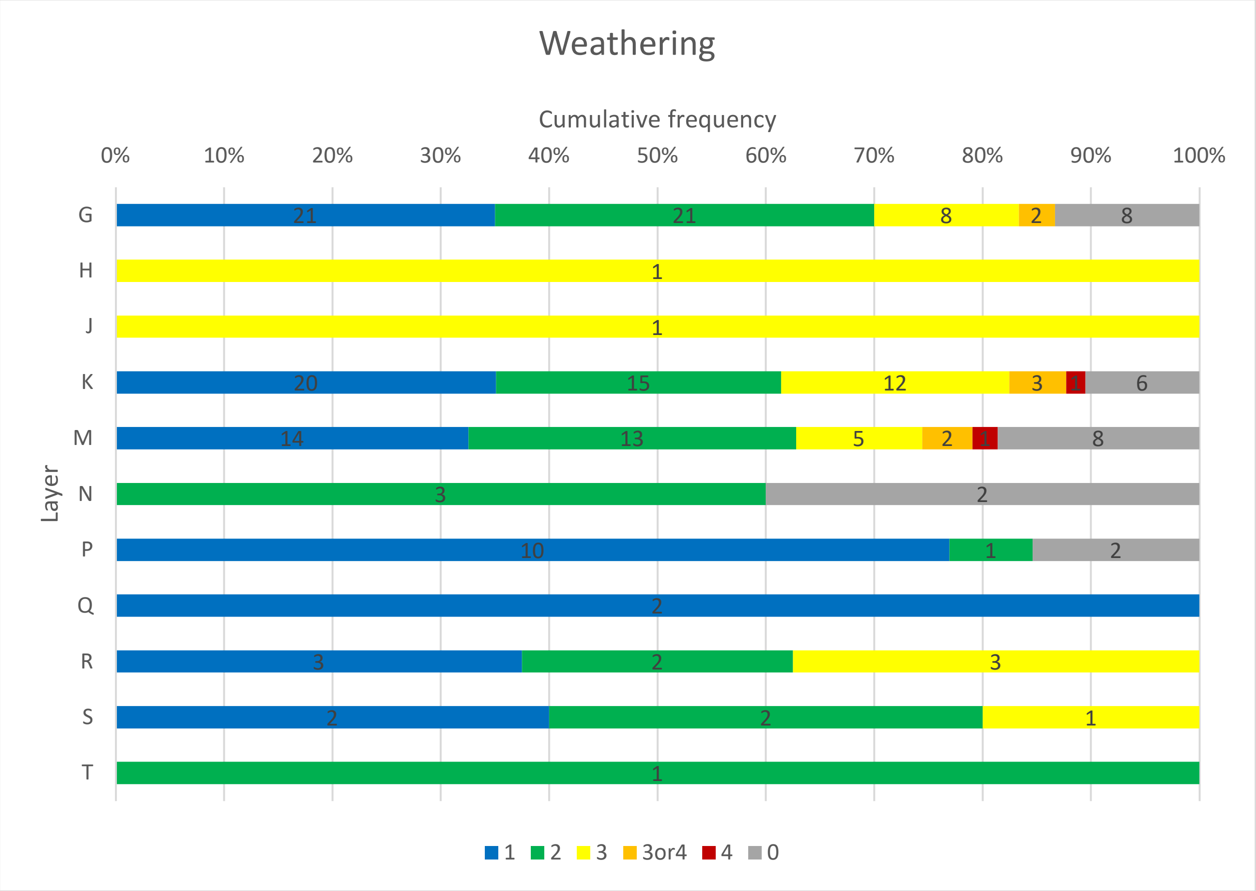


Figure 3.9: Degrees of Weathering modifications by layer. 0 = no modification and 5 = highest degree of modification.

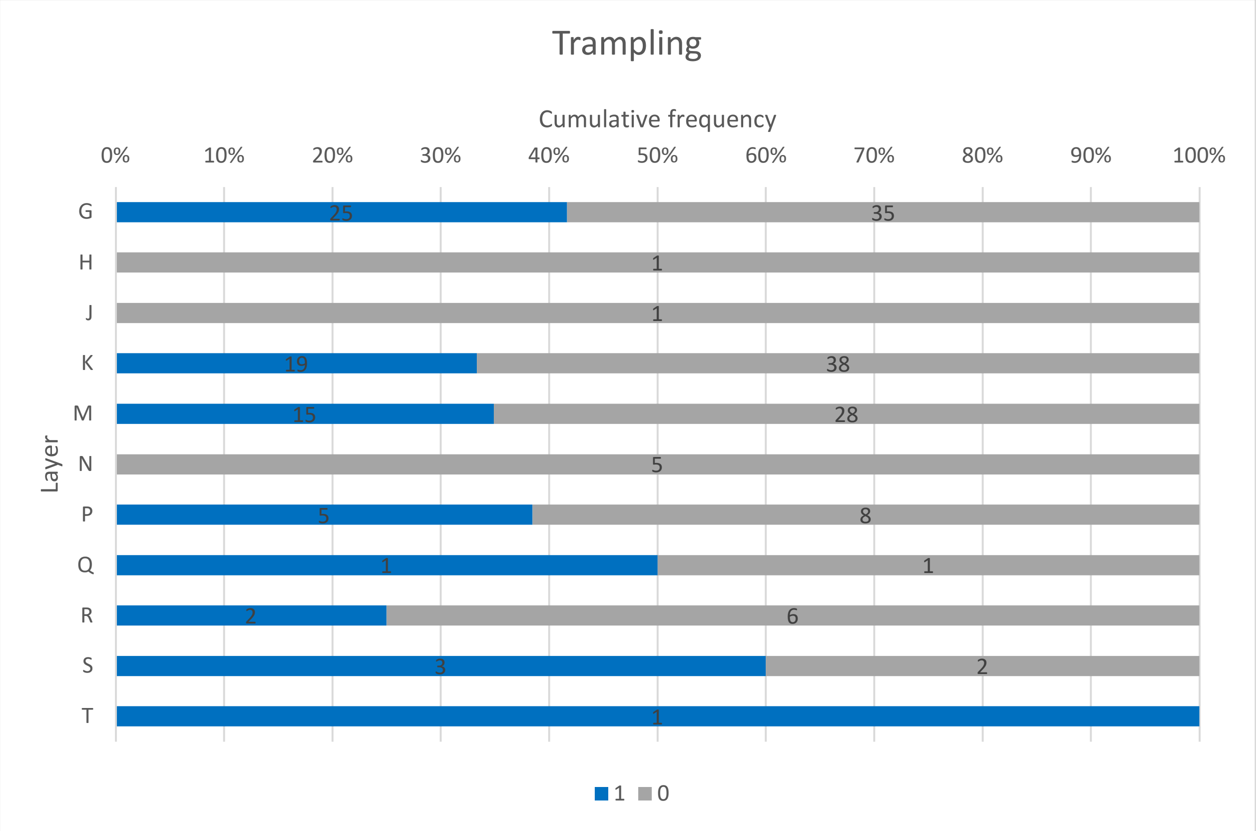


Figure 3.10: Frequency of trampling modifications by layer. 1 = trample present, 0 = no trample.

3.6.2 Predator modifications

80 (38.3%) specimens showed modifications resulting from manducation. Modifications were found on material from all levels except level H (NISP=1) (Table 3.20; Figure 3.11). Punctures (n = 41), crenulated edges (n = 38), and scoring (n = 28) were the most frequent modifications. The greatest variation in modification types were identified in layers G, K, and M. These layers were the only layers in which rodent gnaw was identified on avian remains.

Based on shape and size, small carnivores were the most likely agent behind the majority of scores, punctures and pits identified in the sequence (n = 51) (Fernandez Jalvo and Andrews 2016; Andrews 1990; Laroulandie 2000). However, evidence of bird of prey agency (n=20) was identified in most layers with a NISP > 1. Traces attributed to birds of prey were not identified on remains from the lowest layers in the sequence (R,S,T).

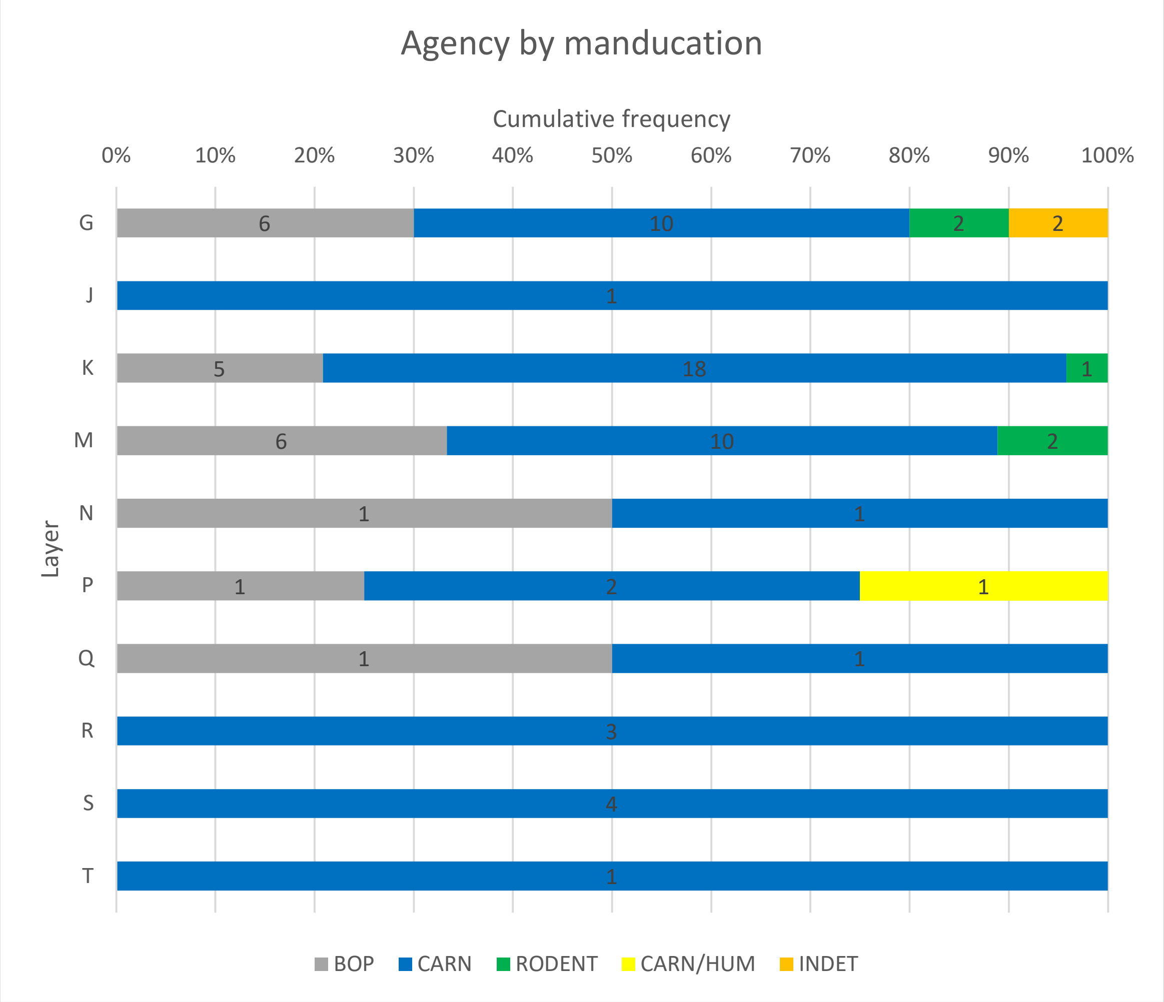


Figure 3.11: Agency as reflected by tooth and beak marks, by layer. BOP = bird of prey, CARN = carnivore, RODENT = rodent gnaw, CARN/HUM = possible human tooth mark, INDET = indeterminate tooth mark.

57.4 % (n = 113) of the NISPtaph displayed traces of digestion (Table 3.21). Of these, 99 (87.6%) showed low levels of acid etching on the bone surface. Few specimens (n = 10) exhibited moderate levels of etching, and a handful (n = 4) showed only light polish of the bone surface. The presence of digestion on bones did not exclude the scavenging of human leftovers. However, dissolution by stomach acid can obscure any traces left by humans (Laroulandie 2000; Fernandez-Jalvo and Andrews 2016).

Table 3.20: Presence of tooth and beak marks by layer detailing number of modifications (NISPmod), percentage of specimens per layer that show manducation modifications (%mod), total number of modifications, and modification type (pit, score, notch, puncture, crenulated edge, or gnaw)

Layer	NISPmod	%mod	Total modification	Pit	Score	Notch	Puncture	Crenulated Edge	Gnaw
G	20	33.3%	27	1	3	2	14	4	3
H									
J	1	100.0%	1					1	
K	24	42.1%	34	2	11	2	4	17	1
M	19	44.2%	31	3	2	1	11	12	2
N	2	40.0%	2				2		
P	4	40.0%	5		2		1	2	
Q	2	100.0%	3		2		1		
R	3	27.3%	5				5		
S	4	80.0%	5		1		2	2	
T	1	100.0%	8		7		1		
Total	80	38.3%	121	6	28	5	41	38	6

Table 3.21: Digestion traces identified in the Waechter avifauna. No etch= no acid etch visible, etch1 = low degree of acid etch visible, etch 2 = moderate degree of acid etch visible. Presence (polish) and absence (no polish) of polish on the bone (Bochenski 2005).

Digestion trace	**No etch**	**Etch 1**	**Etch 2**
Polish	4	85	4
No polish	-	14	6

3.6.3 Human modifications

3.6.3.1 Striations

Striations were identified on nine specimens in the Waechter avifauna, originating in 4 of Waechter’s layers (G, K, M, P) (Table 3.22). The remains belong to five different species, and four of the defined higher taxa groups.

Level G produced two left humeri with transverse cutmarks on the distal ends (G016 - *P. aristotelis* and G053 – *C. livia*, Figure 3.12). Two cut marks were identified on the distal articulation of G016, cutting across the *incisura intercondylaris* this was comparable to severing tendons attaching the humerus to the ulna. The trace on G053 had a classic V-shape but was interrupted at both ends by peeling of the bone cortex. This was due to advanced weathering of the bone surface. The orientation of the cutmarks suggests the purpose behind the action in both cases was disarticulation of the carcass.

Table 3.22: Striations present on specimens from Waechter's avifauna. Includes taxon, common name, element, laterality, number of modifications (n.mod), type of modification (cm = cut mark, scrapes), location on the element, orientation of the modification, and inferred intention behind the mark.

Spec no	Taxon	Common name	Element	Side	n.mod	Type	Location	Orientation	Intention
G016	*Phalacrocorax aristotelis*	shag	humerus	L	2	cm	5	tr	da
G053	*Columba livia*	rock dove	humerus	L	1	cm	distal	tr	da
K005	*Pinguinus impennis*	great auk	coracoid	R	11	cm	2,5	obl	da/df
K021	*Pyrrhocorax graculus*	alpine chough	humerus	L	1	cm	?	tr	df
K037	*Columba livia*	rock dove	humerus	L	1	cm	?	tr	da
K041	*Columba livia*	rock dove	humerus	R	multi	scrapes	234	lo	df
M028	*Columba livia*	rock dove	humerus	R	1	cm?	5	lo/obl	df
P007	*Corvus corax*	raven	femur	L	1	cm	1	tr	df
P008	*Corvus corax*	raven	tmt	R	3	cm	4	obl	df

Of special note was the right coracoid of a Great Auk (*P. impennis*) from layer K (K005; Figure 3.13). 13 cutmarks were identified in two groups on the bone surface. Eleven transverse to oblique striations of varying depth on the dorsal limit of the interior *canalis triosseus* reflected the disarticulation of the coracoid from the humerus, scapula and furcula. A further two fine, oblique striations on the distal ventral surface suggested skinning of the carcass. Of further interest, pathological changes in the bone structure showed a fracture of the coracoid that had healed completely before the carcass was processed. Furthermore, the humeri of an alpine chough (K021) and two rock doves (K037 and K041) also displayed evidence of butchery practices (Figure 3.14). K037 presented with a transverse cutmark on the proximal articulation, which had broken through the bone cortex of the *tuberculum ventrale.* This articulation was securely attached to the scapular girdle. K021 and K041 showed a pair of fine, transverse cutmarks to the mid-shaft, and a series of scrapes longitudinal to the axis of the shaft, respectively. Both modifications reflected defleshing activities.

A single specimen displaying a possible cutmark was identified in Level M (Figure 3.15). The trace, on the distal articulation, had a deeply sloping V-shape and is transverse to the distal condyle. The uncertain status of the striation was amplified by the presence of irregular crenulations along the deltoid crest, accompanied by traces of peeling of the bone surface. The presence of these traces on a single specimen sheds uncertainty of the agent. A crenulated deltoid crest, peeling and a striation could be indicative of human consumption, but may also reflect carnivore agency, the striation then being the product of a sharp tooth score.

Two posterior limb elements of raven (*Corvus corax*) were identified in Level P. P007, a left femur, displayed a shallow striation on the proximal surface. Cutmarks in this position are connected to the disarticulation of the limbs. A set of seven transverse and oblique cutmarks of varying depth were identified along the shaft of a tarsometatarsus (P008, Figure 3.16). These were attributed to skinning activities.

Figure 3.12: G053, Columba livia, left humerus displaying a transverse striation at the distal end.

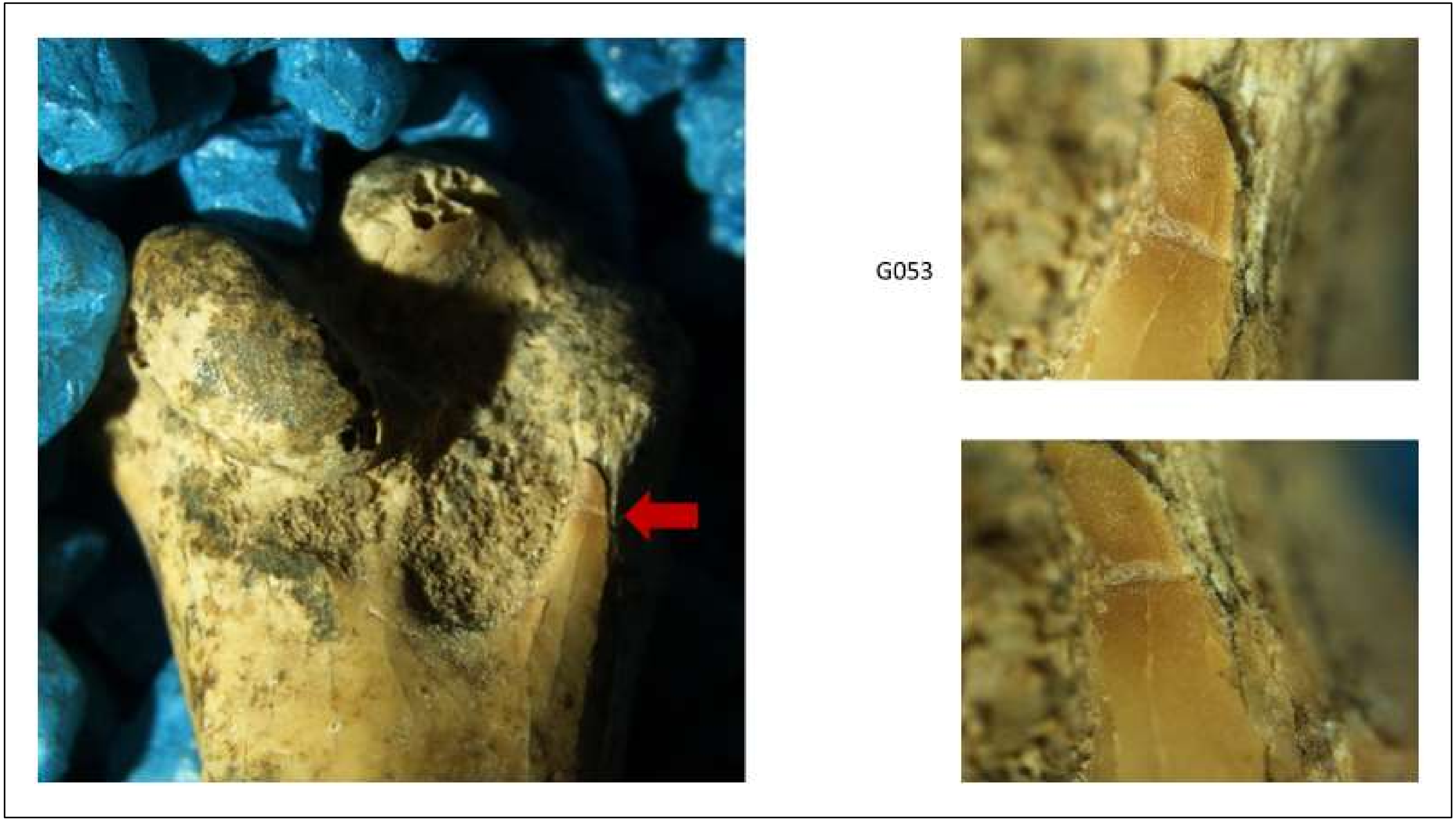
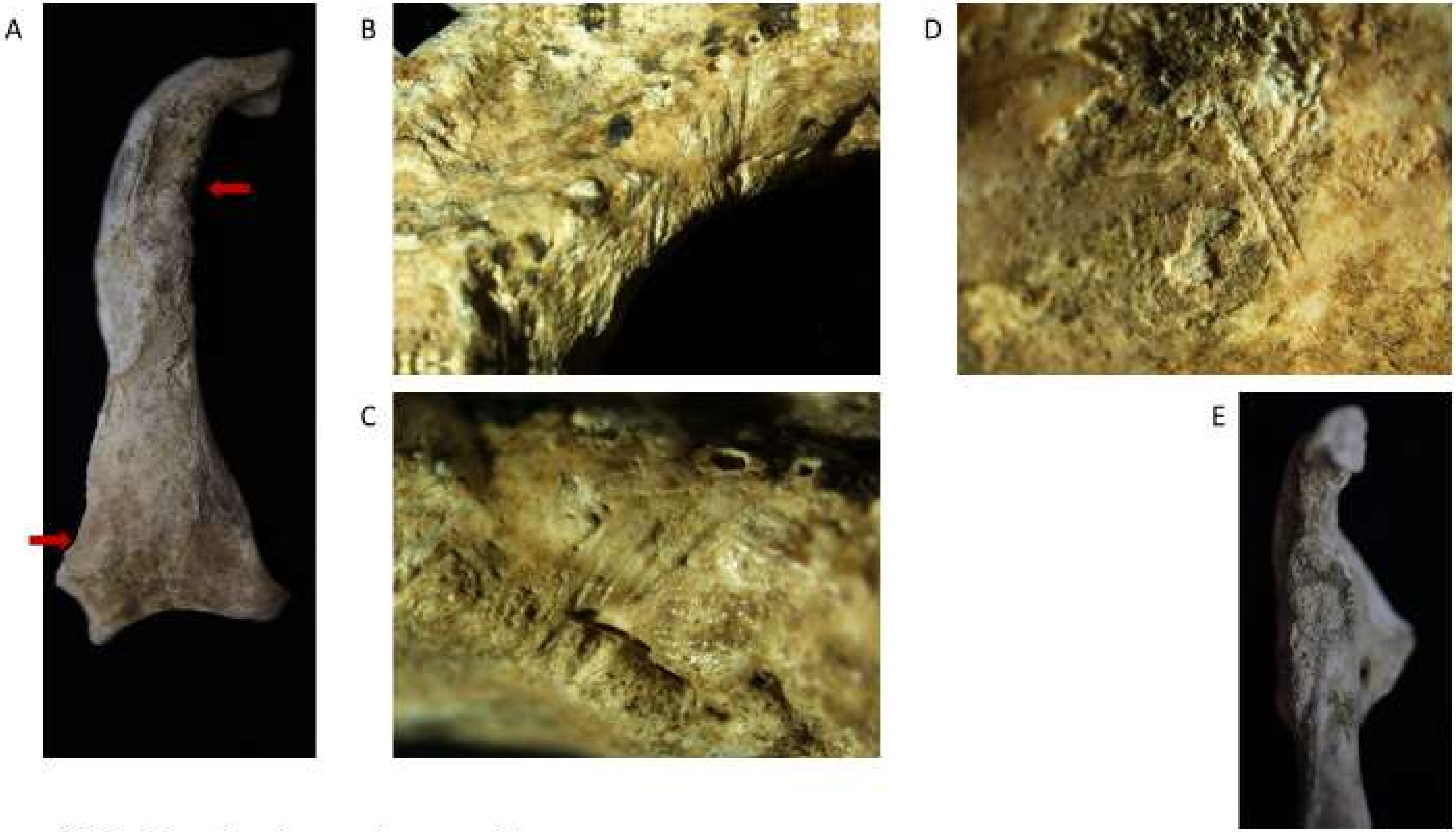
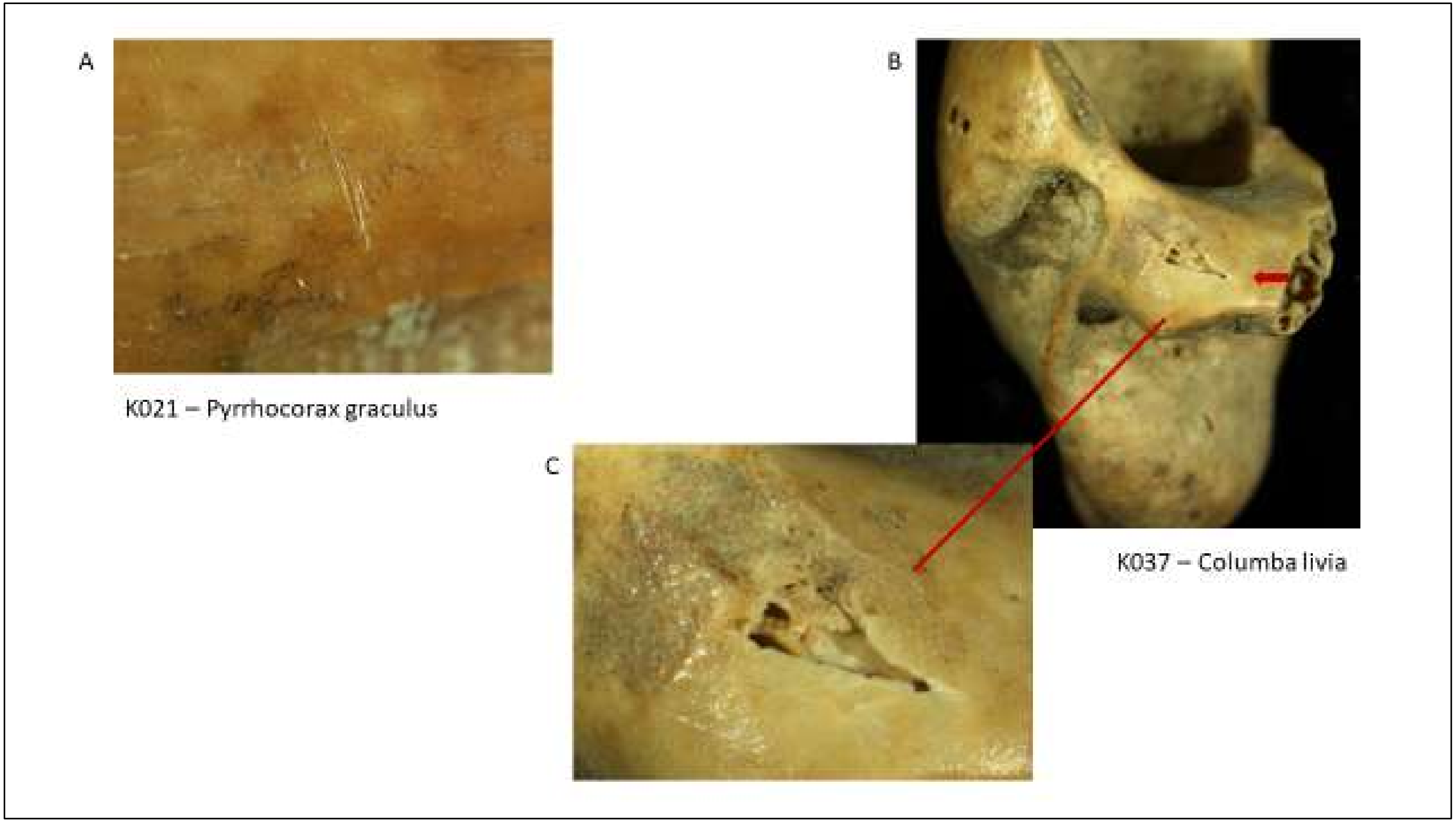


Figure 3.13: K005, Pinguinus impennis, right coracoid displaying a total of 13 cutmarks, which suggested disarticulation and defleshing during butchery.



K005 – Pinguinus impennis, coracoid.

Figure 3.14: A) K021; Transverse striations on the shaft of an alpine chough (P. graculus) humerus. B) K037; A cutmark on the proximal humerus of a rock dove (C. livia) had broken through the bone cortex.



K021 – Pyrrhocorax graculus

K037 – Columba livia

Figure 3.15: M028; A deep v-shaped striation on the distal condyle of a rock dove (C. livia) humeris may a cutmark, but could also be the result of a deep tooth score

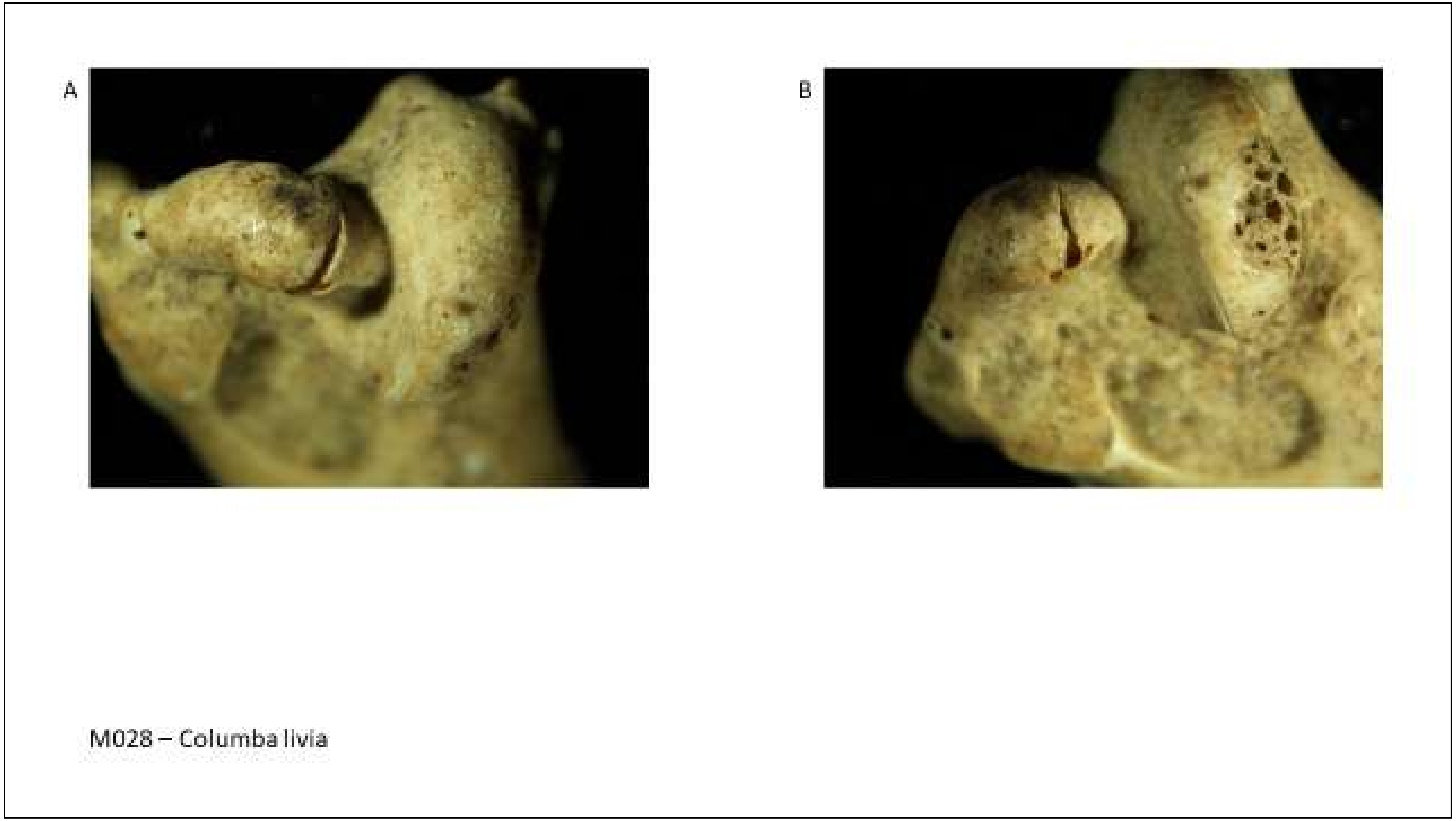


Figure 3.16: P008; Seven cutmarks on the tarsometatarsus of a raven indicating skinning practices.

3.6.3.2 Peeling

A total of five specimens exhibited signs of fresh bone peeling (Table 3.23). All traces were found adjacent to the articular ends where cartilage or robust tendons can tear the bone surface away during disarticulation. While peeling is generally accepted as evidence of human agency, Bochenski observed peeling on the sternum of birds processed by golden eagles (pers. comm. to O'Connor in O'Connor 2005). However, the presence of other traces on some of the specimens make interpretation simpler.

Table 3.23: Specimens displaying traces of peeling. Other mods = other taphonomic modifications present on the specimen.

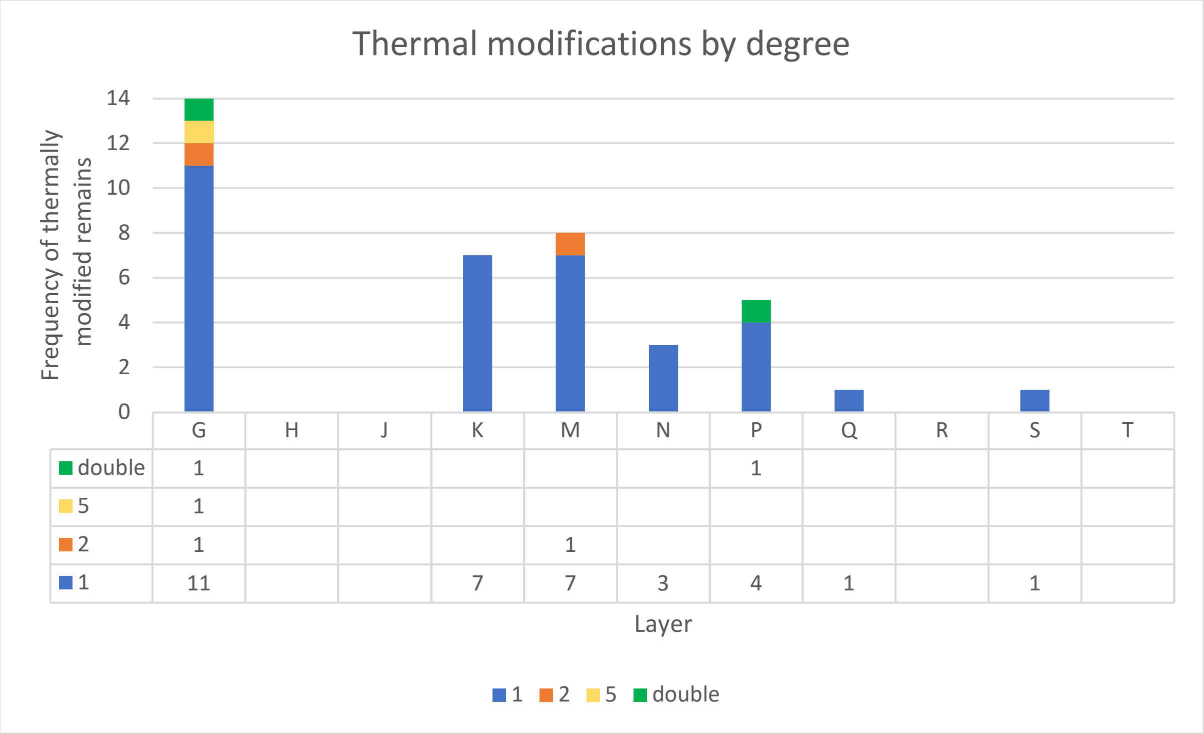
Spec no	***Taxon***	**Element**	**Location**	**Other mods**	**Striation**
G001	*Alectoris rufa*	femur	5	0	0
G055	*Columba livia*	humerus	1	pun	0
K005	*Pinguinus impennis*	coracoid	5	0	cm
P007	*Corvus corax*	femur	1	0	cm
M039	*Columba livia*	ulna	1	0	0
M028	*Columba livia*	humerus	1	cren	cm?

Specimens K005 and P007 both bore clear cutmarks on the bone surface (Figure 3.13). This aligned well with the theory of peeling as a secure signal of human agency (Laroulandie 2000, 2005). Conversely, G055 presented with a puncture attributed to carnivore agency. M028 shows both irregular crenulated edges and an unusual cutmark-like trace on the distal condyles. It is possible this trace was the result of a sharp beak strike.

3.6.3.3 Thermal modifications

Most of the thermal modifications identified in Waechter's avifauna were low grade (level 1, n = 34), presenting as speckling of the bone surface (Figure 3.17). Layer G contained a higher proportion (35.8%, n = 14) and variation (n = 4) of modifications than any other level.

Differential exposure to a heat source wass evident in two different layers, G and P. Specimen G009 (*Aves* sp., radius) showed level 2 thermal modification on one of two fracture surfaces. This was indicative of a differential exposure to heat during cooking/roasting when muscle tissue protects the rest of the bone surface (Blasco and Peris 2009; Finlayson *et al*. 2012). G016 (*P. aristotelis*, humerus) showed level 5 burning only to the distal end of the bone. This suggests direct exposure to the heat source in a limited area, also congruent with roasting while G018 (*P aristotelis*, tibiotarsus) showed speckling at the proximal end and level 3 char midshaft. P005 (*C. livia*, humerus) displayed a discrete double colouration of speckling at the articular ends and a patch of level 2 exposure on the dorsal surface just below the proximal articulation. Specimens from levels H, J, R and T showed no thermal modifications.



	G	H	J	K	M	N	P	Q	R	S	T
🟩 double	1						1				
🟨 5	1										
🟧 2	1				1						
🟦 1	11			7	7	3	4	1		1	

Figure 3.17: Degrees of thermal modifications present by layer. Modofocations were most frequent in layer G. No modifications were identified in layers H, J, R, and T. double = double colouration – more than one degree of modification present on the bone surface.

Pigeon/dove remains were most frequently exposed to heat (n = 18) (Table 3.24). Rock dove remains with thermal modifications were identified in 6 layers. Corvid remains displaying traces of heat exposure were found in 5 layers. All of the modified remains were observed on species mentioned by Cott in his investigation into the tastiness of birds (1946), though he deemed the coot (*F. arta*), shag (*P. aristotelis*) and oystercatcher (*H. oestralegus*) as less palatable. However, it does seem that Neanderthals at Gorham's Cave found the shag edible, as both cut marks and thermal modifications are present on remains of this species.

Table 3.24: Elements showing thermal modification by higher taxa group. Pigeons/doves are the most commonly exposed to fire.

	Layer											Total
Taxa group	**G**	**H**	**J**	**K**	**M**	**N**	**P**	**Q**	**R**	**S**	**T**	
Gamebirds	2				1					1		4
Ducks and geese					2							2
Pigeons/doves	6			5	2	3	1	1				18
cranes and rails	1						1					2
shore birds					1							1
Diving birds	2											2
Corvids	2			2	2		2					8
Indeterminate	1											1

3.6.4 Fragmentation

Fracture analysis of the Waechter avifauna was impeded by recent modifications, which were likely the result of three processes: peri-excavation damage, post-excavation efforts to remove concretions during identification, and inadequate bulk storage in bags that were too small for the number of specimens. The damage was visible as new fractures, flaking on the surface of old fractures, and in some cases, the almost complete destruction of the bone. Any fracture displaying recent damage, or flaking resulting from these processes, was excluded from the fragmentation analysis (Table 3.25).

Twenty-nine specimens showed fracture surfaces that were old or mixed in character. Those of mixed character were not reliable in any interpretation of the fracture patterns. Of the 16 fractures marked as “old”, six displayed a spiral outline, three transverse, and the remaining seven mixed/irregular or stepped outlines. Irregularities in fracture outline are normally indicative of non-human predation (Reitz and Wing 2008). Transverse fractures, right angles, and rough fracture surfaces are the product of trampling. Fragmentation resulting from trampling is additional to the traces of trampling recorded in the section 3.7.1.3.

No discernible pattern indicative of human agency was obvious in the fragmentation patterns of the Waechter avifauna. However, this does not exclude humans as the agent behind the accumulation. The wider context of the fragmented elements can be helpful. For example, G016 (*P. aristotelis*) also displayed cutmarks to the distal end, and K004 (*P. impennis*) was found alongside a coracoid of the same species bearing 13 cutmarks.

Table 3.25: Fractures of 'mix' and 'old' character.

Spec no	**Taxon**	**Element**	**Outline**	**Angle**	**Surface**	**Old/Mix**
G009	*Aves sp.*	radius	sp	mix	mix	old
G010	*Accipitriform*	ulna	tr	right	sm	old
G011	*Accipitriform*	ulna	mix	mix	mix	mix
G016	*Phalacrocorax aristoteles*	humerus	mix	mix	mix	old
G018	*Phalacrocorax aristoteles*	tibiotarsus	tr	right	sm	old
G028	*Sturnus unicolor*	humerus	tr	obl	sm	old
G055	*Columba livia*	humerus	sp	right	rough	old
K023	*Pyrrhocorax pyrrhocorax*	humerus	irreg sp	obscured	obscured	mix
K032	*Columba livia*	femur	sp	mix	mix	mix
K031	*Strix aluco*	humerus	sp	mix	mix	mix
K043	*Columba livia*	humerus	sp	mix	mix	mix
K042	*Columba livia*	humerus	uneven tr	mix	mix	mix
K004	*Pinguinus impennis*	humerus	irreg sp	mix	mix	old
K020	*Pyrrhocorax graculus*	ulna	irreg sp	mix	mix	old
K037	*Columba livia*	humerus	mix	mix	mix	old
K009	*Ardea sp.*	tibiotarsus	sp	mix	rough	old
K025	*Pyrrhocorax pyrrhocorax*	tarsometatarsal	sp	obl	rounded	old
K003	*Accipitriform*	humerus	sp	obl	obscured	old
K013	*Fal.co sp.*	tarsometatarsal	stepped tr	mix	mix	old
M043	*Anatidae?*	humerus	irregular	mix	mix	mix
M042	*Aves sp.*	tarsometatarsal	mix	mix	mix	mix
M013	*Haematopus ostral.egus*	humerus	sp	obl	sm	mix
M003	*Alectoris rufa*	tibiotarsus	sp	right	rough	mix
P002	*Columba livia*	humerus	uneven tr	right	rough	mix
P007	*Corvus corax*	femur	uneven tr	mix	mix	mix
P011	*Pyrrhocorax pyrrhocorax*	ulna	sp	mix	sm	old
P012	*Tadorna ferruginea*	ulna?	uneven sp	mix	mix	mix
P013	*Aves sp.*	acetabulum	irregular	mix	mix	old
R006	*Gavia stellata*	ulna	uneven sp	obl	mix	old

3.7 The Interpretation of Waechter's Avifauna.

3.7.1 Neanderthal Exploitation of birds

Previous studies have identified cut marks, breakage patterns, and burning on raptors, pigeons and corvids at Gorham's Cave (Finlayson *et al.* 2012; Blasco *et al.* 2014, 2016. The material studied were from the inner (level IV) and outer excavation areas (BeSm (Ossm).1 - SSLm (Usm).5), spanning sediments dating between 67, 900 +/- 5150 – 28, 000 years BP (Finlayson *et al.* 2006; Rhodes 2012;). Cutmarks on the wing elements of corvids and raptors were interpreted as evidence of feather collection (Finlayson *et al.* 2012), while cut marks, burns, and specific breakage patterns suggested subsistence-based butchery of pigeons and corvids (Blasco *et al.* 2014; 2016). Taphonomic analysis of the Waechter avifauna adds to this information, expanding the range of species exploited at the site, and extending the horizon of this behaviour at the site.

My analysis of Waechter's avifauna provides unequivocal evidence of Neanderthal bird exploitation in four of five occupation layers, G, K, M, and P (Table 3.22). Radiocarbon dates obtained by Waechter placed Level G at 47,700 +/- 1500 BP and 49,200 +/- 3200 years BP (Waechter 1964). OSL dates procured from more recent excavations place the deposition of levels loosely corresponding to G, K and M between 50-40,000 years BP (Rhodes 2012). Rhodes' (2012) OSL dates and correlations made by Colcutt and Currant (2012) give a best estimate of layer P at between >67,900 +/- 5150 years BP and <89,600 +/- 7700 years BP.

Cutmarks were present on meat-rich bones of rock doves, choughs, and partridges. The feral pigeon, a descendant of the rock dove, inhabits the rocky cliffs in and around Gorham's Cave to the present day, while partridges (albeit re-introduced barbary partridges – *A. barbara*) inhabit open and scrub areas on the rock of Gibraltar (Finlayson 2010; Birdlife Data Zone 2021). The shag (*P. aristotelis*) too would have nested on the cliffs, though instead of feeding right by the cave mouth as it does today, its feeding grounds would have been some kilometres away in coastal waters (Finlayson ibid., 2011; Rodríguez-Vidal *et al.* 2013).

In layer K, 13 cut marks on the coracoid of a great auk (*P. impennis*, K005) signify something quite unique; a now extinct bird exploited by a now-extinct human. The great auk is also present in the avifaunal accumulations at Ibex Cave and Devil's Tower in

Gibraltar (Cooper 1999, Breuil 1922, Garrod *et al.* 1928). Elsewhere remains have been found in Middle Palaeolithic deposits in Italy (Archi, Calabria), Portugal (Layer 2 of Gruta de Figueira Brava, Setubal), and the United Kingdom (La Cotte de St. Brelade, Jersey) (Tyrberg 1998). However, this coracoid from layer K represents the first direct evidence of exploitation of the Great Auk by Neanderthals.

Eleven deep and repeated cutmarks are an artefact of severing the thick tendons that connect the wing to the scapular girdle (Baumel *et al.* 1993). A pair of more superficial cut marks on the ventral surface of the same bone suggest that the bird was skinned before consumption. The great auk was flightless and clumsy on land, both of which made it easy prey for the sailors of the 18th and 19th century who prized the bird for its feathers, meat, oil and fat and hunted it to extinction (Grieve 1885). The last great auks were seen in Newfoundland in 1852 (Halliday 1979). It is unlikely the great auk bred on the rock itself. The few records available on the species, tell that it preferred low-lying rocky ledges to nest upon, close to the water's edge (Bengtson 1984). This means that the Neanderthals at Gorham's Cave must have introduced the auk from the coast, which was up to 5 km from the cave during MIS 5 – MIS 3 (Rodríguez-Vidal *et al.* 2013). Whether the collection of the carcass was the result of hunting or scavenging a washed-up carcass is impossible to discern. However, Grieve describes the ease with which flocks of the bird were collected on land (1885) This suggests that a Neanderthal would not have much trouble capturing a roosting bird if they came upon one.

Cutmarks on the femur and tarsometatarsus of *Corvus corax* remains from level P suggest a different type of exploitation as corvids are not eaten regularly in any culture (Finlayson *et al.* 2012). A raven bone with parallel and equally spaced cutmarks was recovered at Zaskalnaya VI in the Crimea (Majkic *et al.* 2017). This was interpreted as an act of symbolism by the authors. The cutmarks on the Gorham's specimen are not parallel and do not signify the level of symbolism in the Zaskalnaya VI specimen. The significance lies in the purpose. Cutmarks such as those on this meat-poor Raven tarsometatarsus suggests an intention to skin the bird. Nakashema writes that the distinctive black belly of the male common eider (*Somateria mollissima*) is prised above that of the female by the Qikirtamiut of the Belcher Islands (Sanikiluaq, Nunavut) when constructing garments from bird skins (2002). Finlayson (2019) suggests that Neanderthals may have skinned larger birds of prey and utilised the feathers of birds with red and/or black plumage to create personal ornamentations. The raven is a recognized symbol in many present cultures (Chowning 1962; Oosten and Laugrand 2006; Driver 2014) and may have been attractive to Neanderthals (Finlayson *et al.* 2012). As a large bird with glossy, iridescent feathers (Cramp *et al.* 1977-1994), the skin of a raven would have produced eye-catching personal decorations or garments. The cutmarks on these hind limb bones places the earliest non-utilitarian bird exploitation at Gorham's Cave at Level P. Rhodes' (2012) OSL dates and correlations made by Colcutt and Currant (2012) place Level P between 67, 900 +/- 5150 years BP and 89,600 +/- 7700 years BP. The bone originates from a lower stratigraphic level than more recently excavated, securely dated avian remains (Finlayson *et al.* 2012; Blasco *et al.* 2014, 2016), and well below the level of the Neanderthal hashtag (Rodríguez-Vidal *et al.* 2014; >39,000 years BP), pushing back the chronology of the behaviourally modern horizon at the site.

This diversity of habitats in the prey species indicates that Neanderthals at Gorham's Cave were aware of the avian resources available to them, not only in the near vicinity of the site, but also on the margins of the coastal plain. Knowledge of, and exploitation of, marine resources by Neanderthals in Gibraltar is evident in the collection and cooking of large amounts of shellfish (Barton 2000, Finlayson *et al.* 2006; Stringer *et al.* 2008; Fa *et al*. 2016). At both Devil's Tower (Garrod *et al.* 1928; see Chapter 4) and Vanguard Cave (Barton 2000) Neanderthals collected large mussel shells from the coast and brought them to the sites to cook over hearths. In Vanguard, cutmarks on seal bones provide direct evidence of human exploitation of marine mammals (Stringer *et al.* 2008). It would seem that the exploitation of marine taxa was a regular contribution to the diet of Gibraltarian Neanderthals.

Thermal modifications were visible on avian remains from 7 of Waechter's Middle Palaeolithic layers. Low level exposure can be attributed to incidental burning (Stiner *et al.* 1995; Blasco and Peris 2009). This is likely the case in the occupationally sterile layers S, N and Q where no convincing evidence of Neanderthal occupation was found (Waechter 1964). However, similar results can be achieved through cooking practices where flesh has protected the bone from direct exposure. Evidence of differential heat exposure on two bones from layers G and P, along with remains exhibiting higher degrees of exposure in layers G and M (n = 3), suggests that Neanderthals were roasting bird carcasses within the cave (Blasco and Peris 2009; Blasco *et al*. 2014). Known food species account for 84.2% (n = 32) of the thermally modified remains. Pigeons (*C. livia,* n = 18) corvids (*Pyrrhocorax* spp., *Corvus* spp., n = 8), and partridges (*A. rufa,* n = 4), are most frequently exposed to heat. Along with the shag (*P. aristotelis* - layer G, n = 2) and raven (*C. corax* – layer P, n = 2) remains, these species equate to the species in which cutmarks also indicated human agency in the accumulation. Additionally, thermal modifications are found on ducks (layer M: teal - *A. fuligula*, n = 1; long-tailed duck - *C. hyemalis,* n = 1), the common coot (*F. atra*- layers G and P, n = 2), and oystercatcher (*H. ostralegus* – layer M, n = 1) remains. These species highlight the importance of wetland habitats as hunting grounds for Neanderthals, and the scope of their subsistence strategies. Layers S, Q, and N each only show thermal modifications on one taxa group, and collectively contain 13.2% (n = 5) of the thermally modified remains.

The low proportion of remains with human agency does not subtract from their relevance. The scarcity of cutmarks can be explained by the ease with which bird carcasses can be processed manually without the use of lithic implements (Finlayson *et al.* 2012).

It is also possible to cook bird carcasses whole with the feathers on, and for little to no evidence of heat exposure to reach the bone surface at all (Blasco and Peris 2009; Rosell 2001). Thermal exposure may also have contributed to the scarcity. Through experimental work on herpetological material, Ma'ayan Lev of the University of Haifa, Israel found that burned remains of herpetofauna completely disintegrated after 30 minutes of trampling (Lev *et al.* 2020). The moderate levels of trample evident in these occupational layers could be responsible for a presumed lack of burned elements (Figure 3.10). Currant and Price commented on the dearth of mammal bone of any considerable size during recent excavations. They interpreted this as evidence of deliberate cleaning of the living space in order to avoid attracting vermin and larger scavengers like hyenas (*C. crocuta*) (2012). If this is the case, many bird remains would also be removed during cleaning, and the fragile burned elements would likely disintegrate completely.

Of the occupation levels, only level R shows no evidence of human agency in the accumulation of avian remains. Waechter notes that this level held only scant evidence of occupation in the small area he excavated and that it was most likely that the main occupational area was as of yet undiscovered (1964).

3.7.1.1 Other agents contributing to the accumulation

Other agents were responsible for part of the Middle Palaeolithic accumulation at Gorham's Cave. Price (2012) identified owls as largely responsible for the accumulation of the microfaunal sample, while Currant and Price (2012) identified digestion traces from large carnivores on horse, deer, and ibex remains. Eastham (pers. comm.) noted the heavily masticated nature of a *Gyps fulvus* specimen in her possession that I was unable to observe. The bones of this species are sizable, and the traces are therefore likely to belong to a larger carnivore, probably hyena. Spotted hyenas (*C. crocuta*) are recorded in the Gorham's Cave sequence, both by skeletal remains and the presence of coprolites. Other carnivores whose remaisn have been recovered in the sequence are the wolf, the red fox, the wild cat, lynx, leopard, and brown bear (Sutcliffe in Waechter 1964; Currant and Price 2012). Most of the carnivore traces on the avian remains can be assigned to small carnivores. Wild cats, lynx and foxes all take birds as prey. Their agency is observed in the frequency of crenulated edges and punctures on remains in the Waechter avifauna.

57.6% (n = 113) of the avian remains displayed traces congruent with digestion. As in the micromammalian sample. Owls are the most likely agent behind the low-level etching observed on avian remains (Andrews 1990; Laroulandie 2000; Fernandez-Jalvo and Andrews 2016). The pelt of prey animals, swallowed whole, protects the skeletal elements against the owl's stomach acid (Bochenski *et al.* 2018; Marin-Monfort *et al.* 2019). Owls also have less acidic stomach acid than diurnal raptors (Bochenski 2005, Price 2012). However, it is possible some of the digestion traces signify a secondary agency by scavengers (Baumann *et al.* 2020). The digestive footprint of a wild cat aligns well with the levels of digestion observed in the sample (Marin-Monfort *et al.* 2019). A 2019 study showed that light digestion traces dominated in wild cat scats, indicating the pelt of the prey protected remains in this feline's digestive tract (Marin-Monfort *et al.* ibid). Larger carnivores have more acidic gastric fluids, and they tend to consume the entire bone (Andrews 1990). Especially in the case of hyenas, the bone can be completely digested before being deposited as part of the scat (Williams *et al.* 2018).

Two species of owl were present in the Waechter avifauna – the eagle owl (*B. bubo*), and the tawny owl (*S. aluco*) (n = 3). Cooper identified 5 species (2012; *O. scops, B. bubo, A. noctua, S. aluco, A. flammeus*; n = 97). Interesting that apart from one surface find, the only other *B. bubo* were found in LBSmcf.11 which Cooper suggests correlates to layer M on the basis of the juvenile Eagle owl humerus exhibiting same developmental stage as a humerus and ulna found during the 1990's. Whether this is the case or not, the presence of juveniles points to nesting birds during the deposition of layer M. Bochenski *et al.* (2018) assert that eagle owls would not share a cave with human inhabitants, so their presence indicates episodes within Waechter's defined occupations when Neanderthals were absent from the site.

10.7% of the NISP in Waechter's avifauna are the remains of birds of prey (n = 21), compared to 9.6% in Cooper's analysis (n = 234). Whereas Cooper identified nine species of diurnal raptor (*Milvus sp., H. albicilla, N. percnopterus, G. fulvus, A. gentilis, A. nisus, A. chrysaetos, C. cyaneus*), only three were present in Waechter's sample (*H. albicilla, A. gentilis, A. fasciata*). However, Eastham retained a number of kite (*Milvus spp.*) and griffon vulture (*G. fulvus*) remains in her private collection (*pers. comm*. Eastham). All of these species are known to include birds in their diet (Birdlife Data Zone 2021), and they may be responsible for part of the accumulation. Diurnal raptors have stronger stomach acid, and tend not to consume the entire prey animal, tearing it apart before eating it (Bochenski 2002; Croft and Havens 2007; Lloveras *et al.* 2018).

Falcons also tear their prey apart and do not consume the entire carcass (Price 2012; Andrews 1990). Cooper identified three species of falcon in material from recent excavations (2012; *F. naumanni, F. tinnunculus, F. peregrinus*; n = 99). Two species were present in the Waechter avifauna –the common kestrel (*F. tinnunculus*) and the peregrine falcon (*F. peregrinus*). The kestrel is present only in G, K, and M – three of his five occupation layers. Finlayson (2019) proposed that that small falcons and cave-dwelling humans formed a commensal relationship where the falcons fed on rodents that were attracted to the human occupation (Larson *et al.* 2004). Cooper's table shows two concentrations of small *Falconiformes* (F. naumanni, F. tinnunculus) between LBSmcf.2 and LBSmcf.4, and between LBSmcf.8 - LBSmcf.11 (Appendix 4 in Barton, Stringer and Finlayson 2012). Whether this indicates some correlation between these levels is uncertain, but it is interesting that these birds only appear in the sequence in defined intervals.

3.7.2 Ecological interpretations.

Researchers have employed a variety of proxies to reconstruct the climatic and environmental conditions around Gorham's Cave during the Late Pleistocene. Studies of macrofauna (Waechter 1964; Currant and Price 2012; Bernal 2017; Muniz *et al*. 2019), micromammals (Price 2012), herpetofauna (Gleed-Owen and Price 2012; Blain *et al*. 2013), shellfish (Fa *et al*. 2016), birds (Eastham 1997; Cooper 1999, 2012; Finlayson 2006; Finlayson *et al.* 2008, 2016) and have all concluded that conditions in the area were generally stable during this period. The climatic conditions of Gibraltar were not very different from today, though perhaps slightly more humid (Finlayson *et al.* 2008; Jennings *et al.* 2011; Jennings 2012; Rodríguez-Vidal *et al.* 2013). Species that were displaced by the advancing polar front in northern Europe took refuge in southern Iberia, creating a non-analogue community of animal and plant taxa, including humans (Finlayson and Giles-Pacheco 2000; Eynaud *et al.* 2009; Finlayson 2011). They thrived in a landscape dominated by an open coastal plain around the rock of Gibraltar with wetlands occurring around natural freshwater springs and sporadic woodland and shrub copses (Faure *et al.* 2002; Carrión *et al.* 2003, 2008, 2018; Finlayson 2006; Finlayson and Carrión 2007; Bailey *et al.* 2008; Finlayson *et al.* 2008, 2014, 2016; Ward, Gale and Carruthers 2012; Cortes-Sanchez *et al.* 2013; Jimenez-Espejo *et al.* 2013; Rodríguez-Sanchez *et al.* 2013) In light of the wealth of information available from well-documented stratigraphic layers within Gorham's Cave, and at other Gibraltarian sites (Vanguard Cave, Ibex Cave, and Devil's Tower), Waechter's avifauna may seem of little novel value. In the following, I will place the significant results from my ecological analysis into the context of these previous studies.

The distribution of bioclimatic tolerant species in Waechter sequence produced highly significant results when compared to the expected distribution of bioclimatic tolerances across the Palearctic (χ^2 = 22.518, p = <0.001, df = 2). The absence of specialist species and over-representation of moderate to generalist species suggest that the Middle Palaeolithic landscape was more suitable for species which could easily adapt to changes in climate. Finlayson *et al.* found that bioclimatic moderate species to be most common in Gibraltar's Middle Palaeolithic, and that all tolerance categories were present in the collective avifauna of the four sites examined (Gorham's Cave, Vanguard Cave, Ibex Cave, and Devil's Tower Rockshelter) (2016).

The sub-humid climate described by is also visible in the distribution of humidity tolerances in Waechter's layers. Very significant results (χ^2 = 14.830, p = 0.002, df = 3) reflect the over-representation of category D and E (n =12, expected = 6) in the sequence, and indicates that a diverse range of humidity opportunities were present in the landscape surrounding the site. This supports the conclusions of other researchers who inferred sub-humid climate conditions between MIS 5 and MIS 3 with seasonal rains not unlike the present day (Finlayson *et al*. 2008, 2016).

The nesting habitats of species in the Waechter avifauna differed significantly from the expected values for the Palearctic (χ^2 = 11.058, p = 0.004, df = 2). This is related to the topography of Gibraltar. Rocky nesters find ample opportunity to nest on the cliffs of the limestone promontory (Finlayson 2010; Rodríguez-Vidal *et al*. 2013). Finlayson *et al.* noted that rocky nesters dominated Gibraltar's Middle Palaeolithic avifauna (2016).

Chi^2-tests of latitude ranges (χ^2 = 4.709, p = 0.095, df = 2) and temperature tolerances (χ^2 = 0.328, p = 0.849, df = 2) did not produce significant results, but this lack of significant difference to a general palearctic sample is notable in relation to the geographical position of Gibraltar. These results indicate that the avifauna present in the mid-latitude belt between MIS 5 and MIS 3 represented a condensed Palearctic population where cold tolerant, northern species were displaced by the Polar Front. This non-analogue community of taxa is congruent with a glacial refugium and supports the conclusions of previous studies (Carrión *et al*. 2003, 2008, 2018; Finlayson 2006).

3.7.3 Summary

- Remains from the Weachter avifauna show that Neanderthals living at Gorham's Cave exploited at least eleven species of bird. In addition to species harvested in the vicinity of the cave (*C. livia, A. rufa, Pyrrhocorax* spp.), they also incorporated wetland and marine (*A. fuligula, C. hyemalis, P. impennis, P. aristotelis*) species in their diet.
- The exploitation of birds from such diverse habitats indicates that Neanderthals visiting Gorham's Cave in the Middle Palaeolithic had a broad knowledge of the resources available to them in the surrounding landscape.
- A great auk (*P. impennis*) coracoid with thirteen cut marks on the bone surface from layer K (K005) is the first direct evidence of Neanderthal exploitation of this now-extinct bird.

- The ecological information inferred from the taxonomic representation in the Waechter avifauna supports previous studies of the environment and climatic conditions in Gibraltar between MIS 5 and MIS 3 (Carrión *et al.* 2003, 2008, 2018; Finlayson 2006; Bailey *et al.* 2008; Finlayson *et al.* 2008, 2014, 2016; Cortes-Sanchez *et al.* 2013; Jimenez-Espejo *et al.* 2013; Rodríguez-Sanchez *et al.* 2013).

4 Devil’s Tower Rock Shelter

In this chapter, I examine the avian remains of Devil’s Tower Rock Shelter, Gibraltar. Although general taxonomical observations have been made by Bate (Garrod *et al.* 1928) and Cooper (1999), the remains have not been subject to a detailed taphonomic analysis. Given the proximity to other Middle Palaeolithic sites on the Gibraltar peninsula, and the scarcity of information published on the site (Garrod *et al.* 1928; Tillier 1982; Dean, Stringer, and Bromage 1986; Lalueza-Fox and Pérez-Pérez 1993; Currant 2012; Figure 4.1), the present study is aimed at improving our understanding of the birds of this site and their relationship with the Neanderthals who inhabited it. The chapter will begin by providing background context, examining past studies and results previously obtained from the site. I will then describe the avian collection and the results of ecological and taphonomic analyses. Finally, I will discuss these results in the context of the environmental conditions in Gibraltar during the deposition of the sediments at Devil’s Tower, and the possible interactions between Neanderthals and the bird species associated with them at the site.

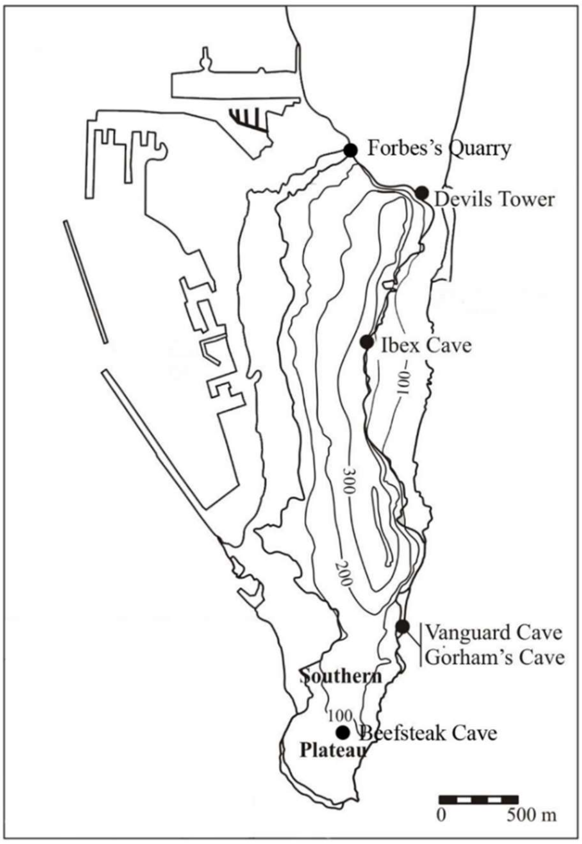


Figure 4.1: Devil's Tower Rock Shelter and other Middle Palaeolithic sites in Gibraltar. Adapted from Shipton et al. 2013.

4.1 Physical setting

Devil's Tower Rock Shelter (36°08'40.6"N 5°20'37.0"W) lies 350 m east of Forbes' Quarry, where the skull of a female Neanderthal (referred to as Gibraltar 1; Rose and Stringer 1997; Buck and Stringer 2015) was found in 1848, and ca. 2.5 km north of Gorham's Cave (Rodriguez-Vidal *et al.* 2004, 2007; Finlayson *et al.* 2006, 2008). The fissure runs at an angle into the north face of the Rock of Gibraltar and has a maximum height of 12 m and a maximum width of 1.2 m, narrowing to a crack approximately four metres from the entrance. The shelter is nine metres above sea level, four metres higher than the isthmus which connects Gibraltar to the Spanish mainland (Garrod *et al.* 1928; Rose and Rosenbaum 1990, 1991; Rose 2000).

4.2 Archaeological investigations

Devil's Tower Rock Shelter was discovered in 1911 by Colonel Willoughby Verner of the Rifle Brigade, a regiment of the British Army based at Gibraltar, and was subject to an investigatory excavation in 1919 lead by the Abbe Breuil (Garrod *et al.* 1928; Breuil 1922). He found it to contain hearths, burnt bones, and calcined lithics attributable to the Upper Mousterian (*ibid.* 1922). Breuil recommended that further investigation was merited, and formal excavations took place over three seasons between 1925 and 1927 directed by archaeologist Miss Dorothy Garrod. Garrod published the excavation report in 1928 (see Table 4.1). The site was considered for further investigation when the Gibraltar Caves Project began new excavations in Gorham's Vanguard and Ibex Caves in the 1990s, but due to the high risk of rockfalls it was decided that extensive safety engineering would be required before any further excavations could take place (Stringer 2012).

4.3 Stratigraphy

Excavations of Devil's Tower by Garrod identified seven distinct layers, where Layers 1-5 contained archaeological material (Garrod *et al.* 1928; Table 4.1; Figure 4.2). Layer 7 was described as a raised beach laid down when sea-level was nine metres higher than at present. At that point in time, Gibraltar would have been an island (Rodriguez-Vidal *et al.* 2013). All the overlying layers were found to consist of windborne sediments but were alternately affected by the presence and absence of a calcareous spring that flowed and ran dry with climatic changes (Garrod *et al*. 1928). Layers 2, 4, and 6 were deposited during such wet periods when calcium carbonate in the spring water impregnated the surrounding sand turning them into tufaceous travertines. Layer 2 also had subdivisions (a-c). Meanwhile, the fine sands of Layers 1, 3, and 5 were the product of deposition in dry periods when there was less activity in the spring (*ibid.* 1928).

Table 4.1: Description of the layers of Devil's Tower Rock Shelter after Garrod et al. 1928.

Layer	Sediment	Thickness	Colour	Charcoal	Fauna	Industry
1	Fine sand	1.3 m - 4.5 m	Light yellow	Scattered	Landshells, mussels, limpets; animal bones, broken by man and burnt	Few rough flakes of quartzite; two fragmented bone compressors
2a	Tufaceous clay	1.5 m	Very dark	Hearths	Landshells, edible seashells; animal bones broken or burnt by man	Two implements and a handful of flakes
2b	Porous tufa	1.5 m	Varying from a tough, sticky clay to a moderately hard travertine	Fragments common, no clearly defined hearths	Landshells, edible seashells, animal bones burnt or broken, small birds, rodents. Bones gnawed by wild animals. Large heap of mussel shells, many blackened by fire	Implements and flakes of quartzite and flint scattered
2c	Crumbling tufa	0.4 m - 1.0 m	Whitish	None	Some bones, small bones and landshells abundant at base	Quartzite flakes
3	Fine sand	0.2 m - 1.0 m	Yellow, merging to reddish inside the fissure	Well-marked hearths	Landshells, edible seashells (thick layers in the hearths), burnt and broken bones, shark tooth	Rough flakes of flint and quartzite, finished implements rare and crude, pebbles from the beach
4	Travertine/tufa	0.1 m - 0.8 m	Brownish grey		Edible seashells, animal bones broken or burnt; human skull (Gibraltar 2)	Flakes of flint and quartzite
5	Fine sand	0.4 m - 1.4 m	Yellow to dark brown inside cave	Small hearths	Landshells, edible seashells, animal bones burnt or broken by man	Implements and flakes exceedingly rare
6	Travertine	0.5 m - 0.75 m	Pink	Single fragment	Small animal bones and landshells	None
7	Raised beach	> 3.5 m				

In addition to the seven layers of the Devil's Tower Rock Shelter, Garrod investigated a 'Wash' area. This area was created through the erosion of terrace deposits containing lithics and faunal material that had originated from all the *in situ* layers. This 'Wash' had formed a protective layer over the deposits and was removed before excavation of the principal deposits could begin (*ibid.* 1928).

Though few studies (Tillier 1982; Dean, Stringer, and Bromage 1986; Lalueza-Fox and Pérez-Pérez 1993) have been conducted exclusively on Devil's Tower since Garrod's initial publication (ibid 1928), material from the site has been included in several studies of Gibraltar in the Middle Palaeolithic (Cooper 1999; Currant 2000; Finlayson 2006; Finlayson *et al.* 2008; Finlayson *et al.* 2016; Bokelmann *et al.* 2019). Additionally, environmental studies based on material from the contemporary sites nearby (Gorham's, Vanguard, and Ibex caves) inform of the landscape and climatic conditions near Devil's Tower during the periods of deposition (Rodriguez-Vidal *et al.* 2004, 2007, 2010, 2013; Finlayson 2006; Finlayson *et al.* 2006, 2008. Carrión and Finlayson 2007; Carrión *et al.* 2008, 2018; Jiménez-Espejo *et al.* 2013; Muniz *et al.* 2019).

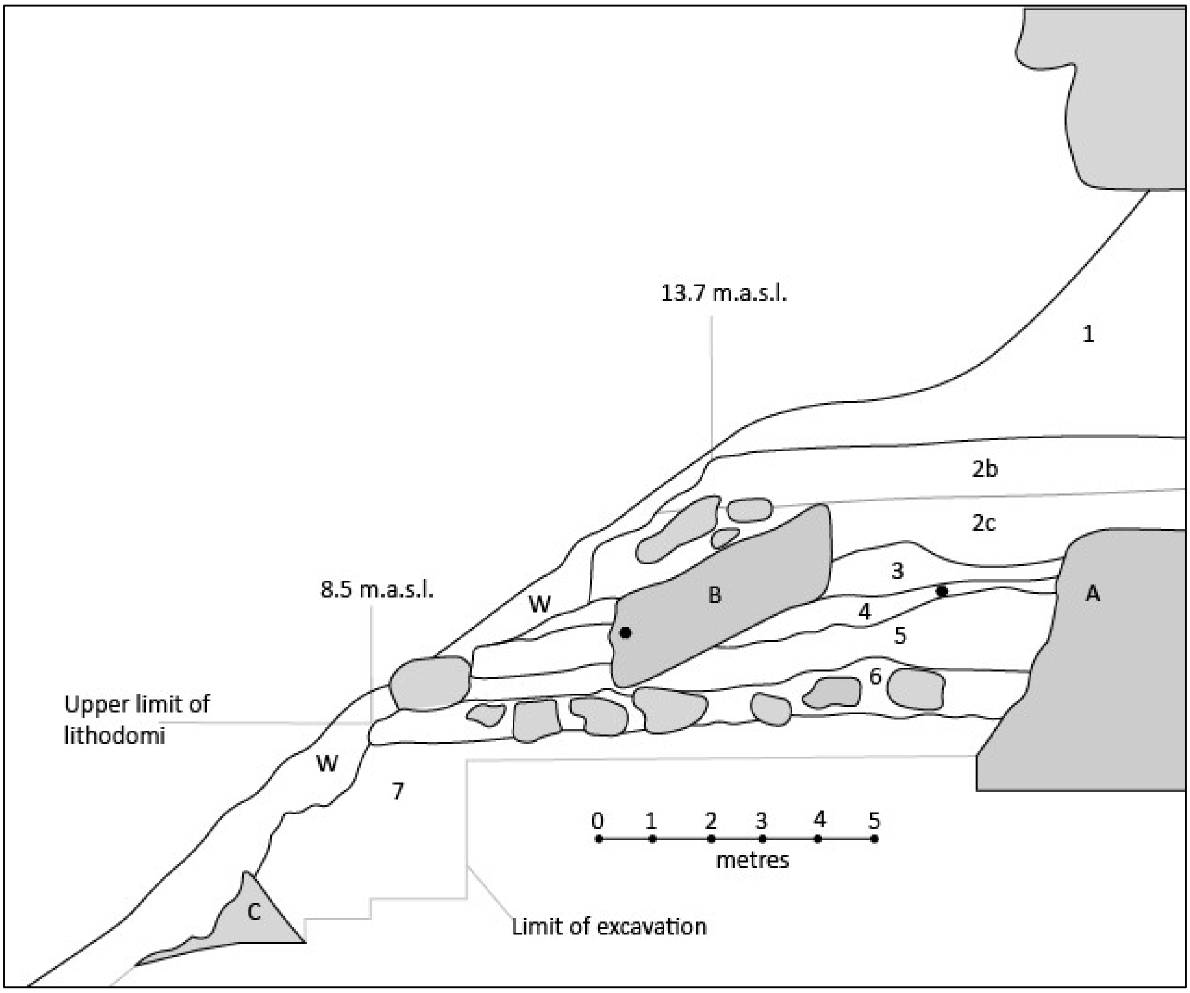


Figure 4.2: The stratigraphy of Devil's Tower Rockshelter . 1. Fine sand. 2. Calcareous tufa. 3. Fine sand. 4. Brownish-grey travertine or tufa. 5. Fine sand. 6. Pink travertine. 7. Raised beach. A. Rocks blocking the fissure. B. Fallen Rock. C. Rampart of rock in front of raised beach. W = Wash material. Black points denote where portions of human skull were found. Lithodomi are bivalve seashells which burrow in solid limestone. Digitalised version of Garrod's hand-drawn stratigraphy (Garrod et al. 1928) made in Adobe Illustrator by Linda Amos.

4.3.1 Chronology

No secure dates have been procured from Devil's Tower Rock Shelter. If the raised beach in Layer 7 did indeed reflect MIS 5e as Garrod (ibid 1928) suggested, then the sediments from Devil's Tower were deposited at some time between then and the end of the Neanderthal occupation, so roughly between MIS 5 and MIS 3. This is the same time frame in which the Catalan Bay sand dunes accumulated to the south of the site, and in which

Vanguard Cave became fully infilled by sand (Rodiguez-Vidal *et al.* 2013; Doerschner *et al.* 2019). Waechter believed the raised beach at Devil's Tower to be contemporaneous with his Layer U at Gorham's Cave (Waechter 1964, Collcutt and Currant 2012). However, Hoyos *et al.* (1994) interpreted the raised beach at Devil's Tower as contemporary with sediments identified at 10 m.a.s.l. at Europa Point on the southern tip of Gibraltar which were aged to the penultimate interglacial (MIS 7a – ca. 143 ka BP). Given that Gibraltar was an island during the maximum highstand of the last interglacial (MIS 5e; Rodriguez *et al.* 2010, 2013), it is likely the occupations happened after this point. A radiocarbon date of >30 ka BP was obtained in the 1960s from a sample taken by Garrod, but the sample was too small to achieve more refined results (Vogel and Waterbolk 1964) and the date is unreliable because advancements in radiocarbon dating have moved on considerably in the last 60 years. Given the available evidence, the sediment at Devil's Tower would therefore appear to have been deposited during periods of aeolian activity, largely during MIS 4 and 3, although further evidence is required to confirm and refine this view.

4.3.2 Lithics

No recent investigation of the Devil's Tower lithic assemblage has been published. Garrod observed that lithics were most prevalent in Layer 2b where the ratio of finished implements to flakes and cores was high, but that Layer 3 yielded clear evidence of a working floor with "abundant" flakes and cores in addition to "many" chips and roughly broken quartzite pebbles (Garrod *et al.* 1928; Table 4.2). Locally occurring jasper, flint from beach pebbles, and quartzite were the most common raw materials utilized in tool production. In total, fewer than 500 lithics were recovered during the excavation with only 43 described in any detail (ibid. 1928). All layers were attributed to the Upper Mousterian tradition, equating to the Typical Mousterian in today's terminology (Bernal 2017).

*Table 4.2: Lithics recovered from Devil's Tower Rockshelter, as described by Garrod (Garrod et al. 1928). Only 43 of the almost 500 lithics were described in any detail. No further counts were published. In Layer 1 * ='a few' fragments were found alongside 6 flakes. In Layer 3 * = flakes and cores were 'abundant' in this layer, prompting Garrod to interpret it as a working floor.*

Layer	**Lithic type**	**Flakes**	**Retouched flakes**	**Blade**	**Cores**	**Discoidal core**	**Typical points**	**Curved points**	**Oblique scraper**	**Side scrapers**	**Retouched sidescrapers**	**End scraper**	**Concave scraper**	**Used as scraper**	**Graver**	**Chopper**	**Disc type implements**	**Hit by two blows**	**Fragments**
1	Quartzite	6																	*
2	Flint			1						4	1		1						
	Chert						2												
	Quartzite					1	3			2	3								
	Jasper			1							1				1		2		
3	Quartzite	*			*								1						
	Jasper			1															
	Chert					1													
	Beach pebble															1			
	Limestone													2					
4	Flint beach pebble																1	1	
5	Flint								1										
	Quartzite					1													
WASH	Quartzite		2					2				1	1						

4.3.3 Human remains

The partial skull of a Neanderthal child (referred to as Gibraltar 2; Garrod *et al.* 1928; Buck and Stringer 2015) was recovered from the hard travertine of Layer 4 in Devil's Tower. The frontal bone and parietal were found one metre apart, 5.5 metres from the cave mouth. In the same layer, a lower jaw, right maxilla and right temporal bone were all found lying close together at the mouth of the cave. The remains were determined to belong to a 3- to 5-year-old male Neanderthal (Garrod *et al.* 1928; Tillier 1982; Dean, Stringer, and Bromage 1986). A study of dental striations by Lalueza-Fox and Pérez-Pérez (1993) suggested that the Devil's Tower child had a more abrasive diet than modern hunter-gatherers. In 2019, a genetic study confirmed the sex as male using DNA extracted from the petrous bone. Testing indicated substantial allele sharing with the Altai Neanderthal, although the quality of the sample prevented further analyses (Bokelmann *et al.* 2019).

4.3.4 Faunal analyses

4.3.4.1. Macrofauna

Dorothea Bate, faunal specialist on the Garrod excavations, identified 25 species of mammal at Devil's Tower (Table 4.3). She interpreted the sample as representative of an occupation following the Last Interglacial. She found the large mammals to be uniformly represented throughout the sequence. Only two species occurred in just a single context - an elephant and a monk seal from the raised beach of Layer 7 (Garrod *et al.* 1928). Currant (2000) re-examined the material and noted that rabbit, wild boar, red deer, and ibex were the dominant species represented at the site.

Table 4.3: The macro-mammalian remains from Devil's Tower Rock Shelter. After Bate in Garrod et al. 1928.

Taxon	**Common name**
Sus scrofa	wild boar
Cervus elaphus	red deer
Bos cf. primigenius	aurochs
Capra pyrenaica	Spanish ibex
Canis lupus	wolf
Ursus arctos	brown bear
Meles meles	European badger
Crocuta crocuta	spotted hyena
Panthera pardus	leopard
Felis cf. silvestris	wildcat
Lynx pardinus	Iberian lynx
Monachus monachus	Mediterranean monk seal
Oryctolagus cuniculus	European rabbit
Equus sp.	horse
Elephas sp.	elephant
Hystrix cristata	porcupine

Bernal included the ungulates from Devil’s Tower in his doctoral thesis where he examined the technology, subsistence and bioclimatic settlement patterns of Iberian Neanderthals (Bernal 2017). He presented counts of material from Breuil (1922) and Garrod (ibid 1928) and assigned habitat zones (Table 4.4). No further study of the Devil’s Tower macrofauna has been done, but studies of macrofaunal remains from other caves in Gibraltar place the site in a rich ecosystem where a variety of species reflect the mosaic type landscape of the exposed coastal plain (Currant 2000; Carrión *et al.* 2003, 2008, 2018; Finlayson 2006; Finlayson *et al*. 2008; Currant, Fernández-Jalvo and Price 2012; Currant and Price 2012; Rodriguez-Vidal *et al.* 2013; Muniz *et al.* 2019).

Table 4.4: Ungulates from Devil's Tower showing frequency of species and of habitat by NISP. Adapted from Bernal (2017).

		Common name	Breuil (1922)	Garrod (1928)	Total
Taxon	*Equus*	horse		3	**3**
	Bos/Bison	cattle		14	**14**
	Capra pyrenaica	Spanish ibex	8	6	**14**
	Cervus elaphus	red deer	8	20	**28**
	Sus scropha	wild boar	4	20	**24**
	Ungulates		**20**	**63**	**83**
Habitat	Rocky	caprids	8	6	**14**
	Wooded	cervids/suids	12	40	**52**
	Plains	equids/bovids		17	**17**

4.3.3.2. Microfauna

Bate identified 33 bird species (see section 4.4), two bat species, several tortoise remains (*Testudo graeca*), some bats, and 'a few' fish remains from Devils' Tower, one of which was identified as a Percoid *cf. Lates* (Garrod *et al.* 1928). Identification of the vole remains from Devil's Tower was conducted by Martin Hinton (Appendix B of Garrod *et al.* 1928) who found that all but five specimens belonged to *Microtus brecciensis*. This fossil species is likely the ancestor of the living species *Microtus cabrerae* (Pita *et al.* 2014). The presence of these voles throughout the sequence points to the presence of open areas, with high soil moisture, and ponds and streams (Luque-Larena and Lopez 2007).

Table 4.5: The micro-mammalian remains from Devil's Tower Rock Shelter. After Bate in Garrod et al. 1928.

Taxon	**Common name**
Talpa europaea	European mole
Crocidura russula	white-toothed shrew
Myotis cf. myotis	greater mouse-eared bat
Tadarida teniotis	European free-tailed bat
Arvicola sp.	water vole
Pitymus sp.	vole
Microtus brecciensis	fossil vole
Apodemus sylvaticus	wood mouse
Eliomys quercinus	garden dormouse

4.3.3.3. Mollusca

Paul Fischer conducted the only published analysis of the fossil mollusca from Devil's Tower (Appendix C in Garrod *et al.* 1928), identifying 12 species of edible marine molluscs in layers 2-6 (Table 4.6). The common limpet (*Patella vulgata*) and the Mediterranean mussel (*Mytilus edulis galloprivincialis*) were especially abundant in Layer 2 (*ibid*. 1928). The marine shells at Devil’s Tower were interpreted as kitchen refuse contemporary with the deposition of sediment and were mostly Atlantic species. This was indicative of human occupation in periods with cooler waters than the present day. Some of the shells showed signs of burning, strengthening the interpretation of marine shell exploitation (Breuil 1922, Garrod *et al.* 1928). In contrast, shells recovered from the raised beach (Layer 7) were mostly Mediterranean species.

Table 4.6: List of marine mollusc species, after Fishcer (Appendix C in Garrod et al. 1928).

Layer	**Species present**	**Dominant Med./Atl.**
1	-	-
2	*Patella vulgata* and var. *conica* *Mytilus edulus* and var. *galloprovincialis* *Patella ferruginea* *Carduim sp.*	Atlantic
3	*Patella vulgata* *Mytilus edulis* and var. *galloprovincialis* *Patella ferruginea* *Septa nodifera* *Lucina borealis*	Atlantic
4	*Patella vulgata* *Mytilus edulis* and var. *galloprovincialis* *Septa nodifera*	Atlantic
5	*Patella vulgata* and var. *major* *Mytilus edulis* and var. *galloprovincialis* *Patella ferruginea* *Pecten jacobaeus* *Patella depressa*	Atlantic
6	*Spondylus gaederopus*	Atlantic
7	chiefly Mediterranean species	Mediterranean

Fischer noted that the mussel shells were exceptionally large in size (ibid. 1928). This was also the case in mussel accumulations excavated at Vanguard Cave where a layer of shells was discovered in a Neanderthal hearth (Barton 2000; Stringer *et al.* 2008). Barton (2000) interpreted the large size of the shells at Vanguard as the result of preferential gathering because a natural collection would not display such uniformity.

4.4 Avifauna

The avifauna of Devil’s Tower Rock Shelter is housed in the Department of Palaeontology at the Natural History Museum, London. Bate distinguished 33 species in her analysis (Garrod *et al.* 1928). All of the identified species are still present in Europe today except the great auk (*Pinguinus impennis)* which is now extinct. Bate concluded that the variety of bird species, along with the other faunal remains pointed towards a much richer and more varied fauna than is present in Gibraltar today. She also commented that a great amount of material remained to be identified, most of which were covered in a cemented matrix (*ibid.* 1928).

Cooper undertook the great majority of the remaining identifications of avifauna at Devil's Tower for her PhD (Cooper 1999). The complete collection of bird remains from Devil's Tower was included in what was the first comprehensive analysis of the Late Pleistocene avifauna of Gibraltar (Cooper ibid.). Cooper's analysis was conducted at site-level rather than at individual layer-levels in order to include the large number of specimens with uncertain stratigraphic information. At some point during Bate's analysis, the secure stratigraphic context of many specimens became lost, and it is now impossible to pinpoint how and when the loss of information occurred. Cooper, in her evaluation, found the taxonomic identifications by Bate to be reliable and included the material in her analysis. However, Cooper did not conduct a taphonomic analysis.

In 2016, Finlayson *et al.* compared the bird species of Devil's Tower along with three other sites in Gibraltar (Gorham's Cave, Vanguard Cave and Ibex Cave) to the bird remains from Zafarraya Cave in Spain. Through their analysis they concluded that Devil's Tower represented part of a rich and varied Middle Palaeolithic ecosystem but remarked that Devil's Tower had some estuarine inclusions that were not present in other Gibraltarian sites (Finlayson *et al.* 2016). Bathymetric maps suggest that a river mouth existed north-east of Gibraltar in the Middle Palaeolithic, flowing over the isthmus into the Mediterranean (Figure 4.3; Cooper 1999; Finlayson and Giles-Pacheco 2000).

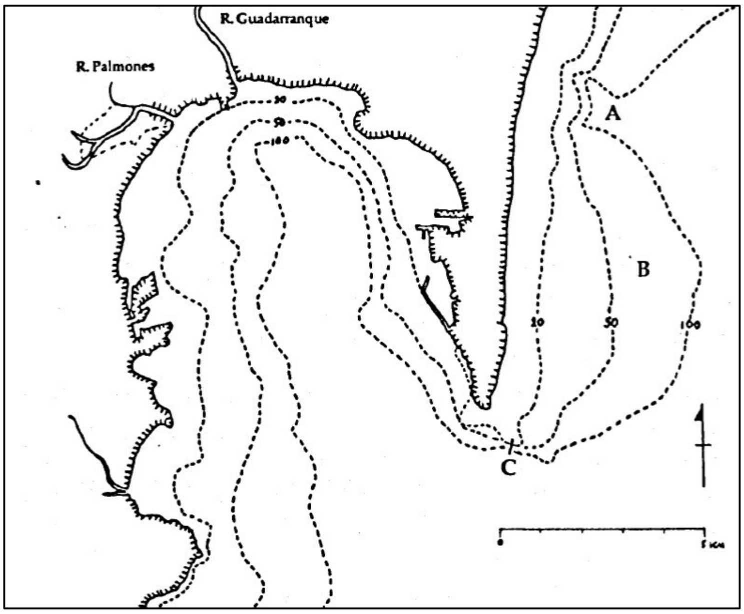


Figure 4.3: Bathymetric map of Gibraltar showing present rivers, a possible third river (A), the coastal plain (B), and a submerged rock outcrop to the south of Europa point (C). Drawn by Cooper (1999, Fig. 6.2) from Admiralty Chart, Sheet 142.

The taxonomic identifications from Devil's Tower in my analysis are those used by Cooper in 1999. In addition to the specimens examined by Cooper, I discovered that part of Garrod's collection had been dispersed into the NHM's taxonomical collection. This included a further sample of 1233 alpine swift (*Tachymarptis melba)*. These specimens have been included in this analysis, bringing the total number of specimens from Devil's Tower Rock Shelter to 3829.

4.4.1 Specimen labelling

Avian remains were labelled with a variety of different layer designations, something which Cooper (1999) noted had resulted in a loss of information. A summary of the layer descriptions and label designations for Devil's Tower, and I how worked with them in this study, is set out in Table 4.7. I made three minor adjustments to the layer organisation to counter the issue of label variation. These are explained in the following three paragraphs.

Layer 2 was divided into three sublayers (2a, 2b, and 2c) by Garrod (ibid). Layer 2a was described as containing hearths, but this was only in a very small portion of the site, and only one bird bone was assigned to it. 2b contained large amounts of marine shells, some blackened by fire and fragments of charcoal, but no defined hearths. Many bird remains were labelled '2a-b'. These remains likely originated from the contact area between sublayers 2a and 2b where the limits were not easy to identify (Garrod *et al.* 1928). Based on this, I grouped labels 2, 2a, 2a-b and 2b into a Layer '2ab'. Layer 2c was described as its own context with no charcoal and appeared as a distinct stratigraphic unit in Garrod's drawing (Figure 4.2). Layer 2c contained 18 avian remains.

Label '3-4' had a NISP of 384. This context most likely covered an area which Garrod described where sediments from Layer 3 filtered in between the hard travertine of Layer 4 after a large boulder fell from above and penetrated the deposits (Garrod *et al.* 1928). The respective NISPs of layers 3 and 4 (n = 211 and n = 4, respectively) suggested that most of the avian remains in layers 3 and 4 originated in Layer 3. However, Layers 3, 3-4, and 4 were examined individually.

Table 4.7: Table showing the layers grouped in this study based on layer descriptions and NISP.

<table>
<tr><th>Garrod's layers</th><th>Layer descriptions
(Garrod <i>et al.</i> 1928)</th><th colspan="2">Labels in NHM records</th><th colspan="2">NISP</th><th>This study</th></tr>
<tr><td>1</td><td>clearly defined unit.
No marine shellfish and scattered charcoals, but some lithics</td><td colspan="2">1</td><td colspan="2">183</td><td>1</td></tr>
<tr><td rowspan="2">2a</td><td rowspan="2">has hearths; single specimen</td><td>2a</td><td rowspan="4">2</td><td>1</td><td rowspan="4">33</td><td rowspan="4">2ab</td></tr>
<tr><td rowspan="2">2a-b</td><td rowspan="2">145</td></tr>
<tr><td rowspan="2">2b</td><td rowspan="2">no defined hearths, blackened material</td></tr>
<tr><td>2b</td><td>192</td></tr>
<tr><td>2c</td><td>distinct, no charcoal</td><td colspan="2">2c</td><td colspan="2">18</td><td>2c</td></tr>
<tr><td rowspan="2">3</td><td rowspan="2">well-marked hearths,
5 shellfish species</td><td colspan="2">3</td><td colspan="2">211</td><td>3</td></tr>
<tr><td colspan="2" rowspan="2">3-4</td><td colspan="2" rowspan="2">384</td><td rowspan="2">3-4</td></tr>
<tr><td rowspan="2">4</td><td rowspan="2">3 shellfish species,
no charcoal</td></tr>
<tr><td colspan="2">4</td><td colspan="2">4</td><td>4</td></tr>
<tr><td>5</td><td>hearth, shellfish, lithics</td><td colspan="2">5</td><td colspan="2">257</td><td>5</td></tr>
<tr><td>6</td><td>no occupation evidence</td><td colspan="2">6</td><td colspan="2">5</td><td>6</td></tr>
<tr><td>-</td><td>wash sediments from layers 1-6 and other unknown units</td><td colspan="2">1?, 5?, ?, Wash, 2bWash, no prov, "Mousterian"</td><td colspan="2">2390</td><td>no prov</td></tr>
</table>

Seven labels were classified as insecure (1?, 5?, ?, Wash, 2bWash, no prov, “Mousterian”). Some of the descriptors allude to a connection with certain secure contexts, but all have been collected under the common title ‘no provenance’. This includes the Wash material that was the only unsecure context described in detail in Garrod’s stratigraphy (Garrod *et al.* 1928). Despite having no secure context, the material from these layers was of Middle Palaeolithic origin because all original contexts were of this age, and some reference will be made to it in the following analyses.

4.5 Taxonomic results

Working with Bate's and Cooper's species identifications and my minor reorganisation of Garrod's layer designations, the following new information on the birds from Devil's Tower can now be determined (Table 4.8). The observed collection consisted of 3,829 (absNISP) specimens, 1,439 of which came from secure contexts (i.e. layers 1 to 6) with a species richness of 67 (absNTAXA). Apodiformes dominated the accumulation, representing 62.8% (n = 2305) of the absNISP and 43.2% (n = 621) of the total specimens from these secure contexts. 2,390 specimens came from insecure contexts (i.e. from the wash deposit or specimens with ambiguously labelled layer designations). The 606 non-Apodiform specimens from insecure contexts were unsuitable in the discussion of chronological changes in species representation but were considered in the overall site interpretation of certain species important to climatic and environmental discussions, e.g. *Somateria sp.* and two species of owl appeared only in these contexts. The dominant species in insecure contexts were of Corvidae, followed by Columbiformes and Galliformes. The NTAXA from insecure contexts was 54.

A total of 660 of 818 non-Apodiform specimens from secure contexts were identified to species: 73 to family, 79 to genus, and 6 to order. 87.6% (n = 717) came from Layers 2ab, 3, 3-4, and 5, with a further 9.7% (n = 79) from Layer 1. Only 2.7% come from layers 2c, 4, and 6 (n = 13, n = 4, n = 5, respectively). Corvidae and Columbiformes dominated the secure assemblage numerically with the rock/stock dove (*Columba livia/oenas*) accounting for 38.1% (n = 312) of the NISP. Choughs (*Pyrrhocorax* spp.) and partridges (*Alectoris* spp.) constituted 37.2% (n = 304) and 6.6% (n = 54), respectively. 27 classifications within secure contexts were represented by a single element. The NTAXA for secure contexts was 47.

Table 4.8: Taxonomic results of the Devil's Tower Rock Shelter avifauna by defined layer including NISP, NTAXA and MNI. MNI is calculated for secure layers only. Apodiformes are not included in the calculation of MNI. 'no prov' = no provenance - the collective total of specimens from insecure contexts. † indicates an extinct species (next 4 pages).

			LAYER									**noprov**	**absolute**
Order	**Genus**	**Species**	**1**	**2ab**	**2c**	**3**	**3-4**	**4**	**5**	**6**	**TOTAL**	**TOTAL**	**TOTAL**
GALLIFORMES													
	Alectoris	*barbara*	0	1	0	0	0	1	2	0	4	0	4
	Alectoris	sp.	6	30	0	4	5	0	5	0	50	57	107
	Coturnix	*coturnix*	0	0	0	0	0	0	0	0	0	1	1
ANSERIFORMES													
	Anas	*platyrhynchos*	0	0	0	1	0	0	0	0	1	0	1
	Anas	*crecca*	0	0	0	0	0	0	1	0	1	0	1
	Anas	sp.	0	0	0	0	0	0	0	0	0	2	2
	Aythya	*fuligula*	0	0	0	0	0	0	0	0	0	1	1
	Somateria	sp.	0	0	0	0	0	0	0	0	0	1	1
	Melanitta	*fusca*	0	0	1	1	0	0	0	0	2	1	3
	Melanitta	*nigra*	0	4	0	3	0	0	0	0	7	3	10
	Clangula	*hyemalis*	0	1	0	1	0	0	0	0	2	0	2
	Mergus	*merganser*	0	0	0	1	0	0	0	0	1	3	4
	Mergus	*serrator*	0	1	0	0	0	0	0	0	1	0	1
	Anatidae	*medium*	0	0	0	1	0	0	0	0	1	1	2
	Anatidae	*small*	0	1	0	0	0	0	0	0	1	0	1
APODIFORMES													
	Tachymarptis	*melba*	104	120	5	78	207	0	97	0	611	1773	2384
	Apus	*apus/pallidus*	0	5	0	2	1	0	2	0	10	11	21
COLUMBIFORMES													
	Columba	*livia/oenas*	5	34	9	72	131	0	59	0	310	138	448
	Columba	*palumbus*	0	1	0	1	0	0	0	0	2	3	5

			LAYER										
Order	**Genus**	**Species**	**1**	**2ab**	**2c**	**3**	**3-4**	**4**	**5**	**6**	**TOTAL**	**noprov TOTAL**	**absolute TOTAL**
GRUIFORMES													
	Porzana	*porzana*	0	0	0	0	0	0	0	0	0	1	1
	Fulica	*atra*	0	0	0	1	0	0	0	0	1	0	1
CHARADRIIFORMES													
	Burhinus	*oedicnemus*	0	0	0	0	0	0	0	0	0	1	1
	Vanellus	*vanellus*	0	0	0	0	0	0	0	0	0	1	1
	Limosa	sp.	0	3	0	0	0	0	0	0	3	0	3
	Scolopax	*rusticola*	0	4	0	1	2	0	2	0	9	9	18
	Scolopacidae		0	0	0	0	0	0	0	0	0	1	1
	Larus	*michahellis*	0	0	0	0	0	0	0	1	1	0	1
	Larus	*fuscus*	1	0	0	1	0	0	0	0	2	0	2
	Uria	*aalge*	0	1	0	0	0	0	0	0	1	1	2
	Alca	*torda*	0	1	0	0	0	0	0	0	1	0	1
	Pinguinus †	*impennis* †	0	0	1	0	0	0	0	0	1	0	1
	Fratercula	*arctica*	0	0	0	0	0	0	0	0	0	1	1
PROCELLARIIFORMES													
	Fulmarus	*glacialis*	0	0	0	0	0	0	0	1	1	0	1
	Calonectris	*diomedea/borealis*	0	0	0	0	0	0	0	2	2	3	5
	Puffinus	*mauretanicus*	0	0	0	0	0	0	1	0	1	0	1
SULIFORMES													
	Morus	*bassanus*	1	0	0	0	0	0	0	0	1	0	1
	Phalacrocorax	*carbo*	0	0	0	0	0	0	0	0	0	1	1
	Phalacrocorax	*aristotelis*	0	0	0	0	0	0	0	1	1	6	7

			LAYER										
Order	**Genus**	**Species**	**1**	**2ab**	**2c**	**3**	**3-4**	**4**	**5**	**6**	**TOTAL**	**noprov TOTAL**	**absolute TOTAL**
ACCIPITRIFORMES													
	Gyps	*fulvus*	2	21	0	0	0	0	0	0	23	39	62
	Aegypius	*monachus*	1	0	0	1	0	0	0	0	2	2	4
	Gyps/Aegypius		0	1	0	0	0	0	0	0	1	4	5
	Hieraaetus	*pennatus*	0	0	0	0	0	0	1	0	1	1	2
	Aquila	*fasciata*	0	0	0	0	0	1	0	0	1	3	4
	Accipiter	*nisus*	2	4	0	1	0	0	1	0	8	6	14
	Accipiter	*gentilis*	2	0	0	1	0	0	0	0	3	2	5
	Circus	*cyaneus*	0	0	0	0	0	0	0	0	0	2	2
	Milvus	sp.	0	0	0	0	0	0	1	0	1	3	4
	Haliaeetus	*albicilla*	1	0	0	0	0	0	0	0	1	1	2
	Aquila/Haliaeetus		0	0	0	0	0	1	0	0	1	5	6
STRIGIFORMES													
	Bubo	*bubo*	0	0	0	0	0	0	0	0	0	1	1
	Strix	*aluco*	0	2	0	0	0	0	0	0	2	9	11
	Athene	*noctua*	0	0	0	0	0	0	0	0	0	6	6
PICIFORMES													
	Picus	*sharpei*	0	0	0	0	0	0	0	0	0	1	1
FALCONIFORMES													
	Falco	*naumanni*	1	1	0	4	1	0	1	0	8	11	19
	Falco	*tinnunculus*	4	10	0	3	2	0	5	0	24	45	69
	Falco	*eleonorae*	0	0	0	0	0	0	1	0	1	1	2
	Falco	*subbuteo*	0	0	0	0	0	0	2	0	2	6	8
	Falco	*peregrinus*	0	2	0	0	0	1	1	0	4	4	8
	Falco	sp. *(small)*	4	7	0	2	0	0	1	0	14	7	21

			LAYER									noprov	absolute
Order	Genus	Species	1	2ab	2c	3	3-4	4	5	6	TOTAL	TOTAL	TOTAL
PASSERIFORMES													
	Cyanopica	*cooki*	0	0	0	0	1	0	0	0	1	1	2
	Pyrrhocorax	*pyrrhocorax*	27	78	0	20	26	0	46	0	197	121	318
	Pyrrhocorax	*graculus*	3	9	2	2	3	0	7	0	26	15	41
	Coloeus	*monedula*	2	3	0	0	0	0	0	0	5	5	10
	Corvus	*corone/frugilegus*	0	2	0	1	0	0	1	0	4	1	5
	Corvidae	*small*	0	1	0	0	0	0	0	0	1	3	4
	Corvidae	*medium*	15	29	0	7	4	0	15	0	70	41	111
	Melanocorypha	*calandra*	0	0	0	0	0	0	0	0	0	1	1
	Hirundo	sp.	0	0	0	0	0	0	0	0	0	2	2
	Sylvia	*atricapilla/communis*	0	0	0	0	0	0	0	0	0	1	1
	Turdus	*torquatus/pilaris/viscivorus*	0	0	0	0	1	0	0	0	1	0	1
	Turdus	sp.	0	0	0	0	0	0	0	0	0	1	1
	Turdus/Sturnus		0	0	0	0	0	0	0	0	0	1	1
	Petronia	*petronia*	0	0	0	0	0	0	0	0	0	2	2
	Prunella	*modularis*	1	0	0	0	0	0	0	0	1	0	1
	Anthus	sp.	0	0	0	0	0	0	0	0	0	1	1
	Carduelis carduelis/	*Linaria cannabina*	0	0	0	0	0	0	0	0	0	1	1
	Carduelis	sp.	0	0	0	0	0	0	0	0	0	2	2
	Fringilla	*coelebs/montifringilla*	0	0	0	0	0	0	0	0	0	2	2
	Fringilla	sp.	0	0	0	0	0	0	1	0	1	0	1
	Emberiza	*calandra*	0	0	0	0	0	0	0	0	0	1	1
	Emberiza	sp.	0	0	0	0	0	0	0	0	0	5	5
	Passeriformes		0	0	0	1	0	0	4	0	5	4	9
INDETERMINATE													
	Aves	sp.	1	0	0	0	0	0	0	0	1	0	1
		NISP	**183**	**377**	**18**	**211**	**384**	**4**	**257**	**5**	**1439**	**2390**	**3829**
		NTAXA	**14**	**22**	**5**	**21**	**11**	**4**	**19**	**4**	**47**	**54**	**67**
		MNI	**25**	**79**	**5**	**42**	**39**	**4**	**46**	**4**	**-**	**-**	**244**

A change in which species was numerically dominant was observed from the rock dove (*C. livia*) in Layers 5, 3-4 and 3 to the red-billed chough (*P. pyrrhocorax*) in Layers 1 and 2ab. A chi^2-test was used to assess whether the observed change was significant. Expected values were calculated by multiplying the total NISP of each species by the relative frequency of remains in each context. The results were significant (p <0.001, df =1; Table 4.9). In layers 3 to 5, the observed frequency of red-billed chough (*P. pyrrhocorax*) remains was below the expected values, while it was almost twice as high as the expected value for layers 1-2ab. Meanwhile, the frequency of rock dove (*C. livia*) remains in layers 3-5 were higher than expected, but in layers 1-2ab, the frequency was less than half of the expected frequency. The shift in dominance could indicate a change in Neanderthal dietary choices.

Table 4.9: Chi^2-test comparing the frequencies of rock dove (C.livia) and red-billed chough (P. pyrrhocorax) in Layers 1-2ab to Layers 3-5. Expected values were based on the proportion of the NISP of both species (%) in each context group.

CHI-SQUARE TEST
Observed (Expected)

	Layers 1 to 2ab	**Layers 3 to 5**	**Total NISP**
P. pyrrhocorax	105 (57)	92 (140)	197
C. livia	39 (87)	262 (214)	301
Sum	144	354	498
Relative frequency of remains	0.2892	0.7108	
Probability			
P. pyrrhocorax	<0.001		
C. livia	<0.001		

The MNI for the secure contexts is 244, of which 231 (94.7%) are from layers 1, 2ab, 3, 3-4, and 5. Apodiformes were excluded from this calculation because the high number of remains would overshadow the other species. A scatterplot of the logNISP against the logMNI for each layer (Figure 4.4) showed that there is a strong positive correlation between the NISP and MNI (Lyman 1994, 2008; Grayson 1984). The higher NISP/MNI values in the high-NISP layers may indicate that more individuals were introduced into the site during deposition. Results of Spearman correlation tests indicated that there was a significant positive association between both the NISP and MNI (rs[8] = .7075, p = 0.05) and the NISP and the NTAXA (rs[8] = . 8503, p = 0.01).

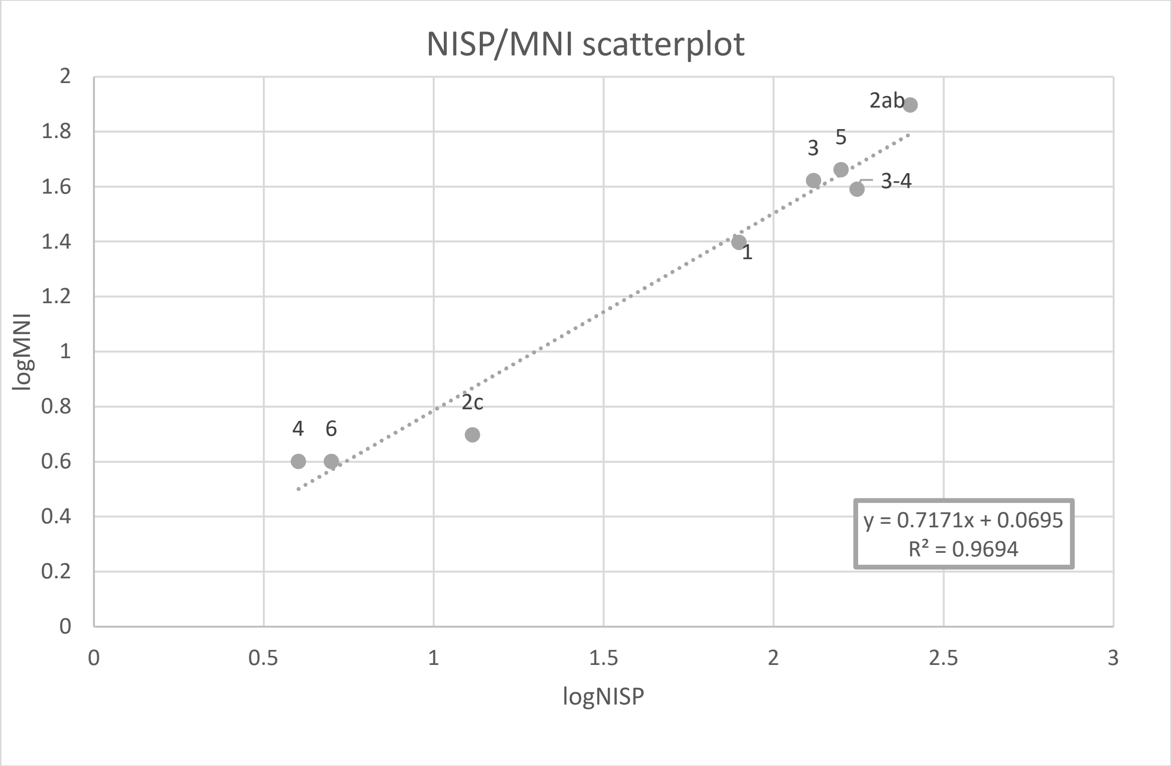


Figure 4.4: Scatterplot of logNISP again logMNI. There is a strong positive correlation between the NISP and the MNI. Layers with evidence of hearth activity show a higher number of individuals. Apodiformes were excluded from the logNISP because they are not included in the calculation of MIN.

4.6 Environmental results

Devil's Tower was included in Finlayson *et al.*'s (2016) interpretation of all Middle Palaeolithic birds in Gibraltar. The species found at Devil's Tower were examined together with species found at three other Gibraltarian sites – Gorham's Cave (see chapter 3), Vanguard Cave, and Ibex Cave to produce their results. Cooper too, in her PhD thesis, included Devil's Tower in an examination of the Middle Palaeolithic Gibraltarian avifauna (Cooper 1999). The following section presents the first examination of ecological markers inferred from the avifauna of Devil's Tower, independent of bird remains from other sites (Table 4.12).

4.6.1 Bioclimatic tolerance

Through a comparison between bird species recovered from four Middle Palaeolithic sites in Gibraltar and Zafarraya Cave, southern Iberia, Finlayson *et al*. (2016) concluded that the Middle Palaeolithic avifauna of Gibraltar showed a dominance of species with bioclimatically moderate (C) tolerances (*ibid* 2016). Category C species were present in 6/8 layers at Devil's Tower (Table 4.10). Their absence from layers 4 and 6 may be an artefact of low NISPs in these contexts (n = 4 and n = 5, respectively). At site-level, all five bioclimatic tolerance categories were represented in the avifaunal sample. This reflected an environment capable of sustaining both generalists with the ability to adapt to climatic fluctuations, and specialists, which had stricter climatic requirements. Specialist species appeared in Layer 1 (*M. bassanus*), and Layer 5 (*P. mauretanicus*).

A chi^2-test performed on the observed frequencies produced a significant result (χ^2 (2, n = 30) = 10.501, p = 0.005; Table 4.11). Moderate to generalist tolerance groups (categories C, D, and E) were grouped to produce workable data. While category B occurred as expected for a site within the Palearctic, specialist species were under-represented and moderate to generalist tolerances were over-represented relative to what was expected.

Table 4.10: Bioclimatic tolerances by layer. A – Specialist, B – Semi-specialist, C – Moderate, D – Semi-generalist, E – Generalist. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Moderate to generalist species were most frequently observed in the sequence.

	Layer (NTAXA)									
TOL	**1**	**2ab**	**2c**	**3**	**3-4**	**4**	**5**	**6**	**FREQ**	**FREQ%**
A	1						1		2	25
B	1	5	2	4	1	1	3	3	8	100
C	7	6	2	4	3		4		6	75
D	2	3	1	5	1	1	2	1	8	100
E	4	6		6	3	1	6		6	75

Table 4.11: Observed and expected frequencies of bioclimatic tolerances. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

TOL	**Observed**	**EPal**	**Expected**
A	2.00	0.315	9.45
B	8.00	0.271	8.13
CDE	20.00	0.414	12.42
sum	**30**		**30**

Table 4.12: *Ecological variables by species present at Devils Tower. After Finlayson, 2011. TOL: bioclimatic tolerance (A= specialist, B= semi-specialist, C= moderate, D= semi-generalist, E= generalist), LAT: latitude range (A= arctic 70°N, B= boreal 60°N, C= temperate 50°N, D= mid-latitude belt (warm species) 40°N, E= subtropical 30°N, F= multilatitude – species occupies several latitude bands), TEM: temperature tolerance (A-E from cold to hot), HUM: humidity tolerance (A-E from arid to wet), Foraging and Nesting habitats (F= forest, O= open, M= mixed F/O, W= wetland, R= rocky, Ma= marine, A= aerial) , diet (E= endotherm, O= omnivore, I= insectivore, H= herbivore, N= necrophyte, M= mixed strategy carnivore, F= fish eater), and Migration behaviours (M= migratory, S= sedentary, P = partially migratory).*

Common name	**Species**	**Order**	**TOL**	**LAT**	**TEM**	**HUM**	**MON**	**Foraging**	**Nesting**	**DIET**	**Migration**
Red-legged Partridge	*Alectoris rufa*	Galliformes	B	D	E	A	M	M	M	O	S
Mallard	*Anas platyrhynchos*	Anseriformes	E	F	B	C		W	W	M	P
Teal	*Anas crecca*	Anseriformes	C	B	B	B		W	W	O	P
Velvet scoter	*Melanitta fusca*	Anseriformes	B	B	B	A		W	W	O	M
Common scoter	*Melanitta nigra*	Anseriformes	B	A	A	C		W	W	O	M
Long-tailed duck	*Clangula hyemalis*	Anseriformes	B	A	A	C		W	W	O	M
Goosander	*Mergus merganser*	Anseriformes	D	B	B	B		W	W	M	P
Red-breasted merganser	*Mergus serrator*	Anseriformes	B	B	B	B		W	W	M	P
Alpine swift	*Tachymarptis melba*	Apodiformes	C	D	D	D	M	A	R	I	M
Rock/stock dove	*Columba livia/oenas*	Columbiformes	D	F	D	D		M	R	O	S
Wood pigeon	*Columba palumbus*	Columbiformes	D	F	C	C		F	F	O	P
Spotted crake	*Porzana porzana*	Gruiformes	C	C	C	C		W	W	O	M
Eurasian coot	*Fulica atra*	Gruiformes	D	F	C	D		W	W	O	P
Eurasian stone curlew	*Burhinus oedicinemus*	Charadriiformes	C	D	D	C		O	O	M	P
Northern lapwing	*Vanellus vanellus*	Charadriiformes	C	F	B	C		W	W	O	P
Woodcock	*Scolopax rusticola*	Charadriiformes	E	C	B	D		F	F	M	M
Yellow-legged gull	*Larus michahellis*	Charadriiformes	B	D	D	A		W	R	O	M
Lesser black-backed gull	*Larus fuscus*	Charadriiformes	C	B	B	B		W	W	O	M
Guillemot	*Uria aalge*	Charadriiformes	C	B	B	D		Ma	R	M	P
Razorbill	*Alca torda*	Charadriiformes	C	B	B	C		Ma	R	M	P
Great auk	*Pinguinus impennis*	Charadriiformes	C	B	B	D		Ma	R	M	P
Northern fulmar	*Fulmarus glacialis*	Procellariiformes	B	B	A	C		Ma	R	M	M
Scopoli's/Cory's shearwater	*Calonectris diomedea/borealis*	Procellariiformes	B	D	E	C		Ma	R	M	M
Balearic shearwater	*Puffinus mauretanicus*	Procellariiformes	A	D	E	A		Ma	R	M	M
Northern gannet	*Morus bassanus*	Suliformes	A	B/D	A	E		Ma	R	M	M
Great cormorant	*Phalacrocorax carbo*	Suliformes	D	B/D	C	D		W	W	F	P
Shag	*Phalacrocorax aristotelis*	Suliformes	D	F	B	B		Ma	R	F	S

Common name	**Species**	**Order**	**TOL**	**LAT**	**TEM**	**HUM**	**MON**	**Foraging**	**Nesting**	**DIET**	**Migration**
Griffon vulture	*Gyps fulvus*	Accipitriformes	C	D	D	B	M	O	R	N	P
Black vulture	*Aegypius monachus*	Accipitriformes	C	D	D	B		O	M	N	S
Booted eagle	*Hieraaetus pennatus*	Accipitriformes	C	D	D	B		M	M	M	M
Bonelli's eagle	*Aquila fasciata*	Accipitriformes	D	D	D	C		M	R	E	S
Goshawk	*Accipiter gentilis*	Accipitriformes	E	C	B	B		F	F	E	S
Sparrowhawk	*Accipiter nisus*	Accipitriformes	E	F	C	D		F	F	E	P
Hen harrier	*Circus cyaneus*	Accipitriformes	E	B	B	B		O	O	M	M
White-tailed eagle	*Haliaeetus albicilla*	Accipitriformes	D	F	B	B		W	W	M	M
Tawny owl	*Strix aluco*	Strigiformes	E	F	C	D		F	F	M	S
Iberian green woodpecker	*Picus sharpei*	Piciformes	C	F	C	B		F	F	O	S
Lesser kestrel	*Falco naumanni*	Falconiformes	C	D	D	B		O	R	M	M
Kestrel	*Falco tinnunculus*	Falconiformes	E	F	C	D		M	R	M	P
Eleonora's falcon	*Falco eleonorae*	Falconiformes	B	D	E	C		A	R	M	M
Hobby	*Falco subbuteo*	Falconiformes	E	F	B	D		A	M	M	M
Peregrine falcon	*Falco peregrinus*	Falconiformes	E	F	D	C		A	R	E	P
Iberian Azure-winged magpie	*Cyanopica cooki*	Passeriformes	C	D	C	B		M	M	O	S
Red-billed chough	*Pyrrhocorax pyrrhocorax*	Passeriformes	E	D	C	D	M	O	R	O	S
Alpine chough	*Pyrrhocorax graculus*	Passeriformes	B	D	C	E	M	O	R	O	S
Jackdaw	*Coloeus monedula*	Passeriformes	C	F	C	B		O	R	O	P
Carrion crow/Rook	*Corvus corone/frugilegus*	Passeriformes	D	F	B	C		O	O	M	P
Calandra lark	*Melanocoypha calandra*	Passeriformes	A	D	E	A		O	O	O	S
Rock sparrow	*Petronia petronia*	Passeriformes	B	D	D	A	M	O	O	O	S
Dunnock	*Prunella modularis*	Passeriformes	C	B/D	B	B	M	M	M	O	P
Corn bunting	*Emberiza calandra*	Passeriformes	B	F	D	C		O	O	O	P

4.6.2 Latitude range, temperature tolerance, and humidity tolerance.

Mid-latitude and multi-latitude species appeared most frequently in the layers of Devil's Tower (Table 4.13). Given the southerly latitude position of Gibraltar within the mid-latitude belt (36°N), this is not unexpected. A chi^2-test comparing the frequency of latitude ranges at Devil's Tower to expected values for current Palearctic distributions confirmed that the prevalence is significant (χ^2 (2, n = 30) = 6.151, p = 0.046; Table 4.14). Arctic and boreal (A, B), temperate, multi-latitude, and category B/D (C, F, B/D), and mid-latitude and sub-tropical (D, E) observed values were grouped to produce workable data. There were fewer category D and E observations than expected (n = 8, expected = 15), and more observations of categories C, F, and B/D. Though the frequency of category A and B was close to the expected value (n = 8; present in 2 and 6 layers, respectively), it was unusual that arctic and boreal species appeared so far south. This incursion of arctic and boreal species was likely due to the displacement of northern species into areas outside their current distribution by the advancing Polar Front during the last glaciation (Eynaud *et al.* 2009). In general, this process led to a concentration of fauna and flora into the habitable mid-latitude belt, creating non-analogue communities during the last glaciation (Cortes-Sanchez *et al.* 2008; Rodriguez-Sanchez *et al.* 2008; Eynaud *et al.* 2009; Finlayson 2011). The arctic species present at Devil's Tower rock shelter are both marine ducks, while the boreal species also include shorebirds, sea birds, and a diurnal raptor. Though temperate species appear in 75% of layers (n = 6), they are represented by only two species: the goshawk (*Accipiter gentilis*) and the woodcock (*Scolopax rusticola*).

Table 4.13: Latitude range by layer. A – Arctic 70°N, B – Boreal 60°N, C – Temperate 50°N, D - Mid-latitude belt, warm, 40°N, E – Subtropical 30°N, F - Multi-latitude (occupies several bands). Table shows number of species (NTAXA) per layer from each latitude range, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Species from the mid-latitude belt, and multilatitude species were most frequent.

	Layer (NTAXA)									
LAT	**1**	**2ab**	**2c**	**3**	**3-4**	**4**	**5**	**6**	**FREQ**	**FREQ%**
A		2		2					2	25
B	1	3	2	3			1	1	6	75
B/D	2								1	12.5
C	1	1		2	1		1		5	62.5
D	6	6	2	5	5	2	8	2	8	100
F	5	8	1	7	2	1	6	1	8	100

Table 4.14: Observed and expected frequencies of Latitude categories. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

LAT	Observed	EPal	Expected
AB	8.00	0.200	6.00
CF - B/D	14.00	0.306	9.17
DE	8.00	0.485	14.55
sum	**30**		**30**

The general distribution of temperature tolerances in the layers of Devil's Tower followed the general distribution of the Gibraltar avifauna (Finlayson *et al.* 2016). Species temperature tolerances reflected a warm to temperate climate where categories B, C and D were most common (Table 4.15). Cold (A) and warm (E) species were each present in 50% (n = 4) of layers. However, their distribution in the sequence was not mutually exclusive with both categories appearing in the same layer several times (layers 2ab, 5, 6). Cold species appeared in four contexts (1, 2ab, 3, and 6) reflecting displaced Arctic species and nesting seabirds. In layers 2ab, 4, and 5 heat tolerant species were represented by the red-legged partridge (*A. rufa*). A chi^2-test did not produce significant differences compared to the expected distribution of temperature tolerances for a Palearctic collection (Table 4.16; χ^2 (2, n = 29) = 0.224, p = 0.894).

Table 4.15: Temperature tolerances by layer. Scale from cold to hot, A – 1-20%, B – 21-40%, C – 41-60%, D – 61-80%, E – 81-100%. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). This shows that theentire spectrum of species tolerances were present, from cold to hot.

	Layer (NTAXA)									
TEM	**1**	**2ab**	**2c**	**3**	**3-4**	**4**	**5**	**6**	**FREQ**	**FREQ%**
A	1	2		2				1	4	50
B	4	5	2	7	1		4	1	7	87.5
C	5	7	1	6	4		4		6	75
D	5	5	2	4	3	2	5	1	8	100
E		1				1	3	1	4	50

Table 4.16: Observed and expected frequencies of temperature tolerances. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

TEM	Observed	Eprop	Expected
AB	11.00	0.416	12.07
C	6.00	0.211	6.11
DE	12.00	0.373	10.82
sum	**29**		**29**

All humidity tolerance categories were found in the sequence (Table 4.17). Species that prefer dry climatic conditions were present in six layers which overlapped in some cases (layers 2ab, 2c, 3, and 5) with species that prefer wet climatic conditions, such as the alpine chough (*P. graculus*). This is a montane species in the present day but was widely distributed in the Middle Palaeolithic alongside the red-billed cough (*P. pyrrhocorax*). The northern gannet is also a wet-tolerant species that appears in Gibraltar in the winter. The relationship between the observed and expected values did not produce significant results when compared using a chi^2-test (χ^2 (3, n = 28) = 6.898. p = 0.075; Table 4.18).

Table 4.17: Humidity tolerances by layer. Scale from arid to humid, A – 1-20%, B – 21-40%, C – 41-60%, D – 61-80%, E – 81-100%. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). This shows that a variety of humidity opportunities were available in the surroundings

	Layer (NTAXA)									
HUM	**1**	**2ab**	**2c**	**3**	**3-4**	**4**	**5**	**6**	**FREQ**	**FREQ%**
A		1	1	1		1	2		5	62.5
B	8	4		5	2		3	2	6	75
C		6		5		2	3	2	5	62.5
D	5	8	3	7	5		7		6	75
E	2	1	1	1	1		1		6	75

Table 4.18: Observed and expected frequencies of humidity tolerances. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

HUM	Observed	EPal	Expected
A	5.00	0.319	8.94
B	6.00	0.217	6.07
C	5.00	0.234	6.55
DE	12.00	0.230	6.44
sum	**28**		**28**

4.6.3 Foraging and nesting habitats

All foraging habitats were recorded in the avifauna of Devil's Tower except Rocky (Table 4.19). Aerial and mixed foragers appeared most frequently. The prevalence of aerial foragers was due to the dominance of alpine swifts (*T. melba*) in the sequence. These insectivores are spring and summer visitors in Gibraltar also in the present day. Open and forest habitats appeared alongside mixed-habitat, reflecting a varied landscape in the area surrounding the site. In addition to terrestrial species, there were strong wetland and marine signals in the avifauna of Devil's Tower. Wetland feeders such as ducks, shorebirds, and the white-tailed eagle indicated the presence of waterbodies close by, while the presence of pelagic species likely reflected nesting colonies of sea birds on the steep cliffs surrounding the rock shelter. The mosaic-type habitat of Middle Palaeolithic Gibraltar has been described before using a variety of proxies (Finlayson 2006; Carrión *et al*. 2008; 2018; Finlayson *et al.* 2008, 2016; Finlayson and Carrión 2007; Blain *et al*. 2013; Rodriguez-Vidal *et al*. 2013). The avifaunal accumulation of Devil's Tower confirms those conclusions but shows a local pelagic signal. No significant results were found when the frequencies from Devil's Tower were compared to the expected values for the Palearctic (χ^2 (3, n = 36) = 1.234, p = 0.745; Table 4.20).

Table 4.19: Frequency of species reflecting foraging habitats per layer. Table shows number of species (NTAXA) per layer that forage in each habitat, and the frequency of each habitat within the sequence (FREQ and FREQ%). This shows that a diverse suite of foraging habitats were available in the immediate surroundings.

	Layer (NTAXA)									
HF	**1**	**2ab**	**2c**	**3**	**3-4**	**4**	**5**	**6**	**FREQ**	**FREQ%**
A	1	2	1	1	1	1	4		7	87.5
F	2	4		4	1		2		5	62.5
N	3	3	1	2	3	2	4		7	87.5
Ma	1	2	1				1	3	5	62.5
O	6	6	1	5	3		4		6	75
W	2	3	1	7			1	1	6	75

Table 4.20: Observed and expected frequencies of foraging habitats. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

HF	Observed	EPal	Expected
F	5.00	0.205	7.37
M	7.00	0.170	6.11
ORA	13.00	0.374	11.05
WMa	11.00	0.307	11.47
sum	**36**		**36**

Rocky nesters dominated the Devil's Tower avifauna (Table 4.21). This was the only nesting habit represented in all eight layers, and the only habitat present in Layer 6 where sea and shore birds were the only taxa. This aligned well with the placement of the rock shelter at the foot of steep cliffs rising above the site and stretching to either side of it. Wetland nesters appeared in five layers and must have been brought to the site from wetland and coastal areas. Forest and mixed-strategy nesters (forest and open) both appeared frequently (n = 5 and n = 6, respectively), while species which only nest in open habitats were observed in only three layers. These were grouped with rocky nesters for significance testing as rocky nesters are essentially also open ground nesters, albeit vertically rather than horizontally. The chi^2-test did not provide significant results despite the dominance of rocky nesters (χ2 (3, n = 36) = 0.929, p = 0.818; Table 4.22).

Table 4.21: Frequency of species present indicating nesting habitat per context. Table shows number of species (NTAXA) per layer that nest in each habitat, and the frequency of each habitat within the sequence (FREQ and FREQ%). This reflects the great variety of nesting opportunities available in the landscape surrounding the site.

	Layer (NTAXA)									
HN	**1**	**2ab**	**2c**	**3**	**3-4**	**4**	**5**	**6**	**FREQ**	**FREQ%**
F	2	4		4	1		2		5	62.5
M	2	1		1	1	1	3		6	75
O		1		1			1		3	37.5
R	9	11	4	6	6	2	9	4	8	100
W	2	3	1	7			1		5	62.5

Table 4.22: Observed and expected frequencies of nesting habitats. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

HN	Observed	Eprop	Expected
F	5.00	0.214	5.78
M	6.00	0.172	4.65
OR	11.00	0.373	10.08
W	5.00	0.241	6.50
sum	**27**		**27**

4.6.4 Specimens from insecure contexts.

Species from insecure contexts did not change the interpretations of the site made via the secure contexts, however they did embellish the record. Twenty one of the 606 specimens from insecure contexts represent 14 species which were not found in the *in situ* deposits. These were excluded from the detailed examination above, but as Devil’s Tower is an entirely Middle Palaeolithic site, they were considered in the interpretation of the site in general (Table 4.23).

- *Bioclimatic Tolerance*

  High occurrences of species with bioclimatic category C were in tune with Finlayson *et al.*'s results for the general Gibraltar Middle Palaeolithic avifauna (2016). Two additional specialist species (A), the calandra lark (*M. calandra*) and eagle owl (*B. bubo*), appear.

- *Latitude Range*

  The relatively high frequencies of mid-latitude belt (D) and multi-latitude (F) species were in accordance with results from the secure contexts. Notable additions were the boreal Atlantic puffin (*F. arctica*), the tufted duck (*A. fuligula*), and the hen harrier (*C. cyaneus*), highlighting the southern displacement of northern species during the last glaciation (Finlayson 2011; Eynaud *et al.* 2009).

Table 4.23: Ecological variables of species only found in insecure contexts, from Finlayson, 2011. TOL: bioclimatic tolerance (A= specialist, B= semi-specialist, C= moderate, D= semi-generalist, E= generalist), LAT: latitude range (A= arctic 70°N, B= boreal 60°N, C= temperate 50°N, D= mid-latitude belt (warm species) 40°N, E= subtropical 30°N, F= multilatitude – species occupies several latitude bands), TEM: temperature tolerance (A-E from cold to hot), HUM: humidity tolerance (A-E from arid to wet), Foraging (HF) and Nesting (HN) habitats (F= forest, O= open, M= mixed F/O, W= wetland, R= rocky, Ma= marine, A= aerial) , diet (E= endotherm, O= omnivore, I= insectivore, H= herbivore, N= necrophyte, M= mixed strategy carnivore, F= fish eater), and Migration behaviours (M= migratory, S= sedentary, P = partially migratory).

Common name	**Taxon**	**Order**	**TOL**	**LAT**	**TEM**	**HUM**	**HF**	**HN**
Quail	*Coturnix coturnix*	Galliformes	D	F	D	D	O	O
Tufted duck	*Aythya fuligula*	Anseriformes	C	B	B	B	W	W
Spotted crake	*Porzana porzana*	Gruiformes	C	C	C	C	W	W
Stone curlew	*Burhinus oedicinemus*	Charadriiformes	C	D	D	C	O	O
Lapwing	*Vanellus vanellus*	Charadriiformes	C	F	B	C	W	W
Puffin	*Fratercula arctica*	Charadriiformes	C	B	B	D	Ma	R
Great cormorant	*Phalacrocorax carbo*	Suliformes	D	B/D	C	D	W	W
Hen harrier	*Circus cyaneus*	Accipirtiformes	E	B	B	B	O	O
Eagle owl	*Bubo bubo*	Strigiformes	E	F	B	D	M	R
Little owl	*Athene noctua*	Strigiformes	D	D	C	C	M	R
Iberian green woodpecker	*Picus sharpei*	Piciformes	C	F	C	B	F	F
Calandra lark	*Melanocorypha calandra*	Passeriformes	A	D	E	A	O	O
Rock sparrow	*Petronia pertonia*	Passeriformes	B	D	D	A	O	O
Corn bunting	*Emberiza calandra*	Passeriformes	B	F	D	C	O	O

- *Temperature and humidity tolerance*

  No species of temperature tolerance A (cold) were present. However, an additional marker for hot (category E) was present in the calandra lark (*M. calandra*). No species that prefer high humidity conditions (category E) appeared in the insecure contexts. At the other end of the scale, arid-tolerant species were the rock sparrow (*P. petronia*) and the calandra lark (*M. calandra*).

- *Foraging and Nesting habitats.*

  All categories of habitats were represented, the majority of which prefer open foraging and nesting habitats (n = 6). Marine foragers included Atlantic puffin (*F. arctica*), while four additional wetland species (tufted duck, *A. fuligula*; spotted crake, *P. porzana*; great cormorant, *P. carbo*; lapwing, *V. vanellus*) highlighted the importance of water sources close to the site.

4.6.5 Higher Taxa.

Specimens that could not be identified to species-level were excluded from the results presented in the section above, but can be included in an analysis of higher taxa groups (Figure 4.5; Table 4.24).

The inclusion of specimens identified as *Alectoris* sp. is a case in point. It is likely that all the partridges present in Devil's Tower belong to the same species (Randi 1996). The red-legged partridge (*A. rufa*) is the Iberian endemic and Bates' classification of the Barbary partridge is a clear case of misidentification. Barbary partridges (*A. barbara*) were introduced to Gibraltar in the 18th Century and there is no way they would have got across the Strait without assistance (Finlayson 2010). Observed at a higher taxa level, partridges were boosted from appearing in three layers, to appearing in six secure layers, and also in the insecure contexts (n = 57).

The family Corvidae also appeared in six secure layers and was boosted by a strong presence in the insecure contexts (n = 187). As a family, corvids represent the most frequently identified species after swifts (nCorvidae = 491). 71 specimens identified as "Corvidae medium" made up a considerable part of the NISP in layers 1 and 2ab. Several species of corvid are known to have been exploited by Neanderthals living in Gibraltar (Finlayson *et al*. 2012; Blasco *et al*. 2016). Another group which featured strongly in both secure and insecure contexts are the pigeons/doves (n= 453). These are also a well-documented food source for Middle Palaeolithic humans (Roger 2004; Blasco *et al.* 2014, 2016; Lloveras *et al.* 2018).

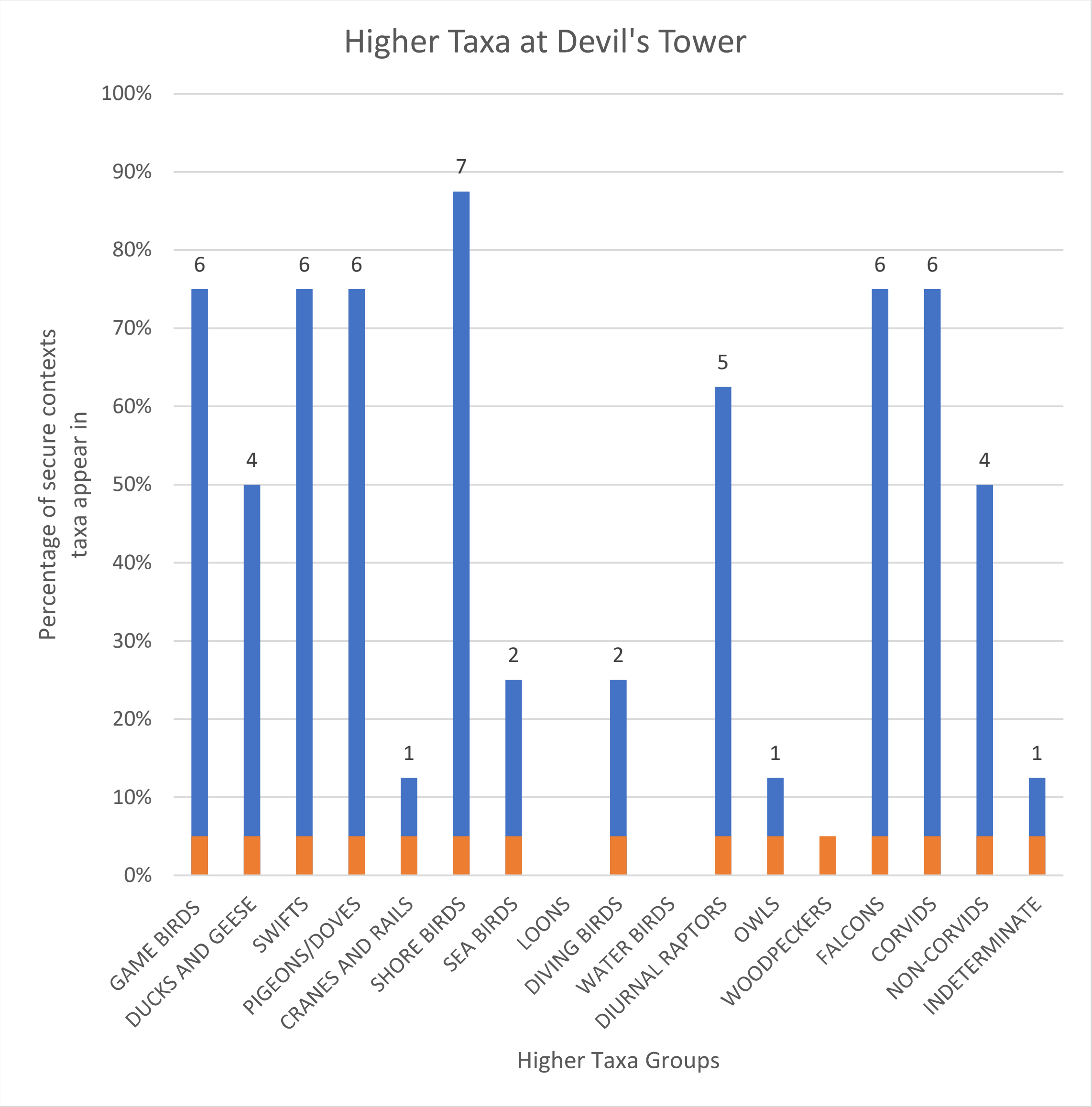


Figure 4.5: Distribution of higher taxa at Devil's Tower. Labels show how many layers each taxa group are present in. An orange block at the base of a column denotes that this group also appears in insecure contexts, but does not effect overall frequency.

Table 4.24: Distribution of higher taxa at Devil's Tower showing NISP and MNI of species grouped into higher taxa group, totals from secure contexts, total of specimens from insecure provenances (noprov total), and absolute total. All = all families. Corvid and non-corvid passerines are split to highlight the importance of corvids. noprov = no provenance.

		Layer								Total	noprov total	Absolute total
Order	**Family**	**1**	**2ab**	**2c**	**3**	**3-4**	**4**	**5**	**6**			
Game birds	All	6	31		4	5	1	7		54	58	112
Ducks and Geese	All		7	1	8			1		17	12	29
Swifts	All	104	125	5	80	208		99		621	1784	2405
Pigeons/Doves	All	5	35	9	73	131		59		312	141	453
Cranes and Rails	All				1					1	1	2
Shore birds	All	1	9	1	2	2		2	1	18	14	32
Sea birds	All							1	3	4	3	7
Loon	All											
Diving birds	All	1							1	2	7	9
Water birds	All											
Diurnal raptors	All	8	26		3		2	3		42	68	110
Owls	All		2							2	16	18
Woodpeckers	All										1	1
Falcons	All	9	20		9	3	1	11		53	74	127
Perching birds	Corvidae	47	122	2	30	34		69		304	187	491
Perching birds	Non-corvids	1			1	1		5		8	24	32
Indeterminate	All	1								1		1
	NISP	183	377	18	211	384	4	257	5	1439	2390	3829
	NTAXA	14	22	5	21	11	4	19	4	47	54	67

Shorebirds featured frequently throughout the sequence (n = 7), appearing in all layers except Layer 4. Godwits (*Limosa* sp.), identified in Layer 2ab, are a genus of migratory waders. Of the two Palearctic species of godwit, both are known to winter in Iberia (Birdlife Data Zone 2021). The black-tailed godwit (*L. limosa*) breeds in temperate latitudes, while the bar-tailed godwit breeds in the arctic (*L. lapponica*) and winters mainly in the southern hemisphere (Birdlife Data Zone, 2021). All charadriiformes present at Devil's Tower except the guillemot (*U. aalge*) and puffin (*F. arctica*) have a reputation of being flavourful according to a study on the palatability of birds conducted by Cott (1946). The degree to which the Great Auk (*P. impennis*) is edible is reflected in its extinction at the hands of humans in the 19th century (Thomas *et al*. 2019).

Several diurnal raptors and falcons could not be identified to species-level. These included the remains of an eagle (*Aquila/Haliaeetus*), a vulture (*Gyps/Aegypius*) and a kite (*Milvus* sp.) from Layers 4, 2ab and 5 respectively, and 14 specimens classified as *Falco* sp. originated in Layers 1, 2ab, 3, and 5. 16 of 18 identified owl remains originated in the insecure contexts. As a group, birds of prey constituted 17.9% of the non-Apodiform sample NISP (n = 256) and 18.9% of the calculated MNI (n = 46). Collectively they appeared in six secure contexts in addition to the insecure context 'no prov' (n = 68).

Ducks appeared in layers 2ab, 2c, 3, and 5. The presence of the genus *Somateria* in the insecure context is a meaningful climate marker. Eider ducks breed in the arctic and prefer cold, dry climatic conditions. Eider ducks are not native to Iberia in the present day (Finlayson 2011; Birdlife Data Zone 2021). Other groups (cranes/rails, woodpeckers, diving birds, and sea birds) were rare occurrences in the sequence and were not embellished by analysis at a higher taxa level. However, it was interesting that the crake (*P. porzana*), shearwater (*P. mauretanicus*), gannet (*M. bassanus*), shag (*P. aristotelis*), and cormorant (*P. carbo*) were all mentioned by Cott (1946) as palatable. He also remarked that the green woodpecker (*P. viridis,* conspecific with *P. sharpei*) tasted good but smelt dreadful.

4.7 Taphonomic results

The section presents the results of the taphonomic analysis of the Devil’s Tower avifauna (Table 4.25). All 818 specimens from secure contexts were included in the analysis. The 606 specimens from insecure contexts were also investigated, but as they could not be attributed to layers, they have been examined separately. Where traces on specimens from insecure contexts contributed to the interpretation of the agency behind the accumulation of bird remains at Devil’s Tower, mention is made citing NHM specimen number and which insecure context the specimen was assigned to. Due to the large amount of Apodiform in the collection, a sample of 242 specimens (8.3%) was selected for taphonomic examination (see: 4.7.6).

4.7.1 Lisibility

The lisibility of the avifauna was generally good (Figure 4.6). Few specimens were significantly obscured by natural processes to prevent the search for taphonomy. In most cases, the lisibility was impaired by concretions, manganese, or rooting. However, the majority of specimens were numbered directly on the bone using black permanent marker, and on some Tippex had been applied before the use of a marker. This practice had the potential to obscure taphonomic traces.

Cleaning damage was identified in all layers except 2c and 6 (Figure 4.7). In layers with a NISP of > 15, the frequency was highest in Layer 2ab. Layers 2, 4 and 6 contained several areas of hard travertine which would make the excavation and cleaning of specimens difficult without employing methods that could damage the surface of small, delicate bird remains. Many specimens contained scrapes made by a metal tool. Garrod also used blasting gelatine on several occasions to break up and clear the travertine levels (Garrod *et al.* 1928), which may explain some of the many recent breaks visible on the material (see Section 4.7.4.).

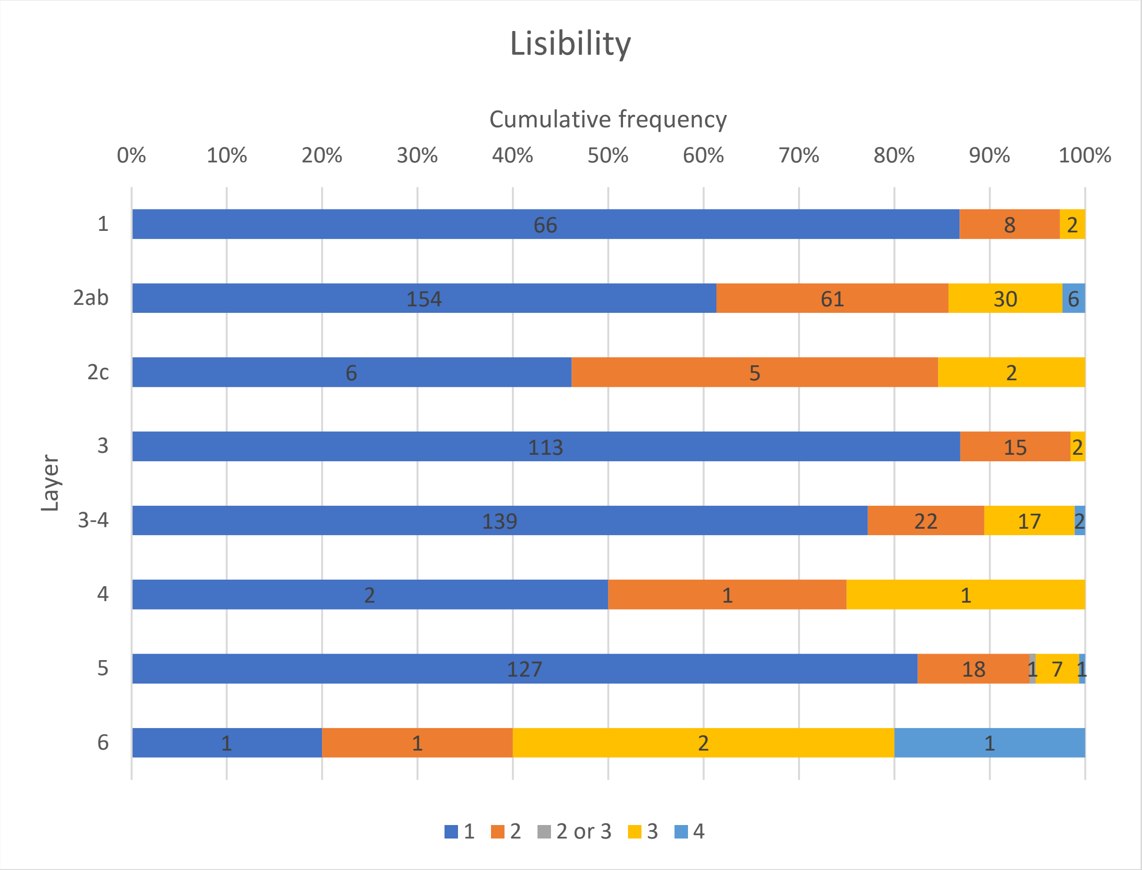


Figure 4.6: Frequency of lisibility ranks by layer on a scale from clear (1) to unreadable (4). Labels are NISP.

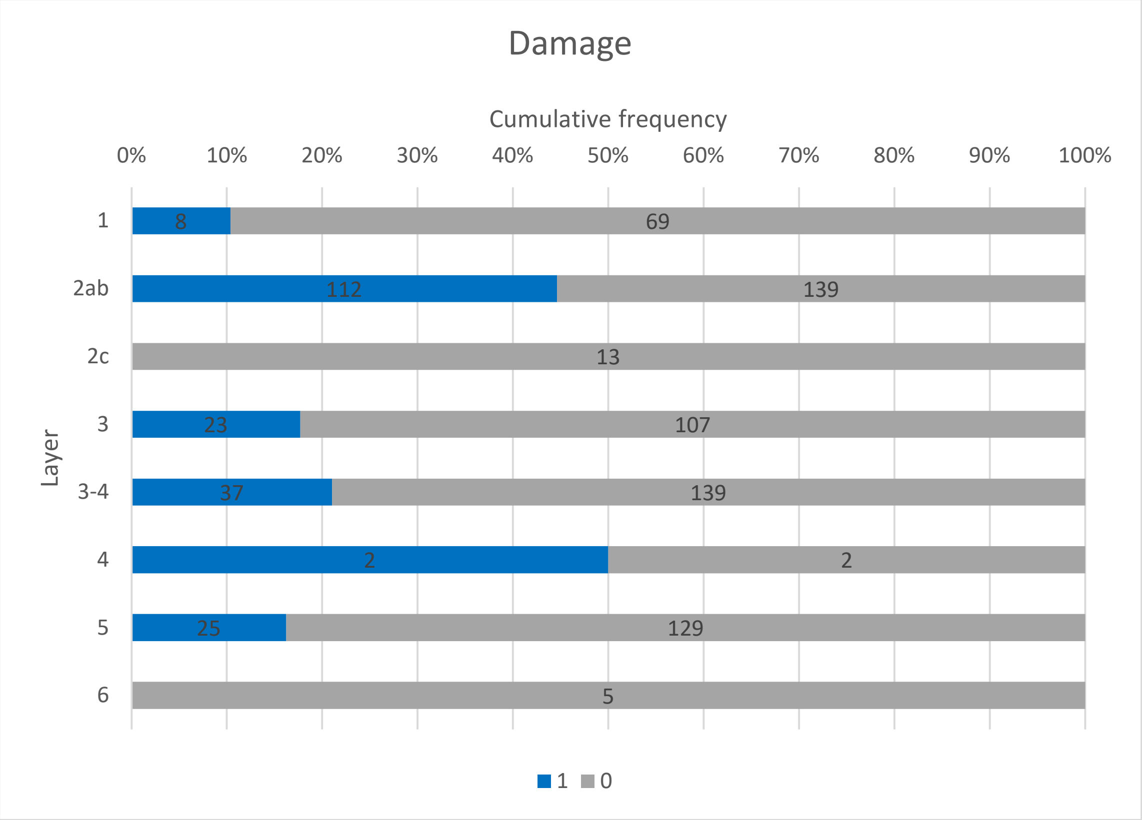


Figure 4.7: Frequency of specimens with recent damage by context. Labels are NISP.

Table 4.25: Presence of taphonomic modifications by level showing layer and NISP, number of modified remains, and percentage of the layer NISP that displayed the modifications.

	Layer 1		**Layer 2ab**		**Layer 2c**		**Layer 3**		**Layer 3-4**		**Layer 4**		**Layer 5**		**Layer 6**	
Modification	**n.**		**n.**		**n.**		**n.**		**n.**		**n.**		**n.**		**n.**	
Concretions	36	45.6%	221	87.7%	8	61.5%	65	49.6%	114	64.77%	4	100.0%	78	49.4%	4	80.0%
Manganese staining	8	10.1%	11	4.4%	1	7.7%	58	44.3%	88	50.00%	1	25.0%	64	40.5%	-	
Trample	29	36.7%	112	44.4%	2	15.4%	51	38.9%	43	24.43%	1	25.0%	63	39.9%	-	
Root etching	50	63.3%	142	56.3%	8	61.5%	103	78.6%	131	74.43%	4	100.0%	122	77.2%	3	60.0%
Weathering	50	63.2%	169	67.1%	12	92.3%	82	62.6%	75	42.61%	3	75.0%	105	66.5%	-	
Human? Toothmark	-		2	0.8%	-		1	0.8%	2	1.14%	-		-		-	
Carnivore toothmark	13	16.5%	28	11.1%	-		8	6.1%	6	3.41%	1	25.0%	5	3.2%	-	
Rodent gnaw	-		1	0.4%	-		-		3	1.70%	-		2	1.3%	-	
Bird of Prey beak mark	1	1.3%	8	3.2%	1	7.7%	10	7.6%	10	5.68%	-		10	6.3%	-	
Indeterminate toothmark	3	3.8%	4	1.6%	-		1	0.8%	8	4.55%	-		5	3.2%	1	20.0%
Digestion	47	59.5%	91	36.1%	10	76.9%	109	83.2%	123	69.89%	2	50.0%	116	73.4%	3	60.0%
Cutmark	1	1.3%	2	0.8%	-		-		2	1.11%	-		1	0.6%	-	
Thermal modification	9	11.4%	14	5.6%	-		4	3.1%	17	9.66%	-		8	5.1%	-	
Peeling	-		1	0.4%	-		-		3	1.70%	-		-		-	

4.7.2 Natural modifications

4.7.2.1 *Concretions, Manganese staining, and Root etching.*

Most specimens displayed a varying degree of concretions (Figure 4.8). These concretions tended to be located on the articular ends, obscuring possible signs of digestion and disarticulation. Layers 1, 3, and 5 had the lowest frequencies of concreted specimens. A higher proportion of concreted specimens and higher frequencies of grade 2, 3, and 4 concretions in layers 2, 4, and 6 may be a sign that water percolated though these layers causing travertines to form.

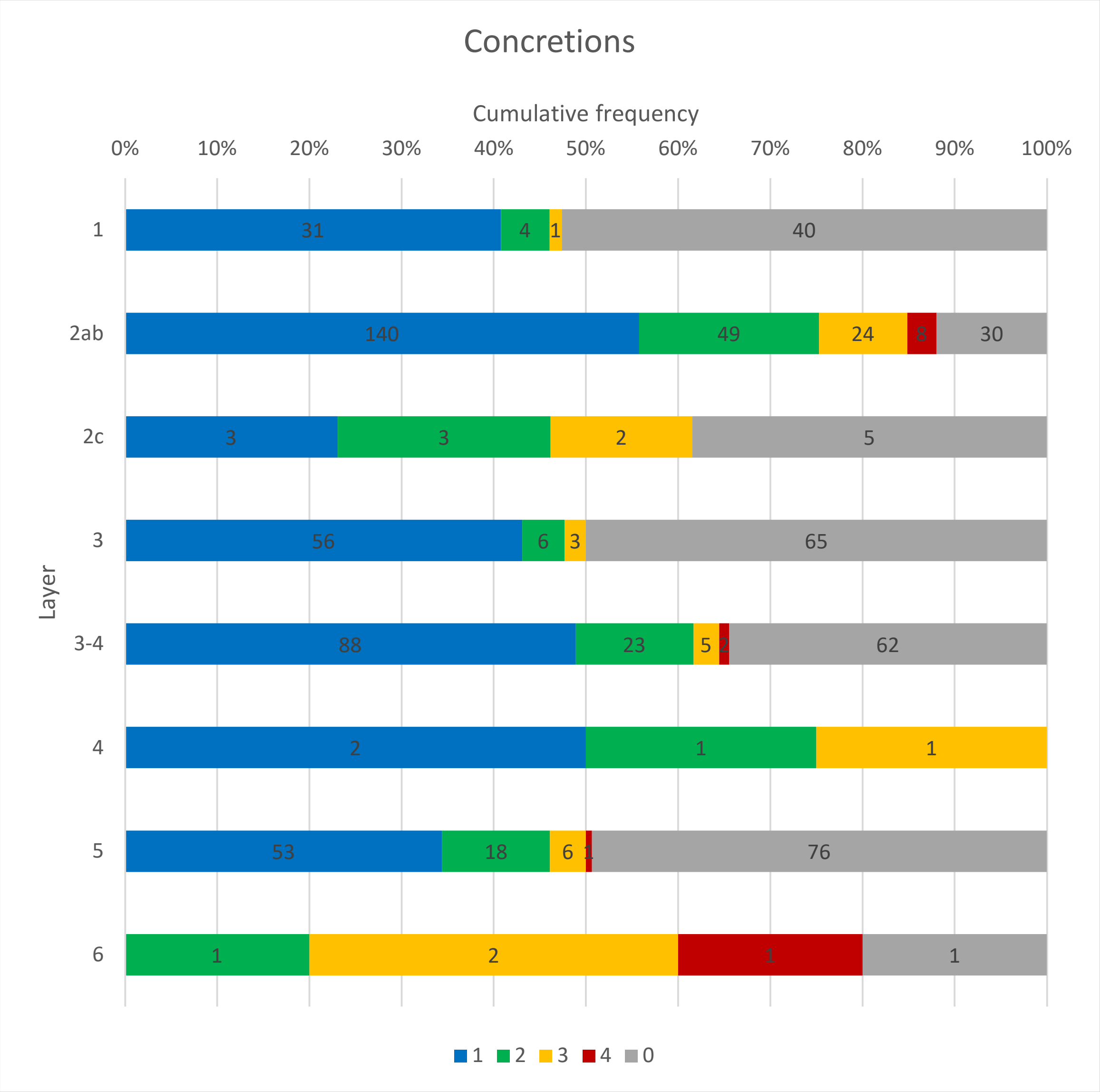


Figure 4.8: Degree of concretion coverage present by context. 1= 0-25%, 2= 26-50%, 3= 51-75%, 4= 76-100%. Labels are NISP.

Manganese oxide staining was uncommon in layers 1, 2, 4 and 6 while between 40 and 50% of remains in layers 3, 3-4, and 5 displayed some degree of staining (Figure 4.9). Less than 10% of specimens in these layers exhibited staining on more than 25% of the bone surface. The low levels of manganese oxide staining despite spring activity in layers 2, 4 and 6 may reflect the open nature of the site. In a closed cave environment damp air lingers, allowing crystals to form on the bone surface (Fernandez-Jalvo and Andrews 2016). In a more exposed location, like a rockshelter, the sediment is more exposed to the elements and is more likely to dry out. 55.2% of specimens displayed evidence of root activity (Figure 4.10). The shallow crevice and generally open nature of the site may have allowed plants to grow unrestricted in the sediments. No rooting was evident on remains in layer 6. This was likely because so few remains were recovered (n = 5) rather than an absence of plants.

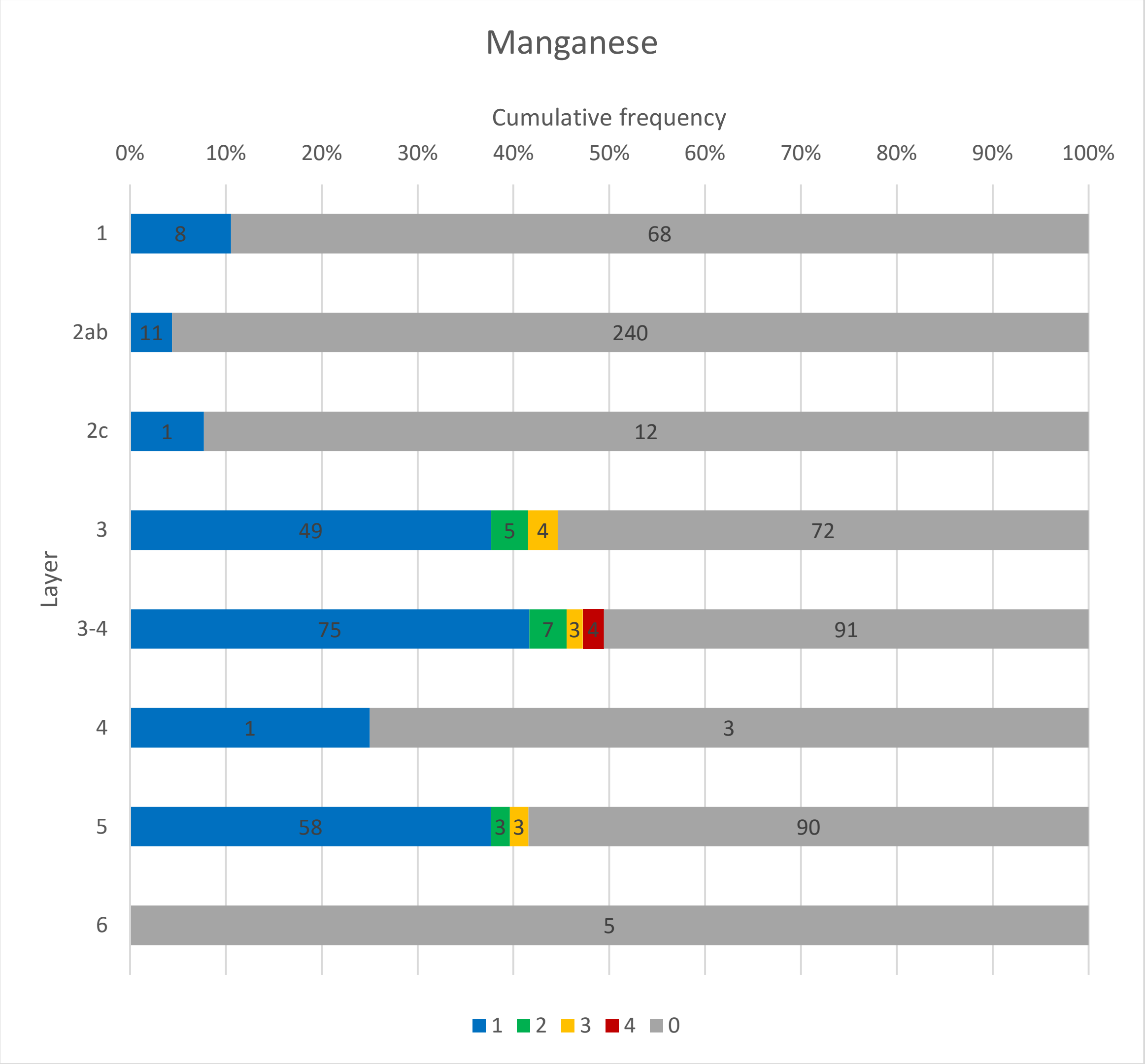


Figure 4.9: Degree of manganese oxide staining by context. 1= 0-25%, 2= 26-50%, 3= 51-75%, 4= 76-100%. Labels are NISP.

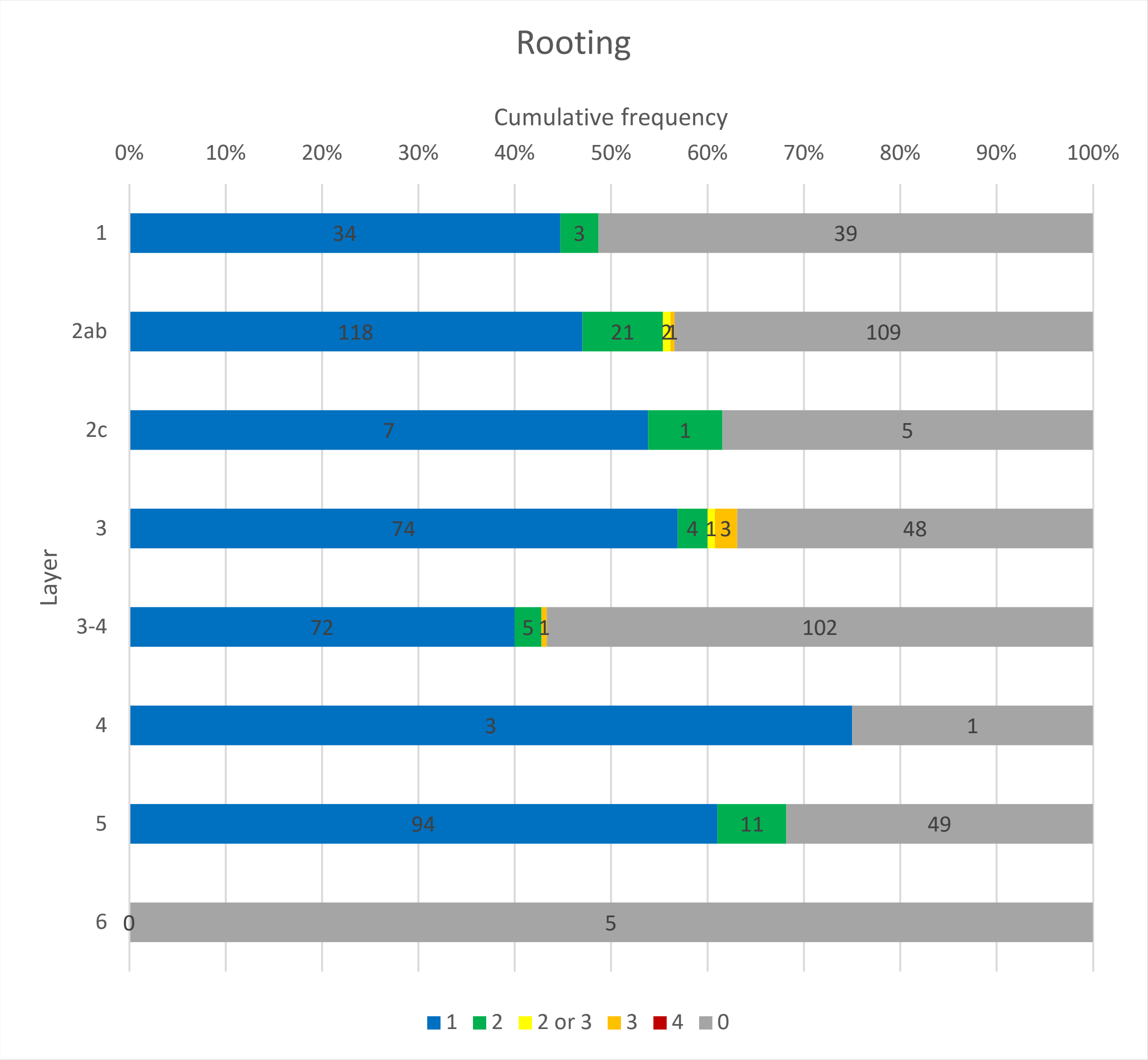


Figure 4.10: Degree of rooting present by context. 1= low level of rooting, 2= moderate level of rooting, 3= significant degree of rooting

4.7.2.2 Weathering

Weathering affected 59% (n = 482) of the Devil's Tower avifauna with the majority of modifications falling into category 1 (n = 405) (Figure 4.11). Layers with a NISP of > 15 showed the same pattern in the frequency of weathering categories with a sharp drop in the count from 1 to 2, and a further drop to 3. No specimens displayed weathering modification beyond category 3. This may reflect the rapid disintegration of specimens after a certain amount of degradation, or it may reflect a collector's bias towards the most identifiable specimens. Weathered specimens were also more likely to be damaged or destroyed in peri- and post- excavation practices.

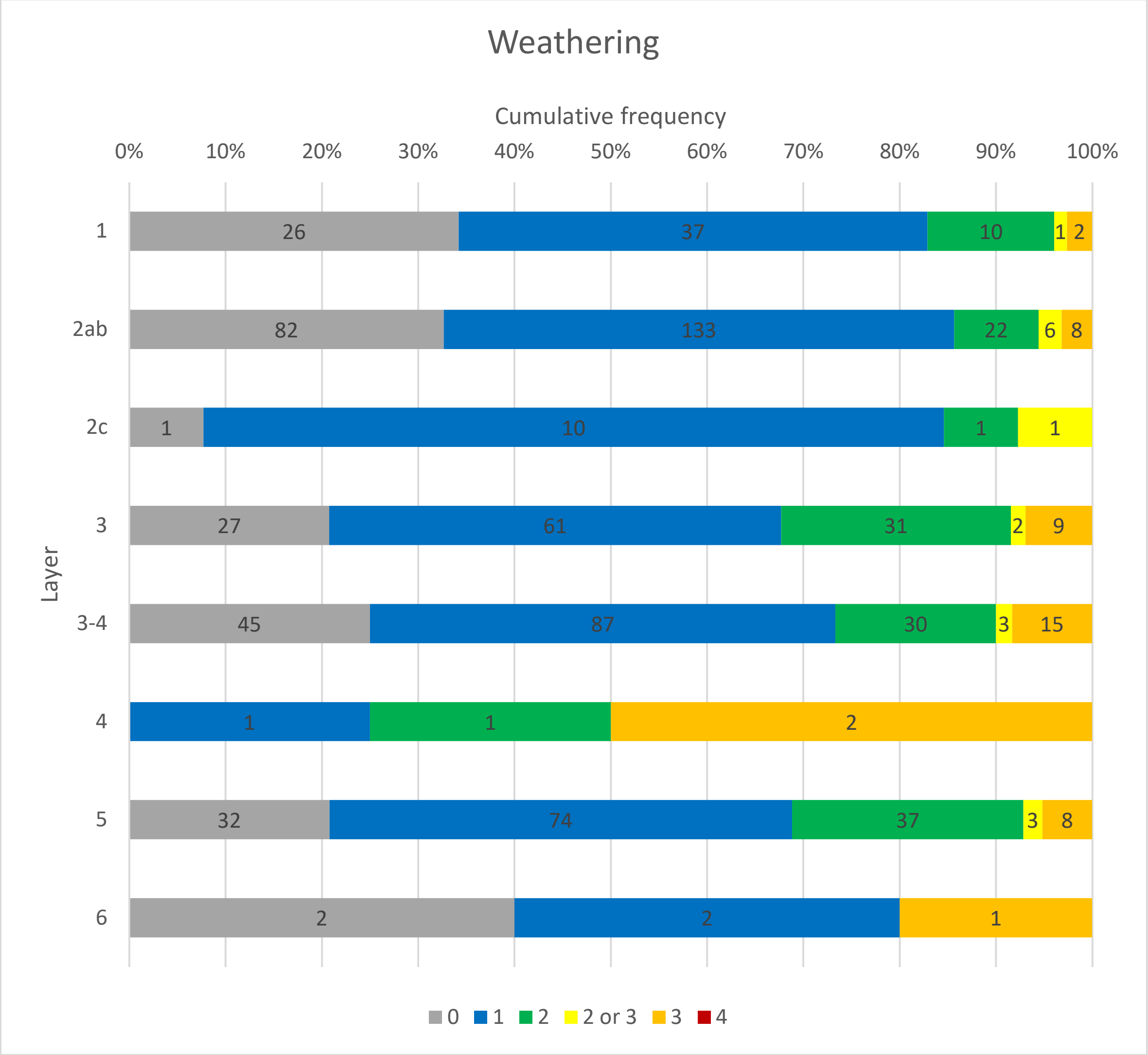


Figure 4.11: Degrees of Weathering modifications by context where 0 = no modification and 5 = highest degree of modification.

4.7.2.3 *Trampling*

Trample was evident in all layers at Devil’s Tower Rockshelter (Figure 4.12). The highest occurrence was found in layers 1, 2ab, 3 and 5 with numbers ranging from 35 - 45% of the specimens. In layers 2c, 3-4, and 4 trampling was found on 15 - 25% of specimens. In general, this was considerably lower than levels found in the Waechter avifauna at Gorham’s Cave (see Chapter 3). This may reflect how the site was used differently by Neanderthals and other large mammals and the frequency of their visits.

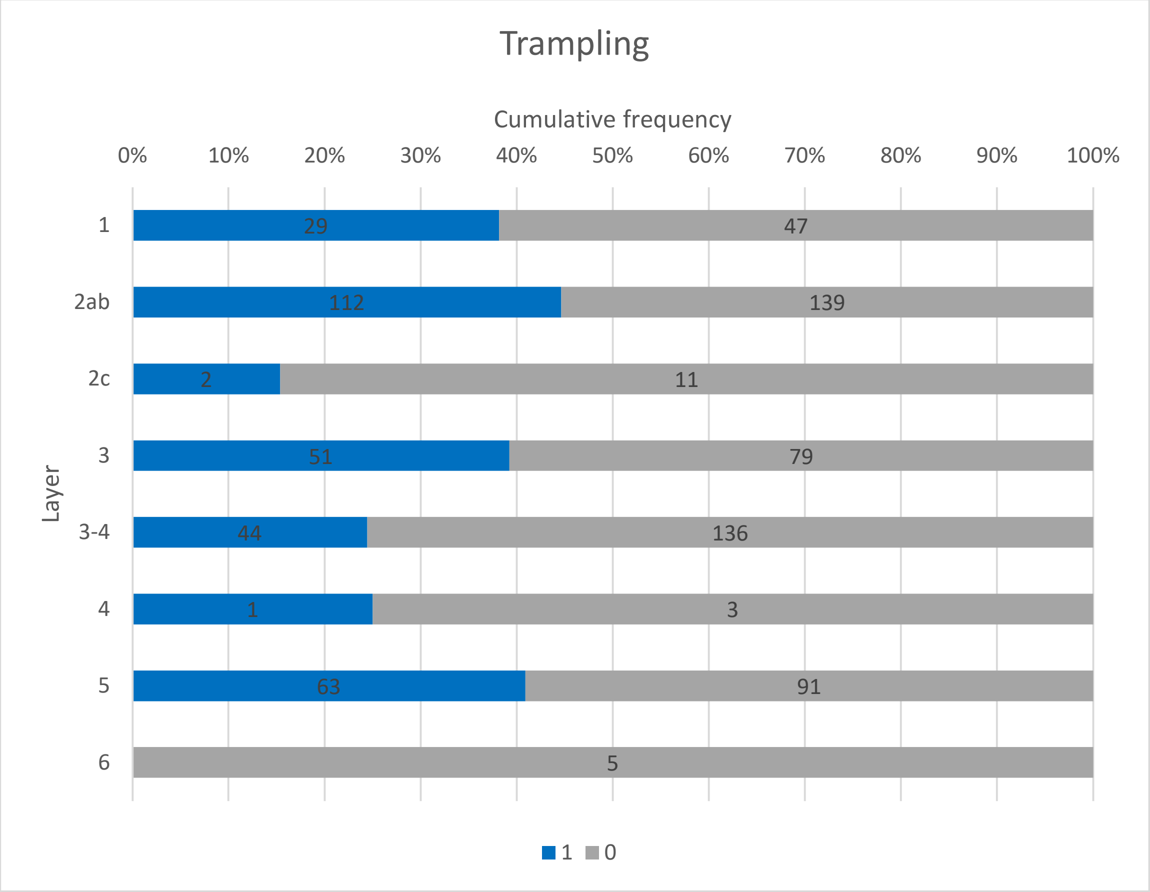


Figure 4.12: Frequency of trampling modifications present by layer.

4.7.3 Predator modifications

A total of 17.2% (NISPmod = 141) of specimens showed modifications resulting from manducation. Modifications were present in material from every layer, and more than one modification could be recorded on any one specimen (Table 4.26; Figure 4.13).

Table 4.26: Presence of tooth and beak marks by context. n. mod=number of modified specimens, %mod= percentage of modified specimens by context, total number of modifications, modification type. Cren = crenulated fracture edges.

				Manducation modifications					
Layer	**n.mod**	**%mod**	**Total modifications**	**Pit**	**Score**	**Notch**	**Puncture**	**Cren**	**Gnaw**
1	17	21.5%	21	0	0	0	15	6	0
2ab	45	17.9%	58	1	4	5	24	24	2
2c	2	15.4%	4	0	0	0	2	2	0
3	20	15.3%	23	0	1	1	12	8	0
3-4	33	18.8%	40	0	2	1	19	15	3
4	1	25.0%	1	0	0	0	0	1	0
5	22	13.9%	28	0	2	1	16	7	2
6	1	20.0%	1	0	0	0	0	1	0
Total	141	17.2%	176	1	9	8	88	64	7

Punctures (n = 88) and crenulated fracture edges (n = 64) were the most frequent modifications. The punctures and pits observed were mostly attributed to smaller carnivore activity due to size (Andrews 1990; Fernández-Jalvo and Andrews 2016), although some specimens exhibited toothmarks of a size attributable to the spotted hyena (*C. crocuta*). Layers 2ab, 3, 3-4, and 5 showed the greatest diversity in the type of trace found on the bone surface. Rodent gnawing was recorded in layers 2ab, 3-4, and 5. Tooth marks of a morphology attributable to humans were present in layers 2ab, 3, and 3-4.

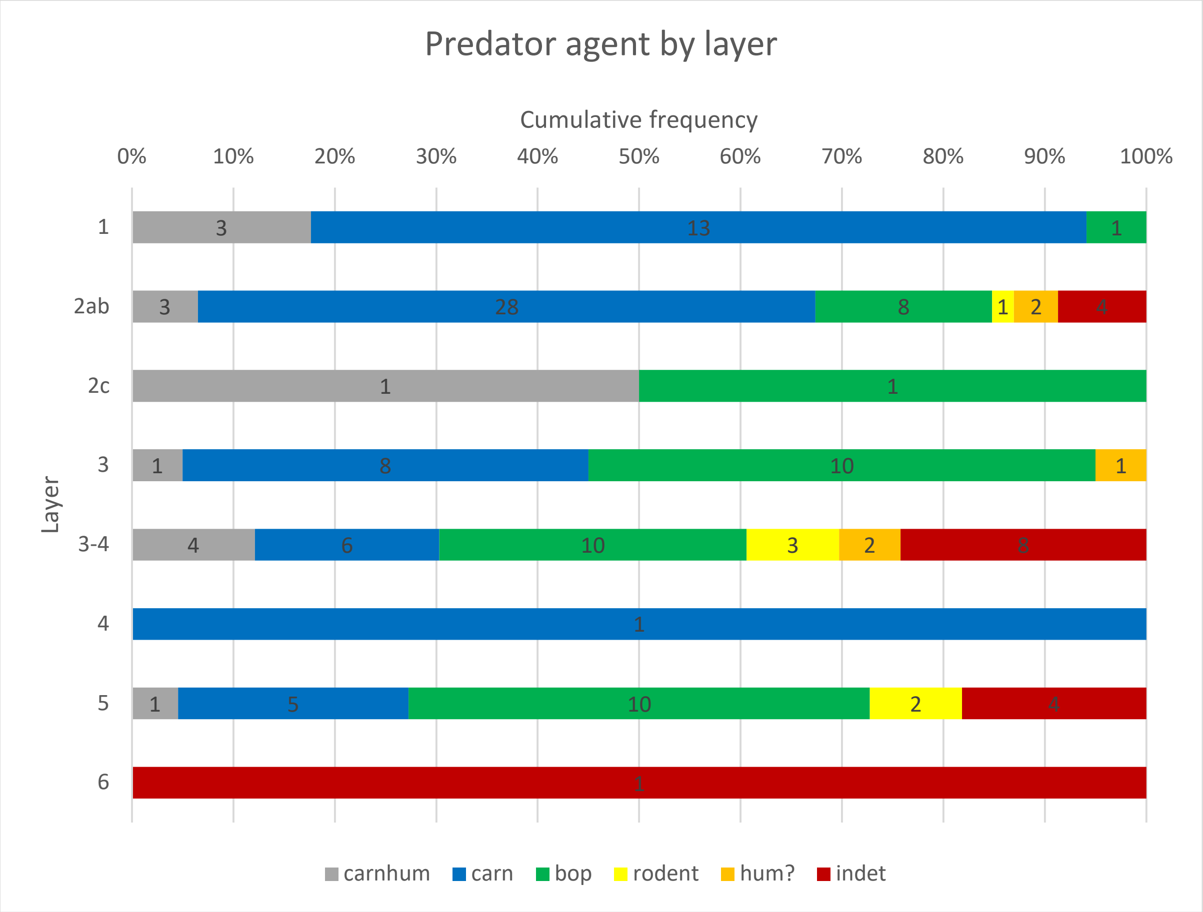


Figure 4.13: Agency in each context as reflected by tooth and beak marks. Carnhum =Carnivore or human, Carn= Carnivore, bop= bird of prey, rodent= rodent, hum?= possible human, indet = indeterminate.

479 specimens (58.6%) of the NISPtaph showed traces of digestion (Table 4.27). Of those, 434 showed only low levels of acid etching on the bone surface. Some specimens showed more advanced stages of acid etching, while 5% showed only a light polishing of the cortex. Low level etching was mostly attributed to owls and small carnivores (Fernández-Jalvo and Andrews 2016). A few incidences of higher etching most likely reflected the agency of diurnal raptors because large carnivores tend to digest the bones of small prey completely (Serjeantson 2009).

Table 4.27: Digestion traces. Polish/no polish denotes the presence or absence of a polished cortex. Etch1, a low level of acid etching, etch 2, a medium level of acid etching.

Digestion trace	No etch	Etch 1	Etch 2
Polish	25	401	38
No polish	-	33	7

4.7.4 Human modifications

4.7.4.1 Striations

Six specimens from four secure contexts (layers 1, 2ab, 3-4, 5) presented with cutmarks (Table 4.28). A further five specimens with cutmarks from insecure contexts (5?, ?, no prov) contributed to the interpretation of Middle Palaeolithic behaviour at Devil's Tower Rockshelter and have therefore been included in this section. Seven species were exploited, six of which were known food birds (Pigeons, ducks, choughs, and partridges). The final specimen was a diurnal raptor; sparrowhawk (*A.gentilis*).

Table 4.28: Specimens marked by striations, snowing spec. no., taxa, element (cmc = carpometacarpal, tmt = tarsometatarsal), laterality, number of modifications (n), type of modifications (cm = cut mark), location by bone zone (1 – 12345, each digit denotes a bone zone), orientation to the long axis of the bone (tr = transverse, lo = longitudinal, obl = oblique), and intent (da = disarticulation, df = defleshing).

Spec no. NHMUK-A-	Layer	Taxon	Common name	Element	Side	n	Type	Location	Orientation	Intent
6642	1	*Corvidae (medium)*	corvid	ulna	R	1	cm	5	tr	da
7240	2ab	*Pyrrhocorax graculus*	alpine chough	tmt	R	2	cm	5	tr	da
7279	2ab	*Melanitta nigra*	common scoter	coracoid	L	2	cm	45	lo/obl	da
7773	3-4	*Columba livia/oenas*	rock/stock dove	femur	L	1	cm	1	tr	da
7866	3-4	*Columba livia/oenas*	rock/stock dove	coracoid	L	3	cm	1	tr	da
8884	5	*Pyrrhocorax pyrrhocorax*	red-billed chough	cmc	R	2	cm	2	tr	da
8769	5?	*Corvidae (medium)*	corvid	ulna	L	1	cm	4	tr	df?
8951	5?	*Acciputer nisus*	sparrowhawk	ulna	R	2	cm	2	obl	df?
1854	no prov	*Pyrrhocorax pyrrhocorax*	red-billed chough	ulna	L	5	cm	1	tr	da
8088	?	*Alectoris sp.*	partridge	ulna	L	1	cm	2	tr	df
8517	?	*Alectoris sp.*	partridge	coracoid	R	9	cm	2	tr/obl	df

An ulna of a medium-sized corvid from Layer 1 displayed a deep transverse cutmark across the *incisura tendinosa* near the distal articulation. This was attributable to the disarticulation of the carpometacarpal and digits from the more meat rich parts of the carcass (Figure 4.14).

Layer 2ab contained a right tarsometatarsal of an alpine chough (*Pyrrhocorax graculus*) (Figure 4.15) and the left coracoid of a common scoter (*Melanitta nigra*) (Figure 4.16). Cutmarks on the distal condyles of the tarsometatarsal suggested a directed effort to separate the phalanges from the upper limb bones. Nicks on the distal coracoid pointed towards an intent to disarticulate the coracoid from the pectoral girdle during butchering activities.

Layer 3-4 contained two specimens, a coracoid and a femur, both identified as rock/stock dove (*Columba livia/oenas*) (Figure 4.17; Figure 4.22). The femur is an attractive meat rich element attached to the pelvic girdle at the acetabulum, while the proximal coracoid attaches to the humerus and scapula. Both specimens showed striations on the proximal articulations congruent with an effort to break down the carcass.

A right carpometacarpal of the red-billed chough (*Pyrrhocorax pyrrhocorax*) from Layer 5 showed two faint transverse cutmarks on the major metacarpal (Figure 4.18), which were likely made in the process of dismembering the wing. It is worth noting that the primary flight feathers attach to the carpometacarpal and that Neanderthals were known to have an affinity for dark feathers (Finlayson *et al.* 2012).

Five specimens with human modifications from insecure contexts displayed cutmarks. Transverse cutmarks on the ulna and coracoid of partridges (*Alectoris sp*.) (Figure 4.19; Figure 4.20), and on the ulnas of two corvids (*Corvidae (medium);* red-billed chough - *P. pyrrhocorax*) (Figure 4.21) reflected butchery practices. However, the oblique character of a cutmark on the proximal shaft of a sparrowhawk ulna (*A. nisus*), along with the placement close to a quill knob, indicated the intention to harvest feathers (Figure 4.22). The cutmark on the sparrowhawk specimen and that on a rock dove femur from layer 3-4 were obscured by marking the bones with a black marker. This was an obstacle in the secure classification of the traces as cutmarks, but examination under magnification provided enough confidence to verify their identification.

A6642 – *Corvidae (medium)*, ulna with deep transverse cut mark.

Figure 4.14: NHMUK-A-6642. Corvid ulna from Layer 1 of Devil's Tower displaying a deep cutmark on the distal articulation. Length = 39 mm. (Photo: Linda Amos. Natural History Museum, London).

A7240 – *Pyrrhocorax graculus* tarsometatarsal with two oblique cutmarks to the medial condyle.

Figure 4.15:NHMUK-A-7240. Alpine chough (P. graculus) tarsometatarsal from Layer 2ab showing two transverse cutmarks on the distal articulation. Length = 29 mm. (Photo: Linda Amos. Natural History Museum, London).

A7279 – *Melanitta nigra,* coracoid with two cutmarks to the distal end.

Figure 4.16: NHMUK-A-7279. Common Scoter (M. nigra) coracoid from Layer 2ab with nicks to the distal dorsal surface. Length = 47 mm. (Photo: Linda Amos. Natural History Museum, London).

A7866 – *Columba livia,* coracoid with one long and two small cutmarks on the proximal end. These traces are partially obscured by mineral deposits.

Figure 4.17: NHMUK-A-7866. Rock dove coracoid from Layer 3-4 showing two shallow cut marks to the proximal articulation made in an effort to disarticulate the scapular girdleLength = 33 mm. (Photo: Linda Amos. Natural History Museum, London).

A8884 – P.P, carpometacarpal with two transverse cutmarks on the major metacarpal.

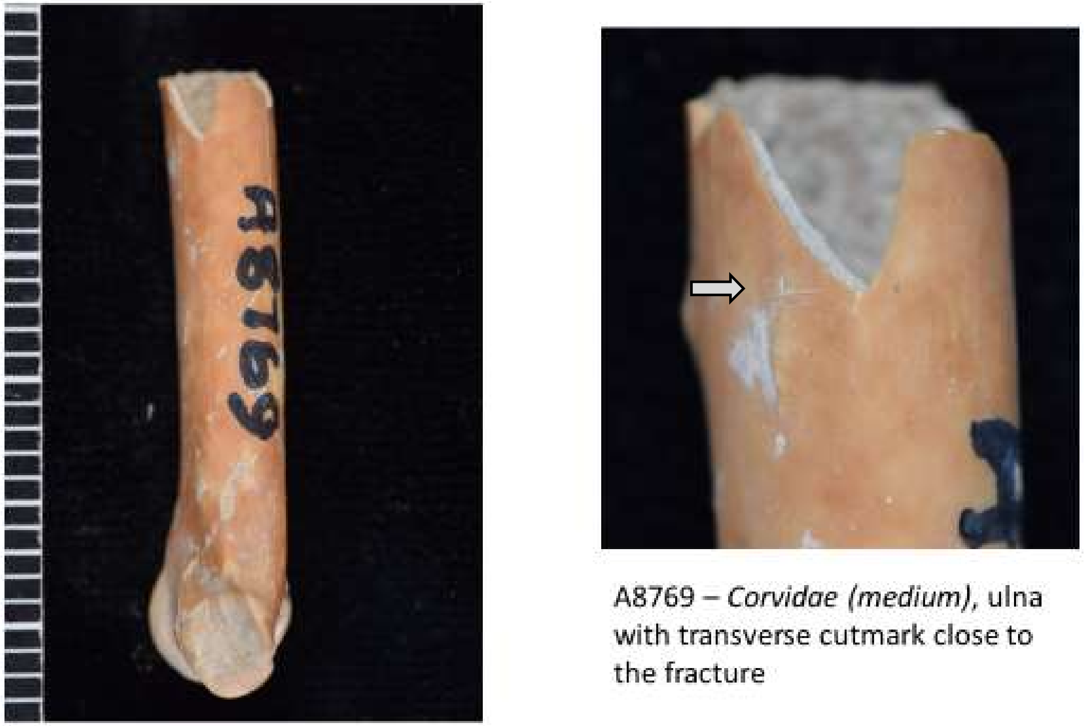
Figure 4.18: NHMUK-A-8884. Red-billed Chough (P. pyrrhocorax) carpometacarpal from Layer 5 with a pair of faint transverse cutmarks on the major metacarpal. Length = 39 mm. (Photo: Linda Amos. Natural History Museum, London).

A8088 – *Alectoris* sp., ulna with a transverse cutmark.

Figure 4.19: NHMUK-A-8088. Partridge (Alectoris sp.) ulna from insecure context with a transverse cutmark to the shaft. Length = 47 mm. (Photo: Linda Amos. Natural History Museum, London).

A8517 – *Alectoris* sp., coracoid with a series of cutmarks on the shaft.

Figure 4.20: NHMUK-A-8517. Partridge (Alectoris sp.) coracoid from insecure context exhibiting a set of cutmarks along the shaft of the coracoid. Length = 31 mm. (Photo: Linda Amos. Natural History Museum, London).



A8769 – *Corvidae (medium)*, ulna with transverse cutmark close to the fracture

Figure 4.21: NHMUK-A-8769. Corvid (Corvidae medium) ulna from insecure context with a single transverse cutmark near the fracture. Length = 25 mm. (Photo: Linda Amos. Natural History Museum, London).

A8951 (left and above) – *Accipiter nisus*, ulna and **A7773** (right) – *Columba livia*, femur.

Figure 4.22: NHMUK-A-8951. Sparrowhawk, proximal ulna, length = 31 mm. A-7773. Rock/Stock dove (C. livia/oenas) proximal femur from Layer 3-4, length = 12 mm. Avian remains from Devil's Tower Rockshelter with striations obscured by black marker. (Photo: Linda Amos. Natural History Museum, London).

4.7.4.2 Peeling

Only four specimens showed evidence of fresh bone peeling (Table 4.29). Three of these were from Layer 3-4 while one was from Layer 2ab; all were from the anterior portion of the skeleton. Three of the specimens exhibited peeling traces on the proximal articulation while the fourth, a scapula, exhibited peeling in connection to a fracture.

Table 4.29: Specimens displaying traces of peeling showing specimen number, layer, taxon, common name, element, and location on the bone. .

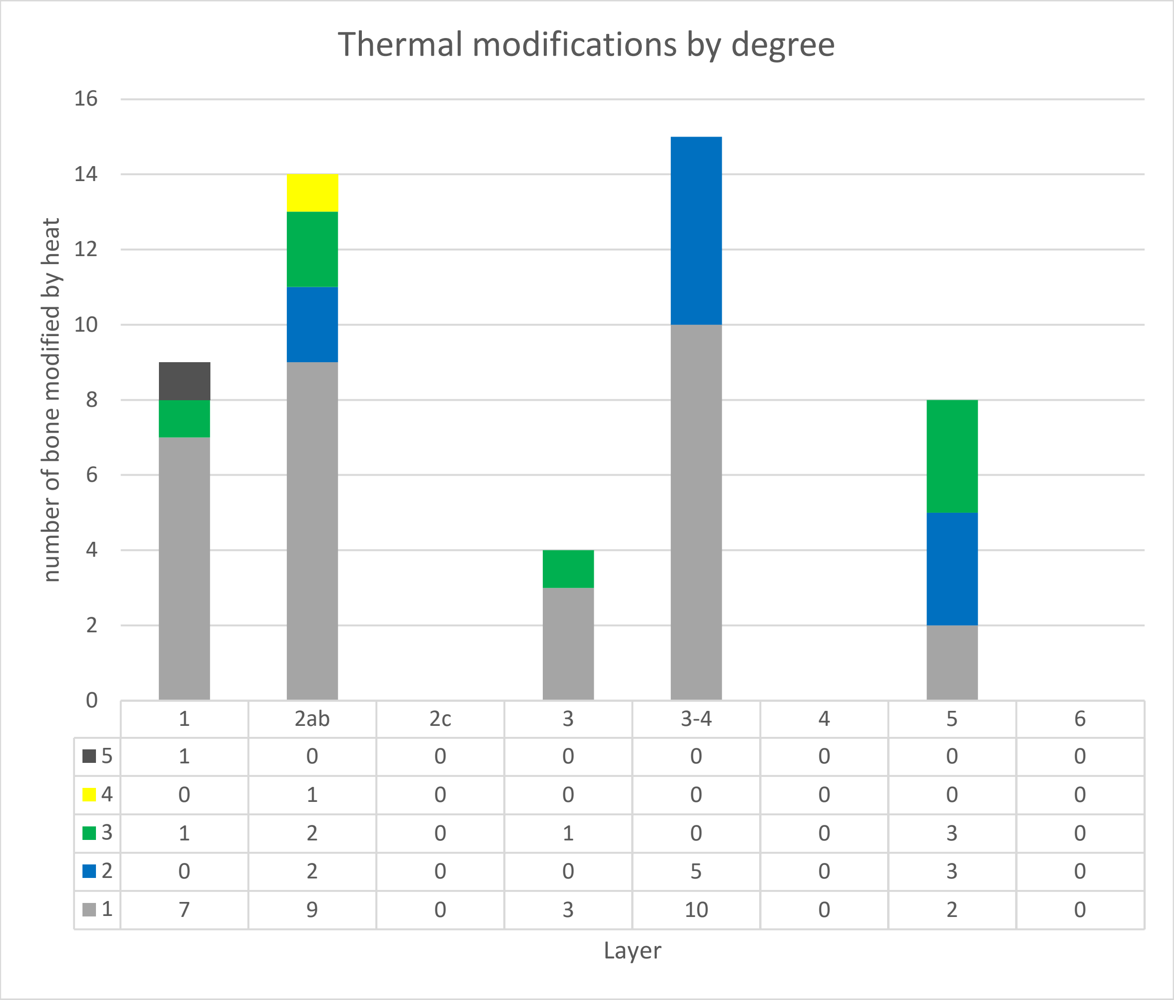
Spec no. NHMUK-A-	**Layer**	**Taxon**	**Common name**	**Element**	**Location**
8973	2a-b	*Alectoris* sp.	partridge	ulna	1
6737	3-4	*P. pyrrhocorax*	red-billed chough	coracoid	1
6735	3-4	*P. pyrrhocorax*	red-billed chough	coracoid	1
7755	3-4	*C. livia/oenas*	rock/stock dove	scapula	3

4.7.4.3 Thermal modifications

Thermal modifications were identified on specimens from five of seven layers and represented 6% of NISPtaph (n = 52). Most modifications were of low grade (n = 33) and presented as speckling on the bone surface (Figure 4.23; Figure 4.24). This may have been the result of incidental burning but could also be due to indirect heat during cooking when flesh partially covered the bone surface (Blasco *et al*. 2014; Laroulandie and Lefevre 2014). All layers showed more than one grade of thermal modification, with layer 2ab being most diverse. Specimens from layers 2c, 4 and 6 showed no thermal modifications.

Pigeons/doves and corvids constituted the majority of the burned elements (n = 33) (Figure 4.24). Along with other known food taxa (game birds, shore birds, ducks), they constituted 86% (n = 43) of the burnt elements. Only seven remains of falcons and diurnal raptors belong to groups outside what is traditionally considered food taxa (Cott 1947; Finlayson 2019).

No differential exposure was evident in any layer, but the thermal modifications did not affect the entire bone surface. This in itself is a differential exposure, indicating that not all parts of the bone were exposed to the heat source equally (Blasco and Peris 2009).



	1	2ab	2c	3	3-4	4	5	6
■ 5	1	0	0	0	0	0	0	0
🟨 4	0	1	0	0	0	0	0	0
🟩 3	1	2	0	1	0	0	3	0
🟦 2	0	2	0	0	5	0	3	0
■ 1	7	9	0	3	10	0	2	0

Figure 4.23: Frequency of degrees of thermal modifications present by layer. Scaled from 1 (speckled) to 5 (calcined).

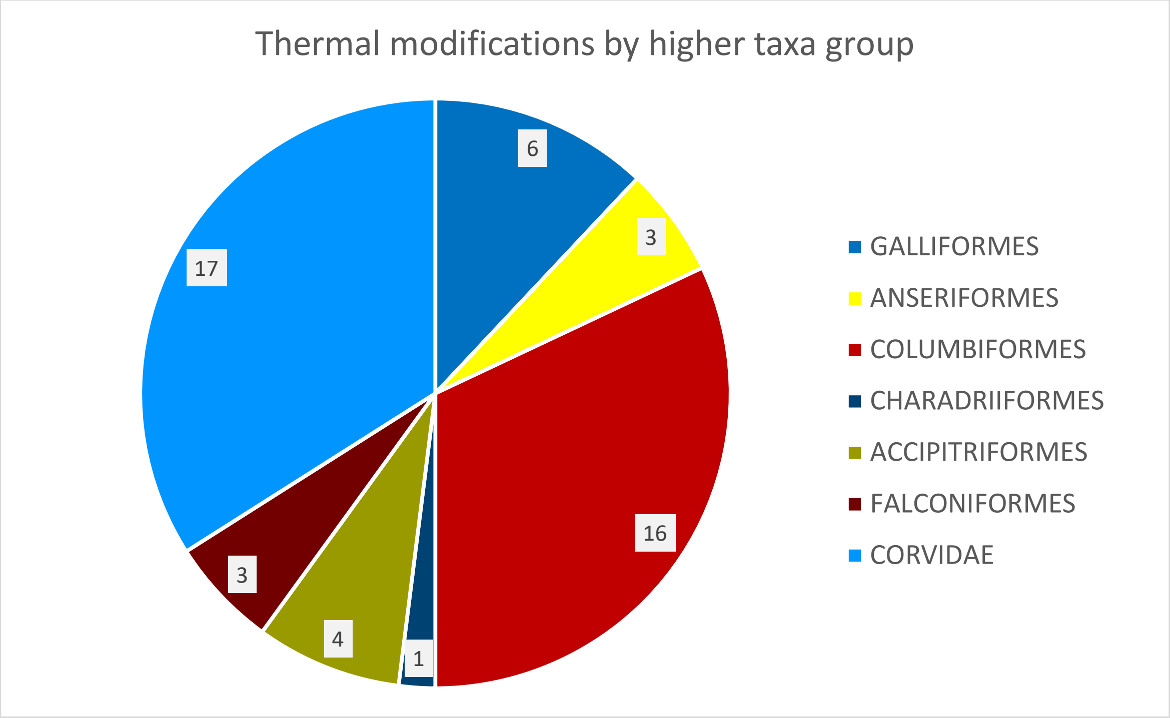


Figure 4.24: Pie chart showing the taxa distribution of elements with identified thermal modifications.

A8937 (left) *Columba livia* tibiotarsus and **A6774** (right) *Alectoris sp.* ulna, both showing thermal modifications.

Figure 4.25: NHMUK-A–8937 Rock dove (C. livia) tibiotarsus, length 38 mm. NHMUK-A-6774 Partridge (Alectoris sp.) ulna, length 40 mm. Specimens showing thermal modifications, both from insecure contexts. (Photo: Linda Amos. Natural History Museum, London)

4.7.5 Fragmentation

Analysis of old fracture patterns on avifauna at Devil's Tower Rockshelter was limited by the high incidences of recent fractures. Based on my observations, I believe that these were primarily the result of two processes: peri-excavational damage due to methods employed during excavation; and post-excavation efforts to remove concretions during identification. The damage was visible as new fractures and flaking on the surface of old fractures. Any fracture displaying recent damage, or flaking resulting from these processes, was excluded from the results of this analysis (Table 4.30).

A total of 422 specimens (51.6%) displayed fractures that were of old or mixed character. Of the 326 fractures that were old in character, 80 displayed a spiral outline, 98 were transverse, four were obscured by concretions, and the remaining 144 were recorded as irregular or mixed in character. Irregularities are usually indicative of a non-human agency (Fernández-Jalvo and Andrews 2016). Transverse fractures were made on dry bone and are usually the result of trampling activities (Fernández-Jalvo and Andrews 2016).

Table 4.30: Fractures of 'mix' and 'old' character by layer and outline.

	1		2ab		2c		3		3-4		4		5		6		Total	
	Old	**Mix**	**Old**	**Mix**	**Old**	**Mix**	**Old**	**Mix**	**Old**	**Mix**	**Old**	**Mix**	**Old**	**Mix**	**Old**	**Mix**	**Old**	**Mix**
Spiral	8	0	35	7	0	0	15	2	12	1	0	0	10	1	0	0	80	11
Transverse	9	1	25	5	1	1	13	2	23	2	0	0	27	1	0	0	98	12
Mix	6	3	9	14	1	1	3	8	3	4	0	0	1	4	0	0	23	34
Longitudinal	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Obscured	0	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	4	0
Irregular	10	4	39	10	0	3	24	7	31	7	1	0	15	6	1	1	121	38
Total	33	9	111	36	2	5	55	19	70	14	1	0	53	12	1	1	422	

Of the 80 spiral fractures, 24 display an oblique fracture angle, and of those only seven have a smooth fracture surface. However, many more have surfaces of a mixed character indicating that some areas are smooth while others are disrupted by later breaks. Some fractures are also partially or completely obscured by concretions and cannot be described in detail. Layers 2c, 4, and 6 contain no spiral fractures.

4.7.6 The Apodiformes

The Apodiformes in the Devil's Tower avifauna account for over 60% (n = 2405) of the total accumulation. In the present day, a number of Alpine swifts (*T. melba*) still roost close to Devil's Tower (Finlayson 2010). It is therefore likely that the presence of these remains is an artefact of former nesting colonies in the cliffs above the site. To assess the assumption that this mass of remains was the result of natural death from nearby colonies, a representative sample of 242 specimens (128 from Garrod's collection, 114 from the specimens which were integrated into the NHM taxonomic collection) was investigated to identify the agency behind the accumulation. The methodology was simplified, only tallying the number of bones showing specific modifications (Table 4.31). It was possible to identify several modifications on any single specimen.

During the general examination in preparation for this sample strategy, it was observed that some Apiodiformes were charred black. This is not assumed to be a sign of exploitation as bones may easily be swept into a fireplace incidentally. Black char signifies a direct heat to the bone surface, whereas cooking meat on the bone leaves a marbled pattern of brown on the bone surface (Stiner *et al.* 1995; Fernández-Jalvo and Andrews 2016).

A total of 197 specimens displayed signs of digestion, indicating that a majority of the Apodiform remains were the result of avian predation. A further 43 specimens showed only natural modifications suggesting natural death conclusive with a breeding colony. No indication of human agency was present in the examined sample. No further investigation was made into the Apodiform accumulation at Devil's Tower Rockshelter.

Table 4.31: Taphonomic results of Apodiform sample showing the collection of origin, number of remains per layer, the frequency of modifications present on the bones, and totals. Natural= only natural modifications, Digested= evidence of digestion, Puncture = evidence of puncture by carnivore or bird of prey, Indeterminate = indeterminate modification.

Collection	Provenance	Total in sample	Natural	Digested	Puncture	Indeterminate
Garrod	Layer 1	18	0	18	0	0
Garrod	Layer 2	6	1	4	1	0
Garrod	Layer 2AB	18	2	16	0	0
Garrod	Layer 2B	10	3	7	0	0
Garrod	Layer 2C	1	0	1	0	0
Garrod	Layer 3	19	0	19	0	0
Garrod	Layer 3-4	18	3	15	0	0
Garrod	Layer 5	20	1	19	0	0
Garrod	WASH	18	2	15	0	1
Taxonomic	no prov	50	23	27	0	0
Taxonomic	no prov	64	8	56	0	0
	Total	242	43	197	1	1

4.8 Interpretation of the Devil's Tower Avifauna

4.8.1 Neanderthal behaviour

The avifaunal remains from Devil's Tower reveal direct evidence of Neanderthal bird exploitation in four Middle Palaeolithic layers of the rock shelter.

Taphonomic and environmental analysis of the avifaunal assemblage indicated that Neanderthals at Devil's Tower regularly took pigeons (*C. livia*), choughs (*P. pyrrhocorax, P. graculus*) and partridges (*Alectoris* spp.), which would have been abundant close to the site. In addition, they likely exploited the estuarine environment to the north (Cooper 1999; Finlayson 1998) as well as the fresh water sources on the plain itself (Faure *et al*. 2002; Finlayson 2006; Rodriguez-Vidal *et al.* 2013), where resident and migratory populations of ducks (*M. nigra*) and shorebirds provided other subsistence opportunities. This diversity of habitats in prey species implies that Neanderthals at Devil's Tower could and did recognize the wide range of hunting opportunities available to them in their surroundings.

The clearest evidence for Neanderthal exploitation of birds were the cutmarks on bones in layers 1, 2ab, 3-4, and 5, as well as on Middle Palaeolithic material from insecure contexts. These indicated that stone tools were used for processing avian carcasses. The cutmarks were found on corvids, pigeons, partridges, a duck, and a diurnal raptor. The location and orientation of the marks suggested disarticulation, defleshing, and possible feather removal as the intention behind the action. Pigeons, corvids, ducks, and gamebirds are well-known food species, and have been exploited by Neanderthals at other sites across Europe (Blasco and Peris 2009, 2012 – Bolomor Cave, Spain; Peresani *et al.* 2011 and Fiore *et al.* 2016 – Fumane Cave, Italy; Finlayson *et al.* 2012 and Blasco *et al.* 2014, 2016 – Gorham's Cave, Gibraltar). Transverse cutmarks on the wing bones of a Sparrow hawk (*A. nisus*) in an insecure context (labelled '5?') and a red-billed chough (*P. pyrrhcorax*) from layer 5 however, suggested an effort to remove the primary feathers. Neanderthals in nearby Gorham's Cave targeted raptors and corvids for their feathers (Finlayson *et al.* 2012; Blasco *et al.* 2014). Feather exploitation is a non-utilitarian practice, and feathers are thought to have been used as personal ornamentation showing the cultural and social status of an individual (Serjeantson 2009; Finlayson 2019).

Despite the relative scarcity of remains with cutmarks (n = 11, 0.3%), they occurred in episodes throughout the deposition of the sequence. Traces of thermal modification on elements from layers 1, 2ab, 3, 3-4, and 5 (n = 50) strengthened this observation. Some of the burnt specimens showed more intense degrees of burning on the articular ends and along fracture edges, which suggested that flesh was covering other areas of the bone surface during heat exposure (Blasco and Peris 2009). All the instances of heat exposure appeared in contexts where hearths have been identified, alongside burned marine shells and burned and broken mammal remains (Garrod *et al*. 1928).

Judging from the results presented by Garrod (1928), the most intense occupation took place during the deposition of in layers 2ab and 3 with less intense occupation episodes in layers 1 and 5 (Table 4.1; Table 4.2; Table 4.32). This coincides with episodes of higher avian species richness (NTAXA) (Table 4.8). In contrast, the NTAXA of the hard travertine/tufaceous layers (2c, 4, and 6) contained no hearths, few lithics, and a dearth of avian taxa (n = 5, n = 4, n = 4, respectively).

Table 4.32: Summary of information from Garrod et al. 1928 combined with results presented in this study. Layers with hard sediment are shaded in grey. NISPx = NISP without Apodiformes. x = presence of charcoal. No data is available for shellfish in Layer 1. Ranking of lithics present 1 = rare, 2 = some, 3 = many. Presence of animal bone modificed by human agency is denoted as 1.

					Garrod *et al*. 1928				**Taphonomy in this study (NISP)**		
Layer	**NISP**	**NISPx**	**NTAXA**	**MNI**	**Hearth present**	**Shellfish NTAXA**	**Presence of lithics (ranked)**	**Burnt and broken mammal bones**	**Specimens with cutmarks**	**Specimens with thermal modification**	**Specimens with peeling**
1	183	79	14	25	scattered charcoal	-	2	1	1	9	
2ab	377	252	22	79	x	6	3	1	2	14	1
2c	18	13	5	5			1				
3	211	131	21	42	x	5	3	1		4	
3-4	384	176	11	39					2	15	3
4	4	4	4	4		3	1	1			
5	57	158	19	46	x	7	2	1	1	8	
6	5	5	4	4		1	1				

Specimens labelled ‘3-4’ likely comprised material from the episode of admixture between layers 3 and 4 observed by Garrod (Garrod *et al*. 1928). This implied that of the 377 bird remains, some of which had traces of human agency, may have belonged to the hard travertine of Layer 4. However, Garrod’s account emphasised that the material that washed into Layer 4 was from the rich hearths of Layer 3. This implied that it was possible to see that the material in the intrusive sediments was burnt. With this in mind, the complete absence of hearths and charcoal in Layer 4 paired with the high frequency of burnt bird bones from layer 3-4 (Figure 4.23; n = 15) indicated that most of the bird material labelled 3-4 originated in Layer 3 where there was ample evidence of Neanderthal occupation, including a lithic working floor and hearths (Garrod *et al.* ibid). The lower MNI (n = 39) to NISP (n = 176) proportion in layer 3-4 compared to other layers with evidence of human agency may also have been an artefact of the admixture. Bones within the intrusive material would be protected from further post-depositional mechanical disturbance within the cracked travertine of layer 4. This would allow more fragile elements to be preserved from each individual carcass. This finds support in that trample was relatively less frequent on the surface of bones in layer 3-4 (24.4%) than other layers with evidence of human agency (35-45% of layers 1, 2ab, 3, 5).

Garrod proposed that the hard travertine layers were deposited under wet climatic conditions, possibly corresponding to seasonal rainfalls, when a calcareous spring was active close to the shelter. Devil's Tower was therefore occupied when this spring was inactive or partially dry and deposits of fine sand or clay were laid down (layers 1, 2ab, 3, 5) (ibid 1928). Working with this hypothesis, cutmarks on a specimen of common scoter (*M. nigra*) might seem to indicate a winter occupation, but juveniles of this species have been recovered from nearby Gorham's Cave, inferring that the species was also present in summer to breed (Cooper 1999). Garrod also highlighted the lack of sun on the site during winter months, likely from her own experience during excavations (Garrod *et al*. 1928). If the wet conditions indeed reflected wet seasonal pulses, this would indicate a seasonal use of the site during dry summer months. Seasonal rainfall cycles in the Middle Palaeolithic did not differ much from the present day; most rainfall happens during winter while summers are mainly dry (Finlayson 2006; Finlayson *et al.* 2008). It follows then that the deposition of sediments and window of occupations at Devil's Tower could reflect a very short period of time - years rather than millennia. The Catalan Bay Sands were actively building against the eastern side of the rock of Gibraltar during MIS 5 – MIS 3 (Rodrigues-Vidal *et al.* 2004, 2013; Muniz *et al.* 2019) and may have accumulated quite rapidly. In Vanguard Cave, > 2 m of sand were found to have accumulated in less than 10,000 years (Droeschner *et al.* 2019).

4.8.2 Other agents contributing to the accumulation

Carnivores and diurnal and nocturnal raptors were active contributors to the accumulation of avifauna at Devil's Tower. Several remains of griffon vulture (*G. fulvus*) from Layer 2ab displayed punctures and crenulations of a size attributable to the hyena; however, most of the manducation modifications on bird bone surfaces were the product of small carnivores. Bate identified the remains of Iberian lynx (*Lynx pardinus*), badger *(Meles meles*) and wildcat (*Felis silvestris*) in the sequence along with larger carnivores such as the brown bear (*Ursus arctos;* whole bones in Layer 3), leopard (*Panthera pardus*) and spotted hyaena (*Crocuta crocuta*). Garrod noted the presence of mammal bones gnawed by animals in Layer 2b (ibid 1928).

Low grade digestion on 434 specimens suggested that owls were important contributors to the avian accumulation. Three species of owl were present at the site. The tawny owl (*S. aluco*) was present in in Layer 2ab, while the eagle owl (*B. bubo*) and little owl (*A. noctua*) featured in insecure contexts. All three species are known from other Middle Palaeolithic contexts in Gibraltar (Finlayson 2019). However, the degree to which Neanderthals and owls coexisted at Devil's Tower was likely limited. Strigiformes would not choose roost in the shelter while humans inhabited it, as the shelter itself is very small in comparison to other cavernous sites nearby (e.g. Gorham's Cave or Vanguard Cave). It is also worth noting that the digestive traces of wild cat agency are similar to those of Strigiformes (Marin-Monfort *et al.* 2019), and that wild cats may therefore have been responsible for some of the digested remains.

The majority of the sampled Apodiform remains showed signs of digestion. All five species of falcon present in the Devil's Tower assemblage are known today to take small birds as prey, though the kestrel (*F. tinnunculus*) and lesser kestrel (*F. naumanni*) prefer small mammals (del Hoyo *et al.* 1994). Finlayson (2019) suggests that falcons may have a commensal relationship with humans in the Middle Palaeolithic, feeding on the micromammals attracted to the site by human refuse. Falcon remains were frequent in both secure and insecure contexts at the site (NISP = 127).

A large number of diurnal raptors were present in the assemblage (NISP = 110). Nine taxa appeared in the accumulation, ranging in size from hawks (*A. nisus*) to vultures (*G. fulvus, A. monachus*). Small to medium sized birds featured strongly in the diet of these raptors (del Hoyo *et al*. 1994; Ferguson-Lees and Christie 2001), except the vultures which feed on the carrion of medium to large mammals (Birdlife Data Zone 2021).

Finally, Neanderthals occupying Devil's Tower introduced the remains of several species of ungulate (Garrod *et al.* 1928; Currant 2000; Bernal 2017), the remains of which likely attracted carrion eaters, both bird and mammal.

4.8.3 Ecological interpretations

I investigated the frequency of ecological variables in the secure contexts of Devil's Tower using tolerances and habitat requirements from Finlayson (2011). However, sample sizes were too low to provide testable data at an intra-site level. That said, as the only available published information regarding the distribution of species in individual levels at Devil's Tower is the presence of shellfish taxa (Fischer -Appendix C in ibid 1928), any new observation of ecological information reflected in the avian species contributes valuable information to the interpretation of Devil's Tower. Therefore, some observations based on intrasite presence and absence are now discussed.

All foraging and breeding habitat types were represented by the avian species in my analysis of the Devil's Tower avifauna, supporting the interpretation of a varied mosaic-type landscape (idem;Table 4.12). The sustained presence of these diverse habitats in the layers of Devil's Tower Rockshelter show that diverse foraging and nesting habitats were available throughout MIS 5 – MIS 3 (Finlayson *et al.* 2016). Bernal's review of habitats reflected in the ungulates of Devil's Tower supported this, showing that rocky (*C. pyrenaica*), forest (*C. elaphus, S. scropha*), and open plains species (*Equus, Bos*) were present in the sample. Bate's interpretation of the mammalian sequence was limited to a general observation of stability, noting an even distribution of species throughout the sequence (Garrod *et al.* 1928). This is also mirrored in the mammalian record of Gorham's Cave and Vanguard Cave (Currant 2000; Currant, Fernandez-Jalvo and Price 2012; Currant and Price 2012).

Avian species with a range of bioclimatic tolerances inhabited the environs around Devil's Tower. Generalist species appeared in all layers in the rockshelter except 2c and 6. In contrast, specialist species were less frequent, appearing on only two layers (1 and 5). These included three species: the sedentary calandra lark (*M. calandra*) and two migratory pelagics - the northern gannet (*M. bassanus*) and Balearic shearwater (*P. mauretanicus*).

While the cold-humid gannet appeared in Layer 1, the hot-arid shearwater appeared in Layer 5. The calandra lark is also a hot-arid tolerant species, but only appeared in an insecure context. All three specialist species are native to the mid-latitude belt. While the pelagic species foraged in the marine environments readily available around Gibraltar, the calandra lark foraged in open landscapes. A wider variety of habitats were represented in the semi-specialist species (n = 5). Wetland and marine foragers featured alongside open and aerial foragers. Open foragers were the only group which contained the whole spectrum of bioclimatic tolerances, indicating that the open coastal plain offered a reliable source of foraging opportunities for birds with a variety of niche requirements (Finlayson 2011).

The latitude range of species in the Devil's Tower avifauna revealed a sustained presence of species which do not regularly breed in the mid-latitude belt today (Finlayson 2010). Eleven of 21 wetland and marine foragers found at Devil's Tower were arctic and boreal species. This reflected a non-analogue community which existed in the thermo-Mediterranean bioclimatic zone of southern Iberia during the last glaciation (Cortes-Sanchez *et al.* 2008; Jennings 2012). This anomaly is also recognized in the flora (Carrion *et al.* 2013, 2018). Boreal wetland and marine species were forced south by the advancing ice sheets (Eynaud *et al.* 2009) and colder water resulting from the release of large quantities of ice from the Laurentide ice sheets (Heinrich events; Bond *et al.* 1993, Andrews *et al*. 1998). Remains of the common scoter (*M. nigra*) were found in layers 2ab and 3 at Devil's Tower complement the remains of subadults of the same species recovered from Gorham's Cave (Cooper 1999, 2000), suggesting that scoters, were breeding within the non-analogue community in Gibraltar and were summer visitors. The gannet, currently a winter visitor to Gibraltar is likely another displaced species, and its presence in Layer 1 likely indicated arrival for the summer breeding season.

Apodiformes were not found in the sterile travertine layers of the rockshelter in any great numbers (only Layer 2c, n = 5). This suggested that the hard travertines were laid down in winter because the swifts (*T. melba, A, apus*) roost on the cliffs during spring and summer months (Finlayson 2010). Garrod (1928) suggested that these layers were deposited in wetter conditions, possibly during seasonal rains. Rainfall in Gibraltar in the present is highly seasonal, with most precipitation falling during winter months (Finlayson *et al*. 2008). The rainfall regimes of MIS 4/3 are thought to be similar, or slightly higher, than the present day (Finlayson *et al.* 2008) and a range of humidity opportunities were available in the landscape (Finlayson 2011; Finlayson *et al.* 2016; Table 4.17). This supports previous studies which noted the importance of precipitation in southern Iberia at this time (Jennings 2007; Jennings *et al*. 2011; Rodrigues-Vidal *et al.* 2013; Carrión *et al*. 2013, 2018).

On an intra-site level, the occupationally sterile travertine layers were populated by the remains of fewer taxa than the occupied layers. All except two species were rocky nesters. Collectively, these layers had a NISP of 27, and NTAXA and MNI of 12. Despite this scarcity of remains, these layers included both boreal and mid-/multi-latitude species ranging from semi-specialist (n = 5) to generalist (n = 2) in bioclimatic tolerance. The temperature and humidity tolerances also indicated a tendency towards species that thrive today in warm-temperate, semi-humid to arid conditions.

Despite the generally stable conditions reflected in the avifauna, and supported by other proxies in Gibraltar, it is possible that a change in the distribution of species between layers 3-5 and 1-2ab reflected a shift in climate. The dominant species in the assemblage changed from rock dove (*C. livia*) to red-billed chough (*P. pyrrhocorax*). Differing seasons of occupancy do not explain this shift as both species would have been resident in Gibraltar during the Middle Palaeolithic. A chi^2- test comparing the distribution of both species between the two layer-groupings gave a significant result in both species (p = <0.001, df = 1;Table 4.9). It is possible that this change in frequencies was due to a change in foraging strategy of the Neanderthals at the site. However, bioclimatic tolerance frequencies also shift from a predominance of generalist species to towards species with moderate bioclimatic tolerances. Furthermore, the chief humidity tolerance shifts from category D (60-80% humid) in layers 5-2ab to B (20-40% humid) in Layer 1. Collectively these data suggest a move towards cooler, more arid conditions. Gentle oscillations between more humid and more dry conditions have been observed through other proxies (Finlayson *et al.* 2004, 2008).

4.8.4 Summary

- The Devil's Tower Avifauna consisted of 3,829 specimens with a species richness (NTAXA) of 67, and a MNI of 244. 2,905 of the total remains were swifts, which would have formed large breeding colonies at the site during summer months (Finlayson 2010).

- The discovery of cutmarks on 11 bones from multiple layers in the depositional sequence provides the first conclusive evidence that Neanderthals exploited birds at Devil's Tower.
  Ten of the cut-marked bones indicated that the birds were exploited for dietary purposes.
- Thermal modifications were also present on the bones of game birds, pigeons, corvids, shorebirds, and ducks, implying roasting of bird carcasses for consumption.
- The oblique characteristics of a cutmark on the proximal shaft of a Sparrowhawk ulna (*A. nisus*) pointed to the harvesting of feathers.
- Ecological tolerances of the birds in the Devil's Tower accumulation exhibited characteristics of a non-analogue community during MIS 5 – 3, although sample sizes are low to make firm conclusions. Arctic ducks and boreal marine species appeared in a wider avifauna centred around the mid-latitude belt (Finlayson *et al.* 2016).
- The Devil's Tower avifauna has a strong marine signal. This is not seen in other Gibraltar sites (Finlayson *et al.* 2016) and may be a reflection of the excellent nesting opportunities provided by the sheer cliff face surrounding the site. This would attract marine foragers such as the shag, the northern gannet, and the Balearic shearwater.

5 Cova Negra

This chapter presents my analysis of bird remains excavated during the 20th Century at Cova Negra, Spain. These have not been studied previously from a taphonomic perspective. Cova Negra offers an opportunity to examine an avifauna from an inland site on the Iberian Peninsula, at a latitude of ~40°N. Given the proximity to other known Mousterian sites and the recent developments in the dating of the site (Villaverde *et al.* 2014; Richard *et al.* 2019), this assemblage can add to our understanding of Neanderthals in Iberia in the Late Middle Pleistocene. In this chapter, I first introduce the site, providing background information relevant to the deposition of the avian remains. I then investigate the ecological information that can be inferred from the avian species present in the site before moving on to a taphonomic examination of the bone surfaces to identify the agency behind the accumulation. Finally, I discuss the results in regard to Neanderthal bird exploitation at the site and their use of the surrounding landscape.

5.1 Physical setting

Cova Negra (38° 57′ 54.17″ N, 0° 29′ 46.58″) lies on the margin of the Albaida River valley near the town of Xàtiva in the Province of Valencia, Spain (Martinez Valle *et al.* 2016; Eixea *et al.* 2020; Figure 5.1). Other prominent Neanderthal sites in the Valencian Community include Abrigo de la Quebrada (Eixea *et al*. 2014; Real *et al.* 2019, 2020), Cova Foradà (Lozano *et al.* 2013), Cueva de Bolomor (Blasco and Peris 2009, 2012ab; Arsuaga *et al.* 2012), and El Salt (Garralda *et al.* 2014; Leierer *et al.* 2019; Marin-Monfort *et al.* 2021). The site is 30 km from the Mediterranean coast, at an altitude of 100 m.a.s.l. It is situated 20 m above the current riverbed at the base of the calcareous mountain Serra Grossa and is one of many conduits in a karstic system (Arsuaga *et al.* 1989). Cova Negra was declared a Municipal Nature Park in 2006 and, along with 57 hectares of the surrounding landscape, is a Cultural Heritage Site (Cova Negra cave – Xàtiva Tourist 2020).

The cave has a large, circular entrance that faces east, measuring 18 m in width and up to 18 m in height (Figure 5.2). It comprises a single chamber that is 25 m long with a surface area of ~500 m^2. It contains a sequence of 36 levels (capas), divided into 15 units and six sedimentary phases (Arsuaga *et al.* 2007; Eixea *et al.* 2020).

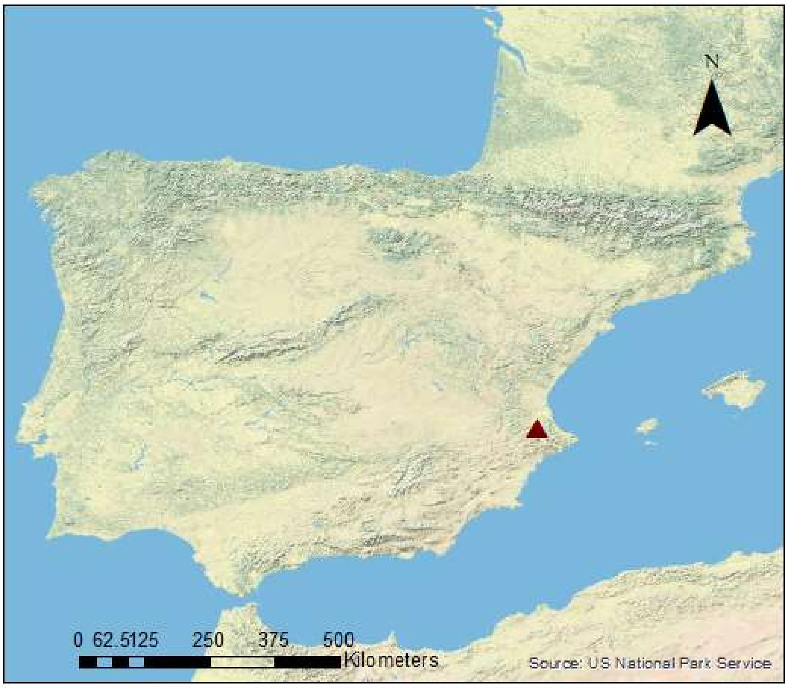


Figure 5.1: Map of Iberia with the location of Cova Negra marked by a triangle.

Figure 5.2: Cova Negra in the Albaida River Valley. The cave mouth is approximately 18x18 m. at the mouth and lies 20 m. above the river Albaida. Photo: Eixea et al. 2020.

5.2 Archaeological investigations

The first excavations of Cova Negra were directed by Viñes between 1928 and 1932. Viñes attributed the sequence to the Mousterian (Viñes 1929, 1942). Unfortunately, his premature death prevented the publication of further findings (Eixea *et al*. 2020). In the 1950s, investigations were continued by Jordá (Jordá 1953; Villaverde 1984). His team excavated a large part of the cave in defined sectors (Figure 5.3). These sectors varied in surface area, some covering as much as 40 m^2. The sediments were removed in arbitrarily defined spits ranging from 5 to 20 cm in thickness. Little attention was paid to the relationship between archaeological material and different stratigraphic units at the time of excavation (Arsuaga *et al.* 2007). Publications from this effort were limited to synthesis works that did not provide much detail about the industrial character of the site (Eixea *et al.* 2020)

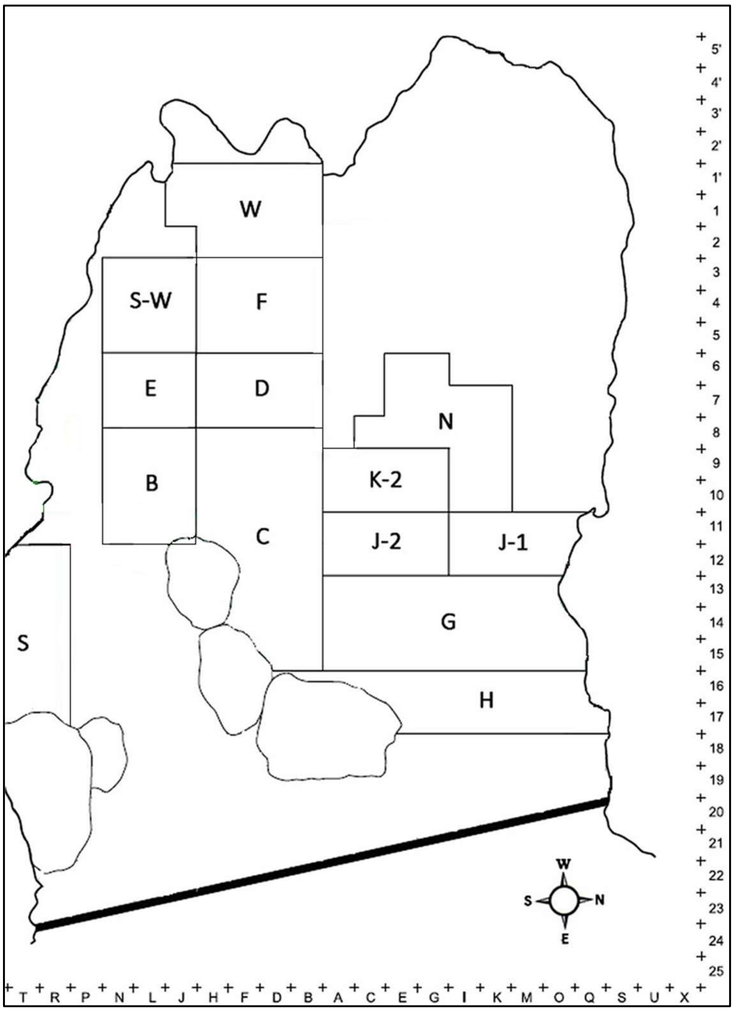


Figure 5.3: General plan of Cova Negra showing the size and placement of the excavated sectors. The plan is adapted from Eixea et al. 2020.

In the 1980s, Villaverde continued fieldwork at the site, studying the lithic industry for his PhD thesis. He aimed to clarify the stratigraphy and chronology of the site and place it within the greater context of the European Middle Palaeolithic (Villaverde 1984; Eixea *et al.* 2020). Villaverde concluded that human occupation of the site consisted of short intervals spaced between long periods of abandonment. He based his conclusion on the construction of simple hearths and the use of limited areas of the cave floor (10-12 m^2) during each occupation episode. He also observed repeated changes in the location of occupation events within the site (Villaverde *et al.* 2009; Villaverde 2009). Villaverde and Eixea undertook excavations from 2013-2017 with the intention to better understand the stratigraphic sequence and refine the site chronology (Eixea *et al.* 2020).

In the following summary, the emphasis is on results from Sector C, which is where the bird remains in this thesis originate (see: Section 5.3.2).

5.2.1 Stratigraphy

The stratigraphic sequence was established by Fumanal (Fumanal 1986; Fumanal and Villaverde 1997), who identified 36 levels. These were later unified into 15 units and grouped into six climatic phases (Villaverde 2009; Fumanal and Villaverde 2009) (Table 5.1). The exact stratigraphic sequence differed from sector to sector due to the short and episodic nature of human presence at the site (Villaverde 1984).

- Phase A corresponded to the deepest units in the sequence (Unit XV). The sediment was archaeologically sterile, likely because frequent flooding of the Albaida river prevented occupation. No dates have been obtained from this phase.
- Phase B (units XIV, XIII) was a cold phase characterised by gelifraction processes. During this phase, an increase in organic components was attributed to sporadic human occupation. Thermoluminescence dates on sediment placed unit XIV at 117 +/- 17 ka BP (Arsuaga *et al.* 2007).
- Phase C (Unit XII) presented an interruption of the previous cold conditions. Here, soil formation reflected a warmer climate with seasonal humidity pulses. Two sets of dates have been procured from unit XII; thermoluminescence on sediment placed this level between 107+/-17 and 96+/-14ka BP (Arsuaga *et al*. 2007). However, recent ESR (electron spin resonance) dates placed the unit at 273+/-26 ka BP (Richards *et al*. 2019)

- Phase D was an erosive phase with clear indications of colder environmental conditions. However, there were milder pulses within the cold climate period and variable humidity levels, which coincided with human influences in the accumulation. Dates are available for three units in Phase D. Unit XI was dated by ESR to 261+/-42 ka BP, while thermoluminescence on burnt flint placed unit VIII at 255+/-20 ka BP and 206+/-23 ka BP, and unit V at 235+/-21ka BP. ESR dating, however, placed unit V at 168+/-20 ka BP and 146+/-34 ka BP (Richards *et al.* 2019; Villaverde *et al.* 2014).
- Phase E (unit IV) was another interruption in occupation, appearing as a preserved clay horizon within a palaeosol. This phase contained soil formation, and there was evidence of seasonal rainfall and warmer temperatures. Thermoluminescence on sediment placed unit IV at between 53 +/- 8 ka BP and 50 +/- 8 ka BP (Arsuaga *et al.* 2007).
- There was significant environmental aridity in the final phase of the sequence (F; units III-I). ESR dates placed unit III between 206+-/21 ka BP and 193+-/19 ka BP (Fumanal 1986; Fumanal and Villaverde 1997; Villaverde *et al*. 2014; Richard *et al.* 2019).

Table 5.1: The sedimentary sequence of Cova Negra showing correlation of unit, capa (Sector C only), and Phase along with information regarding climate, sediment type, dates, lithics type, and human agency identified on faunal remains. After Villaverde et al. (2009, 2014), Eixea et al. (2020), Arsuaga et al. (2007), Martinez-Valle et al. (2016), Richard et al. (2019).

Phase	**Climate**	**Unit**	**Capa (sector C)**	**Sediment**	**Dates**	**Lithics type**	**Fauna**
F	Arid conditions, warm Mediterranean climate	**I**	1, 2	Some stones (6-10cm) in clays		Well defined Levallois	
		II	3	Gravels and stones (7-10cm) in silty sands			
		III	4, 5	Abundant stones and sub-rounded gravels in silty stands	ESR 206+-/21ka, 193+-/19ka		IIIb; bone with both cutmarks and carnivore gnaw
E	Warm with seasonal rainfall	**IV**	6, 7	Subangular stones decreasing in size towards the bottom in clayey silt with sands, becoming laminated towards the bottom	TL (sediment) 53+/-8ka, 50+/-8ka		Cervids and equids; abundant cutmarks
D	Progression from cold, moist to cold, dry	**V**	8, 9	Angular to subangular stones >5cm increase; in silty sands	TL (burnt flint) 235+/-21ka ESR 168+/-20ka; 146+/-34ka		
		VI	10, 11	Some stones in clayey silts with fine sands		Discoid and Quina	
		VII	12, 13, 14	Stones increase, and some carbonated concretion in silty sands			
		VIII	15, 16, 17	Some gravels and stones with carbonated concretions in silty sands; clayey towards the bottom	TL (burnt flint) 255+/-20ka, 206+/-23ka		
		IX	18, 19	Gravels in silty sands		Discoid and Quina	
		X	20	Some gravels (1-3cm) in sandy silt laminations			
		XI	21	Sub-rounded stones (5-10%) in silty sands	ESR 261+/-42ka	Levallois	
C	Warmer conditions with seasonal humidity pulses	**XII**	22, 23, 24	Blocks in silty sands	TL (sediment) 107+/-17ka to 96+/-14ka ESR 273+/-26ka		
B	Starts cool and humid, ends harsh	**XIII**	25, 26, 27	Subangular blocks in sands		Discoid and Quina	
		XIV	28 29, 30	Stones 1-3cm and gravels in laminated silty sands, sands and clayey silt and sands	TL (sediment) 117+/-17ka		
A	Warm and humid	**XV**	31-36	Marl			

5.2.1 Chronology

Initial dating efforts ascribed the accumulation of sediments in Cova Negra to between 117+/-17 ka BP (MIS 5e) and 50+/-8 ka BP (initial Würm/MIS3) (Arsuaga *et al.* 2007) (Table 5.2). However, further dates procured through thermoluminescence on burnt flint contradicted these results (VIllaverde *et al.* 2014), suggesting a Middle Pleistocene chronology (MIS 8-6) for the sequence instead. Richard *et al.* (2019) further investigated the chronology of the site. ESR/U-series dating was employed on herbivore teeth from four contexts. The resulting dates between 273+/-26 ka and 146+/-34 ka supported Villaverde *et al.* (2014) in placing the Neanderthal occupation of Cova Negra to the end of the Middle Pleistocene. OSL dating of the sequence is underway to clarify the site chronology (Eixea *et al.* 2020).

Table 5.2: Dates procured from Cova Negra. TL= thermoluminescence, ESR= electron spin resonance; ka= thousand years, MIS= marine isotope stage.

Phase	**Unit**	**Method**	**Material dated**	**Age**	**Mis**	**Reference**
E	IV	TL	sediment	53+/-8 ka; 50+/-8ka	3	Arsuaga *et al.* 2007
C	XII	TL	sediment	107+/-17ka; 96+/-14ka	5c-d	Arsuaga *et al.* 2007
B	XIV	TL	sediment	117+/-17ka	5e	Arsuaga *et al.* 2007
D	V	TL	burnt flint	235+/-21ka	7-8	Villaverde *et al.* 2014
D	VIII	TL	burnt flint	255+/-20ka;206+/-23ka	7-8	Villaverde *et al.* 2014
C	XII	ESR	herbivore tooth	273+/-26ka	8	Richard *et al.* 2019
D	XI	ESR	herbivore tooth	261+/-42ka	7-8	Richard *et al.* 2019
F	III	ESR	herbivore teeth	206+-/21ka; 193+-/19ka	6-7	Richard *et al.* 2019
D	V	ESR	herbivore teeth	168+/-20ka; 146+/-34ka	6-5	Richard *et al.* 2019

5.2.2 Lithics

There was a low density of lithics across the site, consistent with sporadic episodes of occupation (Villaverde 1984). The industrial sequence was typologically homogeneous and showed similarities to the Mousterian of other western Mediterranean regions (Arsuaga *et al.* 1989). The raw materials used were of semi-local origin, with a 20-25 km catchment area from the site (Eixea *et al.* 2020). Studies of the lithic material revealed fragmented operative chains, which coincided with the short duration of occupations at the site (Villaverde *et al.* 2014; Eixea *et al.* 2020). The proportion of retouched lithics in sector C varied from 33.3 % in Unit I to 71.4 % in unit V (Table 5.3).

Table 5.3: Distribution of lithics in Sector C by level. After Villaverde 1984.

	Unit													
	I	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**	**XIII**	**XIV**
Total	63	42	75	40	14	12	15	59	49	20	8	59	26	3
Retouched	21	23	26	23	10	4	7	27	25	8	4	41	17	2
%Retouched	33.3	54.8	34.7	57.5	71.4	33.3	46.7	45.8	51.0	40.0	50.0	69.5	65.4	66.7

5.2.3 Human remains

The remains of at least seven Neanderthal individuals have been recovered from Cova Negra, comprising two adults, one adolescent and four infants (Crusafont Pairo 1976; Arsuaga *et al.* 1989, 2007; Bermudez de Castro 1992) (Table 5.4). This assessment was based on cranial and dental remains. Additionally, postcranial remains have been excavated from the cave, representing immature individuals (Arsuaga *et al.* 2007). Most of the remains originated from the upper part of the sequence (III-VIII), while a single remain was from the lower units (XI-XII). Most of the remains excavated during Jordá's field season came from sector E, and the remains found by Villaverde in 1987 were a result of a section collapse in that same sector (Arsuaga *et al.* 2007). No human remains have been found in Sector C, although Sectors G, B, D, and E are directly adjacent (Figure 5.3).

Table 5.4: Human remains from Cova Negra. After Arsuaga et al. 2007.

Inventory no.	Specimen	Side	Age	Sector	Level	Year
Parietal I	parietal	right	adult	-	IV-VIII	1930
Parietal II	parietal	right	adolescent	-	VIII	1931
CN 42164a	frontal fragment	left	immature	E	V-VII	1951
CN 42164b	parietal fragment	left	immature	E	V-VII	1951
CN42170-7310	parietal fragment	left	immature	E	III-V	1951
CN42170-7311	parietal fragment	left		E	III-V	1951
CN42170-7312	occipital fragment		immature	E	III-V	1951
CN42170-7313	parietal fragment	right		E	III-V	1951
CN42174	parietal fragment	right		E	Mousterian	1987
CN42174a	parietal fragment	left	immature	E	Mousterian	1987
CN42174b	parietal fragment	left	immature	E	Mousterian	1987
CN7755	mandibular fragment	right	immature	DE	XI-XII	1951
CN42175	upper 4th premolar (crown)	left		E	Mousterian	1987
CN42175	upper 2nd deciduous molar (crown)	left	immature	E	Mousterian	1987
CN42175	upper first molar (crown)	left		E	Mousterian	1987
CN7755	lower 2nd deciduous molar	left	immature	DE	XI-XII	1951
CN7856	Upper 1st incisor	right	young adult	F	I-II	1953
CN42165	radius	right	immature	E	VI-VII	1951
CN42166	4th metatarsal	right	immature	E	III-V	1951
CN42167	3rd metatarsal	right	immature	E	III-V	1951
CN42168	distal femur	right	immature	G	II-III	1953
CN42169	proximal femur	right	immature	G	II-III	1953
CN42171	distal fibula		immature	B	VII-VIII	1950
CN42318	distal femur (diaphysis)	right	adolescent	B	VI-VII	1950

5.2.1 Fauna

Faunal remains were first examined by Obermaier (Vines 1929), followed by Royo Gomez (1942), but these studies did not produce detailed interpretations (Villaverde *et al.* 1996). In 1977 Perez Ripoll embellished the faunal records, examining the material from Jorda's excavations (Table 5.5). He separated the finds by excavation sector. Villaverde *et al.* conducted a review of the macrofauna from recent excavation seasons (Phases D, E, F) (1996) (Table 5.6). Like the episodes of human occupation, the concentration of faunal remains varied across the area of the cave (Villaverde *et al.* 2014).

5.2.1.1 Macrofauna

The macrofaunal remains from Cova Negra were insufficient to give a detailed interpretation of the site's environmental conditions (Villaverde *et al.* 2014). However, Villaverde *et al*. (2014) distinguished some trends, especially in s D, E and F, where there was a progressive increase of caprines and a decrease of horse and bovines. Additionally, species that indicate cool and moist conditions (roe deer *C. capreolus*; wild boar *S. scropha*) were present in Phase F, alongside open and forest species (brown bear *U. arctos*; beaver *C. fiber*), suggesting the presence of a variety of habitats available in the vicinity of the site.

Though the abundance of individual species varied throughout the sequence, the continuous presence of cervids suggested the persistence of woodland habitats (Villverde *et al.* 2014). Gallery forest formations would have persisted along the river providing shelter for deer and other woodland species (Villaverde *et al.* 2014). Horses were also present throughout the sequence. Along with the narrow-nosed rhinoceros and bovines, horses inhabited open landscapes. In Unit VI, the large number of horse remains implied a more open terrain than in units V-IV, where an increase in deer and a reduction of horses and bovines suggested an expansion of forested areas (Villaverde *et al.* 1996).

Villaverde *et al.* (1996, 2014) identified up to eight species of carnivore, including the cave lion (*Pantera spelaea*) identified in the 1950s (Table 5.5; Table 5.6; Table 5.7). Furthermore, the lower units contained large numbers of hyaena coprolites. Carnivores might have been responsible for the changing ratios of faunal remains found in the accumulation. However, taphonomic analyses revealed a complicated depositional history. Carnivore toothmarks are frequent on the remains. Some remains showed cut marks resulting from human agency along with evidence that carnivores subsequently gnawed these. This suggested a rapid succession of human and carnivore occupation (Villaverde *et al.* 1996; Villaverde and Martinez Valle 1992).

Table 5.5: Presence (X) and absence (blank) of faunal remains from all Cova Negra sectors, by unit. The table is adapted from counts made by Perez Ripoll 1977.

		Units													
Taxon	**Common name**	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**	**XIII**	**XIV**
Palaoeloxodon antiquus	straight-tusked elephant														x
Dicerorhinus	rhinoceros species	x	x	x	x	x				x	x				
Equus cabellus	horse	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Bos primigenius	aurochs	x	x	x	x	x	x	x	x				x		x
Capra pyrenaica	iberian bex	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Rupicapra rupicapra	chamois	x		x	x	x						x	x		
Cervus elaphus	red deer	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Capreolus capreolus	roe deer	x		x											
Sus scrofa	wild boar	x	x		x	x									
Macacus sylvanus	barbary macaque						x								
Ursus arctos	brown bear	x							x						
Crocuta crocuta	spotted hyaena	x										x	x	x	x
Canis lupus	wolf			x					x	x	x				
Vulpes vulpes	red fox	x													
Panthera spelaea	cave lion	x										x	x	x	
Panthera pardus	leopard	x		x	x										x
Lynx lynx	Eurasian lynx	x		x	x		x	x	x				x		
Felis silvestris	wild cat	x													
Castor fiber	beaver	x		x	x		x			x			x		
Oryctolagus cuniculus	rabbit	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Arvicola sapidus	water vole				x		x	x	x	x	x	x	x	x	x
Microtus sp.	vole species				x										
Elyomis quercinus	garden dormouse									x					
Allocircetus bursae	extinct hamster species									x	x				
Myotis myotis	greater mouse-eared bat			x		x	x		x	x	x	x	x		x
Miniopterus schreibersi	common bent-wing bat									x			x		
Testudo sp.	tortoise species	x	x	x	x	x	x	x	x	x	x	x	x	x	x

Table 5.6: NISP of macromammals identified in the south-western section by Villaverde et al. 1996.

Taxon	**Common name**	**IIIA**	**IIIB**	**IV**	**V**	**VI**
Caprinae	goat species	8	74	28	6	2
Capra pyrenaica	Iberian ibex	1	1			
Hemitragus sp.	tahr species	13	58	24	2	2
Cervidae	deer species	8	12	36	12	5
Cervus elaphus	red deer	2	4	13	7	1
Capreolus capreolus	roe deer		2			
Dama dama	fallow deer	1	2	11	8	6
Bovidae	wild cattle species	1	6	8	4	5
Bos primigenius	aurochs				1	
Equus caballus	horse	2	37	38	12	23
Equus sp.	horse species			2	1	
Stephanorhinus sp.	narrow-nosed rhinoceros	1				
Dicerorhinus sp.	rhinoceros species	1	1			
Sus scropha	wild boar		2	1	1	
Carnivora	carnivore species				2	
Canis lupus	wolf		5	8		1
Vulpes vulpes	red fox	1	3			
Lynx lynx	Eurasian lynx	2				
Panthera pardus	leopard	1				1
Crocuta crocuta	spotted hyaena			2		
Ursus arctos	brown bear		1			
Castor fiber	beaver	2				
Oryctolagus cuniculus	rabbit	94	337	368	41	75
Total		**138**	**545**	**539**	**97**	**121**

Table 5.7: NISP of faunal remains from Sector C of Cova Negra, identified by Perez Ripoll (1977).

Sector C		**Unit**														
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	
	sup/inf (m)	0	0.5	0.65	0.9	1.15	1.35	1.7	2.05	2.35	2.55	2.65	2.9	3.3	3.7	
Taxonomical ID	**Common name**	0.5	0.65	0.9	1.15	1.35	1.7	2.05	2.35	2.55	2.65	2.9	3.3	3.7	4.15	**Total**
Dicerorhinus hemitoechus	narrow-nosed rhinoceros				1	7										8
Equus caballus germanicus	horse	6	1	9	2	3		1	4	6	3	6	3		2	46
Bos primigenius	aurochs	1			1			1	5							8
Capra pyrenaica	Iberian ibex	8	1	1	1	2	2		2				5	1		23
Rupicapra rupicapra	chamois				1											1
Cervus elaphus	red deer	2		1	1	3		1	1	15	10		6	5	2	47
Crocuta crocuta	spotted hyaena												1	1	1	3
Felis sp.	felid (small/medium)											1		1		2
Lynx lynx	Eurasian lynx			1	1											2
Castor fiber	Eurasian beaver						2			1						3
Oryctolagus cuniculus	rabbit	2	1	11	22	19	20	97	778	761	206	157	344	105	21	2544
Arvicola sapidus	water vole								4	4		1	7	2	1	19
Testudo sp.	tortoise species				1	1						2		4	5	13
Aves	unidentified bird species	1		6	27	26	25	47	157	121	41	37	147	69	9	713

5.2.1.2 Microfauna

Taphonomic studies of the microfauna from Cova Negra showed that nocturnal birds of prey and carnivores were responsible for accumulating rodents and insectivores in the cave (Villaverde *et al.* 2014; Guillem 2009). The distribution of microfaunal remains was also associated with the intensity of human occupations (Villaverde *et al.* 2009, 2014). Environmental interpretations drawn from the presence and absence of micromammals point towards oscillations between cold and warmer climatic phases (Guillem 2009). Phases B and C both contain species that prefer humid conditions, such as shrews and moles (*Sorex* sp. and *Talpa* sp.), but whereas B was a cooler phase, C was warm, leading insectivores to decline while voles and murine species expanded. Phase D progressed from cold and moist towards cold and dry conditions with alternating mild pulses, observed in the disappearance of insectivores as in Phase C. In Phase F, the micromammals reflected the drier conditions indicated by the sedimentary interpretations. However, the presence of bats denotes mild conditions like those of the Mediterranean zone in the present day (Villaverde *et al.* 2014).

Of the 15 species of bat recovered from the sediment, there was evidence of breeding and hibernating colonies seen in the presence of both juvenile bat remains and those of advanced age. Breeding colonies demand a calm environment, a direct indicator that human occupations were rare (Guillem 2009). This reinforced the interpretation of short, sporadic episodes of human occupation (Table 5.8) (Villaverde *et al.* 2009, 2014).

Table 5.8: Bat remains identified by Villaverde et al. 2006. Values are NISP.

Species	**Common name**	**III**	**IV**	**V**	**VI**	**Total**
R. ferrumequinem	greater horseshoe bat	1	1	2	1	5
R. hipposideros	lesser horseshoe bat	1	1			2
R. euryale	Mediterranean horseshoe bat			1	1	2
R. mehelyi	Mehely's horseshoe bat				1	1
M. nattereri	Natterer's bat	2	2			4
M. myotis	greater mouse-eared bat	6	4	8	2	20
M. blythii	lesser mouse-eared bat		1			1
B. barbastellus	western barbastelle	1				1
P. auritus-austriacus	brown long-eared bat	1	1	1		3
M. schreibers	screibers' long-fingered bat	1	1	3	1	6
Pipistrellus sp.	pipistrelle	1	1			2
Total		**14**	**12**	**15**	**6**	**47**

5.3 The Cova Negra Avifauna

5.3.1 Previous studies

Avifauna remains from Cova Negra were first mentioned by Perez Ripoll (1977), who identified 2425 *Aves* sp. remains in the whole site, 713 of which came from Sector C (Table 5.7). No further investigation was made into the bird remains until archaeornithologist Mrs Anne Eastham studied them. Eastham identified the remains to species-level but did not publish a detailed report. In comparison to the remains that she studied from Gorham's Cave, Gibraltar, she commented on the stability and continuity of the species found throughout the Cova Negra's stratigraphic sequence (Eastham 1989). The collection remains in Mrs Eastham's care to this day. In 2016 Martinez-Valle *et al.* examined 249 bird remains from the west sector of unit IIIb (Table 5.9). This material was excavated during more recent seasons (MartinezValle 2009). The sample consisted of 22 species. Human manipulation and consumption was evident on 93 remains, covering 12 species. This study examines whether bird exploitation occurs during other occupation episodes.

Table 5.9: Bird remains from Level IIIb of Cova Negra showing NISP, MNI and frequency of bones with human modifications (nmod) per species. After Martinez-Valle et al. 2016.

Birds	**NISP**	**MNI**	**nMod**
Columba livia/oenas	110	14	47
Pyrrhocorax graculus	20	6	10
Pyrrhocorax pyrrhocorax	12	6	3
Pyrrhocorax sp.	3	2	14
Corvus sp.	7	1	3
Corvus monedula	4	3	1
Pica pica	2	1	
Garrulus glandarius	1	1	
Falco tinnunculus	1	1	
Falco naumanni	2	2	1
Athene noctua	2	2	
Alectoris sp.	4	4	1
Apus melba	3	2	
Pytonoprogne rupestris	1	1	1
Hirundo rustica	1	1	
Hirundinidae	1	1	
Scolopax rusticola	1	1	
Coracias graculus	1	1	1
Turdus merula	1	1	1
Fringillidae	4	3	5
Indet.	67		5
Total	**247**	**53**	**93**

Mrs Eastham granted me access to study the taphonomy of the avifaunal collection in her possession in 2018. The results of this study form the remainder of this chapter, together with the presentation of novel interpretations of the bioclimates at the site, based on the presence/absence of bird species across different stratigraphic units. I have relied on the taxonomic identification of bird species made by Mrs Eastham (1989).

The avifauna remains of Mrs Eastham's collection bared evidence of lengthy storage. Recent damage was widespread, likely due to specimens being kept together in large bulk bags. Some specimens had been varnished, a practice which can obscure original taphonomic traces. Others had been glued together to correct recent fractures. There is a majority of large-sized fragments (size > two bone zones) in the collection, indicating a preference for the recovery of larger, identifiable fragments during excavation. No spatial information beyond sector and unit was available for the bird material.

The original excavation team allocated numbers to most of the bones using a marker pen directly on the surface. I assigned a letter-and-number code in the format of X000 to specimens without an inventory number. These numbers were solely for use in this thesis, and numbers were not marked on the specimens.

5.3.2 Selection of Sector C

While creating an inventory of the avian material in the possession of Mrs Eastham, Sector C stood out as the sector in which the highest number of Middle Palaeolithic units were represented by bird remains (Figure 5.5). This presented a unique opportunity to extract a sample of the entire sequence of Cova Negra during the restricted time in which the material was made available.

Table 5.10: Distribution of remains by sector and unit in the collection kept by Mrs Anne Eastham. X indicates that bird bones were present in the given context.

	Unit													
Sector	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**X&XI**	**XII**	**XIII**	**XIV**
B		x	x	x	x					x		x		x
C			x	x	x	x	x	x	x	x	x	x	x	x
D	x	x	x			x								
D/E	x								x			x		
E	x		x	x	x	x	x							
F	x			x	x	x	x	x	x	x	x	x	x	
G	x	x	x	x	x	x	x	x						
H	x	x					x							
J1/J2							x	x	x	x	x			
K1/K2	x				x	x	x		x	x				
B-edge	x		x		x									
entrada				x	x									

Sector C has a surface area of 33.6 m^2 (8.4x4m) and is located at the centre of the cave, oriented along the central axis (Figure 5.3). The stratigraphic sequence consists of many thin natural layers that vary in colour, of which layers (capas) 10-13 (60 cm) are sterile. The sterile base stratum begins at a depth of 4.15 m below the surface (layer/capa 31) and reaches a depth of 5.15 m (layer/capa 38). The material was excavated in 1950 (Jorda 1953; Villaverde 1984; Eixea *et al.* 2020).

5.3.3 Contextual decisions

The context units used in this thesis are the sedimentary units determined by the original excavators and noted on specimen bags. Unit X&XI likely includes material retrieved from the boundary between units X and XI and all the material from unit XI. This may indicate that it would be pertinent to combine the NISPs of both X and X&XI into a single context. However, I have chosen to keep this as a separate context due to the lower NISP from unit X&XI in contrast to overlying unit X. There is also a taphonomic difference in the material reflected in the frequencies of thermal modification (see page 39).

5.4 Taxonomic results

Based on Eastham's identifications, the avifauna from Section C at Cova Negra consisted of 768 specimens from 12 units (Table 5.11). Of these, 741 were identified to species, 12 to genus, and 1 to order. Fourteen specimens could not be identified beyond *Aves* sp., and 11 classifications were each represented by a single element. The number of species identified was 32 (NTAXA).

Columbiform remains were most abundant (n = 423). Of these, 411 (53.5 %) belonged to the rock dove (*C. livia*). The red-legged partridge (*A. rufa*) was the second most frequent species identified in the remains (n = 105). Five species of corvid were present in seven of 12 units, including the raven (*C. corax*), the carrion crow (*C. corone*), and the Eurasian jay (*G. glandarius*). In total, corvid remains constituted 13.9 % of the sample (n = 107). The alpine chough (*P. graculus*) was the third most plentiful species by NISP (n = 79). The alpine swift (*T. melba*) accounted for 6.1 % of the remains (n=47) and was present in units V through XIII.

More than half of all specimens came from units VIII, IX, and X (57.4 %, n = 441). These units also had the highest MNI and NTAXA values (Unit VIII = 56/18, Unit IX = 36/12, Unit X = 36/12). A scatterplot showing the relationship between NISP and the MNI indicated a positive relationship between them. Spearman correlation tests indicated that there was a significant positive association between both the NISP and MNI (rs[12] = .9666, p = <0.001) and the NISP and the NTAXA (rs[12] = . 9717, p = <0.001). The NISP, MNI and NTAXA were greater in units VIII – XIV than in units III-VII where Villaverde (1984) identified the highest intensity of human activity. However, if humans were the source of the accumulation, this may indicate that Sector C was more heavily utilised in earlier phases of occupation than during the deposition of the upper units.

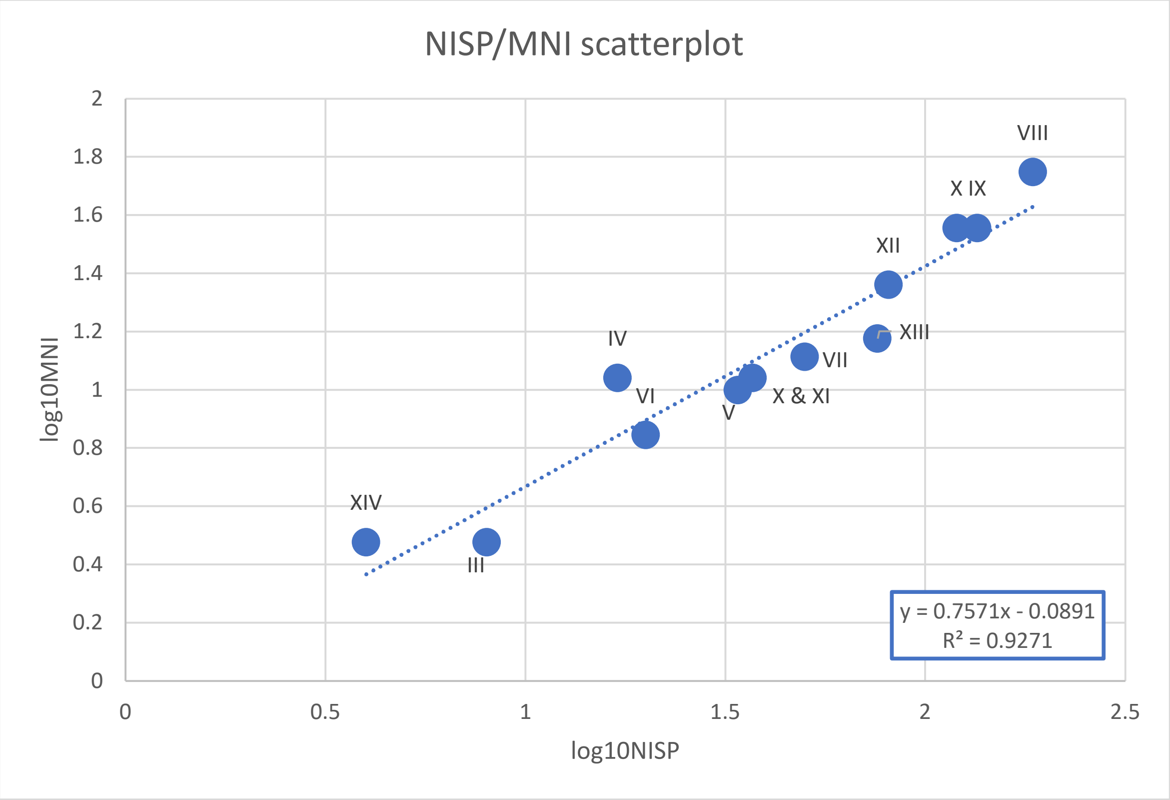


Figure 5.4: Scatterplot showing the relationship between NISP and MNI.

Table 5.11: Taxonomic results for Cova Negra Sector C based on Eastham's identifications, showing counts, NISP per unit, NISP per species, total NISP, MNI, and NTAXA.

			Unit												
Order	**Genus**	**Species**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**X & XI**	**XII**	**XIII**	**XIV**	**Total**
GALLIFORMES															
	Alectoris	*rufa*	1		3	2	7	37	22	11	8	9	5		105
	Coturnix	*coturnix*								1					1
ANSERIFORMES															
	Spatula	*querquedula*						1							1
	Mareca	*penelope*							2	3					5
	Anas	*platyrhynchos*						3	5		4	3	3	1	19
	Anas	*crecca*						1		1	1				3
APODIFORMES															
	Tachymarptis	*melba*			1	2	1	14	9	9	3	4	4		47
COLUMBIFORMES															
	Columba	*livia/oenas*	5	11	22	10	31	87	71	59	20	44	50	1	411
	Columba	*palumbus*							1			1			2
	Streptopelia	*turtur*						9							9
	Streptopelia	sp.							1						1
CHARADRIIFORMES															
	Scolopax	*rusticola*				1									1
SULIFORMES															
	Phalacrocorax	*aristotelis*								1					1
ACCIPITRIFORMES															
	Accipiter	*nisus*										1	1		2
STRIGIFORMES															
	Strix	*aluco*						1							1
	Athene	*noctua*						2		1					3
FALCONIFORMES															
	Falco	*naumanni*						1		1					2
	Falco	*tinnunculus*		1				3		1					5
	Falco	*eleonorae*						1							1
PASSERIFORMES															
	Garrulus	*glandarius*					2				1				3
	Pyrrhocorax	*pyrrhocorax*	2				7	4	7			1			21
	Pyrrhocorax	*graculus*		3	7	4		4	9	24		15	11	2	79
	Pyrrhocorax	sp.					1	8	1						10
	Corvus	*corone*		1	1			1							3
	Corvus	*corax*						1							1
	Turdus	*philomelos*							3						3
	Turdus	*viscivorus*				1	1	1	2			3	1		9
	Monticola	*saxatilis*						1							1
	Monticola	*solitarius*						1	1						2
	Oenanthe	*oenanthe*											1		1
	Passeriformes									1					1
INDETERMINATE															
	Aves	sp.		1				5	1	7					14
NISP			**8**	**17**	**34**	**20**	**50**	**186**	**135**	**120**	**37**	**81**	**76**	**4**	**768**
MNI			**3**	**11**	**10**	**7**	**13**	**56**	**36**	**36**	**11**	**23**	**15**	**3**	**217**
NTAXA			**3**	**3**	**5**	**6**	**6**	**19**	**12**	**11**	**6**	**9**	**8**	**3**	**28**

5.5 Environmental and climate results

This section outlines the results of my ecological analysis of Cova Negra. Only specimens identified to species were included (ecoNISP = 741). The environmental variables for each species were tabulated in Table 5.14.

5.5.1 Bioclimatic tolerance

The bioclimatic tolerances of species in Cova Negra revealed an environment dominated by birds with few climatic restrictions (

Table *5.12*). Generalist and semi-generalist species (categories E and D) were present in 11 and 12 units, respectively, while moderate species (category C) appeared in 10 units. A single semi-specialist species (Alpine chough, *P. graculus*; category B) was present in nine units. No bioclimatic specialist species were present in the sequence.

The frequencies observed at Cova Negra were compared to the expected distribution for the Palearctic in order to assess whether the differences were significant. Categories D and E were grouped to produce workable data due to low expected values. A chi^2- test provided a highly significant result (Table 5.13; χ^2 (3, n = 42) = 67.805, p = <0.001). The observed frequencies of generalist species (categories D and E) were much higher than expected in a current Palearctic accumulation. The observed absence of category A specialist species was unexpected because these were expected to be the most prolific of species.

Table 5.12: Bioclimatic tolerances by unit. A – Specialist, B – Semi-specialist, C – Moderate, D – Semi-generalist, E – Generalist. After Finlayson 2011. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). No specialist species were present in the sequence.

	Unit (NTAXA)													
TOL	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**X&XI**	**XII**	**XIII**	**XIV**	**FREQ**	**FREQ%**
A													0	-
B		1	1	1		2	1	1		1	1	1	9	75.0
C	1		2	2	2	5	4	5	3	2	2		10	83.3
D	1	2	2	2	3	6	4	4	2	3	3	1	12	100.0
E	1	1		1	1	5	2	1	1	3	2	1	11	91.7

Table 5.13: Observed and expected frequencies of bioclmatic tolerances. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

Category	Observed	EPal	Expected
A	0.00	0.315	13.23
B	9.00	0.271	11.38
C	10.00	0.280	11.77
DE	23.00	0.134	5.62
sum	**42**		**42**

Table 5.14: Ecological variables by species after Finlayson, 2011. TOL: bioclimatic tolerance (A= specialist, B= semi-specialist, C= moderate, D= semi-generalist, E= generalist), LAT: latitude range (A= arctic 70°N, B= boreal 60°N, C= temperate 50°N, D= mid-latitude belt (warm species) 40°N, E= subtropical 30°N, F= multilatitude – species occupies several latitude bands), TEM: temperature tolerance (A-E from cold to hot), HUM: humidity tolerance (A-E from arid to wet), Foraging and Nesting habitats (F= forest, O= open, M= mixed F/O, W= wetland, R= rocky, Ma= marine, A= aerial) , diet (E= endotherm, O= omnivore, I= insectivore, H= herbivore, N= necrophyte, M= mixed strategy carnivore, F= fish eater), and Migration behaviours (M= migratory, S= sedentary, P = partially migratory).

			Ecological Variables							
Common name	**Taxon**	**Order**	**TOL**	**LAT**	**TEM**	**HUM**	**Foraging**	**Nesting**	**Diet**	**Migration**
Red-legged partridge	*Alectoris rufa*	Galliformes	C	D	D	C	O	O	O	S
Common quail	*Coturnix coturnix*	Galliformes	D	F	D	D	O	O	O	M
Garganey	*Spatula querquedula*	Anseriformes	C	C	B	B	W	W	O	M
Wigeon	*Mareca penelope*	Anseriformes	C	B	B	B	W	W	O	M
Mallard	*Anas platyrhynchos*	Anseriformes	E	F	B	C	W	W	M	P
Teal	*Anas crecca*	Anseriformes	C	B	B	B	W	W	O	P
Alpine swift	*Tachymarptis melba*	Apodiformes	C	D	D	D	A	R	I	M
Rock dove	*Columba livia*	Columbiformes	D	F	D	D	M	R	*O*	*S*
Wood pigeon	*Columba palumbus*	Columbiformes	D	F	C	C	F	F	O	P
Turtle dove	*Streptopelia turtur*	Columbiformes	D	F	C	C	M	M	O	M
Woodcock	*Scolopax rusticola*	Charadriiformes	E	C	B	D	F	F	M	M
Shag	*Phalacrocorax aristotelis*	Pelecaniformes	D	F	B	B	Ma	R	F	S
Sparrowhawk	*Accipiter nisus*	Accipitriformes	E	F	C	D	F	F	E	P
Tawny owl	*Strix aluco*	Strigiformes	E	F	C	D	F	F	M	S
Little owl	*Athene noctua*	Strigiformes	D	D	C	C	M	R	M	S
Lesser kestrel	*Falco naumanni*	Falconiformes	C	D	D	B	O	R	M	M
Kestrel	*Falco tinnunculus*	Falconiformes	E	F	C	D	M	R	M	P
Eurasian jay	*Garrulus glandarius*	Passeriformes	D	F	C	D	F	F	O	S
Red-billed chough	*Pyrrhocorax pyrrhocorax*	Passeriformes	E	D	C	D	O	R	O	S
Alpine chough	*Pyrrhocorax graculus*	Passeriformes	B	D	C	E	O	R	O	S
Carrion/hooded crow	*Corvus corone*	Passeriformes	D	F	B	C	O	O	M	P
Raven	*Corvus corax*	Passeriformes	E	F	B	B	M	R	M	S
Song thrush	*Turdus philomelos*	Passeriformes	C	B/D	C	C	F	F	O	P
Mistle thrush	*Turdus viscivorus*	Passeriformes	D	F	C	C	F	F	O	P
Rufous-tailed rock thrush	*Monticola saxatilis*	Passeriformes	B	D	E	C	R	R	O	M
Blue rock thrush	*Monticola solitarius*	Passeriformes	D	D	C	C	R	R	O	P
Eurasian wheatear	*Oenanthe oenanthe*	Passeriformes	D	F	B	B	O	O	O	M

5.5.2 Latitude range

Latitude ranges were dominated by species that inhabit the mid-latitude belt (D) and multiple latitude bands (F) (Table 5.15). Both categories appeared in all 12 stratigraphic units. Four units (VIII, IX, X, X&XI) contained boreal species (category B), represented by two species of duck (*A. crecca* and *M. penelope*). The present distribution of these ducks is much further north (60°N; Finlayson 2011) than Cova Negra. Another duck species (*S. querquedula*) was one of two temperate species (category C); the other being the woodcock (*S. rusticola*). These species appeared in units VIII and VI, respectively. The song thrush (*T. philomelos*) was present in unit IX. No arctic (category A) or subtropical (category E) species were present in the studied sample.

In general, the latitude ranges of species at Cova Negra reflected a diversity of species centred around the cave's geographical position (ca. 40°N) along with some scattered northern species presumably displaced by the ice sheets in the north (Eynaud *et al.* 2009). A chi^2-test test showed a significant difference between the observed values and those expected in the Palearctic (χ^2 (3, n = 31) = 14.648, p = 0.002; Table 5.16). The frequency of multi-latitude species was higher than expected, while the expected frequencies were higher for all other categories. However, the lower-than-expected values in lumped category DE may be due to the complete absence of category E species, as category D species were present in all 12 units.

Table 5.15: Latitude ranges by unit. A – Arctic 70°N, B – Boreal 60°N, C – Temperate 50°N, D - Mid-latitude belt, warm, 40°N, E – Subtropical 30°N, F - Multi-latitude (occupies several bands). After Finlayson 2011. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Categories D and F were represented in all 12 units, while A and E are absent

	Unit (NTAXA)													
LAT	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**X&XI**	**XII**	**XIII**	**XIV**	**FREQ**	**FREQ%**
A													0	-
B						1	1	2	1				4	33.3
B/D							1						1	8.3
C				1		1							2	16.7
D	2	1	3	3	3	8	5	5	2	4	3	1	12	100.0
E													0	-
F	1	3	2	2	3	8	4	4	3	5	5	2	12	100.0

Table 5.16: Observed and expected frequencies of Latitude categories. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5). Categories A and B were lumped as higher-latitude species, categories C and B/D as temperate, and categories D and E as mid-latitude to produce workable data.

Category	Observed	EPal	Expected
AB	4.00	0.200	6.20
C-B/D	3.00	0.160	4.97
DE	12.00	0.485	15.03
F	12.00	0.145	4.50
sum	**31**		**31**

5.5.3 Temperature and humidity tolerances

Temperature and humidity tolerance values indicated a warm-temperate, sub-humid climate at Cova Negra (Table 5.17;

Table *5.19*) with moderate rainfall levels. This was reflected in the presence of categories C and D (40 %-80 % warm/sub-humid) birds in all 12 stratigraphic contexts and the absence of species that prefer cold and dry conditions (Category TEM A and HUM E). One category E (hot) species, the rufous-tailed rock thrush (*M. saxatilis*), appeared in unit VIII.

Humidity tolerances indicated that species which prefer moderate to humid climatic conditions were more prevalent than those that prefer dry conditions. There were no category A (dry) species present in the sequence, while the humid-tolerant (category E) alpine chough appeared in 75% of units (n = 9). Six of the nine species that showed a preference for colder temperatures (TEM B) and five of the seven that require drier (HUM B) conditions were partially or wholly migratory. These included ducks (*A. crecca, S. querquedula, M. Penelope*), the woodcock (*S. rusticola*), and the wheatear (*O. Oenanthe*).

Chi^2-tests produced significant results in both categories (TEM χ^2 (4, n = 35) = 23.959, p = <0.001; Table 5.18; HUM χ^2 (3, n = 38) = 31.679, p = <0.001; Table 5.20). A scarcity of temperature tolerance categories A and E combined with a higher-than-expected frequency of category C and D species pointed towards an avifauna adapted to the warm climatic conditions typical of the mid-latitudinal geographic position and topographic setting of the site. The higher-than-expected frequencies of species with high humidity tolerances and a deficit of species that prefer dry conditions indicated a more humid climate in the area than in the present day.

Table 5.17: Temperature tolerances by unit on a scale from cold to hot; A – 1-20 %, B – 21-40 %, C – 41-60 %, D – 61-80 %, E – 81-100 %. After Finlayson 2011. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Temperate to warm species were featured most frequently.

	Unit (NTAXA)													
TEM	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**X&XI**	**XII**	**XIII**	**XIV**	**FREQ**	**FREQ %**
A													0	-
B	0	1	1	1		5	2	3	2	1	2	1	10	83.3
C	1	2	1	2	3	8	6	3	1	5	3	1	12	100.0
D	2	1	3	3	3	4	3	5	3	3	3	1	12	100.0
E						1							1	8.3

Table 5.18: Observed and expected frequencies of temperature tolerances. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

TEM	Observed	EPal	Expected
A	0.00	0.146	5.10
B	10.00	0.271	9.47
C	12.00	0.211	7.37
D	12.00	0.143	5.01
E	1.00	0.230	8.05
sum	**35**		**35**

Table 5.19: Humidity tolerances by unit on a scale from arid to humid; A – 1-20%, B – 21-40%, C – 41-60%, D – 61-80%, E – 81-100%. After Finlayson 2011. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Species that prefer wetter environments appeared at higher frequencies.

	Unit (NTAXA)													
HUM	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**X&XI**	**XII**	**XIII**	**XIV**	**FREQ**	**FREQ%**
A													0	-
B						4	1	4	1		1		5	41.7
C	1	1	2	2	2	8	6	2	2	4	3	1	12	100.0
D	2	2	2	3	4	5	3	4	3	4	3	1	12	100.0
E		1	1	1		1	1	1		1	1	1	9	75.0

Table 5.20: Observed and expected frequencies of humidity tolerances. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

Category	Observed	EPal	Expected
A	0.00	0.319	12.14
B	5.00	0.217	8.23
C	12.00	0.234	8.88
DE	21.00	0.230	8.74
sum	**38**		**38**

5.5.4 Foraging and nesting habitats

Foraging requirements of the bird species at Cova Negra reflected a landscape with a mixture of open and forested habitats (Table 5.21). Species with open and mixed foraging strategies featured in all 12 stratigraphic units. Rock thrushes (*M. solitarus, M. saxitilis*) appeared in two units, taking advantage of the cliffs around the cave to find food, while swifts, present in nine units, were aerial insectivores. The shag constituted the only marine forager and was present only in Unit X. Wetland and forest foragers were each present in seven units. The duck species (wetland) were present in the lower portion of the sequence (VIII-XIV), while forest foragers were recorded from units VI to XIII except for unit X.

In order to produce workable data for significance testing, the observed values of aerial (A), open (O), and rocky (R) foragers were combined into a general open category, and wetland and marine foragers were combined into a single category (

Table *5.22*). A chi^2-test produced significant results (χ^2 (3, n = 50) = 10.234, p= 0.017), confirming that the observed frequencies deviated from the expected values in a current Palearctic distribution. Wetland and marine species were underrepresented, while there were more open (AOR) and mixed species than expected. Fewer than expected forest species reflected the open character of the landscape.

Table 5.21: Foraging habitat by unit; A = aerial, F = forest, M = mixed (forest and open), Ma = marine, O = open, R = rocky, W = wetland (Finlayson 2011). Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Mixed and Open foragers appear in all 12 units.

	Unit (NTAXA)													
HF	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**X&XI**	**XII**	**XIII**	**XIV**	**FREQ**	**FREQ %**
A			1	1	1	1	1	1	1	1	1		9	75.0
F				2	2	2	3		1	3	2		7	58.3
M	1	2	1	1	1	5	1	3	1	1	1	1	12	100.0
Ma								1					1	8.3
O	2	2	3	2	2	5	3	4	1	3	3	1	12	100.0
R						2	1						2	16.7
W						3	2	2	2	1	1	1	7	58.3

Table 5.22: Observed and expected frequencies of foraging habitats. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

Category	**Observed**	**EPal**	**Expected**
F	7.00	0.205	10.23
M	12.00	0.170	8.49
AOR	23.00	0.307	15.35
WMa	8.00	0.319	15.93
sum	**50**		**50**

Wetland and forest nesters were equivalent to those that foraged in those habitats (Table 5.23). The rocky nesters were present in all 12 units, represented by ten species. Among them were the choughs, swifts, rock dove, and falcons. These species would have found roosts not only in the cliffs around the cave but inside the cavern itself. Finlayson (2019) suggests that kestrels may have developed a commensal relationship with humans, attracted by the rodents feeding on human refuse. Species that prefer to nest in open landscapes, game birds (*A. rufa, C. coturnix*) and Passeriformes (*C. corone, O. oenanthe*), were present in 11 units.

A chi^2-test produced highly significant results (χ^2 (4, n = 38) = 14.989, p= 0.005; Table 5.24). The observed values exceeded those expected for rocky (R) and open (O) nesters, while mixed (M) and wetland (W) were underrepresented. Woodland nesters (F) generally appeared as expected.

Table 5.23: Nesting habitat by unit; F = forest, M = mixed (forest and open), O = open, R = rocky, W = wetland (Finlayson 2011). Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Rocky and Open nesters appear most frequently.

	Unit (NTAXA)													
HN	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**X&XI**	**XII**	**XIII**	**XIV**	**FREQ**	**FREQ %**
F				2	2	2	3		1	3	2		7	58.3
M						1							1	8.3
O	1	1	2	1	1	2	1	2	1	1	2		11	91.7
R	2	3	3	3	3	10	5	7	2	4	3	2	12	100.0
W						3	2	2	2	1	1	1	7	58.3

Table 5.24: Observed and expected frequencies of nesting habitats. Expected frequencies are calculated by multiplying the sum of observations by the expected Palearctic frequency (EPal) (see section 2.5).

HN	Observed	EPal	Expected
F	7.00	0.214	8.13
O	11.00	0.238	9.06
M	1.00	0.172	6.54
R	12.00	0.135	5.13
W	7.00	0.241	9.15
sum	**38**		**38**

5.5.5 Higher Taxa

Diurnal raptors, falcons and owls appeared in 5 of 12 stratigraphic units (42%) (Table 5.25; Figure 5.5). Falcons and owls were present in units VIII and X, while the sparrowhawk (*A. nisus*) only appeared in the lower part of the sequence (units XII and XIII). In total, bird of prey remains amounted to 1.8 % of the total avifaunal sample (n = 14). On a higher resolution, raptors accounted for between 1.2 % and 5.9 % of each unit's remains.

Corvids appeared in all stratigraphic units, represented by five species across three genera. Of them, the raven (*C. corax*) and choughs (*Pyrrhocorax* spp.) are rocky nesters and would be an expected presence on the cliff face around the cave (Cramp *et al.* 1977 - 1994). The same can be said of the rock dove (*C. livia*), which was also present in all 12 units. Along with the swifts, which would have formed a breeding colony within the cave itself, the presence of these species may represent a natural attritional accumulation (Laroulandie 2000). However, corvids and pigeons are among the species known to be exploited by Neanderthals (Finlayson *et al.* 2012; Blasco *et al.* 2014, 2016; Lloveras *et al.* 2018).

It is more difficult to explain the presence of other frequently occurring groups such as gamebirds (Galliformes) (83 %) and ducks and geese (Anseriformes) (58 %) because these species do not naturally feature in cave environments and must have been introduced to the site by an external agent. Taphonomic research of bird remains from other Middle Palaeolithic sites proved that humans were partially responsible for the accumulation of game birds and Anseriformes in the sediment (Blasco and Peris 2009, 2012; Peresani *et al.* 2011; Fiore *et al.* 2016). Therefore, it is tempting to suggest that the higher frequencies of pigeons, crows, and gamebirds also indicate human exploitation at Cova Negra. However, direct evidence is required to draw any valid conclusions.

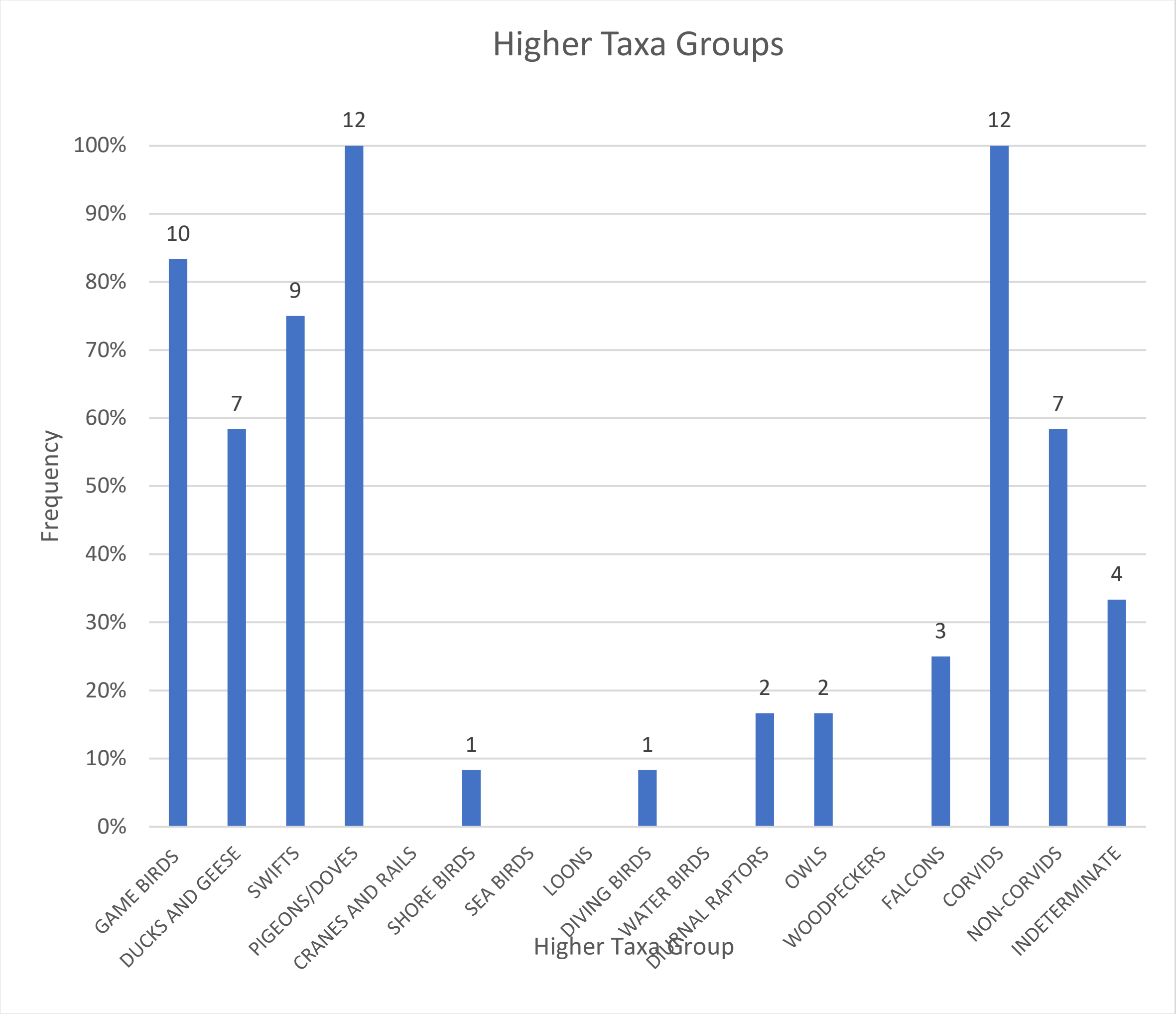


Figure 5.5: Frequency of bird groups at Cova Negra. Doves/Pigeons and Crows are present in all units while diving birds and shorebirds each feature in only one unit.

Table 5.25: Presence of higher taxa groups showing counts per unit, total NISP, NTAXA, frequency of presence in the stratigraphic units, and relative frequency.

			Unit														
Common name	**Order**	**Family**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**X & XI**	**XII**	**XIII**	**XIV**	**Total**	**Freq**	**Freq%**
GAME BIRDS	GALLIFORMES	ALL	1		3	2	7	37	22	12	8	9	5		106	10	83%
DUCKS AND GEESE	ANSERIFORMES	ALL						5	7	4	5	3	3	1	28	7	58%
SWIFTS	APODIFORMES	ALL			1	2	1	14	9	9	3	4	4		47	9	75%
PIGEONS/DOVES	COLUMBIFORMES	ALL	5	11	22	10	31	87	72	59	20	45	50	1	423	12	100%
CRANES AND RAILS	GRUIFORMES	ALL															
SHOREBIRDS	CHARADRIIFORMES	ALL								1					1	1	8%
SEABIRDS	PROCELLARIIFORMES	ALL															
LOONS	GAVIIFORMES	ALL															
DIVING BIRDS	SULIFORMES	ALL				1									1	1	8%
WATER BIRDS	PELICANIFORMES	ALL															
DIURNAL RAPTORS	ACCIPITRIFORMES	ALL										1	1		2	2	17%
OWLS	STRIGIFORMES	ALL						3		1					4	2	17%
WOODPECKERS	PICIFORMES	ALL															
FALCONS	FALCONIFORMES	ALL		1				5		2					8	3	25%
CORVIDS	PASSERIFORMES	CORVIDAE	2	4	8	4	9	18	17	24	1	16	11	2	116	12	100%
NON-CORVIDS	PASSERIFORMES	NON-CORVIDS				1	1	3	6	1		3	2		17	7	58%
	INDETERMINATE	ALL		1				5	1	7					14	4	33%
		NISP	**8**	**17**	**34**	**20**	**50**	**186**	**135**	**120**	**37**	**81**	**76**	**4**	**768**		
		NTAXA	**3**	**4**	**5**	**6**	**6**	**18**	**12**	**12**	**6**	**9**	**8**	**3**	**32**		

5.6 Taphonomic results

This section presents the results of the taphonomic analysis of the Cova Negra avifauna (Table 5.26).

5.6.1 Lisibility

The lisibility of the sample was generally good (Figure 5.6). Most impairments observed were the product of concretions and manganese deposits on the bone surfaces (see below). As mentioned in Section 5.3, recent modifications such as crushing during storage and the use of a marker pen, glue, and varnish on the bone surface also impaired the lisibility of some specimens.

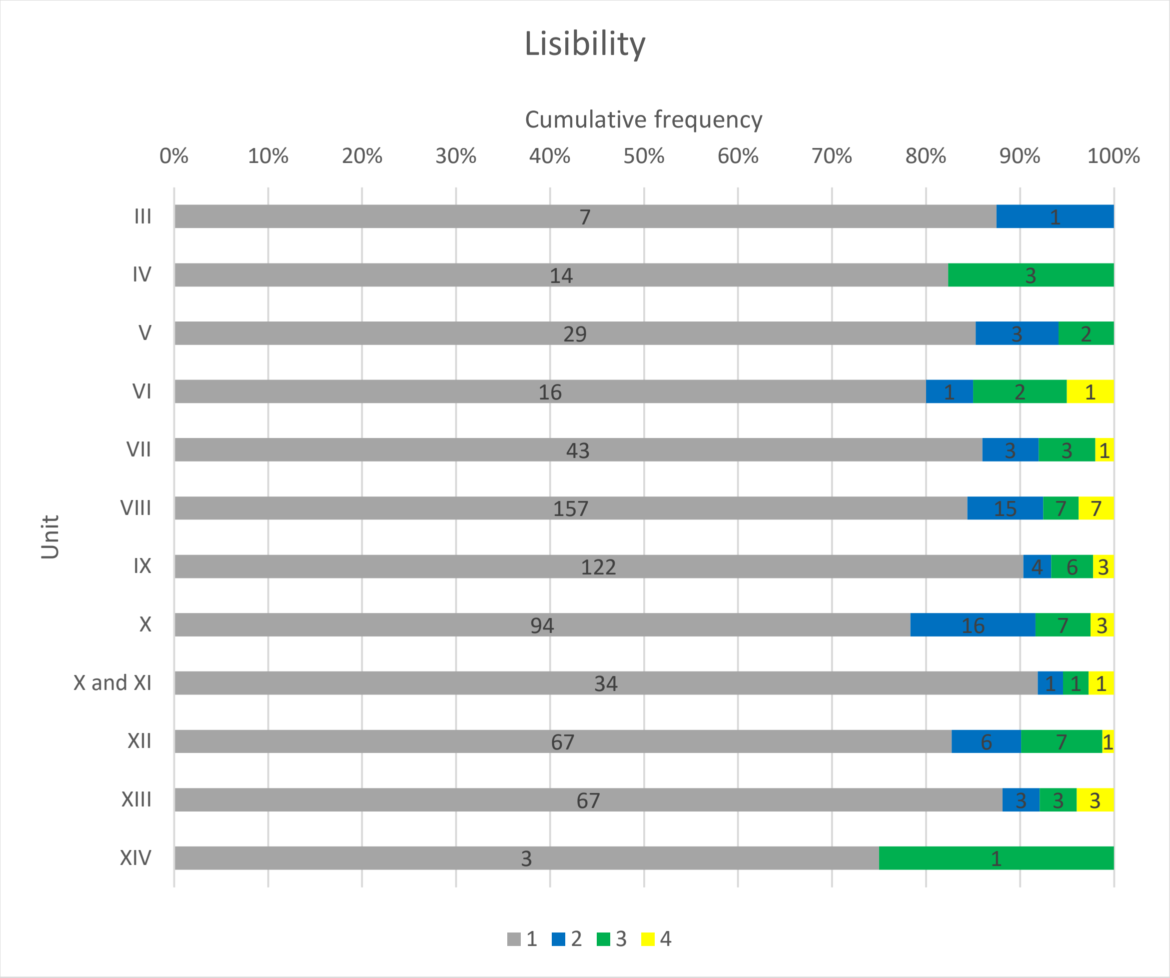


Figure 5.6:Lisibility of specimens by unit. 1=clear; 2= mostly clear, some issues; 3= some major issues; 4= unreadable.

Table 5.26: Taphonomic results by unit showing the count of modifications and percentage of NISP modified per unit (%).

Unit	Concretions	Manganese staining	Trample	Root etching	Weathering	Carnivore toothmark	Rodent gnaw	Bird of prey beak mark	Indet. Toothmark	Digestion	Cutmark	Thermal modification	Peeling
III	2	4	3	8	7	6		1		3	2	1	
	25.0%	*50.0%*	*37.5%*	*100.0%*	*87.5%*	*75.0%*		*12.5%*		*37.5%*	*25.0%*	*12.5%*	
IV	12	13		14	15	5		2		15		4	
	70.6%	76.5%		82.4%	88.2%	29.4%		11.8%		88.2%		23.5%	
V	13	22	7	25	22	14	1			8	5	10	
	38.2%	*64.7%*	*20.6%*	*73.5%*	*64.7%*	*41.2%*	*2.9%*			*23.5%*	*14.7%*	*29.4%*	
VI	9	14	7	12	16	4		3	1	10	2	7	
	45.0%	*70.0%*	*35.0%*	*60.0%*	*80.0%*	*20.0%*		*15.0%*	*5.0%*	*50.0%*	*10.0%*	*35.0%*	
VII	20	46	15	39	41	9	1	10		17	5	18	1
	40.0%	*92.0%*	*30.0%*	*78.0%*	*82.0%*	*18.0%*	*2.0%*	*20.0%*		*34.0%*	*10.0%*	*36.0%*	*2.0%*
VIII	89	173	38	130	117	49		23		94	2	25	
	47.8%	*93.0%*	*20.4%*	*69.9%*	*62.9%*	*26.3%*		*12.4%*		*50.5%*	*1.1%*	*13.4%*	
IX	40	123	24	99	108	26		26	1	84	1	7	
	29.6%	*91.1%*	*17.8%*	*73.3%*	*80.0%*	*19.3%*		*19.3%*	*0.7%*	*62.2%*	*0.7%*	*5.2%*	
X	62	108	36	91	94	17		25		59	4	9	
	51.7%	*90.0%*	*30.0%*	*75.8%*	*78.3%*	*14.2%*		*20.8%*		*49.2%*	*3.3%*	*7.5%*	
X&XI	19	29	3	26	29	7		10		29	1		
	51.4%	78.4%	8.1%	70.3%	78.4%	18.9%		27.0%		78.4%	2.7%		
XII	54	75	31	76	69	20	1	10		40	3	5	
	66.7%	*92.6%*	*38.3%*	*93.8%*	*85.2%*	*24.7%*	*1.2%*	*12.3%*		*49.4%*	*3.7%*	*6.2%*	
XIII	43	65	32	68	65	12	2	10		50	1	3	2
	56.6%	*85.5%*	*42.1%*	*89.5%*	*85.5%*	*15.8%*	*2.6%*	*13.2%*		*65.8%*	*1.3%*	*3.9%*	*2.6%*
XIV	3	4		3	3	2				1		1	
	75.0%	*100.0%*		*75.0%*	*75.0%*	*50.0%*				*25.0%*		*25.0%*	

5.6.2 Natural modifications

5.6.2.1 *Concretions, Manganese staining and Root etching.*

Concretions were present on specimens throughout the sequence (Figure 5.7). The lowest concentration of concretions appeared in units III (25%, n = 2) and IX (29.6%, n = 40) while the highest concentrations occurred in units IV (70.6%, n = 12), XIII (66.7%, n = 54), and XIV (75%, n = 3). Though NISPs were low in units IV and XIV, these frequencies coincided with already identified humid phases (Villaverde *et al.* 2014).

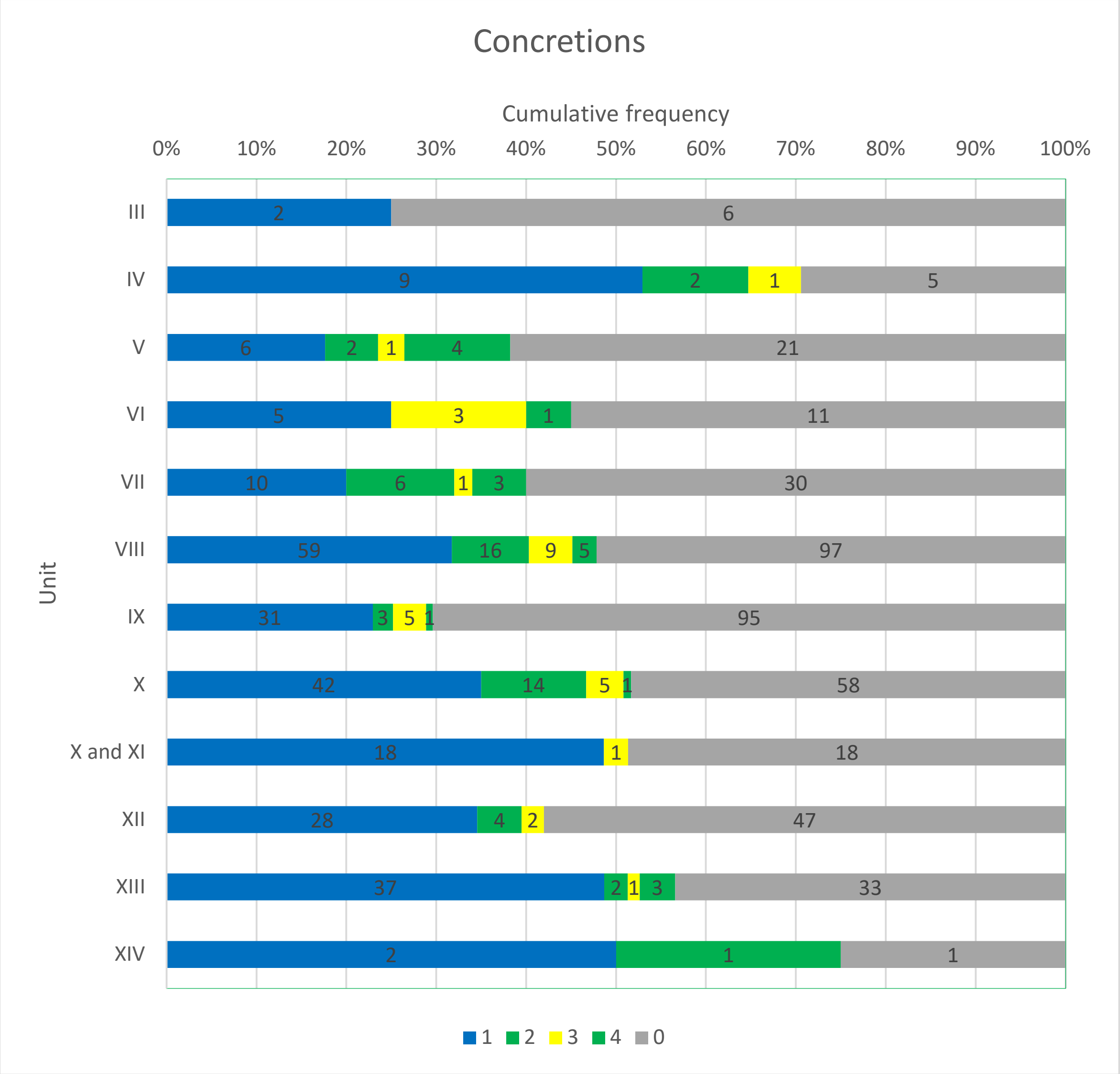


Figure 5.7: Degree of concretions present by unit. 1= 1-25%, 2= 26-50%, 3= 51-75%, 4= 76-100%, 0= no concretion.

Moderate to high frequencies of manganese-oxide staining were present throughout the sequence affecting between a minimum of half to all specimens in any given unit (Figure 5.8). As with concretions, the lowest level of manganese staining occurred in level III. However, Unit IX di not show the same trend.

Rooting damage was visible at moderate to high levels throughout the sequence (Figure 5.9). The cave has a wide, east-facing opening (Eixea *et al.* 2020). This would allow sunlight to penetrate the chamber, promoting photosynthesis. The presence of rooting supports the theory that Cova Negra's occupational events were short, sporadic, and concentrated in different small areas of the cave, leaving other areas undisturbed where plants may take root and grow.

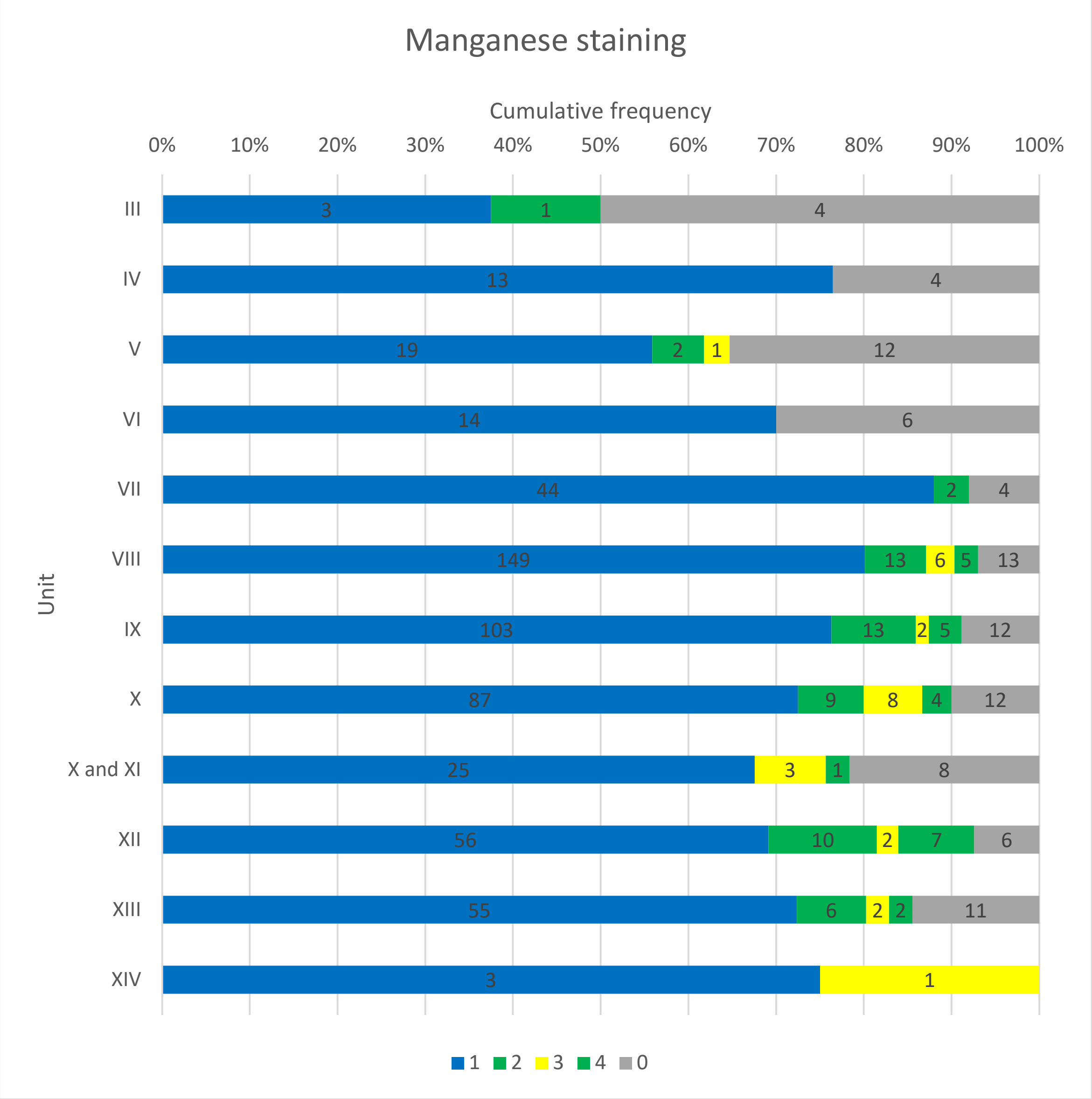


Figure 5.8: Degree of manganese oxide staining by unit. 1 = 1 - 25%, 2 = 26 - 50%, 3 = 51 - 75%, 4 = 76 - 100%.

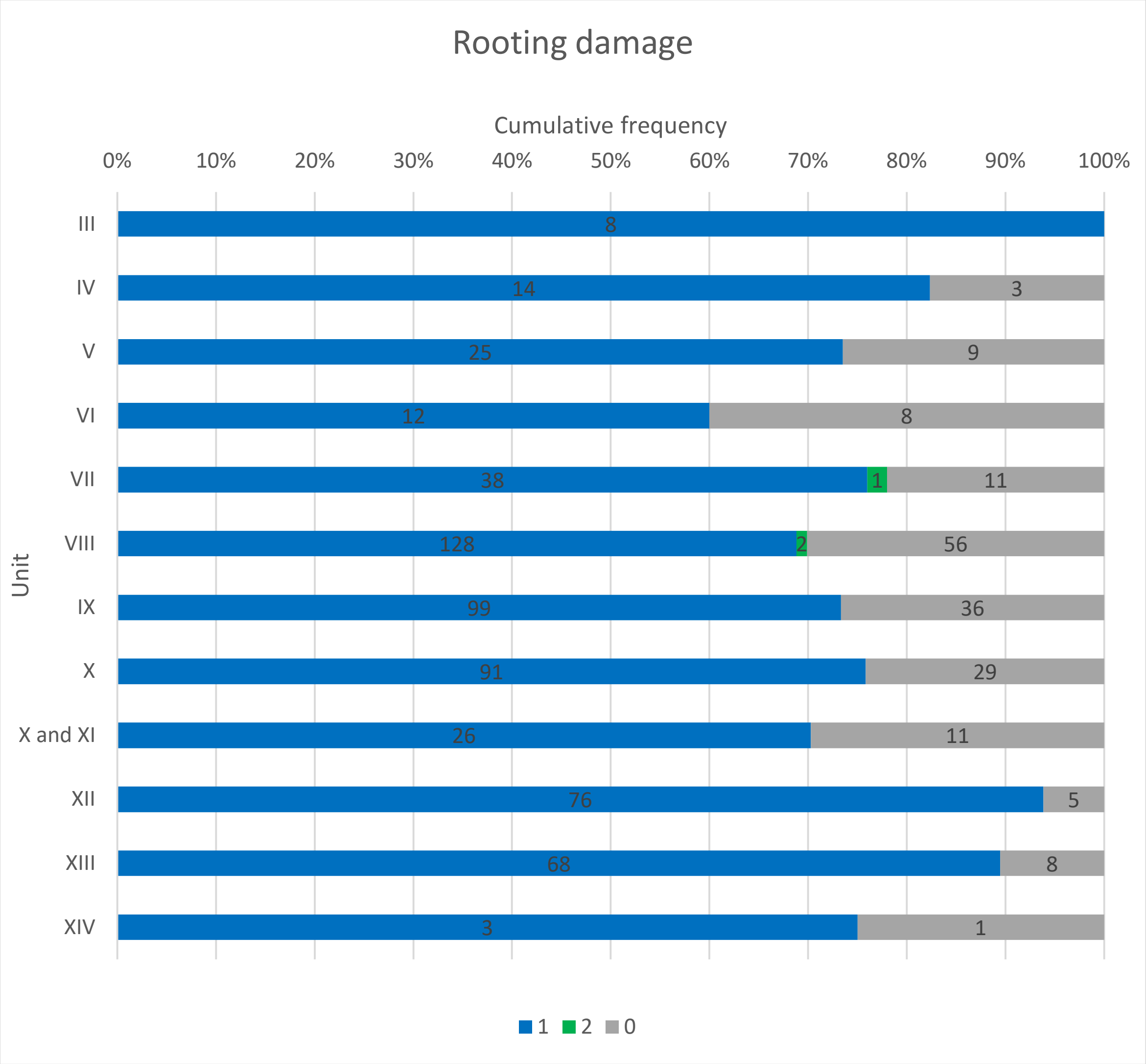


Figure 5.9: Presence of acid etch from rooting by level. 1= low level of root etch, 2= moderate level of root etching.

5.6.2.2 Weathering and Trample

Weathering was present in all units, varying from light (1) to heavy (4) (Figure 5.10). Most of the affected specimens (n= 522) were weathered to degree 1 or 2, while only a handful of specimens showed degree 4 damage (n = 5). This was congruent to the degradation pattern seen in bird bones by Bochenski & Tomek (1997), who observed that bird bones weather slowly at first but then suddenly deteriorate more rapidly. The regular distribution of degrees of weathering was similar throughout the site, pointing towards a generally stable environment with no external forces influencing the rate of weathering. Trampling was evident in 10 of 12 units (Figure 5.11), appearing on 30 - 42% of remains in units III, VI, VII, X, and XI. Low levels of trample indicate little influence from external agents such as Neanderthals and large predators during the accumulation (Fernández-Jalvo and Andrews 2016).

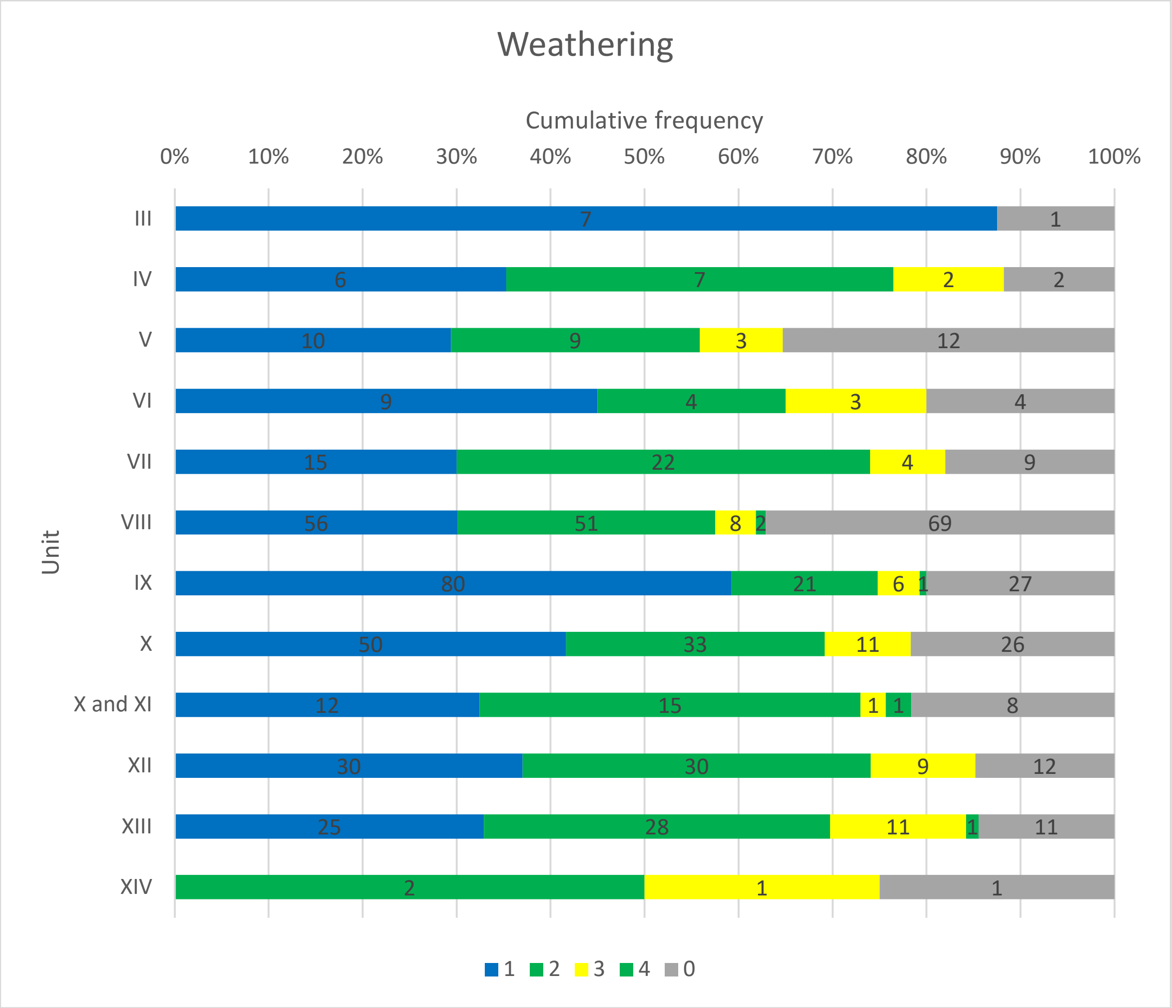


Figure 5.10: Degrees of Weathering modifications by unit on a scale from WEATH0 = no modification to WEATH5 = highest degree of modification.

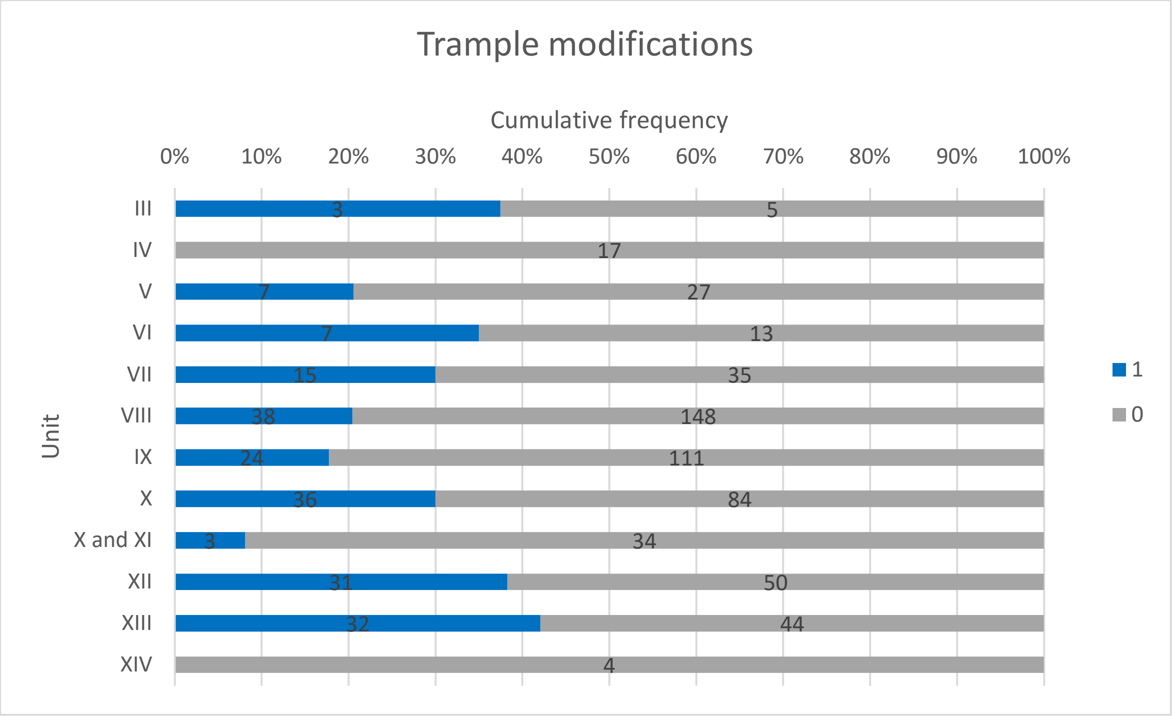


Figure 5.11: Number of trampled specimens per unit. 1 = trample present, 0 = no trample.

5.6.3 Predator modifications

303 specimens (39.5 %) showed modifications resulting from predator manducation. Any single specimen may display more than one modification. Tooth and beak marks were present on material from every unit (Table 5.27). Punctures and crenulated edges were the most frequently identified traces. Punctures of an oval to round shape along with the presence of pitting indicated small carnivore agency (Fernández-Jalvo and Andrews 2016) (Figure 5.12). No remains bore toothmarks attributable to larger carnivores like hyaenas (*C.crocuta*). Irregularly shaped punctures and scores indicated that avian agents contributed to the accumulation in all units except V and XIII. This was also observed in the micromammal remains studied by Guillem (2009). Rodent gnaw was identified in units V, VII, X, XII, and XIII, but only in low frequencies.

Low-level acid etching from digestion was the most frequent type of predator modification observed (n = 352) (Figure 5.13). This is attributable to nocturnal birds of prey and small carnivores (Andrews 1990, Fernández-Jalvo and Andrews 2016). Higher levels of acid etch (n = 33) were likely the product of diurnal birds of prey, while larger carnivores were probably responsible for the advanced stage of etching visible on one specimen in level X&XI, as these were more likely to consume the entire carcass (Serjeantson ibid; Andrews ibid).

Table 5.27: Presence of tooth and beak marks by context. n. mod=number of modified specimens, %mod= percentage of modified specimens per unit, the total number of modifications per unit (more than one modification may be present on any one specimen), and modification type.(pun=puncture; cren=crenulated edges).

				Manducation modifications					
Unit	**n.mod**	**%mod**	**total modifications**	**score**	**notch**	**pit**	**pun**	**cren**	**gnaw**
III	7	87.5%	13	2	0	2	4	5	0
IV	7	41.2%	12	0	0	1	6	5	0
V	15	44.1%	27	2	0	3	16	5	1
VI	8	40%	12	0	0	2	6	4	0
VII	20	40%	25	1	0	4	7	12	1
VIII	72	38.7%	109	7	4	7	43	49	0
IX	53	39.3%	68	3	0	1	37	27	0
X	44	36.7%	58	2	5	0	25	24	1
X & XI	17	45.9%	29	1	0	0	23	5	0
XII	31	38.3%	39	3	2	2	17	14	1
XIII	27	35.5%	32	2	1	1	17	9	2
XIV	2	50%	4	0	0	1	3	0	0
TOTAL	**303**	**39.5%**	**428**	**23**	**12**	**24**	**204**	**159**	**6**

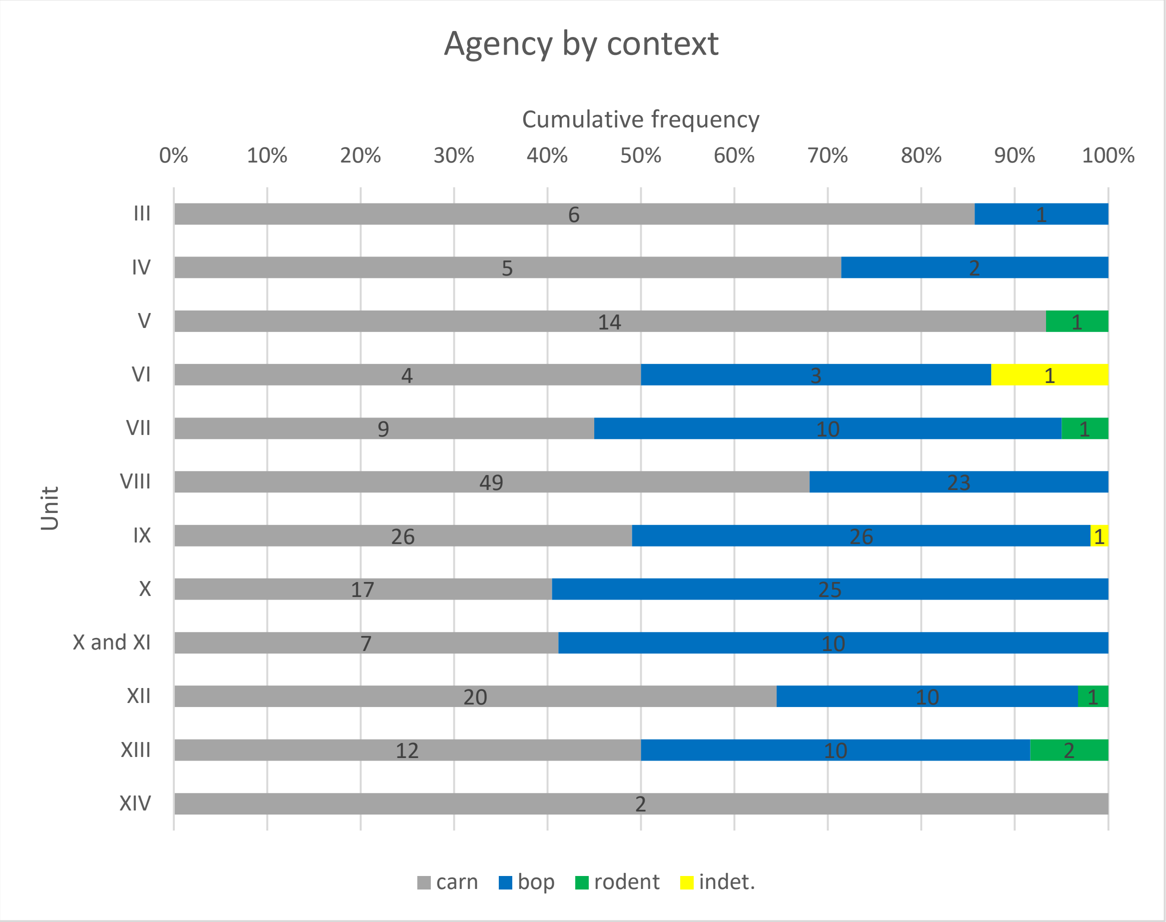


Figure 5.12: Agency as reflected in tooth and beak marks, by unit; carn=carnivore toothmark, bop=bird of prey beak mark, rodent=rodent gnaw, indet= toothmark of indeterminate origin.

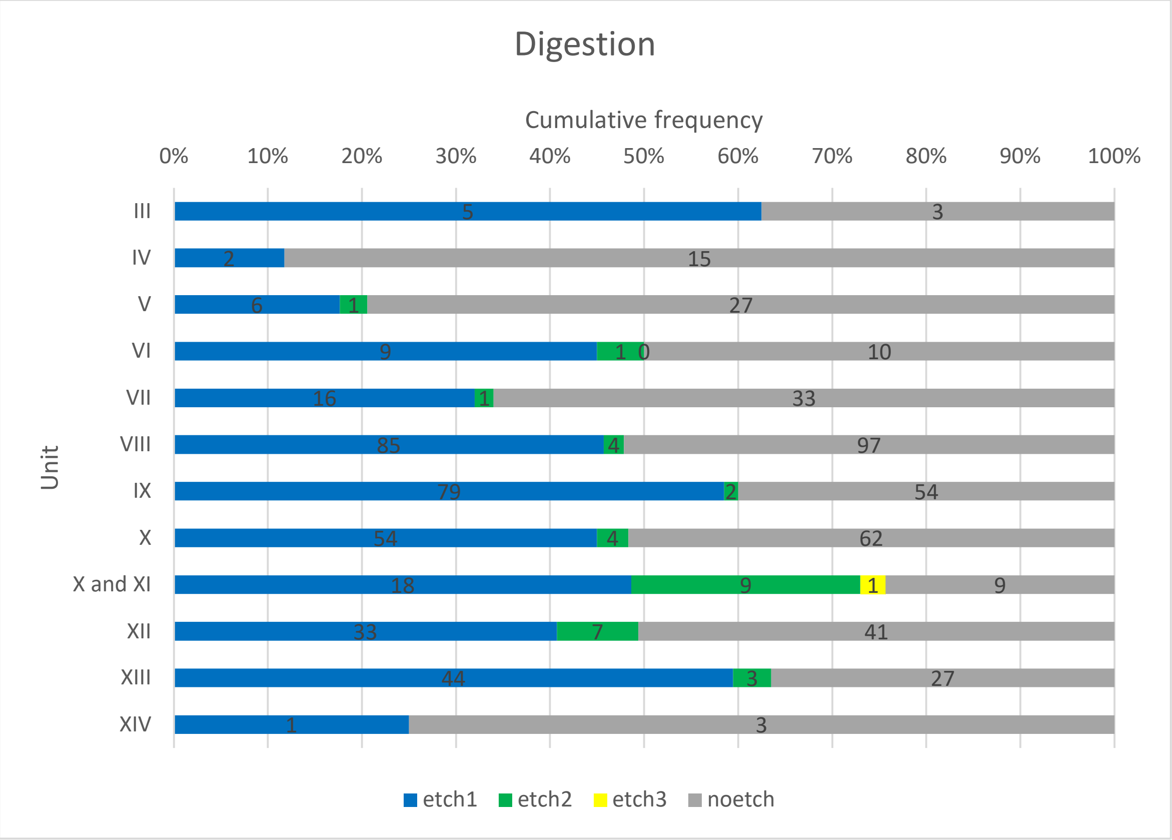


Figure 5.13: Digestion traces per stratigraphic unit.

5.6.4 Human modifications

5.6.4.1 Striations

A total of 26 bone specimens from ten of the 12 units in Sector C exhibited striations that derived from human agency (Table 5.22). The seven species included pigeons, corvids, ducks and partridges. One specimen in particular, a shag (*P. aristotelis*) coracoid, displayed multiple striations to suggest that it was part of a disarticulated carcass. The striations are described in greater detail below, grouped by climatic Phase (Fumanal 1986).

In Phase B, a single rock dove (*C. livia*) coracoid from Unit XIII presented multiple striations on the distal portion of the ventral aspect (Figure 5.14). The marks varied in orientation and depth. They were deepest near the *proc. lateralis*; these oblique cuts lead to the fracture of the extremity of this feature from the main element. On the central surface of the ventral aspect, transverse striations were shallower, and cuts of moderate depth were present slightly more proximal on the shaft. All of these striations were present on the ventral surface of the element, which was exposed during the disarticulation of the scapular girdle from the sternum.

Table 5.28: Specimens marked by striations. By unit, climatic phase, taxon, element, laterality, number of striations (nMod), type of striation (cm=cutmark/scrape), location of striation (location on the element), orientation of striation in relation to the main axis of the bone (tr=transverse, obl=oblique, lo= longitudinal, and intention (da=disarticulation, df=defleshing).

Unit	**Phase**	**Coll. No.**	**Taxon**	**Common name**	**Element**	**Side**	**nMod.**	**type**	**location**	**orientation**	**intention**
III	F	10041	*Columba livia*	rock dove	femur	l	5	cm	2	obl	da
III	F	A001	*Pyrrhocorax pyrrhocorax*	red-billed chough	scap	r	2	cm	3	obl	df
V	D	CN97	*Alectoris rufa*	red-legged partridge	humerus	l	2	cm	5	lo/tr	da
V	D	8018	*Columba livia*	rock dove	ulna	r	2	cm	5	tr	da
V	D	10018	*Columba livia*	rock dove	cmc	r	2	scrape/cm	23	lo/tr	df
V	D	8017	*Corvus corone*	rock dove	ulna	r	5	cm	1	lo	da
V	D	CN92	*Columba livia*	rock dove	femur	l	multi	scrapes	caudal	lo/tr	df
VI	D	10306	*Columba livia*	rock dove	coracoid	r	1	cm	2	obl	df
VI	D	CN124	*Columba livia*	rock dove	humerus	r	1	cm	5	lo/tr	da
VII	D	10130	*Columba livia*	rock dove	humerus	l	2	cm	5	lo	da
VII	D	10134	*Alectoris rufa*	red-legged partridge	femur	r	2	cm	5	obl	da
VII	D	CN177	*Columba livia*	rock dove	humerus	l	2	scrapes&cm	3	lo/obl	df
VII	D	10137	*Columba livia*	rock dove	tmt	l	3	cm	3	x	df
VII	D	CN176	*Garrulus glandarius*	eurasian jay	humerus	l	4	cm	5	tr	da
VIII	D	1134	*Columba livia*	rock dove	humerus	r	1	cm	5	0	da
VIII	D	1126	*Pyrrhocorax pyrrhocorax*	red-billed chough	humerus	l	4	cm	2	tr	df
IX	D	2075	*Columba livia*	rock dove	humerus	r	1	cm	2	lo	df
X	D	2313	*Columba livia*	rock dove	cmc	r	1	cm	1	lo	da
X	D	1586	*Alectoris rufa*	red-legged partridge	tmt	r	1	cm	5	lo	da
X	D	2344	*Mareca penelope*	eurasian wigeon	tmt	l	2	cm	2	tr	df
X	D	1576	*Phalocrocorax aristoteles*	shag	coracoid	l	multi	cm	12	tr	da
X and XI	D	2521	*Columba livia*	rock dove	coracoid	l	1	cm	1	lo	da
XII	C	2929	*Columba livia*	rock dove	coracoid	r	1	cm	4	obl	df
XII	C	3045	*Columba livia*	rock dove	humerus	r	2	cm	3	x	df
XII	C	3055	*Columba livia*	rock dove	tbt	l	2	cm	5	lo	da
XIII	B	CN3179	*Columba livia*	rock dove	coracoid	r	multi	cm	345	tr/obl	da/df

Figure 5.14: CN3179. The right coracoid of a rock dove (C. livia) from unit XIII displaying multiple striations resulting from disarticulation and defleshing processes. Scale = 1mm.

Phase C, equivalent to Unit XII, Figure 5.15). A humerus (Spec. no. 3045) and a coracoid (Spec. no 2929) displayed striations made during defleshing activities. On the distal end of a tibiotarsus (Spec. no. CN3055), a pair of longitudinal striations on the articulation surface were the product of cuts made to disarticulate the hind limb.

Phase D contained 20 specimens with striations distributed unevenly throughout units XI to V. Units X&XI (Spec. no. 2521) and IX (Spec. no. 2075; Figure 5.16) each produced a single specimen with longitudinal striations interpreted as defleshing modifications. Both elements belonged to rock doves (*C. livia*). It is possible the coracoid from unit X&XI originated from sediments belonging to Unit X. Unit VI also contained the remains of two rock doves with striations related to the disarticulation and defleshing of the carcasses (Spec. no. 10306; Figure 5.17; Spec. no. CN124). In unit VIII, a red-billed chough (*P. pyrrhocorax*) humerus (Spec. no. 1126) with four transverse striations indicating defleshing practices was found alongside a rock dove humerus with a striation at the distal end, indicating disarticulation of the wing from the more nourishing breast.

Each of the four bones from Unit X (Phase D) represented a different species. A rock dove carpometacarpal (Spec. no. 2313) had a longitudinal cut mark on the proximal end, which likely occurred during disarticulation of the lower wing from the ulna. Two tarsometatarsals displayed further evidence of exploitation. While a red-legged partridge (*Alectoris rufa*) element (Spec. no. 1586) displayed a cut mark at the distal articulation, the same element of a wigeon (*Mareca penelope;* Spec. no. 2344) showed two transverse cutmarks that relate to skinning or defleshing activities. The proximal coracoid of a shag (*P. aristotelis*) (Spec. no. 1576) presented a series of transverse cuts distal to the *cotyla scapularis,* which likely resulted from an effort to separate the coracoid from the scapula and humerus.

Units VII and V (both Phase D) each contained five specimens with striations produced through human butchery practices. Rock dove elements from both units suggested disarticulation and defleshing practices (Spec. no. 8018, 10018, CN92, 10130, CN177, 10137). A complete ulna in Unit V (Spec. no. 8018; Figure 5.19) had two transverse striations modifications congruent with cuts made to disarticulate the ulna from the carpometacarpal. Disarticulation was also evident in the modifications of a red-legged partridge humerus (*A. rufa*, Spec. no. CN07; Figure 5.20) and a carrion crow ulna (*C. corone*, Spec. no. 8017) from the same context. The red-legged partridge is also present in Unit VII in the form of a femur bearing oblique cut marks to the distal portion of the element (Spec.

no. 1586), while corvids are represented in this unit by the Eurasian jay (*G. glandarius,* Spec. no. CN176). The modifications on these elements were made during disarticulation of the hind limb and wing, respectively.

In Phase F, a single rock dove (*C. livia*) femur from Unit III displayed a series of five oblique cutmarks to the shaft (Spec. no. 10041; Figure 5.21). The marks were shallow and recurrent in orientation, signalling defleshing activities. A set of marks on a scapula from the same indicate defleshing of the carcass for consumption.

Figure 5.15: CN3055. The distal tibiotarsus of a rock dove (C. livia) displaying a pair of longitudinal cutmarks (see arrow) on the articular surface (Phase C). Scale = 1mm.

Figure 5.16: CN2075. The right humerus of a rock dove (C.livia) displaying longitudinal cutmarks related to defleshing activities. This is the only specimen from unit IX (Phase D) with striations. The mark is partially obscured by the use of a permanent marker on the bone surface. Scale = 1mm.

Figure 5.17: 10306. The left coracoid of a rock dove (C. livia) from Unit VI (Phase D) with an oblique striation to the ventral shaft of the coracoid. The cut mark is partially obscured by manganese oxide deposits on the bone surface (see arrow). Scale = 1mm.

Figure 5.18: CN1576. The proximal coracoid of a shag (P. aristotelis) from Unit X (Phase D) displaying cutmarks congruent with the disarticulation of the scapular girdle. Scale = 1mm.

Figure 5.19: 8018. A complete right ulna of a rock dove (C. livia) from Unit V (Phase D) with transverse cutmarks to the distal end.Scale = 1mm.

Figure 5.20: CN97. Multiple cutmarks on the distal humerus of a red-legged partridge (A. rufa) from unit V (Phase D). Scale = 1mm.

Figure 5.21: Rock dove femur from Unit III (Phase F), showing a series of shallow cutmarks to the shaft.

5.6.4.2 Peeling

Only three specimens showed evidence of peeling (Table 5.29). Two originated in Unit XIII, and one came from Unit VII in the middle of the sequence. Two specimens (Spec. no. 10134 and CN3179) also exhibited cutmarks congruent with disarticulation practices (see: Striations), supporting the human agency behind these peeling modifications.

Table 5.29: Specimens displaying traces of peeling.

Coll. No.	**Sector**	**Phase**	**Unit**	**Taxon**	**Common name**	**Element**	**Location**
10134	C	D	VII	*Alectoris rufa*	red-legged partridge	femur	5
10275	C	B	XIII	*Columba livia*	rock dove	femur	5
CN3179	C	B	XIII	*Columba livia*	rock dove	coracoid	areas

5.6.4.3 Thermal modifications

Thermal modifications appeared on specimens from all examined units except unit X&XI (Figure 5.22). Level 1 (speckled) and level 4 (grey) modifications were most frequent in the sequence, indicating indirect and direct heat exposure of the bone surface, respectively (Fernández-Jalvo and Andrews 2016). Level 5 modification (calcination) was present at low frequencies in units VI and VIII. Level 1 exposure may result from incidental burning from naturally occurring fire sources. Still, the presence of other degrees of char on specimens of the same species in the same contexts seems to indicate an intentional exposure of multiple carcasses to a heat source (Table 5.30).

The presence of entirely charred bone elements (Figure 5.23) implies exposure to fire after removing flesh from the bones (Fernandez-Javlo and Andrews 2016). Their survival also indicates that they were not much disturbed after deposition, as trampled burnt bone quickly disintegrates (Lev *et al.* 2020). This supports the interpretation of occupation events at Cova Negra being of short, sporadic nature (Villaverde *et al.* 2014).

Table 5.30 Frequency of thermal modification by species.

		Degree of thermal modification						
Taxon	**Common name**	**1**	**2**	**3**	**4**	**5**	**Total**	**%total NISP**
Alectoris rufa	red-legged partridge	3	0	0	5	1	9	8.6
Mareca penelope	garganey	0	0	0	2	0	2	40.0
Anas platyrhynchos	mallard	0	0	0	1	0	1	5.3
Anas crecca	teal	1	0	0	1	0	2	66.7
Columba livia	rock dove	24	1	1	19	1	46	11.2
Streptopelia turtur	turtle dove	1	0	0	3	0	5	55.5
Streptopelia sp.	dove	0	0	0	1	0	1	100.0
Pyrrhocorax pyrrhocorax	red-billed chough	6	0	0	0	0	6	28.6
Pyrrhocorax graculus	alpine chough	8	1	0	4	0	13	16.5
Pyrrhocorax sp.	chough	0	0	0	1	0	1	10.0
Turdus viscivorus	mistle thrush	1	0	0	0	0	1	11.1
Aves sp.	bird	2	0	0	1	0	3	21.4
Total		**46**	**2**	**1**	**38**	**2**	**90**	

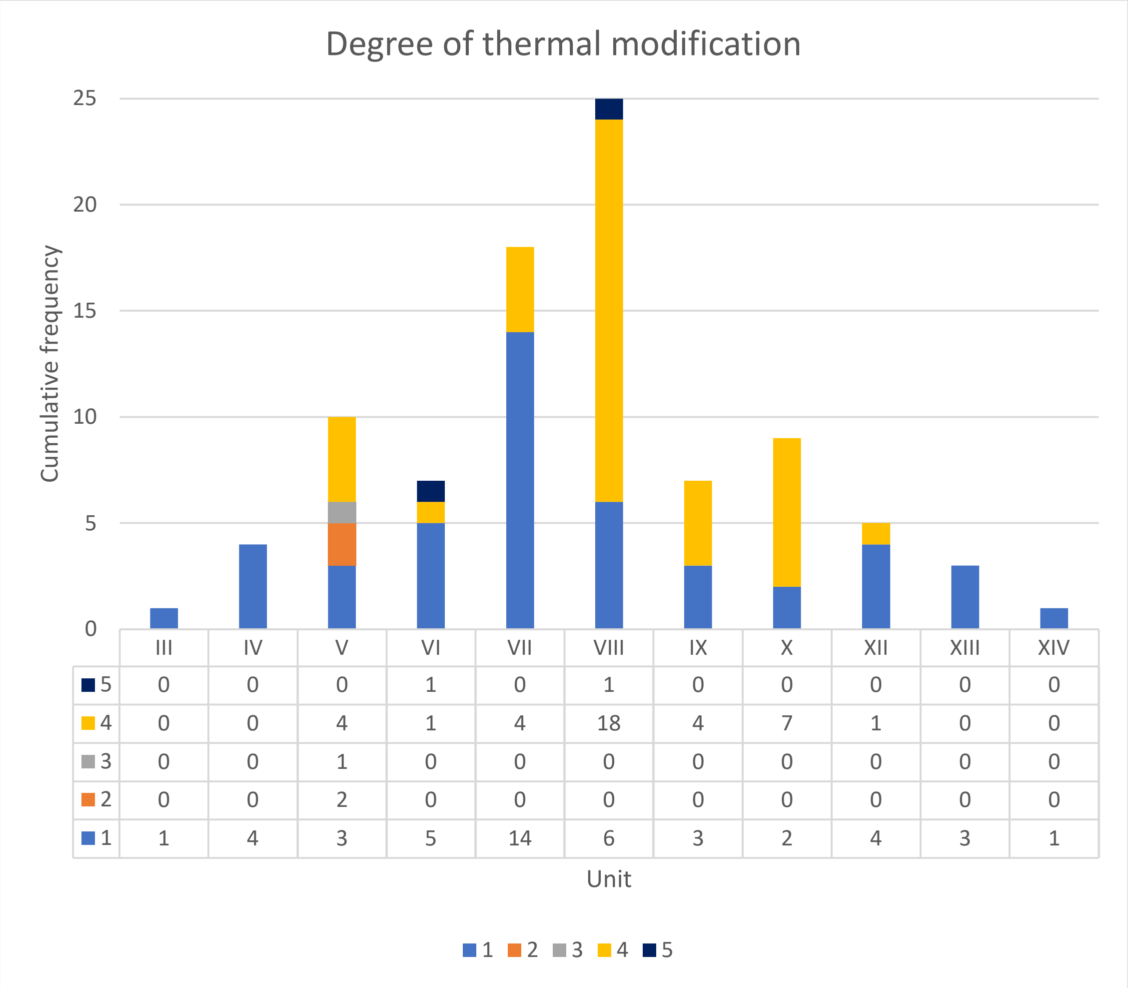


Figure 5.22: Bar chart illustrating the degree of thermal modification on specimens by the stratigraphic unit.

Figure 5.23: 8021. A rock dove (C. livia) tarsometatarsus with Level 4 thermal modifications, indicating exposure to a heat source after removing any flesh from the bone. Scale = 1mm.

5.6.5 Fragmentation

Peri- and post-excavation damage limited the analysis of the fragmentation patterns in the Cova Negra avifauna. Specimens presenting with recent fractures and flaking of fracture surfaces that obscured the original fractures were not considered in this section.

362 specimens (47.1%) exhibited fractures that were old (made on green bone, or dry bone close to the time of deposition) or mixed (partially obscured by recent post-depositional fractures but broken initially close to the time of deposition) in character (Table 5.31). Those with mixed character contributed to an understanding of the original frequency of fractured specimens but were not reliable in the interpretation of fracture patterns. Of the 303 specimens with fractures of old character, 132 displayed a spiral outline, and 74 were transverse. Transverse fractures were made on dry bone and result from trampling activities.

Table 5.31: Fractures of 'mixed' and 'old' character by unit and outline.

		Fracture outline						
Unit	**Fracture type**	**Spiral**	**Transverse**	**Mix**	**Irregular**	**Longitudinal**	**Obscured**	**Total**
III	*old*	3	1	0	2	0	0	**6**
	mix	0	0	0	0	0	0	**0**
IV	*old*	7	0	0	0	0	0	**7**
	mix	2	0	0	1	0	0	**3**
V	*old*	5	4	0	2	0	0	**11**
	mix	1	0	2	1	0	0	**4**
VI	*old*	5	4	0	0	0	0	**9**
	mix	0	0	1	0	0	0	**1**
VII	*old*	13	5	2	5	0	0	**25**
	mix	0	0	0	0	0	0	**0**
VIII	*old*	29	22	1	24	0	0	**76**
	mix	2	0	5	4	1	0	**12**
IX	*old*	22	18	2	17	1	0	**60**
	mix	7	0	7	5	0	0	**19**
X	*old*	20	9	1	15	0	0	**45**
	mix	2	0	6	4	0	0	**12**
X & XI	*old*	0	0	0	0	0	0	**0**
	mix	0	0	0	0	0	0	**0**
XII	*old*	11	7	0	19	0	0	**37**
	mix	0	0	3	0	0	0	**3**
XIII	*old*	15	4	0	5	0	1	**25**
	mix	2	0	3	0	0	0	**5**
XIV	*old*	2	0	0	0	0	0	**2**
	mix	0	0	0	0	0	0	**0**
Total	*old*	132	74	6	89	1	1	**362**
	mix	16	0	27	15	1	0	

A total of 72.7 % (n = 96) of the spiral fractures showed an oblique fracture angle. Still, only 33.3% (n=44) also exhibited the smooth fracture surface resulting from the twisting motion used when a carcass is disarticulated by hand (Laroulandie and Lefevre 2014). Other fractures of spiral and oblique character displayed roughened surfaces indicative of dry bone fracture (Fernandez-Javlo and Andrews 2016). Others were rounded by digestive acids, which could indicate scavenging of bones discarded after human consumption (ibid 2016).

5.7 Interpretation of the avifauna from Sector C at Cova Negra

In this section, I discuss the results of my taphonomic and ecological analyses of Cova Negra Sector C. First, I discuss the implications of Neanderthal bird exploitation at Cova Negra, then I will discuss the evidence of other species contributing to the accumulation. Finally, I evaluate the climate and environmental results in relation to other proxies from earlier studies.

5.7.1 Neanderthal exploitation of birds at Cova Negra

The identification of several striations on the surfaces of a total of 26 bird bones from a collection of 768 specimens from Sector C of Cova Negra, as well as other bones exhibiting thermal damage (n = 90), is evidence of the human exploitation of birds, presumably for food, at this cave during the Middle Pleistocene.

The appearance of cutmarks and scrapes was congruent with the practice of disarticulation and defleshing of carcasses for consumption. This has been reported at several Middle Palaeolithic sites elsewhere in Europe (Blasco and Peris 2009, 2012 – Bolomor Cave, Spain; Peresani *et al.* 2011 and Fiore *et al.* 2016 – Fumane Cave, Italy; Finlayson *et al.* 2012 and Blasco *et al.* 2014, 2016 – Gorham's Cave, Gibraltar). Many of the same bird species consumed at these sites were also found at Cova Negra with these modifications, including rock dove (*C. livia*, n = 17), corvids (*P. pyrrhocorax*, n = 2*; G. glandarius*, n = 1; *C. corone*, n = 1), game birds (*A. rufa*, n = 3), and ducks (*M. penelope*, n = 1).

It is clear that the consumption of birds occurred during multiple occupation episodes because the 26 human-modified bones and thermal damage appeared across several stratigraphic units in the deposit. Most of the avian remains bearing human modifications (n = 20/26) were found within the six stratigraphic units of climate Phase D. Each unit contained at least one modified bone. The remaining bones were recovered from climate phases B, C, and F (n= 1, n = 3, n = 2, respectively).

Of the eight specimens recovered from unit III (Phase F; ESR 206 +/- 21 ka BP; 193 +/- 19 ka BP; Richards *et al.* 2019), cut marks were found on a red-billed chough (*P. pyrrhocorax*) and a rock dove (*C. livia*), and a further single specimen showed traces of thermal modification. Martinez-Valle *et al.* (2016) investigated the avian remains from IIIb, identifying 249 bones, 75 of which bore cutmarks. However, these remains originated in the south-western sector of the cave. Occupations in the more recent Cova Negra units were concentrated in this area (Villaverde *et al.* 2009). One possible explanation is that section C was outside the main area used for processing bird carcasses by the time unit III was deposited. Underlying Phase E (unit VI) contained no bones with cutmarks. However, thermal modifications on bones from this phase were a strong indicator of human agency.

Phase D, consisting of several climatic oscillations during a period of overall cooler climatic conditions, had a collective NTAXA of 26. It contained all but two of the species present at the site. Seven of these species exhibited cutmarks and scrapes, and 59 specimens were modified by fire. The discovery of a modified shag (*P. aristotelis*) bone in Unit X was the most unusual specimen from this phase. Cut marks on the specimen congruent with the dislocation of the coracoid from the scapular girdle confirmed human agency. Unlike its relative the great cormorant (*P. carbo*), the shag does not venture inland. It is a marine species that nests on coastal cliffs, feeding on fish. The presence of this species at Cova Negra infers that the bird was transported to the cave from the Mediterranean coast, which is currently c. 30 km to the east. During the Middle Palaeolithic, lower sea levels meant that the coast was even further away (Moreno *et al.* 2005). This expands the Neanderthal's catchment area and indicates that they possessed intricate knowledge of marine resources, which we see at sites in southern Iberia (Stringer *et al.* 2008; Fa *et al.* 2016; Cortés-Sánchez *et al.* 2019; Zilhao *et al.* 2020). This concentration of human agency within Phase D is evidence of continuous avian exploitation by Neanderthals throughout the minor oscillations of this cold phase.

Thermal modifications were present in all but one unit (X&XI) and were found on 6.2 % of the bones within these units (n = 90). Evidence for fireplaces in the cave came from Villaverde *et al.* (1996), who noted temporally discrete, simple hearths in several locations across the south-western sectors. He inferred that a similar pattern of hearths could be drawn from the results of earlier investigations elsewhere the cave. The survival of many bird specimens with thermal modifications of Level 4 and above (n = 40) fit well with Cova Negra's interpretation as a sporadically inhabited site because burned microfaunal remains are brittle and disintegrate after a moderate amount of trample (Lev *et al.* 2020).

Other than the unidentified fragments, all of the 90 specimens exposed to thermal sources were known edible species (Cott 1947; Finlayson 2019). A total of 52 were pigeons/doves, and a further 34 were game birds, ducks and choughs (Table 5.30). Three species of duck showed thermal modifications (*A. crecca, A. platyrhynchos, M. penelope*). Thermal exposure by human agency was reinforced in the case of the wigeon, which also bore cutmarks. Although mallards could have conceivably inhabited the river flowing close to the cave, the Wigeon and Teal prefer open wetlands and coastal areas and would have wintered in the area (Birdlife International 2021; Burns 1987). While these species were more likely harvested from the closest large water body, Lake Bellus, which is 5 km to the south of Cova Negra, it is also possible they were brought from the more distant coast, which is 30 km away. The garganey (*S. querquedula*) displayed no signs of human agency but would also have been introduced to the site from an open wetland area (Birdlife International 2012). The garganey is also migratory and would only appear in the area briefly on passage to and from wintering grounds in tropical Africa (Finlayson 2011; Cramp *et al*. 1977-1994). Interestingly, ducks were only present in the lower part of the sequence (units XIII-VIII). This may indicate a change in foraging strategies at Cova Negra from Unit VII onward, or it may indicate the drainage of a local waterbody as the climate slowly became more arid during Phase D (Fumanal 1986).

Sustained exploitation of avian resources throughout the several climatic oscillations recorded in the sediments at Cova Negra, as evidenced by butchery and cooking modifications, showed that the Neanderthals who used the site considered birds a regular part of their diet. The regularity of bird exploitation was highlighted by the fact that these occupations were sporadic and of short duration (Villaverde *et al.* 1996). This suggests that birds exploitation did not only happen at base camps where supplies were plentiful, and energy could therefore readily be expended on low-calorie yield resources such as birds and small game. Bird exploitation has been identified at nearby Bolomor Cave in MIS 6. The earliest bird exploitation in unit XIII of Cova Negra was in MIS 8, but the earliest bird exploitation in Iberia dates to MIS 9 at Gran Dolina, Atapuerca (Blasco *et al.* 2013).

5.7.2 Other agents contributing to the avian faunal accumulation

Previous investigations determined that carnivores denning at Cova Negra in between human occupation episodes contributed to the accumulation of mammalian remains (Villaverde *et al.* 1996). However, large predators capable of taking down horse, deer and aurochs (e.g. wolf, bear, cave lion, hyaena, leopard) were not reflected in modifications on the avian remains investigated in this thesis. This was mainly because larger predators tend to consume the entire bird carcass, completely digesting the bone (Andrews 1990).

Toothmarks comparable to small and medium-sized carnivores were present on avian remains from all 12 units at Cova Negra. Guillem (1995, 2009) identified red fox (*V. vulpes*) and beech marten (*Martes fiona*) as accumulators of small mammals in the cave. Traces found on avian remains were also congruent with predators of this size range. However, no mustelid remains have been recorded at the site (Guillem 2009). Lynx (*L. lynx*) and wild cat (*F. silvestris*) were both identified in Sector C by Perez Ripoll (1977), the only carnivores he observed in that sector, except for the spotted hyaena in units XII-XIV. Rodents, though not a primary agent in the accumulation, also frequented the cave. Bird remains in units XIII, XII, VII, and V bore marks congruent with rodent tooth marks.

Rodents featured in the prey spectrum of both nocturnal and diurnal birds of prey. Finlayson (2019) suggested that small falcons adapt to become commensal with humans in cave sites, preying on rodents that were attracted to human middens. Small falcon remains were present in units X, VIII, and IV, all of which produced some evidence of human occupation. However, because these occupations were irregular in nature (Villaverde *et al*. 2014), it is uncertain whether the falcon population at Cova Negra engaged in such a commensal relationship with humans. Nevertheless, leftover scraps from carnivores denning within the cave would have attracted rodents that the falcons would prey upon (Larson *et al*., 2004). The sparrow hawk (*A. nisus*), usually a forest forager (Finlayson 2011; Birdlife Data Zone, 2020), was present in units XIII and XII and likely contributed to the avian accumulation in those units.

Beak modifications present on bird remains in all units except units V and XIV indicated that birds of prey regularly introduced prey to the cave despite the scarcity of direct skeletal evidence. Digestion traces were generally light, which was indicative of birds of prey and small carnivores as the agents (Serjeantson 2009; Fernandez-Javlo and Andrews 2016). 73% of bones showing beak modifications also exhibited digestion traces (Figure 5.24). This was typical of nocturnal birds of prey. Owl remains in VIII and X were likely to represent nesting and roosting birds in periods between human occupations.

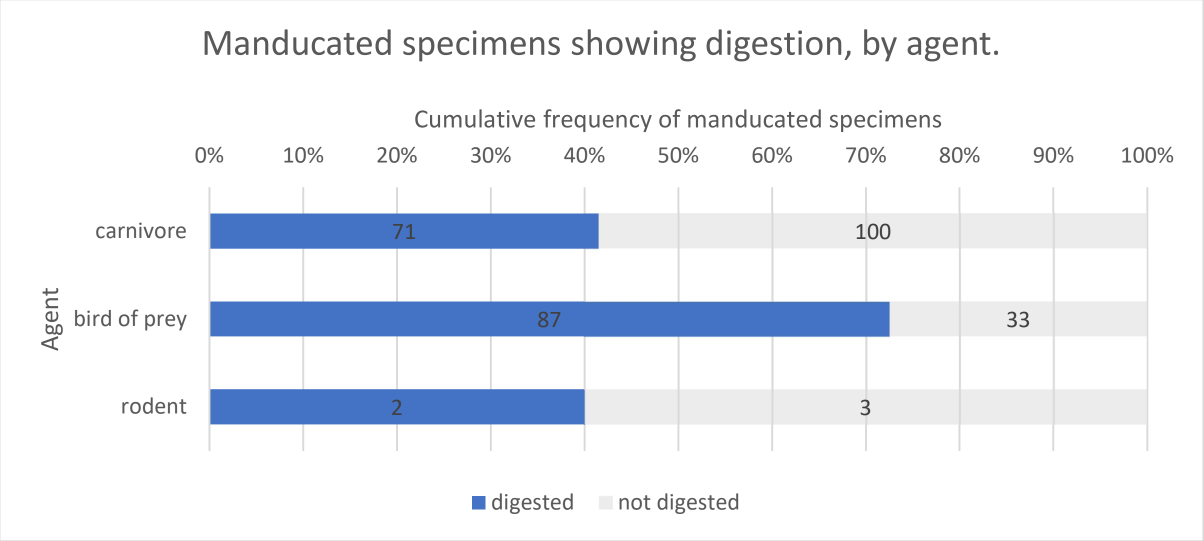


Figure 5.24: Bar chart showing the proportion of digested and not digested elements that also bear manducation modifications

5.7.3 Ecological interpretations

Several studies have aimed to describe the environment and climate conditions at Cova Negra during the Middle Pleistocene. These results were based on the analyses of macromammals, micromammals and sediments (Table 5.1; Fumanal 1986; Eastham 1989; Villaverde *et al*. 1996; Guillem 2009). In this section, I discuss whether the bird results of Cova Negra support or reject these conclusions.

The ecological variables represented by bird species reflected a population generally suited to the latitude in which the site lies (ca. 40°N; Table 5.16; Table 5.15). There was a tendency towards species that prefer warm and humid conditions, with few exceptions; boreal duck species appeared in four units (X&XI-VIII). Their presence corresponded to a cool climatic phase (Phase D). While local conditions in Iberia, close to the Mediterranean, may not have changed drastically, the ice sheets to the north extended in this phase, displacing boreal and arctic species further south (Eynaud *et al.* 2009; Finlayson 2011). The garganey is a temperate duck that also appeared in the sequence in unit VIII. The woodcock, another migratory temperate species that migrates south in the winter, was present in unit VI, one of the warmer oscillations within the generally cool Phase D.

The alpine chough, a native of higher altitudes in the present day, was the most specialist species present in the sequence, appearing in nine stratigraphic units. Tolerance categories B-E are present in almost all units throughout the sequence. The absence of category A (specialist) species was conspicuous and contributed to the highly significant chi-squared results, along with the higher-than-expected observed frequencies of generalist species (p

= <0.001). It is worth noting that very few non-corvid passerine species featured in the sequence (n= 17). This may be due to differential preservation of small, fragile bones or a collector's bias towards larger specimens due to methods employed during excavation (Discamps and Faivre 2017). In any case, the absence of species with specialist bioclimatic tolerances should not be interpreted as an absence of them in the ecosystem.

Temperature and humidity tolerance frequencies reflected temperate to warm conditions with moderate to high humidity levels (Table 5.17; Table 5.18;

Table *5.19*; Table 5.20). This is consistent with the geographical position of the site but reflected a significant difference from the expected values for current distributions in the Palearctic (p^{TEM} = <0.001, p^{HUM} = <0.001). Boreal and temperate duck species, along with the shag, raven, lesser kestrel, and wheatear, prefer drier conditions (Category B) and only appeared in the lower levels of the sequence (XIII-VIII, except XII). The gradual aridification during Phase D may have resulted in desiccation of water bodies leading to the ducks relocating or a change in the foraging habits of the local Neanderthals, such as using the cave in a different season. After Unit VIII, the mallard also disappeared, supporting that it inhabited the same environment as the other ducks, despite possessing different ecological traits. The appearance of the category E (hot) rufous-tailed rock thrush (*M. saxatilis*) in Unit VIII supported the interpretation of this sub-phase as a warm oscillation (Villaverde *et al.* 2014). This was the only occurrence of category E temperature tolerant species in the sequence.

The foraging and nesting habitats of bird species at Cova Negra reflected a mosaic type landscape with open plains and woodlands close to the cave. This was supported by the mammalian record, where forest and open foragers appeared in all units of the sequence. Varying frequencies of those species, foremostly equids and cervids, allowed Villaverde *et al.* (1996) to propose the expanse and retreat of forested areas in tune with overarching climatic phases. Avian remains reflected a presence of forest or mixed foragers in all 12 units, suggesting the continuous presence of at least some woodland areas. Wetland habitats were no longer represented after VIII with the disappearance of ducks; however, the beaver was present in IIIb, indicating the persistence of gallery forest formations along the riverbank. Rocky habitats on the cliffs around the cave were widely used for nesting but were extensive enough to also function as foraging habitats for rock thrushes (*M. solitaris, M. saxatilis*). The Albaida river provided wetland species with a habitat closer to the cave. While the woodcock may have frequented the wooded areas along the riverbank, ducks more likely represent species brought from open water further afar.

5.7.4 Summary

- Neanderthal bird exploitation is documented at Cova Negra by 26 bones with cutmarks and 90 bones with a variety of thermal modifications from units dating between MIS 5-8 (ESR; Richard *et al*. 2019).
- The presence of bird exploitation at a site with sporadic, short occupation episodes (Villaverde 1984) indicates that bird consumption was not solely a supplemental subsistence to large game but a usual resource for a mobile population.
- Species such as ducks and the shag reflect the wide catchment area of the Neanderthal foragers who used the site, stretching as far as the Mediterranean Sea 30 km to the east.
- Middle Palaeolithic Cova Negra stood in a mosaic type landscape that provided diverse habitats for both foraging and nesting species. Ducks frequented wetlands nearby while pigeons and choughs nested in the rocky cliffs around the cave. Woodland species featured in the gallery forests sustained by the Albaida river flowing below the cave.
- The climate fluctuated through warmer and cooler phases but supported a range of warm-temperate species throughout the deposition of the sedimentary sequence. The presence of boreal and temperate species during cool phase D reflected the southern displacement of species by advancing ice sheets in the north (Eynaud *et al.* 2009).

6 Scladina Cave

This chapter presents the results of a taphonomic investigation of avian remains from Scladina Cave, Belgium. This site is located in northwest Europe, beyond the geographical scope of most current studies of Neanderthal bird exploitation, which are mainly focused on mid-latitude localities of Europe (Appendix 1). Studies of the avifaunas of two sites containing Middle Palaeolithic material have been conducted in the United Kingdom, but neither produced evidence of human exploitation (Currant and Eastham 2012; Stewart and Jacobi 2015). Scladina represents a new opportunity to explore Neanderthal behaviour in a different, northerly, environmental setting during the last ice age cycle. Scladina Cave is a well-known archaeological site that has been excavated continuously over the last half century, recording spatial information and sieving sediments in accord with modern methodologies (Otte *et al*. 1992; Otte *et al.* 1998; Bonjean *et al.* 2014; Toussaint and Bonjean *et al.* 2014). However, its avian collections have not been examined until now. The chapter begins with an overview of past fieldwork undertaken with a focus on the Middle Palaeolithic levels in the cave. I then provide a summary of the key taxonomic finds associated with these levels that have recently been classified by the head of the Scladina Avifauna Project Mr. Quentin Goefette. My individual contribution then follows with a detailed analysis of the taphonomy of the same assemblage.

6.1 Physical Setting

Scladina Cave (50°29′2″N, 5°1′32″E, 138 m.a.s.l) is situated on the western flank of a hilltop overlooking Ri de Pontine, a tributary of the river Meuse in Namur Province, Belgium (Figure 6.2; Bonjean *et al.* 2011). The cave formed within a Visean limestone massif and is located 30 m above the valley floor and 7 m from the hill summit, facing east. It comprises a cylindrical karst structure that is up to 40 m long, six metres high, and between six and 20 metres wide (Figure 6.3; Pirson *et al.* 2018; Lopez-Garcia *et al.* 2017). A small terrace extends in front of the cave. Recent speleological prospections indicated that the cave likely extends for a further 12 metres (Pirson *et al.* 2018). Towards the back an aven opens to the plateau above where a 60 m^2 sinkhole has formed (Bonjean *et al.* 2002). The cave joins up with Saint-Paul Cave and Sous-Saint-Paul Cave, two nearby karstic sites discovered in the 1950s (Bonjean *et al.* 2014).

Scladina is the most recently discovered of several Palaeolithic cave sites in the Meuse basin. The others, which were first excavated in the nineteenth century, include Spy (Fraipont and Lohest 1887; Semal *et al.* 2009; Naito *et al.* 2016; Pirson *et al.* 2018; Fernandez-Javlo and Andrews 2019), Trou de l'Abîme at Couvin (Toussaint *et al.* 2010; Pirson *et al.* 2009); Walou (Stewart and Parfitt 2011; Toussaint *et al.* 2017), Engis (Fraipont 1936; Tillier 1983), La Naulette (Leguebe and Toussaint 1988; Toussaint and Pirson 2006), Fonds de Forêt (Trinkaus and Ruff 1989), and Goyet (Hamy 1873; Toussaint 2006).

Figure 6.1: The geographical position of Scladina Cave, marked by a star.

Figure 6.2: Location of Scladina Cave in relation to the river Meuse. From Pirson et al. (2018).

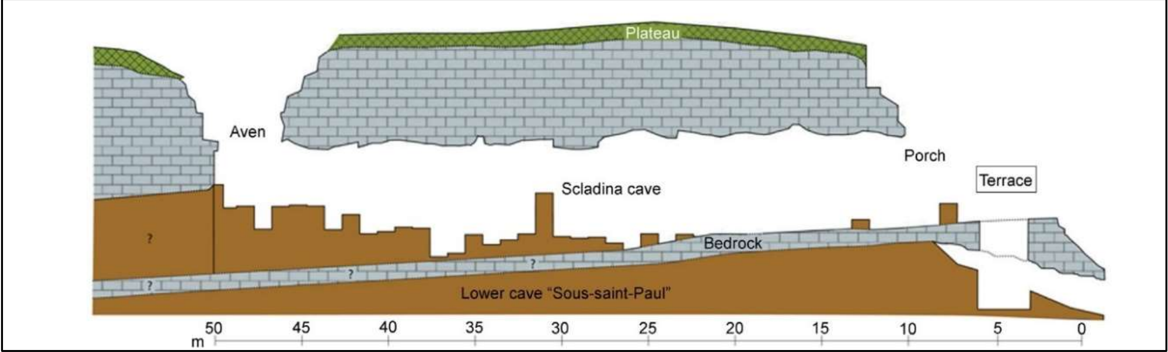


Figure 6.3: Layout of Scladina Cave showing the depth from the entrance and the position of the aven From Lopez-Garcia et al. (2017).

6.2 Archaeological Investigations

Scladina Cave was discovered in 1971 by local speleologists. They found Middle Palaeolithic artefacts in its upper sediments and reported them to Prof. Marcel Otte at the University of Liège (Otte *et al.* 1992; Otte *et al.* 1998; Pirson *et al.* 2018). Investigations of the cave have been ongoing since 1978. While other caves in the basin were excavated in the nineteenth century, the work at Scladina Cave has been undertaken using recent excavation methods, including modern sieving protocols and 3-D recording of artefacts (Otte *et al.* 1992; Otte *et al.* 1998; Bonjean *et al.* 2014). Current excavations are carried out by Archéologie Andennaise, a non-profit organization, in collaboration with the University of Liège.

6.2.1 Stratigraphy

Scladina Cave contains a complex 15 m deep sedimentary sequence that ranges in age from the late Middle Pleistocene to the Holocene according to a range of dating methods (Pirson *et al.* 2008). The sequence comprises 130 stratigraphic layers, which in turn have been grouped into 30 units (Pirson *et al.* 2018). A number of studies have been undertaken at the site including on the archaeology (Otte *et al.* 1998; Toussaint and Bonjean 2014); sedimentology (Gullentops and Deblaere 1992; Haesaerts *et al.* 2016; Benabdelhadi 1998; Ellwood *et al.* 2004; Pirson 2007), palynology (Bastin 1990, 1992); palaeontology (Cordy 1992; Simonet 1992; Lopez-Garcia *et al.* 2017), dating (synthesis in Bonjean 1998; Toussaint *et al.* 1998; Pirson 2007; Pirson *et al.* 2008, 2014), and others (Pirson *et al.* 2018)(Figure 6.4; Table 6.1; Table 6.2).

Table 6.1: Legend of material used to obtain dates in Figure 3 by font colour and type. After Pirson et al 2018.

		Font type		
Dating method	**font colour**	normal	*italic*	**bold**
^{14}C	**black**	bone	Calcite (in situ and reworked speleothems)	Teeth (accurately positioned in the stratigraphic system)
U/Th	**blue**	In situ speleothem	reworked speleothem	Neanderthal mandible (gamma spectrometry)
TL	**red**	sediment	in situ speleothem	Burnt flint (TL) Sediment (IRSL)
U/Th-ESR	**green**	bone	-	-

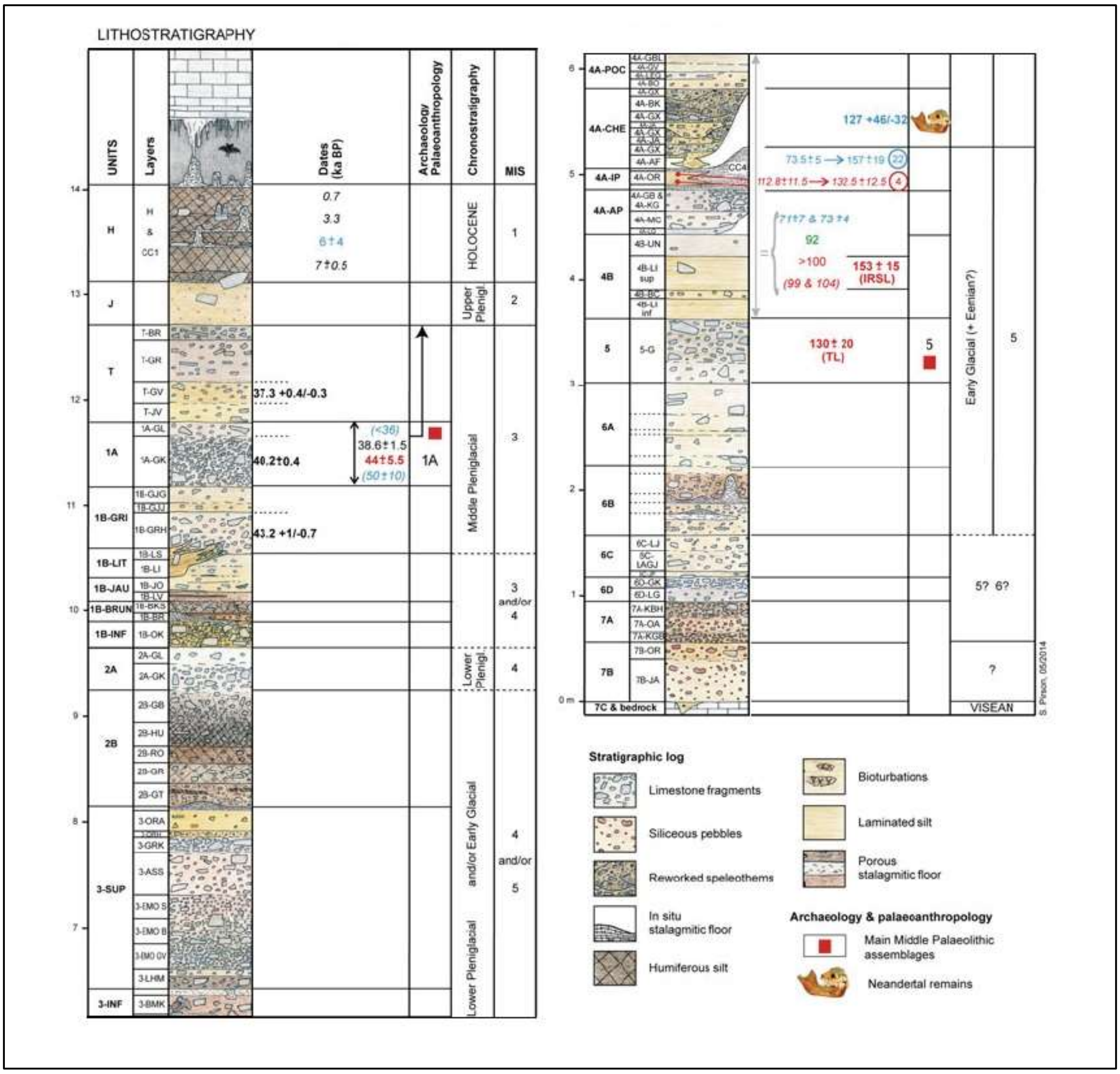


Figure 6.4: Stratigraphy of Scladina Cave adapted from Pirson et al 2018. See Table 2 for legend of the materials employed for each dating estimate. Circled numbers= number of dates for CC4 interval. Problematic dates in brackets.

Table 6.2: Stratigraphic context of the Scladina avifauna showing original 'Old' unit, present Unit, Layer, Environmental, Sedimentary, Palynological, Anthracological, faunal and Climatological information along with Chronostratigraphic information and correlation to marine isotopic stage (MIS). After Bonjean et al 2014; Pirson et al 2018. Additional references within table. The main assemblages are highlighted in blue.

Old unit	**Unit**	**Layer** (Pirson 2007)	**Environment**	**Sedimentary**	**Palynology**	**Charcoal**	**Micromammal**	**Large mammal**	**Magnetic susceptibility** (Elwood *et al.* 2004)	**MIS**	**Chronostratigraphy**
	H			Reworked palaeosol Pirson et al 2008), 10 generations of staligmatic floors; numerous badger burrows (Pirson 2007)	Interglacial signatures in speleotherms (CC1) (Bastin 1992)					1	Holocene
	J									2	Upper Pleniglacial
38	T	T-BR/T-GR	Cold steppe								
39		T-GV									
40	**1A**	1A-GL	Cold steppe (climatic improvement)	Deep frost episode and carbonate cementation at top of Layer 1A (Pirson 2007)	High herb count, hardy climate, open steppe landscape (Pirson *et al.* 2008)		Cold conditions and a and drier climate than at present (Lopez-Garcia *et al.* 2017)	196 burned bones. No other human agency (Abrams *et al.* 2010)		3	Middle Pleniglacial
1A		1A-GK									
1B	1B-GRI	1B-GJG		In situ palaeosol at top of layer (Haesaerts 1992).							
	1B-GRI	1B-GRH									
	1B-BRUN	1B-BKS		Reworked palaeosol (Pirson 2007)	Relatively high amounts of trees, dominated by boreal taxa. Maximum pollen count in sequence. (Pirson et al 2008)						
	1B	1B-INF		Deep frost episode separates from above (Pirson 2007).							
2	2A		Cold and dry	New loess input: cryoturbation (Pirson *et al.* 2008)	High herb count steppe taxa; very dry and cold (Pirson et al 2008)		Poor and polluted (Cordy 1992; Pirson 2007)	Studied together with remains from former Layer 2B	Cold and dry	4	Lower Pleniglacial
	2B		Interastadial (climatic improvement)	Reworked humic palaeosol (Pirson 2007).	High *Picea* and *Pinus*, high values of ferns. humid boreal environment (Bastin 1992; Pirson et al 2008)	Numerous fragments, local coniferous trees	Dominance of temperate taxa from open field (Cordy 1992)				Lower Pleniglacial and/or Early glacial

Old unit	**Unit**	**Layer** (Pirson 2007)	**Environment**	**Sedimentary**	**Palynology**	**Charcoal**	**Micromammal**	**Large mammal**	**Magnetic susceptibility** (Elwood *et al.* 2004)	**MIS**	**Chronostratigraphy**
3	3-SUP	3-ORA	Climatic improvement	Reworked palaeosol topped by a staligmatic floor (Pirson 2007)	Low pollen count, forest steppe Pirson et al 2008)					4 and/or 5	
		3 - ORH 3-GRK	Cooling	Thick, platy structure and small cryoturbations (Pirson 2007).	*Pinus*, *Juniperus*, *Betula*; steppic environment with some boreal trees. (Bastin 1992; Pirson et al 2008)						
		3-ASS 3-EMO	No signature	Torrential flow and run off			Mixture of taxa: temperate forest and colder milieus (Cordy 1992)	Mixture of taxa: temperate forest and colder milieus (Simonet 1992)	Irregular, but suggests cooling		
	3-INF			Reworked palaeosol (Pirson 2007)	Open steppe (Pirson *et al.* 2008)						
4A	4A-POC		Boreal forest-steppe		Boreal, steppic herbs, large amount of pinus, scattered pollen of malacophyll trees, mainly Betula. Monolete spores of fern suggest local humidity. Court-Picon & Damblon in Pirosn 2007; Pirson *et al.* 2008.		60% temperate forest taxa, return of chiroptera and insectivores, disappearance of arctic taxa. Cordy 1992.	75% forest taxa (50% Dama dama) Simonet 1992. Assigned to 4A as investigations from 1991-2003 showed 4B to be extremely poor in faunal remains	Climatic improvement		
	4A-CHE			Gulley, possibly a melting channel (Pirson 2014)		*Pinus*, but maybe intrusive. Pirson *et al.* 2008.			Climatic improvement		
	4A-IP		Boreal to temperate forest	Interface with 4A-CHE: thick platy structure (4-6 mm) indicative of a deep frost episode (Pirson 2007).					Climatic improvement	5	Early glacial (+Eemian?)
	4A-IP	CC4	Transition from temperate to boreal	Stalagmitic floor	Malacophyll trees; ulmus quercus, faxinus and Carpinus coexisiting with Pinus and Picea. Monolete fern spores linked to a rise of humidity. Decrease of temperate taxa (Court-Picon & Damblon in Pirson 2007; Pirson *et al.* 2008)				Climatic improvement		
	4A-IP	4A-OR	Forest steppe, or even cold, steppic conditions in palynology, but charcoal temperate.	Interface with 4A-CHE: thick platy structure (4-6 mm) indicative of a deep frost episode (Pirson 2007).	25-30% tree pollen pinus juniperus betula. Almost no temperate taxa. (Court-Picon & Damblon in Pirosn 2007; Pirson *et al.* 2008).	*Quercus*, *fraxinus*, *malaceae* in good agreement with CC4. Pirson *et al.* 2008			Climatic improvement		

Old unit	Unit	Layer (Pirson 2007)	Environment	Sedimentary	Palynology	Charcoal	Micromammal	Large mammal	Magnetic susceptibility (Elwood *et al.* 2004)	MIS	Chronostratigraphy
	4A-AP	4A-KG	Boreal to temperate forest		Juniperus and Pinus (65%), macrophyll temperate taxa appear (quercus and ulmus) (Court-Picon & Damblon in Pirosn 2007; Pirson *et al.* 2008.)	*Quercus, Populus, Prunus*; along with palynological data can point to warming towards climatic improvement in 4A-IP. Pirson *et al.* 2008.			Climatic improvement		
4B	4B		Arid, open, cold steppe	Run-off and settling	Open steppe. Mainly Pinus and Juniperus. Rise in conifers towards 4A. (Court-Picon & Damblon in Pirson 2007; Pirson *et al.* 2008, Bastin 1992.)		Cold steppe taxa, disappearance of arctic taxa, forest taxa, insectivores and bats. Strong return of collared lemming (Cordy 1992)		Climatic improvement?		
5	**5-G**		Cold, steppe, open landscape	Solifluction; Clear periglacial climatic signature. Upper part of cryosol starting in Unit 6A. Indicates deep frost (Pirson 2014).	Top half of 5 yields steppe taxa. Many herbs. Cold steppe environment. bottom yields mesophilous trees. (Pirson *et al.* 2008)	Partially boreal environment. *Pinus, Juniperus, Betula*. Low levels of *Quercus*. Cold, steppic, open landscape. (Court-Picon & Damblon in Pirosn 2007; Pirson *et al.* 2008)	Return of arctic species, persistence of forest taxa (Cordy 1992) Cold, dry environment and climate. (Lopez-Garcia *et al.* 2014)	3625 burned bones, six chamois, bears make up 65.8% of NISP, cutmarks on large and small game Daujeard *et al.* (2016)	Cooling		
6	6A		Temperate	Thick platy structure on top	High *Picea* and *Tilia* values and small amounts o *Quercus* and *Carpinus* (Bastin 1992)		Temperate forest taxa, presence of chiroptera (Cordy 1992)	75% forest taxa			
	6B		Forest steppe	Three stalagmitic floors	Dominance of conifers. (Pirson 2007)						

6.2.2 Palynology and Charcoal

Pollen from the sediments of Scladina Cave was first studied in the 1980s (Schneider in Otte *et al.* 1983, Bastin & Schneider 1984; Schneider 1986a, 1986b; Bastin 1990,1992), and again in the mid-2000s (Pirson 2007; Pirson *et al.* 2008). A total of 98 plant taxa, including 21 species of trees and shrubs and 56 species of herbs, forbs, and ferns, have been identified (Pirson *et al.* 2008). In general, the sequence describes transitions between open steppe vegetation and temperate boreal forest. In Layer 1A (MIS 3) a high count of herbs reflects an open steppe landscape and a harsh climatic period (Pirson *et al.* ibid.). Cold, steppe environments were prevalent throughout MIS 5 (Layers 3, 4, 5), but with fluctuating presences of boreal pollen, including malacophyll (soft leaf) species, which pointed towards high humidity (Bastin 1990, 1992; Pirson 2007; Pirson *et al.* 2008, 2014). Anthracological studies of charcoal from layers 2B to 4A are coherent with the palynological data (Pirson *et al.* 2008, 2014).

6.2.3 Human remains

The remains of a juvenile Neanderthal were found in Unit 4A between 1993 and 2006. These included a right hemi-mandible, and 18 teeth and skull fragments. They were not in primary context and likely date to MIS 5a or MIS 5b (Rasmussen *et al.* 2014; Pirson *et al.* 2014). Dental maturation (Toussaint *et al.* 2014) and histological studies (Smith *et al.* 2014) point towards an age of eight years old at the time of death of the individual. The morphology of the skull fragments seem to suggest the child is female, but this is not confirmed (Toussaint *et al*. 2014). Isotope studies conducted on the child's remains have provided insights into Neanderthal diet (Bocherens *et al.* 1997, 1999a, b; Bocherens 2014, El Zaatari *et al.* 2014) and ancient DNA analysis has shed light on its genetic diversity (Orlando *et al.* 2005, Orlando and Hänni 2014).

6.2.4 Fauna

Tens of thousands of faunal remains were recovered throughout the sequence at Scladina Cave (Patou-Mathis 1998; Dauejard *et al*. 2016; Pirson *et al*. 2018). Table 6.3 shows the NISP and ratios of faunal remains from Unit 1A and Unit 5, the two main faunal assemblages of the cave. Unit 1A is dominated by carnivores (n = 5,276 or 77% of the total assemblage; Figure 6.5) including cave bear and hyena, while the main herbivores present included horse, bovids and woolly rhinoceros. Human agency in this unit is less apparent. Out of almost 35,000 remains, only 196 showed traces of thermal modification from use as a source of fuel (Abrams *et al.* 2010). No other clear anthropogenic modifications were identified in the assemblage (Bonjean *et al*. 2014). In Unit 5, human agency is well-documented through the presence of cutmarks and thermal modifications on 3,625 bone surfaces (Bonjean *et al.* 2014; Daujeard *et al.* 2016). At least six entire chamois were brought into the cave and processed in order to obtain skins, meat, tendons and marrow (Patou-Mathis 1998). Few specimens show marks produced by scavenging canids (Patou-Mathis ibid). Eighteen butchery marks on the coxal bone of a hare (Bonjean *et al.* 2011) also points towards small game exploitation.

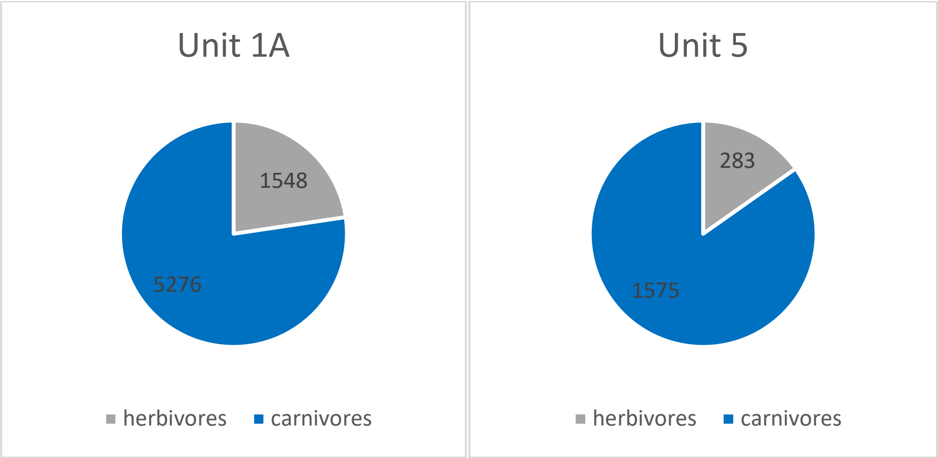


Figure 6.5: Pie charts illustrating the proportion of carnivore to herbivore remains in Unit 1A and Unit 5.

Table 6.3: Macromammal species identified in Units 1A and 5. After Patou-Mathis 1998 and Daujeard et al. 2016. Taxonomic identifications are as reported by the principle investigators. indet = indeterminate.

Taxon	**Common name**	**NISP 1A**	**%NISP 1A**	**NISP 5**	**%NISP 5**
Cervus elaphus	red deer	73	1.1	27	1.4
Dama dama	fallow deer	0	0	16	0.9
Rangifer tarandus	reindeer	41	0.6	11	0.6
Capreolus capreolus	roe deer	3	0	4	0.2
Megaloceros giganteus	Irish elk	14	0.2	0	0
Cervid indet	deer, indet.	69	1	11	0.6
Rupicapra rupicapra	chamois	19	0.3	138	7.4
Capra ibex	ibex	0	0	7	0.4
Sus scrofa	wild boar	0	0	6	0.3
Bison priscus/Bos primigenius	steppe bison/aurochs	302	4.4	0	0
Equus hydruntinus	wild ass	42	0.6	0	0
Equus (caballus)	horse	546	7.9	16	0.9
Coelodonta antiquitatis	woolly rhinoceros	170	2.5	31	1.7
Mammuthus primigenius	woolly mammoth	35	0.5	16	0.9
Ungulate indet.	herbivore, indet.	234	3.4	0	0
Total herbivores		**1548**	**22.5**	**283**	**15.1**
Ursus spelaeus	cave bear	0	0	1232	65.8
Ursus arctos	brown bear	0	0	21	1.1
Ursus spelaeus/Ursus arctos	"cave bears"	4215	61.3	0	0
Crocuta crocuta spelea	cave hyaena	633	9.2	12	0.6
Canis lupus	wolf	43	0.6	160	8.6
Cuon priscus	dhole	9	0.1	0	0
Cuon sp.	dhole	0	0	7	0.4
Vulpes vulpes	red fox	0	0	68	3.6
Alopex lagopus	arctic fox	0	0	12	0.6
Vulpinae	foxes	100	1.5	0	0
Panthera (Leo) spelaea	cave lion	6	0.1	16	0.9
Panthera pardus	leopard	0	0	7	0.4
Lynx sp.	lynx	1	0	0	0
Felis silvestris	wild cat	0	0	1	0.1
Meles meles	badger	21	0.3	3	0.2
Martes martes	pine marten	0	0	1	0.1
Carnivores indet.		248	3.6	35	1.9
Total carnivores		**5276**	**76.8**	**1575**	**84.2**
Rodents		**2**	**0**	**0**	**0**
Lagomorphes		46	0.7	13	0.7
total NISP		**6872**		**1871**	

The first examination of micromammals from Scladina was conducted by Cordy (1992), who identified 21 different taxa in different units of the cave terrace deposits. A revision of Cordy's collections by López-García *et al.* (2017) (Table 6.4) has added several new species, including four species of bat and two rodent species. Their results suggest that mean annual temperatures at the site were lower in MIS 5 than the present day, and that vegetation surrounding the cave was mainly composed of boreal to temperate forest. It was also possible to distinguish MIS substages 5a and 5c as more humid, temperate periods within MIS 5 because of the presence of species requiring more humid conditions than those of the cooler, drier substages (Lopez-Garcia *et al*. 2017). Blain *et al.* (2014) examined herpetofauna remains from MIS 5 units at Scladina and Sous-Saint-Paul. They identified three amphibians, two lizards and two snakes that together reflect a mosaic of environments around the cave, including slow water forest streams and humid meadows. This fits well with the mosaic-type, forested and open MIS 5 landscapes proposed by palynological studies (Pirson 2007; Pirson *et al.* 2008). Micromammal species present in MIS 3 imply a colder and drier climate than today existed (Haesaerts *et al.* 1999, 2011; Lopez-Garcia *et al.* 2017). Taphonomic examination of microfaunal remains points to nocturnal and diurnal birds of prey as contributing to the accumulation (Lopez-Garcia *et al.* 2017).

Table 6.4: *Presence of micromammals in layers from the terrace deposits corresponding to MIS 3 and 5 as identified by Lopez-Garcia et al (2017). Layer I = MIS3, Layers IV-VII = MIS5. MIS = marine isotope stage.*

				MIS 5					
			MIS 3	**MIS 5a**				**MIS 5c**	
	taxon	**layer** / **common name**	**I**	**IV**	**V ocre**	**V**	**VB**	**VI**	**VII**
insectivores	*Erinaceus europaeus*	hedgehog				x	x	x	
	Talpa europaea	mole		x	x	x	x	x	x
	Sorex gr. *araneus*	common shrew		x	x	x	x	x	
	Sorex minutus	pygmy shrew			x			x	x
	Neomys anomalus	mediterranean			x				
	Crocidura sp.	musk shrew			x				
bats	*Myotis mystacinus* s.l.	whiskered bat	x		x		x	x	x
	Myotis cf. *daubentoni*	Daubenton's bat					x	x	
	Barbastella barbastellus	western			x				
	Miniopterus schreibersii	common bent-			x				
rodents	*Arvicola amphibius*	water vole	x	x		x	x	x	x
	Lemmus lemmus	Norwegian	x			x			
	Lagurus lagurus	steppe lemming	x		x	x	x		
	Dicrostonyx torquatus	arctic lemming	x			x	x		x
	Microtus arvalis	common vole	x	x		x	x	x	x
	Microtus agrestis	field vole	x	x	x	x	x	x	x
	Microtus oeconomus	tundra vole	x	x	x	x	x	x	x
	Microtus gregalis	narrow-headed	x	x	x	x	x	x	x
	Microtus (*Terricola*) *subterraneus*	European pine				x	x	x	x
	Chionomys nivalis	European snow	x				x	x	x
	Clethrionomys glareolus	bank vole	x	x	x	x	x	x	
	Cricetus cricetus	European hamster							x
	Cricetulus migratorius	migratory							
	Sicista betulina	northern birch							x
	Apodemus gr. *sylvaticus-flavicollis*	wood mouse/yellow-			x	x	x	x	x
	Eliomys quercinus	garden dormouse						x	
	Glis glis	edible dormouse			x				
	Marmota marmota	alpine marmot			x				
	Spermophilus citellus	European ground			x	x			

6.2.5 Material culture

A total of 18,566 lithic artefacts have been recovered from the cave excavations (DiModica and Bonjean 2004). The majority were from the Middle Palaeolithic and from Unit 5 (n = 14,069) and Unit 1A (n= 3,236). These layers are the two most significant in terms of my own analyses. 1,261 lithics were recovered from other sedimentary units, but do not represent any meaningful occupations (Di Modica and Bonjean 2004, 2005).

The Unit 5 assemblage is the richest in the sequence. It dates to MIS 5 and contained evidence for the Neanderthal exploitation of small and large game, and for stone tool manufacture (Bonjean *et al.* 2014; Pirson *et al.* 2018; Di Modica 2010). Raw materials recovered from Unit 5 are diverse, including flint nodules from distant sources. These were acquired alongside local quartz and quartzite pebbles, limestone, and chert in the production of a Quina-type Mousterian assemblage (Bonjean *et al.* 2011, Pirson *et al.*

2018). Hammerstones were used in stone tool manufacture as well as bone retouchers, some of which were made from cave bear bones (Di Modica 2010; Abrams *et al.* 2014). More than 1,000 burned bone fragments pointed towards the presence of one or more hearths (Bonjean *et al.* 2014).

The Unit 1a assemblage is the second richest of the sequence. It represented one of the more recent Neanderthal occupation episodes in Europe, dating to between 40,210 + 400/−350 BP and 37,300 + 370/−320 BP (Bonjean *et al*. 2009). Due to post-depositional processes, the material of Unit 1A is in a poorer state of preservation than Unit 5. Local flint and quartzite pebbles dominate in the production of lithics of Mousterian tradition with Charentian affinities (Di Modica 2010) (Figure 6.5). More than 50 fragments of a black, friable rock were recovered from Unit 1A and were interpreted as a pigment imported to the site by Neanderthals. Geochemical analysis identified the material as a highly siliceous graphitic siltstone; the first non-manganese oxide black pigment recorded from the Middle Palaeolithic. Raman spectroscopy analysis unambiguously pinpointed the source as a Cambrian formation of very limited extent in the area of Franquenies, ca. 40 km north east of Scladina (Bonjean et al. 2015). Burnt bones in this layer testify to the use of bone as fuel (Abrams *et al.* 2010). During this period, human occupation was concentrated in two living spaces; one in the main body of the cave, and one close to the aven (Bonjean *et al.* 2002; Pirson 2007; Pirson *et al.* 2008; Bonjean *et al.* 2014).

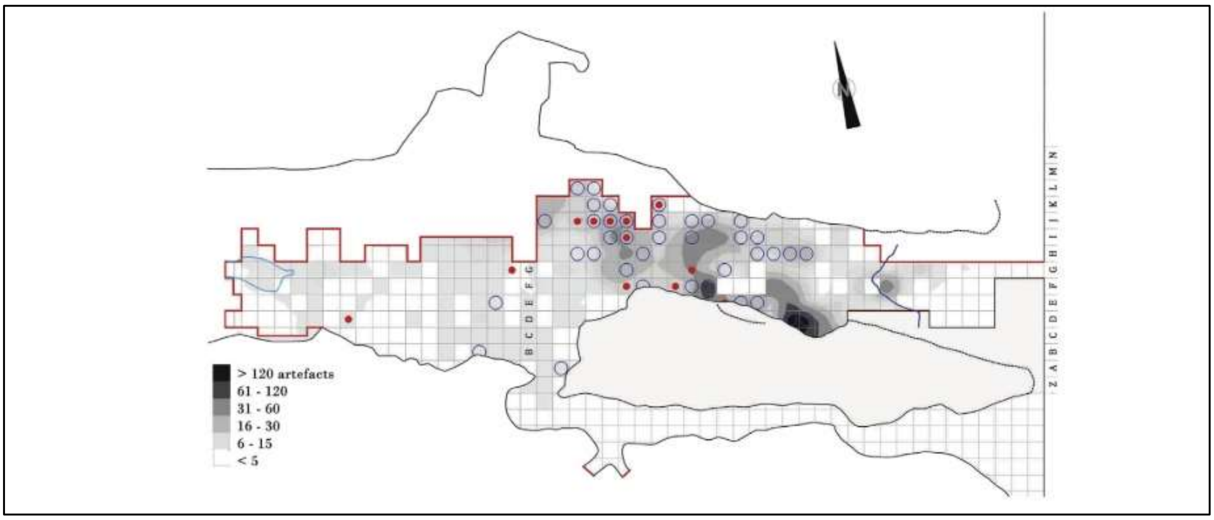


Figure 6.6: Distribution of black pigment (red dots), burned bones (blue circles), and lithic artefact concentrations (grey zones) in units 1A, T, and Z-INF in the excavated area of Scladina Cave. From Bonjean et al. (2015).

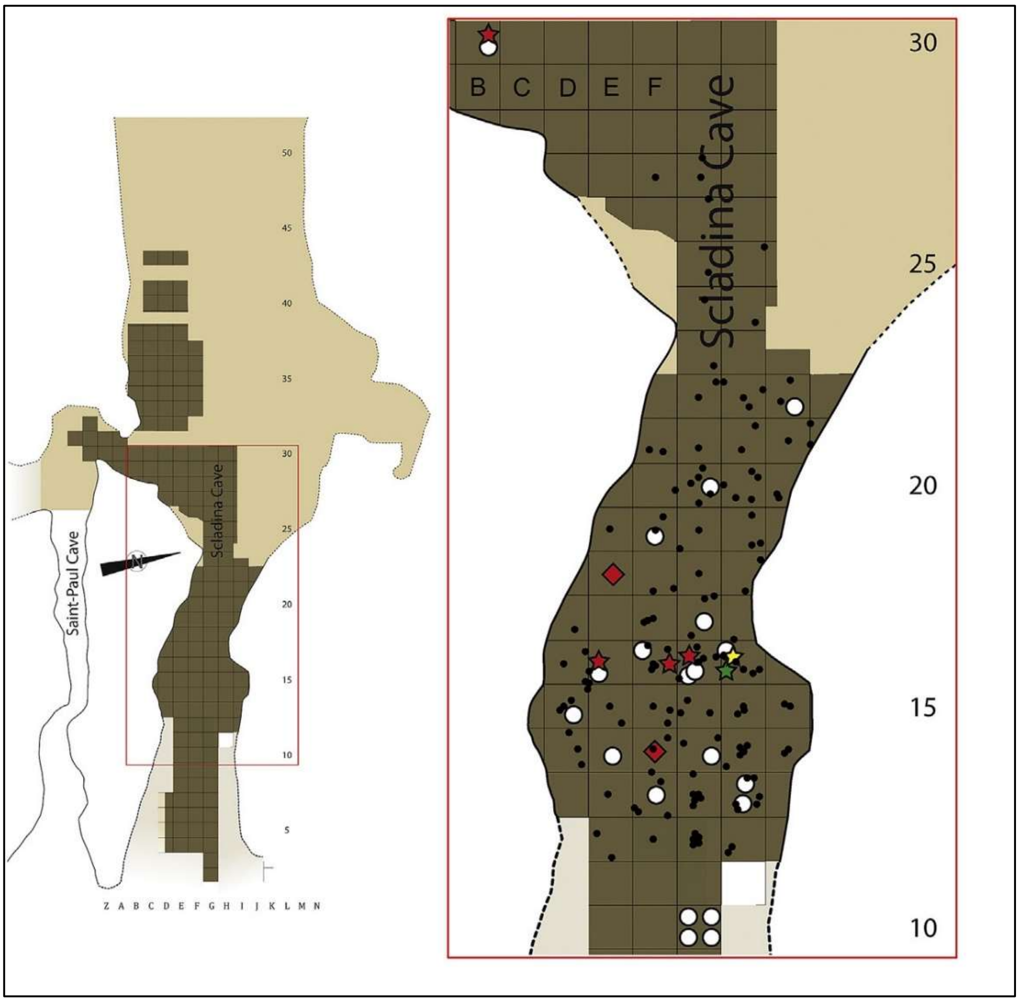


Figure 6.7: Extent of the main occupation deposit in Unit 5 showing lithics (black dots); retouchers made from bear bone (red, yellow, and green stars) and other bone (white dots); unused bear bone splinters (red diamonds). From Abrams et al. (2014).

6.3 The avifauna from Scladina Cave.

Taxonomic identification of the Scladina avifauna was conducted by Quentin Goefette of the Royal Belgian Institute of Natural Sciences at the Museum of Natural Sciences in Brussels, Belgium. He is the Head of Avifaunal Research at Scladina Cave. The investigation of the avian remains is a collaboration between Mr. Goefette and myself and features in both our theses. My taphonomic analyses will inform his thesis, and Mr. Goefette has consented that I make some observations on the taxonomic data to facilitate my regional comparative studies. Our results on Scladina Cave will be published jointly based on a fair and equal contribution from both researchers. An in-depth interpretation of the taxonomic representation of Scladina will be presented in Goefette's PhD thesis. The taxonomic interpretations presented below are wholly the work of the author.

The avifauna remains were recovered from 22 layers/layer groupings of the stratigraphic sequence of Scladina Cave. These derive from multiple fieldwork seasons undertaken by Belgian authorities, who employed both unit and layer designations when recording the cave stratigraphy (see Table 6.2, reproduced from Pirson *et al.* 2018). As the avian sample is not large (n = 81), I have used the marine isotope stage designations established by the Scladina team to group some specimens into larger sample sizes, while referring to individual layers, layer groupings, or units whenever necessary. My designations are as follows:

- **MIS 2**

  This comprises Unit J, which is Upper Palaeolithic/Aurignacian (Pirson 2007; Pirson *et al.* 2008). A single specimen from this Unit (Sc2014-399-1) carries no contextual information. The specimen is outside the scope of this study but will be mentioned in the taphonomy section due to the presence of cutmarks.

- **MIS 3 group**

  MIS 3 is organised into two divisions.

  1) <u>MIS 3 – Late Middle Palaeolithic / Early Upper Palaeolithic (MP/UP):</u> Units 38 and 39 belong to the Middle or Upper Palaeolithic and equate to Layer T. A single specimen marked T-GN from the area around the aven is allocated to this period. However, Layer T-GN does not exist in the sequence and is likely the result of a recording failure. As the specimen is from the main Layer T, it will be included with Units 38 and 39.

  2) <u>MIS 3 (MIS 3):</u> Layers 40 and 1A are equivalent to the most recent Neanderthal occupation phase (c. 40 - 43 ka; Figure 3). These correlate to the Unit 1A assemblage mentioned in 6.2.5. During this period, two different living spaces were identified within the cave. The middle section of Unit Z-INF (an aven collapse) is contemporaneous with Unit 1A, attested by the cross-contextual refitting of lithic debris (Pirson 2007). Therefore, the specimen from Layer Z3-4 is included in this group. The single specimen from Layer 1B is also from MIS 3 and is included in this group.

- **MIS 5 group**

Three stratigraphic units belong to MIS 5 (Layers 3, 4, and 5). As each layer reflects independent accumulation episodes separated by several millennia, they will be assessed in the following sub-divisions:

1) MIS 5 – Layer 3 (MIS 5-3): All specimens marked as originating in Layer 3.

2) MIS 5 – Layer 4 (MIS 5-4): All specimens originating from contexts within the greater designation of 'Layer 4' (4, 4A, 4A-GR, 4A-GX1) (c. 100 ka; Figure 3). The contexts in Layer 4A below stalagmitic floor CC4 are reworked by post depositional processes. After the formation of CC4 during MIS 5, a channel developed in the sediment, cutting down into the stratigraphy as far as Layer 5. The sediment that fills this erosive feature consists of reworked sediment from elsewhere in the sequence. It is within these reworked sediments that the juvenile Neanderthal was discovered (Pirson *et al.* 2005). Sediments deposited above CC4 were deposited subsequent to the creation and filling of the channel feature (Pirson *et al.* 2005, Pirson 2007).

3) MIS 5 – Layer 5 (MIS 5-5): All contexts attributed to Layer 5 in both the interior area of the cave and the old terrace deposits. Context Vb originates from the old stratigraphy in the terrace deposits. Context "5+6" is from the interface between Layers 5 and 6 (*pers. comm.* G. Abrams 2019). A specimen from square F36 with no exact layer information is likely from Layer 5 by the depth information provided and has been included here. This sub-division correlates to the Unit 5 assemblage.

- **MIS 6**

  One single specimen is from Layer Via. This is a designation from the older stratigraphic descriptions and originates from the upper part of Unit 6.

- **Other Z-contexts (MIS 1)**

  Additional Z-contexts were ascribed to the sediments that accumulated in the area of the aven collapse after it opened in MIS 3. Pirson (2007) made correlations with the main sequence of the cave, ascertaining that Z-HUM is equivalent to the Holocene Unit H. Hence specimens marked with layers Z1, Z1-TE, Z1 a Z3, and the specimen from square I41 (Sc2009-232-2) are from this context which is outside the scope of this study.

6.4 Taxonomic results

Of the 81 specimens (NISP) from Scladina Cave, 60 were identified beyond class (*Aves* sp.) 35 of which were identified to species, 6 to genus, 1 to family and 18 to order (Table 6.5; Appendix 5). Of the 22 original layers with avifauna, half were represented by a single element, and three specimens were not assigned to any exact one, although, other contextual information allowed the allocation of these specimens to stratigraphic units (see: section 6.3). There were twelve species (NTAXA). The avian faunal material ranged in age from MIS 6 to MIS 1. 59 % of the remains (n = 48) belonged to the MIS 5 group, and a further 31 % (n = 25) in the MIS 3 group. The remaining 10 % (n = 7) were found in layers belonging to MIS 1, 2, and 6. Layers 1A (n = 18) and 5 (n = 23) represent the main occupation levels in the site (Bonjean *et al*. 2014).

The modest sample was dominated by Galliformes (n = 39 or 48.9 %), of which capercaillie (*Tetrao urogallus*) was the most abundant. Game birds like the capercaille and black grouse (*L. tetrix*) may have inhabited the wooded landscape directly around the cave. Anseriformes constituted a further 13.5 % of the collection (n = 11), reflecting the presence of water bodies. Seventeen classifications were represented by a single element. 19.7 % of the specimens (n = 16) were not securely identified beyond class and were excluded from any ecological interpretation. Three specimens (3.7 %) were of the order Passeriformes, representing two different size comparisons.

Remains from MIS 1 and MIS 2 fell outside the scope of this study and were excluded from the ecological and taphonomic interpretations. NISPs in the MIS 6 group (n=1) and MIS 3 – MP/UP group were too small for statistical analysis (Hawkins 2019). The following taxonomic and ecological comparisons are therefore limited to comparisons between MIS 3 and the MIS 5 groups (Table 6.5). However, other context groups were included in the taphonomic analysis.

The MNI present in the MIS 5 and MIS 3 was 55, 48 of which come from contexts MIS 3, MIS 5-4 and MIS 5-5. The higher NISP in these contexts was due to the presence of more individuals in the accumulation rather than differential preservation (Lyman 1994). The presence of more individuals during periods of human occupation suggests low levels of attritional accumulation in Scladina Cave and hints at an external agency. The ten remains from Layer 3 (MIS 5-3) constitute only two individuals, one each of the species recorded as present in that context.

The relationship between NISP and MNI was tested by linear regression. The scatterplot showed a positive relationship between the values.

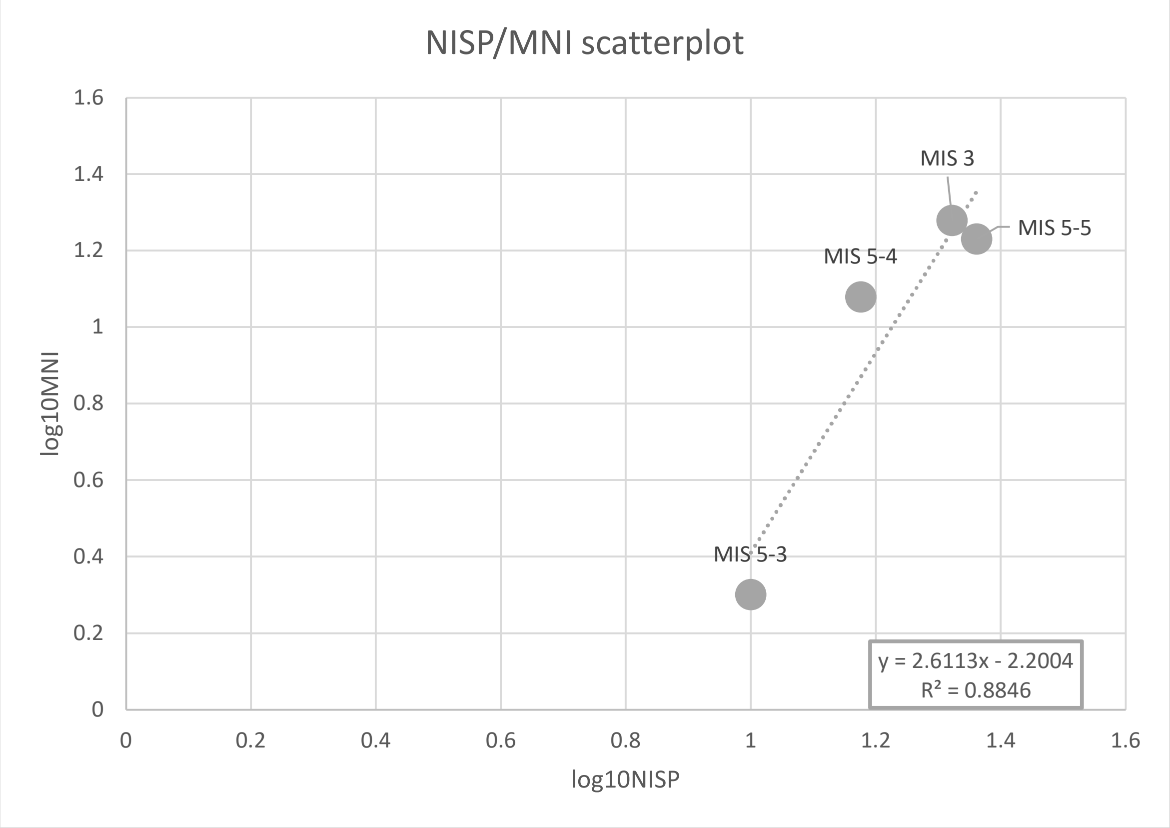


Figure 6.8: Scatterplot of the relationship between NISP and MNI.

Table 6.5: Taxonomic representation of the Scladina avifauna grouped as explained in section 6.3, showing NISP and NTAXA per context, levels included in each context, and total specimens per species.

	MIS Stage	**MIS 3**	**MIS 5**		
Taxon	**Layers**	**40 - 1A - 1B - Z3-4**	**3**	**4 - 4A**	**5 - Vb – 5+6**
GALLIFORMES					
Tetrao	*urogallus*	**1**	8	5	3
Lyrurus	*tetrix*	**2**	0	2	2
Lagopus	sp.	**1**	0	1	0
Lagopus sp./	*Lyrurus tetrix*	**0**	0	0	1
Gallliformes size	*Tetrao sp.*	**0**	0	0	3
Gallliformes size	*Lyrurus tetrix*	**0**	0	1	0
Gallliformes size	*Lagopus sp.*	**1**	2	0	0
ANSERIFORMES					
Anser	*albifrons/serrirostris*	**0**	0	0	1
Anser	sp.	**0**	0	0	1
Anatidae size	*Anas acuta*	**1**	0	0	0
Anseriformes size	*Anas platyrhynchos*	**1**	0	1	1
COLUMBIFORMES					
Columba	cf. *palumbus*	**1**	0	0	0
SULIFORMES					
Phalacrocorax	*carbo*	**0**	0	1	0
ACCIPITRIFORMES					
Accipiter	*nisus*	**1**	0	0	0
Accipitriformes size	*Aquila/Gyps*	**1**	0	0	0
STRIGIFORMES					
Bubo	*scandiacus*	**0**	0	1	0
Asio	*otus/flammeus*	**0**	0	0	1
PASSERIFORMES					
Passeriformes small	(size *Coccothraustes)*	**2**	0	0	0
Passeriformes size	*Emberiza citrinella*	**1**	0	0	0
INDETERMINATE					
Aves size	*Tetrao urogallus*	**1**	0	2	2
Aves size	*Tetrao* sp.	**0**	0	0	2
Aves size	*Lyrurus tetrix*	**0**	0	0	2
Aves size	*Lagopus* sp.	**1**	0	0	0
Aves size	*Anser* sp.	**1**	0	0	1
Aves size	*Columba livia*	**1**	0	0	0
Aves size	*Numenius phaeopus*	**0**	0	0	1
Aves	middle	**0**	0	0	1
Aves	middle/large	**3**	0	0	0
Aves	sp.	**1**	0	1	1
	NISP	**21**	**10**	**15**	**23**
	NTAXA	**11**	**2**	**6**	**7**
	MNI	**19**	**2**	**12**	**17**

6.5 Environmental and climate results

Due to the small sample size, the following ecological analysis was conducted for MIS 3 and MIS 5 (MIS 5-5, MIS 5-4, MIS 5-3) only. MIS 3 correlates to Unit 1A, while MIS 5-5 correlates to the Unit 5 assemblage. It was not possible to produce meaningful significance tests with the available data. Environmental variables for species included in the interpretation can be found in Table 6.7.

6.5.1 Environmental tolerances

Birds with moderate bioclimatic tolerances were most frequent and were present in all layers (Table 6.6). These include the black grouse (*T. tetrix*), the capercaillie (*T. urogallus*), and the yellowhammer (*E. citrinella*). Generalist species were present in three layers (MIS 5-5, MIS 5-4, and MIS 3), but occurred in both MIS stages. Frequencies of other tolerance levels were too low (all < 3) to offer substantive observations. However, it is interesting that specialist (A) and semi-specialist (B) species only appeared in MIS 5 (MIS 5-5 and MIS 5-4 respectively), while category D (semi-generalist) species appeared in both MIS 5 and glacial MIS 3.

Table 6.6: Bioclimatic tolerances by context. A – Specialist, B – Semi-specialist, C – Moderate, D – Semi-generalist, E – Generalist. After Finlayson 2011. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Moderate to generalist species appear most frequently.

	Context (NTAXA)					
TOL	**MIS 3**	**MIS 5-3**	**MIS 5-4**	**MIS 5-5**	**FREQ**	**FREQ%**
A				1	1	25
B			1		1	25
C	3	1	2	2	4	100
D	1		1		2	50
E	2		1	1	3	75

Table 6.7: Ecological variables by species after Finlayson, 2011. TOL: bioclimatic tolerance (A= specialist, B= semi-specialist, C= moderate, D= semi-generalist, E= generalist), LAT: latitude range (A= arctic 70°N, B= boreal 60°N, C= temperate 50°N, D= mid-latitude belt (warm species) 40°N, E= subtropical 30°N, F= multilatitude – species occupies several latitude bands), TEM: temperature tolerance (A-E from cold to hot), HUM: humidity tolerance (A-E from arid to wet), Foraging and Nesting habitats (F= forest, O= open, M= mixed F/O, W= wetland, R= rocky, Ma= marine, A= aerial) , diet (E= endotherm, O= omnivore, I= insectivore, H= herbivore, N= necrophyte, M= mixed strategy carnivore, F= fish eater), and Migration behaviours (M= migratory, S= sedentary, P = partially migratory).

Species	**Common name**	**Order**	**TOL**	**LAT**	**TEM**	**HUM**	**Foraging**	**Nesting**	**Diet**	**Migration**
Tetrao urogallus	capercaillie	Galliformes	C	B/D	B	B	F	F	*O*	*S*
Lyrurus tetrix	black grouse	Galliformes	C	C	B	C	M	M	O	S
Anser albifrons/serrirostris	white-footed/bean goose	Anseriformes	A	A	A	A	O	O	O/H	M
Anas acuta	Pintail	Anseriformes	C	B	B	B	W	W	O	M
Anas platyrhynchos	mallard	Anseriformes	E	F	B	C	W	W	M	P
Columba palumbus	wood pigeon	Columbiformes	D	F	C	C	F	F	O	P
Phalacrocorax carbo	great cormorant	Suliformes	D	B/D	C	D	W	W	F	P
Accipiter nisus	sparrowhawk	Accipitriformes	E	F	C	D	F	F	E	P
Bubo scandiaca	snowy owl	Strigiformes	B	A	A	B	O	O	E	M

Latitude category B/D reflects species which inhabit the boreal zone, but which have relict montane populations in the mid-latitude belt. These were the most frequently occurring species at Scladina Cave (n = 4), represented by two taxa: the great cormorant (*P. carbo*), and the capercaillie (*T. urogallus*) (Table 6.8). In the context of Scladina, these species merged with the purely boreal species (B) which were represented by only a single species in MIS 3 (pintail - *A. acuta*). Other categories all had values < 4. Species which may occupy multiple latitude bands and temperate species each appeared in three contexts. The temperate black grouse (*L. tetrix*) and multilatitude mallard (*A. platyrhynchos*) were present in both MIS 5 and MIS 3, while other multilatitudinal taxa (*C. palumbus, A. nisus*) were only identified in MIS 3. Arctic species (snowy owl - *B. scandiaca*, white-footed/bean goose - *A. albifrons/serrirostris*) occurred in MIS 5 (MIS 5-4 and MIS 5-5). No category D or E taxa (mid-latitude belt, warm and subtropical) appeared in the collection. This is not unexpected given the geographic location of the site (50°N).

Table 6.8: Latitude range by context. A – Arctic 70°N, B – Boreal 60°N, C – Temperate 50°N, D - Mid-latitude belt, warm, 40°N, E – Subtropical 30°N, F - Multi-latitude (occupies several bands). Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Boreal species were most frequent.

	Context (NTAXA)					
LAT	**MIS 3**	**MIS 5-3**	**MIS 5-4**	**MIS 5-5**	**FREQ**	**FREQ%**
A			1	1	2	50
B	1				1	25
B/D	1	1	2	1	4	100
C	1		1	1	3	75
D					0	-
E					0	-
F	3		1	1	3	75

Only species with cold to moderate temperature tolerances were identified in the sequence (Table 6.9). This reflected the latitude ranges of the taxa present. Species with high cold tolerance equate to the arctic species and were only present in MIS 5 while those with moderate tolerances were present in MIS 5-4 and MIS 3. Category B species are present in all layers. No species with high humidity tolerance (E) were present in the sample (Table 6.10). Species with moderate to low humidity tolerances were most frequent (n = 9) and categories B, C and D appear in both MIS 5 and MIS 3. The white-footed/bead goose (A. albifrons/serrirostris) only featured in MIS 5-5.

Table 6.9: Temperature tolerances by context. Scale from cold to hot, A – 1-20 %, B – 21-40 %, C – 41-60 %, D – 61-80 %, E – 81-100 %. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Cold-tolerant species were most frequent.

	Context (NTAXA)					
TEM	**MIS 3**	**MIS 5-3**	**MIS 5-4**	**MIS 5-5**	**FREQ**	**FREQ%**
A			1	1	2	50
B	4	1	3	3	4	100
C	2		1		2	50
D					0	-
E					0	-

*Table 6.10: Humidity tolerances by context. Scale from arid to humid, A – 1-20 %, B – 21-40 %, C – 41-6 0%, D – 61-80 %, E – 81-100 %***.** *Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Moderate humidity tolerances were most frequent.*

	Context (NTAXA)					
HUM	**MIS 3**	**MIS 5-3**	**MIS 5-4**	**MIS 5-5**	**FREQ**	**FREQ%**
A				1	1	25
B	2	1	2	1	4	100
C	3		2	2	3	75
D	1		1		2	50
E					0	-

Four foraging habitats were reflected in the species present in Scladina Cave: forest, open, mixed (forest and open), and wetland (Table 6.11). Woodland taxa appeared in all four layers but were more diverse in MIS 3 where they were represented by three species (*T. urogallus, C. palumbus, A. nisus*). Wetland and mixed foragers species featured in both MIS3 and MIS5. Mixed foragers were represented by a single species (*L. tetrix*), while wetland species were more diverse (n = 4). The only instance of an open forager was the snowy owl in MIS 5-4, while MIS 5-3 only reflected forest foragers (*T. urogallus*). Five categories of nesting habitat were reflected in the Scladina sample (Table 6.12). Forest, Open, mixed and Wetland nesters were equivalent to the same species in foraging habitats.

Table 6.11: Foraging habitats by context. A= aerial, F = forest, M = mixed open and forest, Ma = marine, O = open, R = rocky, W = wetland. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Forest and mixed foragers were most frequently observed.

	Context (NTAXA)					
HF	**MIS 3**	**MIS 5-3**	**MIS 5-4**	**MIS 5-5**	**FREQ**	**FREQ%**
A					0	-
F	3	1	1	1	4	100
M	1		1	1	3	75
Ma					0	-
O			1	1	2	50
R					0	-
W	1		2	1	3	75

Table 6.12: Nesting habitats by context. F = forest, M = mixed open and forest, O = open, R = rocky, W = wetland. Table shows number of species (NTAXA) per layer that exhibited each tolerance category, and the frequency of each tolerance category within the sequence (FREQ and FREQ%). Forest and mixed nesters were most frequently observed.

	Context (NTAXA)					
HN	**MIS 3**	**MIS 5-3**	**MIS 5-4**	**MIS 5-5**	**FREQ**	**FREQ%**
F	3	1	1	1	4	100
M	1		1	1	3	75
O			1	1	2	50
R					0	-
W	1		2	1	3	75

6.5.2 Higher taxa groups

By examining higher taxa groups rather than species level, more of the remains recovered from Scladina were able to be included in my analysis (Table 6.13; Figure 6.9). This was important because low numbers weakened the results of the previous ecological analysis. By zooming the focus out to higher taxa levels, more specimens became eligible for analysis. This was not a perfect approach, but an earnest attempt to work with the material available in this thesis.

The NISP of game birds (Galliformes) rose with the inclusion of specimens not identified securely beyond genus and order, but as the capercaillie was present in all four layers, the frequency does not change (n = 4). Anseriformes (ducks and geese) did not increase in the frequency and remained present in three layers as indicated by the species level analysis.

Table 6.13: The distribution of higher taxa groups at Scladina Cave.

Common name	Order	Family	MIS 3	MIS 5-3	MIS 5-4	MIS 5-5
Game birds	Galliformes	All	5	10	9	9
Ducks and geese	Anseriformes	All	2		1	3
Swifts	Apodiformes	All				
Pigeons/doves	Columbiformes	All	1			
Cranes and rails	Gruiformes	All				
Shore birds	Charadriiformes	All				
Sea birds	Procellariiformes	All				
Loons	Gaviiformes	All				
Diving birds	Suliformes	All			1	
Water birds	Pelicaniformes	All				
Diurnal raptors	Accipitriformes	All	2			
Owls	Strigiformes	All			1	1
Woodpeckers	Piciformes	All				
Falcons	Falconiformes	All				
Corvids	Passeriformes	Corvidae				
Non-corvids	Passeriformes	Non-corvids	3			
	Indeterminate	All	**8**		**3**	**10**
		NISP	**21**	**10**	**15**	**23**
		NTAXA	**11**	**0**	**6**	**7**

In owls (Strigiformes), the inclusion of a specimen of long/short-eared owl (*Asio otus/flammeus*) increased the observed frequency of nocturnal birds of prey to two, both observations in MIS 5 (MIS 5-5 and MIS 5-4). At this higher taxa level, the sparrowhawk (*A. nisus*) was joined in MIS 3 by a larger member of the same order (Accipitriformes – diurnal birds of prey), comparable by size to an eagle or vulture (Accipitriformes size = *Gyps/Aquila*). Finally, two different sizes of non - corvid Passeriformes (perching birds) were identified in MIS 3.

Galliformes and Anseriformes are both well-known food species (Cott 1947; Serjeantson 2009; Finlayson 2019). Modifications made during human consumption were present on bird remains of these orders at Middle Palaeolithic sites in Spain (Bolomor Cave – Blasco and Peris 2009; Cova Negra IIIb – Martinez-Valle *et al.* 2016), Germany (Salzglitter Lebenstadt - Gaudzinski-Windheuser and Niven 2009), France (Pie Lombard – Romero *et al.* 2017), and Italy (Fumane Cave - Peresani *et al.* 2011; Fiore *et al.* 2016).

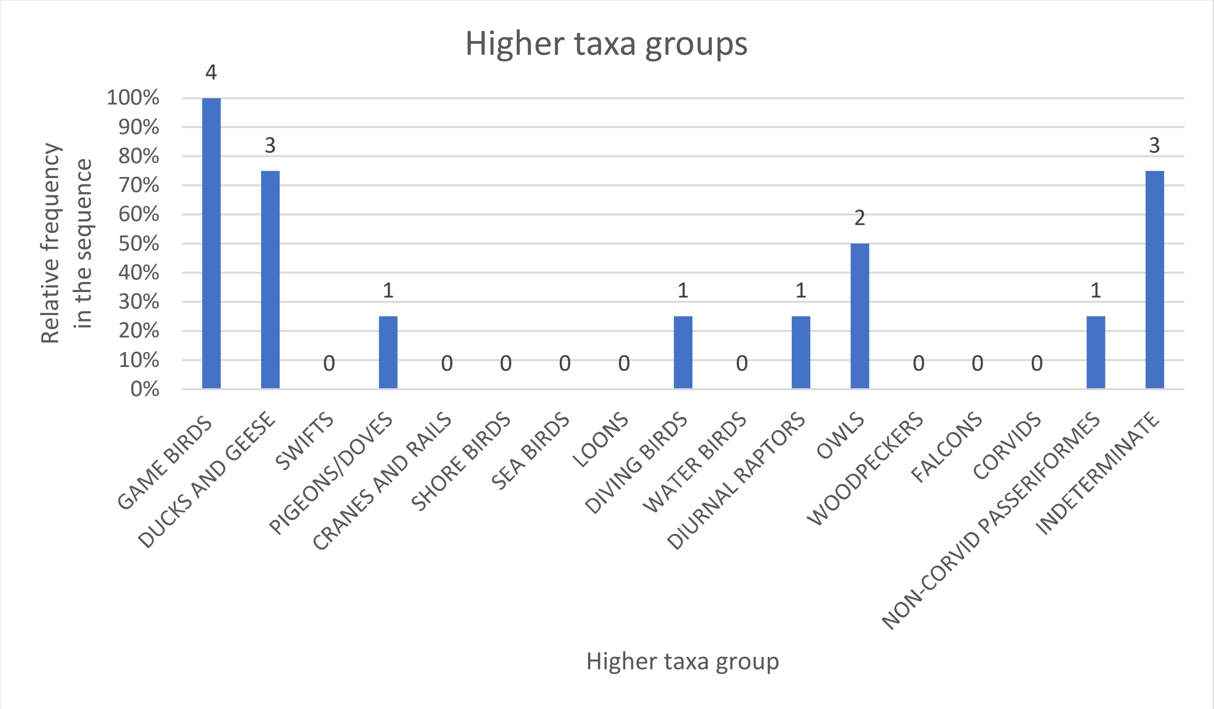


Figure 6.9: Relative frequencies of higher taxa groups at Scladina Cave. Actual frequencies are labelled above each column.

6.6 Taphonomic results

In this section the results of taphonomic analysis of the avifauna from Scladina Cave are presented. NISPtaph was 74 and included all remains in all contexts, excluding 7 specimens from MIS1 and MIS 2 (Table 6.14). However, the single specimen from MIS 2 is mentioned due to the presence of human agency. The collection was in generally good condition, with no peri- and post- excavational damage visible on the specimens. This reflected the careful excavation techniques employed at Scladina (Bonjean *et al.* 2014). Lisibility (Figure 6.10) was generally good throughout the sequence with a dip in MIS 5-4. 25 % (n = 20) of specimens show a Lisibility rank above 2. One specimen in MIS 5-5 was too obscured to interpret at all.

Table 6.14: Presence of taphonomic modifications by context/context group designations. The percentages indicate the relative frequency of these modifications per context group.

	MP/UP trans		**MIS 3**		**MIS 5 - 3**		**MIS 5 - 4**		**MIS 5 - 5**		**MIS 6**	
	38,39,T-GN		40, 1A, 1B, Z3-4		3		4, 4A		5, Vb, 5=6, F36		Via	
Concretions	2	50.0%	15	71.4%	7	70.0%	2	13.3%	12	52.2%		
Manganese staining	4	100.0%	19	90.5%	10	100.0%	13	86.7%	20	87.0%	1	100.0%
Trample	2	50.0%	4	19.0%	2	20.0%	2	13.3%	6	26.1%	1	100.0%
Root etching	2	50.0%	3	14.3%	1	10.0%	6	40.0%	7	30.4%		
Weathering	3	75.0%	16	76.2%	10	100.0%	12	80.0%	17	73.9%		
Human? Toothmark							1	6.7%				
Carnivore toothmark			10	47.6%	8	80.0%	5	33.3%	12	52.2%	1	100.0%
Rodent gnaw									1	4.3%		
Indet. Toothmark	1	25.0%										
Digestion			10	47.6%	3	30.0%	2	13.3%	4	17.4%		
Cutmark	1	25.0%					2	13.3%	3	13.0%		
Thermal modification									1	4.3%		
Peeling									1	4.3%		

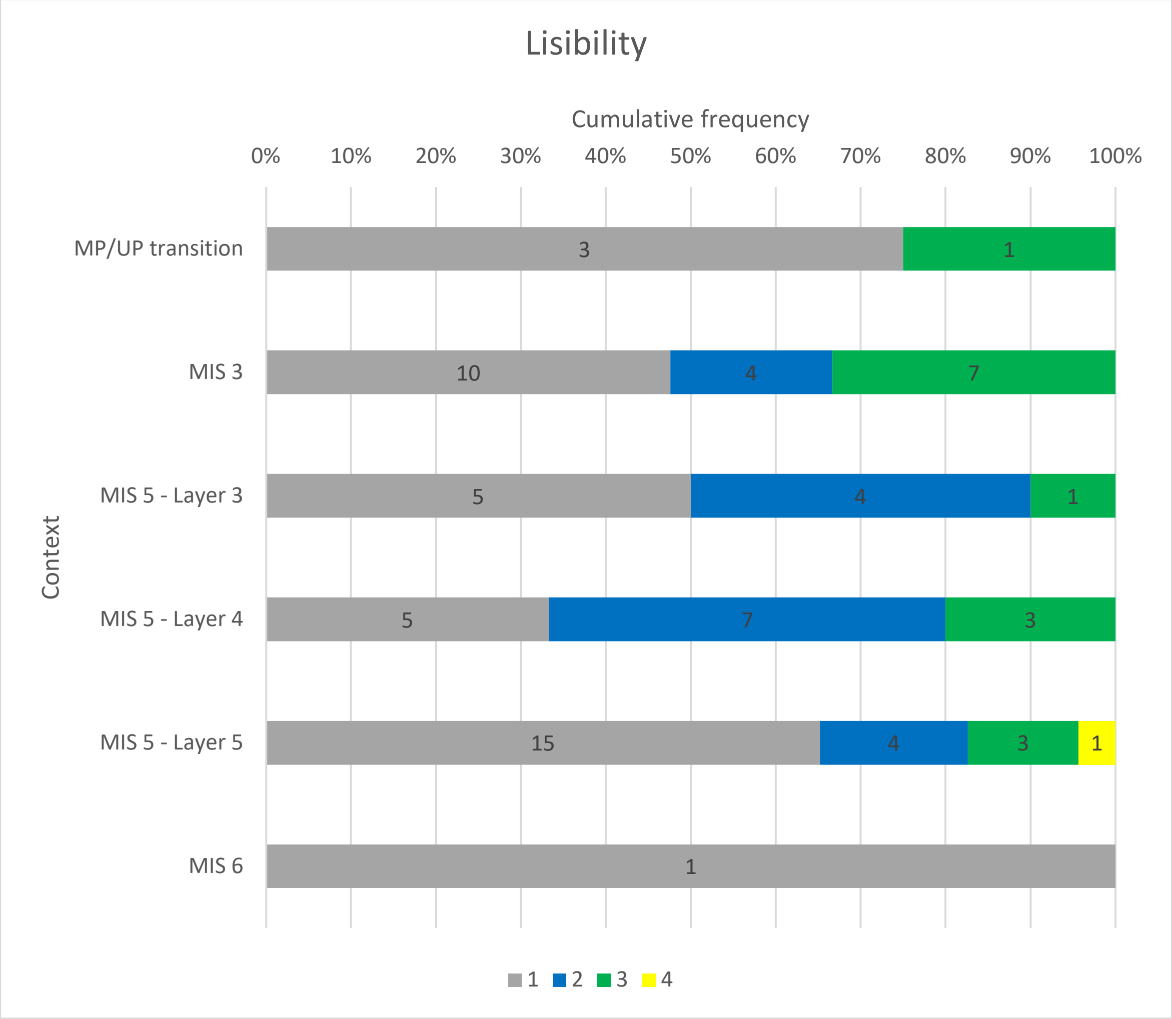


Figure 6.10: Proportion of Lisibility rank by context on a scale from clear (1) to unreadable (4).

6.6.1 Natural modifications

6.6.1.1 *Concretions, Manganese staining and Root etching.*

The frequency of concretions on the bone surfaces varied from context to context (Figure 6.11). Fewest concretions were found in MIS 5-4. This level has been subject to post-depositional processes that may have contributed to the lack of adhesion (Pirson 2007; Pirson *et al.* 2008, 2014). The heaviest concretions are found in MIS 3. No concretions were observed on the single specimen from MIS 6. A total of 67 specimens (95 %) displayed some degree of manganese staining (Figure 6.12). The highest levels were in MIS 3 (n = 15, 71.4 %) and MIS 5-5 (n = 12, 52 %) with the difference possibly indicating a higher level of humidity within the cave in MIS 3.

There was some evidence of rooting on the bone surfaces (n = 20), but only at low levels (Figure 6.13). Those specimens displaying any degree of rooting originated in areas of the cave that allowed sunlight to penetrate and drive photosynthesis. Specimens from MIS 3 and MP/UP contexts are closer to the aven, while the material in MIS-4 and MIS 5 were deposited where sunlight could have entered through the main opening (Figure 6.2).

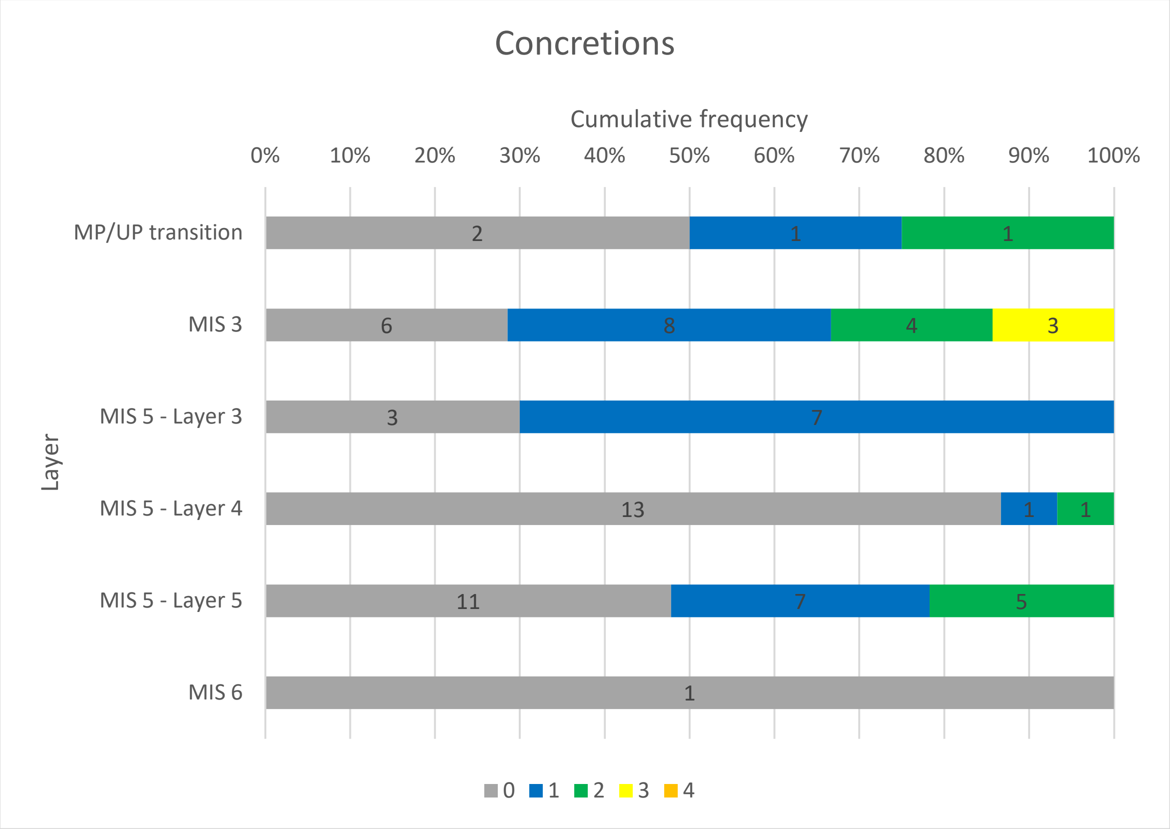


Figure 6.11: Degree of concretions present by context. 1 = 0-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%, 0 = no concretions.

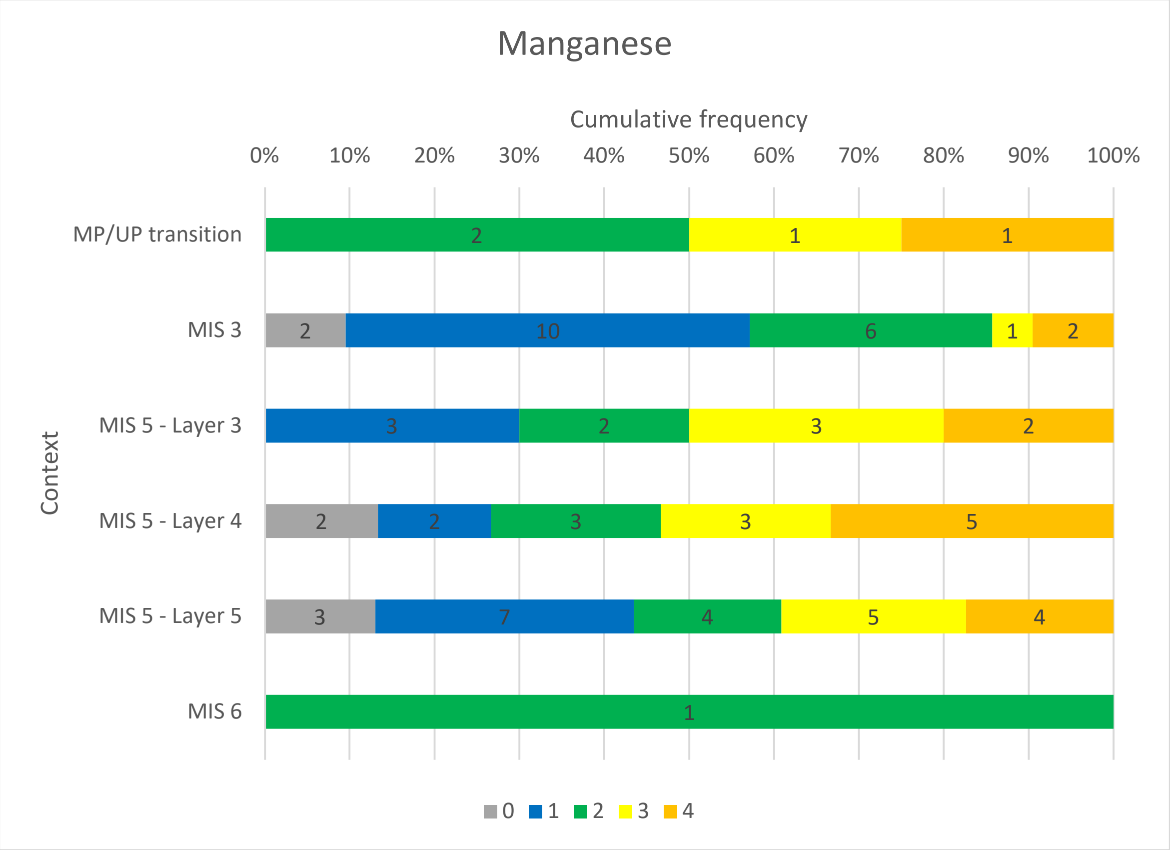


Figure 6.12: Degree of manganese oxide staining by context. 1 = 0-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%, 0 = no manganese oxide.

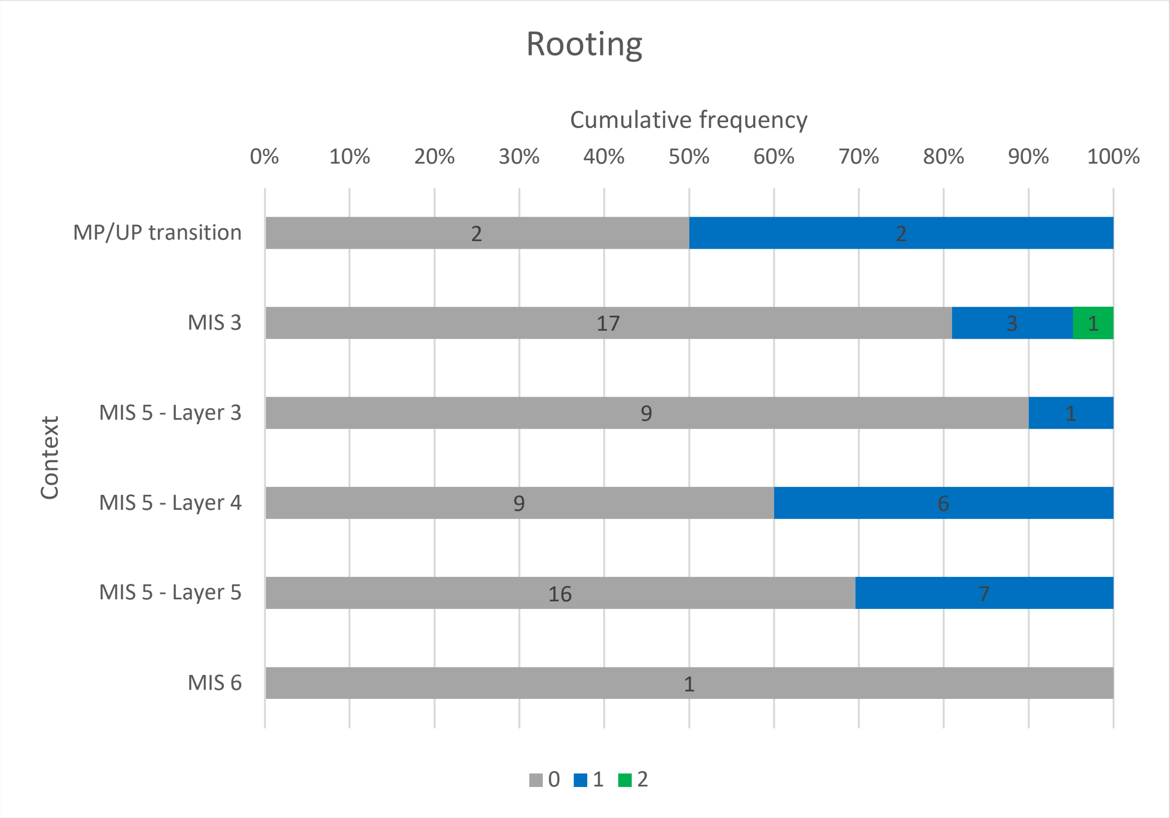


Figure 6.13: Degree of rooting present by context. 1 = low level of rooting, 2 = moderate level of rooting, 0 = no rooting.

6.6.1.2 Weathering

49 remains displayed some level of weathering (Figure 6.14). In line with observations made by Tomek and Bochenski (1997), only three stages of weathering were apparent on the material, not including stage 0 (no weathering). These stages were present in all contexts except MIS 6 where no weathering was evident.

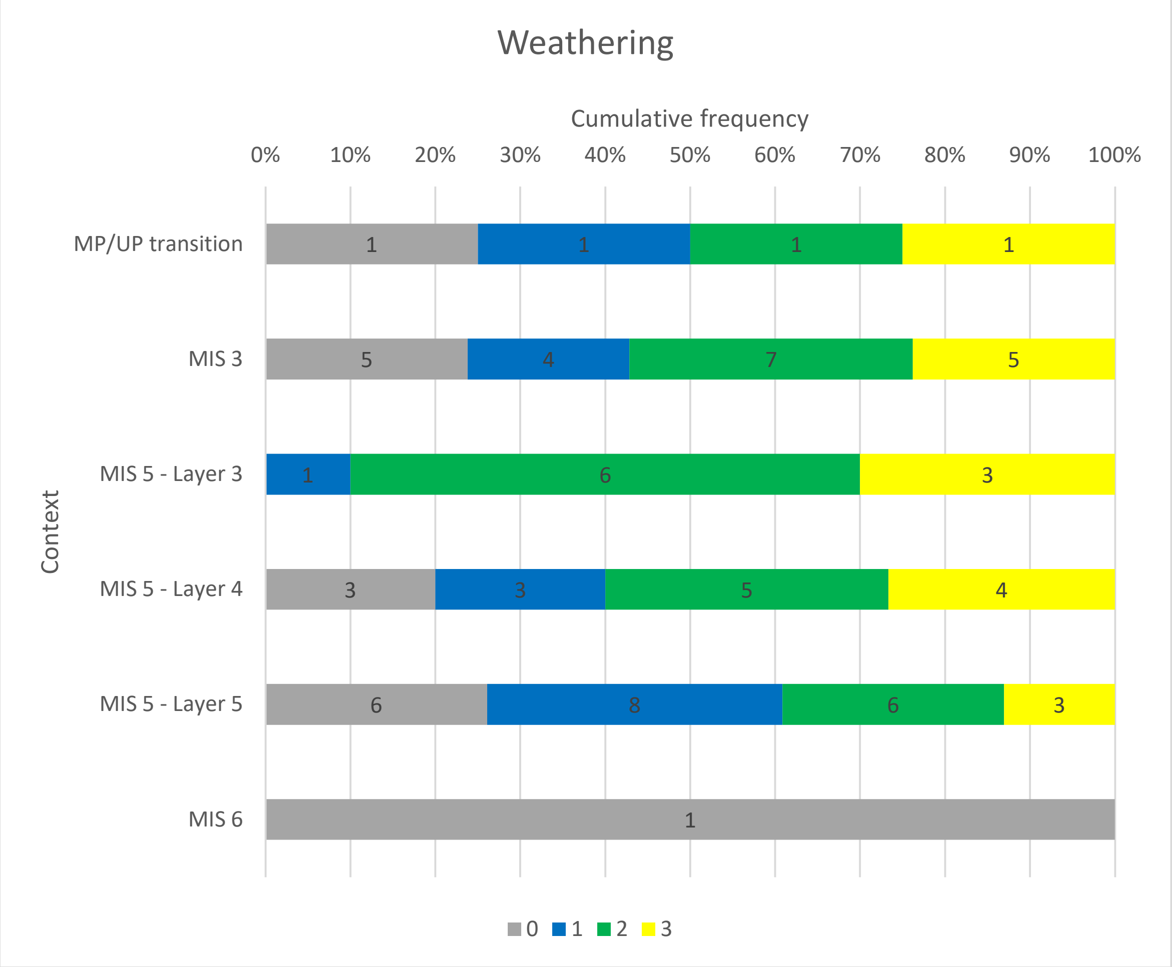


Figure 6.14: Degrees of Weathering modifications by context where 0 = no modification and 5 = highest degree of modification.

6.6.1.3 Trampling

Trample appeared at a low frequency in all contexts (Figure 6.15). Sample sizes were too small to interpret beyond presence and absence. The slightly higher frequency in context groups MIS 3 and MIS 5-5 can be explained by higher NISPs rather than as evidence of higher instances of trampling.

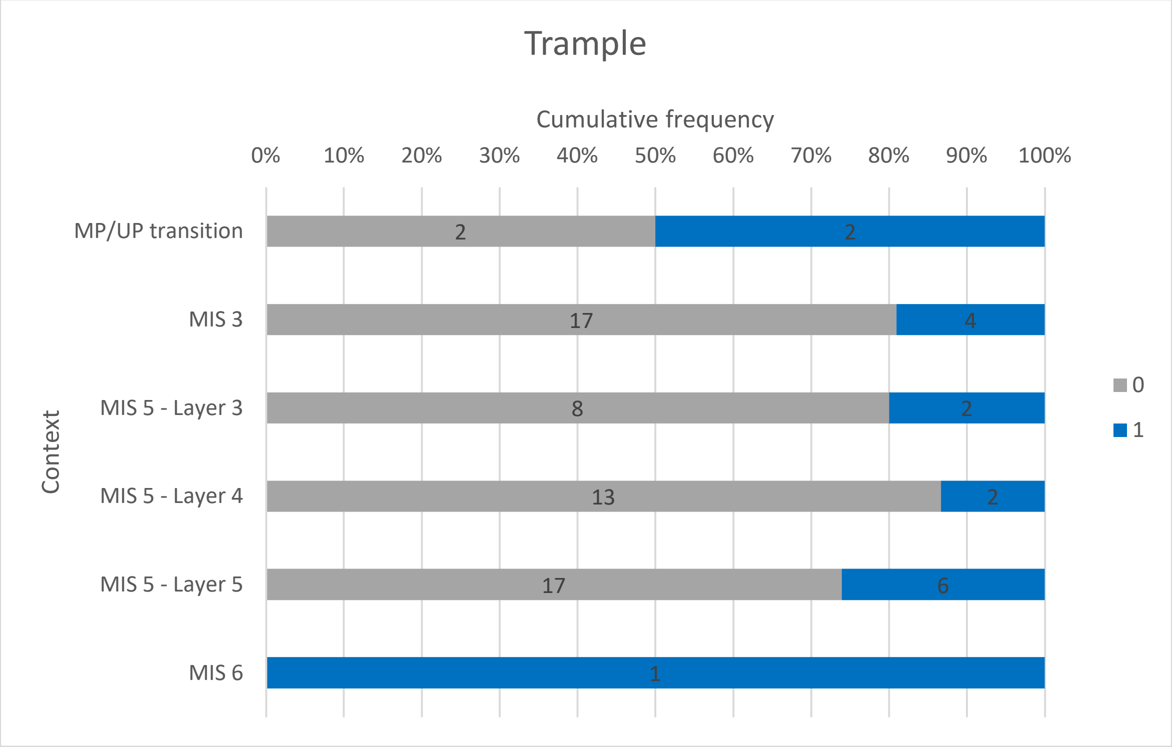


Figure 6.15: Frequency of trampling by context. 0 = no trample, 1 = trample present.

6.6.2 Predator modifications

Forty-three (53%) specimens showed modifications resulting from manducation. Modification was found on material from all contexts pointing towards a steady deposition of prey throughout the sequence. The number of modified specimens, percentages of sample per context, and types of modification present are tabulated in Table 6.15. More than one trace may be recorded on any one specimen.

Mammalian carnivores were responsible for all but three of the manducation modifications. Of the remaining three, one was the result of rodent gnawing, one was indeterminate in nature, and one may be the result of human manducation due to the size and shape of the puncture (Laroulandie 2005; Blasco *et al.* 2014). However, the lack of other manducation traces attributable to humans makes this less likely. No modifications could be securely ascribed to avian predators (Figure 6.16).

25 % (n = 20) of the NISPtaph show traces of digestion (Table 6.16). Most specimens show only low levels of acid etching to the bone surface (n = 16). Two specimens show a higher degree of acid etching, and a further two specimens show a light polish of the bone surface, but no etching.

Table 6.15: Presence and type of manducation modification by context group denoting number of modifications (NISPmod), percentage of modified specimens per context group (%mod), and type of modification (pitting (pit), scoring (score), notch, puncture (punc), crenulated edges (cren/chew), gnaw).

			Type of modification					
	NISPmod.	**%mod**	**Pit**	**Score**	**Notch**	**Punc**	**Cren/chew**	**Gnaw**
MP/UP transition	1	25.0%				x	x	
MIS 3	10	47.6%	x	x	x	x	x	
MIS 5 - 3	8	80.0%		x	x	x	x	
MIS 5 - 4	6	40.0%		x	x	x	x	
MIS 5 - 5	13	56.5%		x	x	x	x	x
MIS 6	1	100.0%					x	
MIS 1	3	60.0%				x		
MIS 2	1	33.3%	x		x			

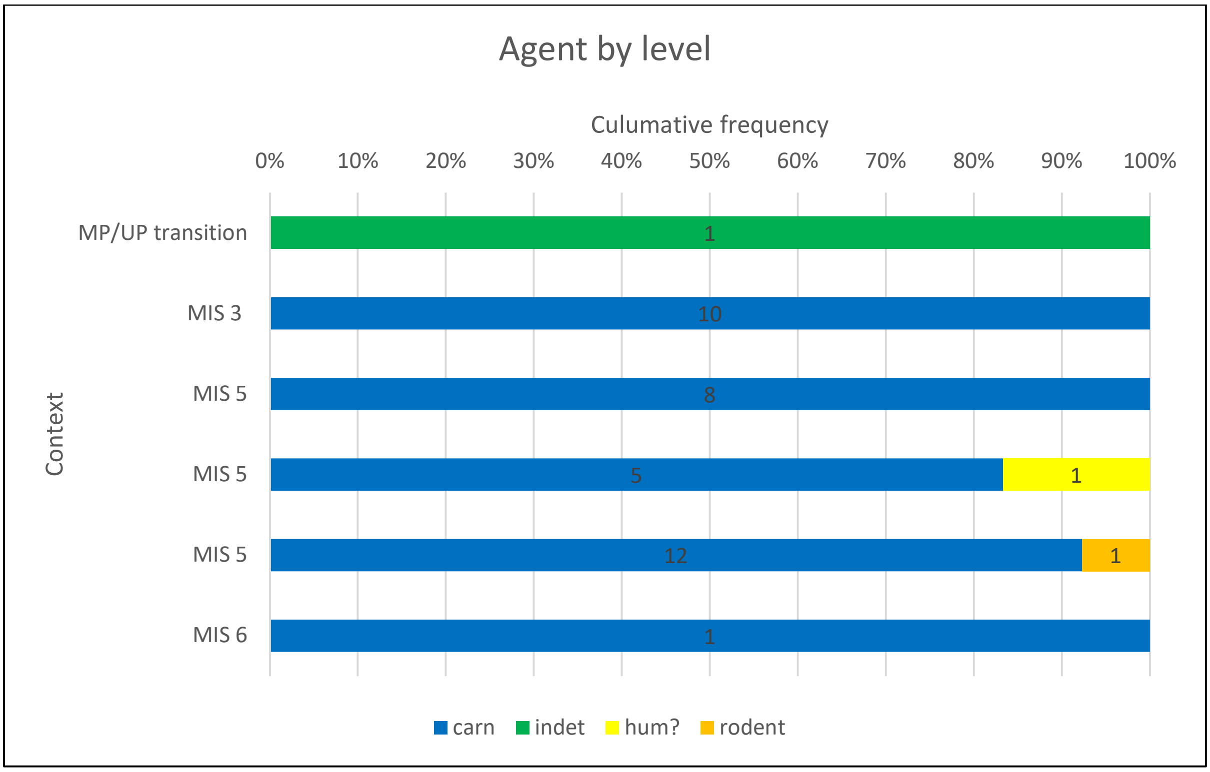


Figure 6.16: Agency as reflected by manducation modifications, by context carn = carmivore, indet = indeterminate, hum? = possible human).

Table 6.16: Digestion traces on bone surfaces.

Digestion trace	**No etch**	**Etch 1**	**Etch 2**
No polish	60	12	0
Polish	2	4	2

6.6.3 Human modifications

6.6.3.1 Striations

Seven specimens displayed striations that were the product of human agency (Table 6.17). These specimens originated in four different contexts; one from MP/UP (Layer 39), two specimens from MIS 5-4 (4), three specimens from MIS 5-5 (5), and a single specimen from MIS 2 (J) which is of Aurignacian origin and therefore falls outside the scope of this study.

In the MP/UP transition context group, Layer 39 contained the right humerus of an *Aves size Lagopus sp* with striations (Figure 6.17). A set of oblique scrapes on the proximal shaft (zone 2) suggested defleshing activities, as did two oblique cut marks at the distal fracture. Two transverse cut marks at the proximal articulation indicated an effort to disarticulate the wing from the scapular girdle.

Two specimens with striations were found in Layer 4 (Context group MIS 5-4). The complete left carpometacarpal of a Capercaillie (*Tetrao urogallus*) presented with two small, parallel cutmarks on the proximal articulation (Figure 6.18). This placement suggests incidental contact between the lithic and bone during disarticulation of the wing elements. A set of striations was also evident close to the proximal fracture of a Great Cormorant humerus (*P. carbo*). These traces were deep and accompanied by microstriations/scrapes proximal to the main incisions. It is likely the intent was to deflesh the carcass (Figure 6.19; Binford 1981).

Layer 5 (Context group MIS 5-5) produced three specimens with striations (Figures 6.24-26). The right tibiotarsus of a black grouse (*L. tetrix*) presented with a faint oblique cutmark to the distal articulation, comparable to disarticulation of the hind limb (Figure 6.20).

A longbone fragment less than 15 mm long exhibits two types of striation (Figure 6.21). Longitudinal scrapes down the centre of the fragment point towards defleshing activities. The oblique cutmark is likely incidental to this process. The dimensions of this fragment indicate identifications as capercaillie (*T. urogallus*) or a black grouse (*L. tetrix*).

A heavily weathered portion of a radius identified as *Aves size Anser sp.* (possible goose) also displays various types of striation (Figure 6.22). Close to the rounded fracture, two oblique marks are likely the product of a chopping motion to break the bone when it was fresh. Towards the other end of the specimen, oblique cutmarks indicate a defleshing or skinning of the wing.

Table 6.17: Bird remains with striations on the bone surface detailing the element (hum = humerus, cmc = carpometacarpal, tbt = tibiotarsus, rad = radius), laterality (l = left, r = right, ? = indeterminate), number of striations (multi = multiple), type of striation (cm = cutmark, cm? = possible cutmark), location, orientation (obl = oblique, tr = transverse, lo = longitudinal), and intent (da = disarticulation, df = defleshing).

Collection Reference	**MIS Group**	**Layer**	**Taxon**	**Element**	**Side**	**N.**	**Type**	**Location**	**Orientation**	**Intent**
Sc 1991-145-15	MIS 3	39	*Lagopus* sp.	hum	l	multi	scrapes & cm	123	obl/tr	df/da
Sc 1985-30-1	MIS 5-4	4	*Tetrao urogallus*	cmc	l	2	cm	1	obl	da
Sc 1986-72-3368	MIS 5-4	4	*Phalacrocorax carbo*	hum	l	2	cm	3	tr	df
Sc 1983-194-53	MIS 5-5	5	*Lyrurus tetrix*	tbt	r	1	cm?	5	obl	da
Sc 1985-116-1	MIS 5-5	5	Aves size *Tetrao* sp.	longbone	?	2	scrape & cm	?	lo/obl	df
Sc 1985-910-309	MIS 5-5	5	Aves size *Anser* sp.	rad	?	4	cm/chop	14	tr	df
Sc 2014-399-1	MIS 2	J	*Mergus merganser/serrator*	cmc	r	8	cm	123	tr/obl	da/df

Sc1991-145-15, square E33, Layer 39 (MP/UP transition); *Aves size Lagopus sp.*, right humerus.

Figure 6.17: Aves size Lagopus sp. from Layer 39 with multiple striations. Length = 41 mm.

Sc1985-30-1, square I21, Layer 4 (MIS 5-4);
Tetrao urogallus, left carpometacarpal.

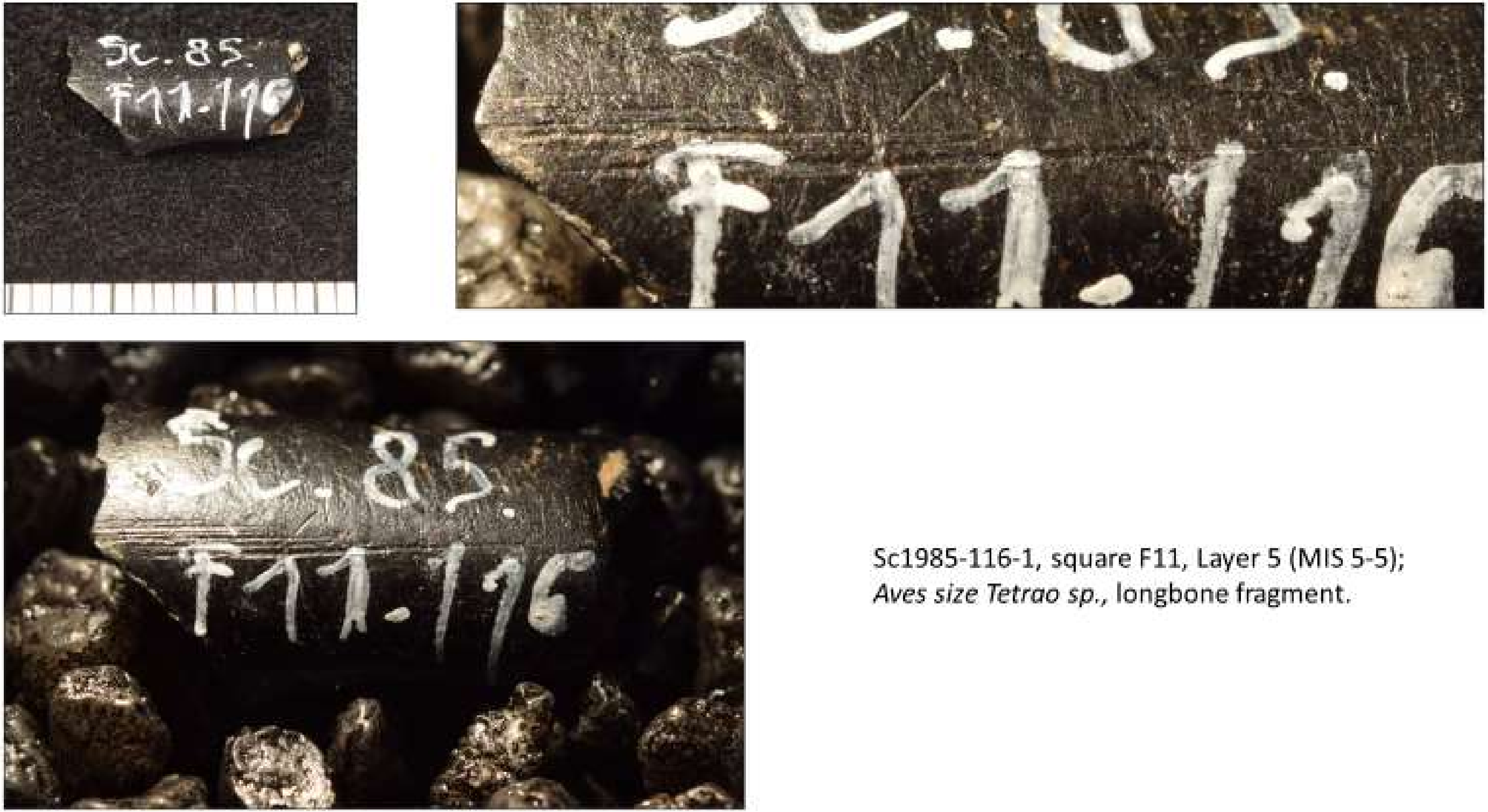
Figure 6.18: Tetrao urogallus carpometacarpal from Layer 4 with striations on the proximal articulation. Length = 52 mm.

Sc1986-72-3368, square H17, Layer 4 (MIS 5-4);
Phalacrocorax carbo, left humerus.

Figure 6.19: Phalacrocorax carbo humerus from Layer 4 with striations by the proximal fracture. Length = 93 mm.

Sc1983-194-53, square F13, Layer 5 (MIS 5–5);
Tetrao tetrix, right tibiotarsus.

Figure 6.20: The right tibiotarsus of a Black Grouse from Layer 5. Length = 20 mm.



Sc1985-116-1, square F11, Layer 5 (MIS 5-5);
Aves size Tetrao sp., longbone fragment.

Figure 6.21:Longbone fragment from Layer 5 with two types of striation on the surface.

Sc1985-910-309, square F20, Layer 5 (MIS5-5); *Aves size Anser sp.*, radius.

Figure 6.22: Radius with cut marks from Layer 5. Likely goose. Length = 55 mm.

6.6.3.2 Peeling

A single specimen, the left coracoid of a capercaille (*T. urogallus;* Sc1986-29-3, sq. F17) from Context MIS5-5 (Layer 5+6) displayed peeling at the fracture edge. However, this specimen also presented with a carnivore toothmark at the proximal articulation. It is therefore likely that the peeling was the result of fresh bone breakage during consumption by carnivores.

6.6.3.3 Thermal modifications

A long bone fragment identified as *Aves size Tetrao sp*. from MIS 5-5 (Layer 5) displayed level 3 thermal modification over the entire surface, including the fracture edges. This full exposure indicates that the entire fragment was exposed directly to a heat source after the flesh was removed from it (as testified by scrapes and a cutmark on the specimen, Figure 6.21). No other remains showed any degree of thermal modification. Hearths were documented in Layer 5 (Bonjean *et al.* 2014). The lack of material with thermal modification may be due to differential preservation of friable, burnt material in a site where most of the material has been subject to post-depositional processes (Lev *et al.* 2020).

6.6.4 Fragmentation

Fifty-four specimens (66.7%) displayed fractures that were old (made on green bone) or mixed (partially obscured by fractures made on dry bone after deposition) (Table 6.18). Of the 46 ‘old’ fractures, 17 displayed a spiral outline, 4 are transverse, and 25 are of mixed or irregular character. Irregularities were indicative of non-human agency while transverse fractures were made on dry bone and are usually the product of trampling (Fernández-Jalvo and Andrews 1990).

Table 6.18: Fractures of 'mix' and ‘old’ character by context and outline.

	MP/UP transition		**MIS 3**		**MIS 5 - 3**		**MIS 5 - 4**		**MIS 5 - 5**		**MIS 6**		**total**	
	old	mix	old	mix	old	mix	old	mix	old	mix	old	mix	old	mix
Spiral	1	1	1	0	3	0	6	1	5	1	1	0	17	3
Transverse	0	0	3	0	1	0	0	0	0	0	0	0	4	0
Mix	1	0	1	0	0	0	0	1	5	1	0	0	7	2
Irregular	1	0	7	0	3	2	2	0	5	1	0	0	18	3
Total	3	1	12	0	7	2	8	2	15	3	1	0	54	

The 17 spiral fractures originated from all main context groups, and 8 individual layers (39, 1A, 3, 4, 4A, 5, Via). 64.7 % (n = 11) of spiral fractures displayed an oblique fracture angle, and of those seven had a smooth fracture surface. These three characteristics together are indicative of human agency. A further four spiral oblique fractures had fracture surfaces that were either mixed in character (partially obscured by later flaking/fractures) or obscured by concretions. The two main occupation Layers (1A and 5) contained 1 and 5 spiral fractures, respectively.

6.7 Intrasite Spatial Distribution

The spatial distribution of avian bones from Scladina Cave was plotted onto a plan of the site in Adobe Illustrator (Figure 6.23; Figure 6.24; Figure 6.25; Figure 6.26). In MIS 5-5 (Figure 6.23), specimens bearing human modifications were concentrated between 10 and 25 metres from the cave entrance. This was the area of the main occupation at this level (Bonjean *et al*. 2014). Specimens found in this area also bear traces made by small carnivores. Where the cave joins with Saint Paul cave, two specimens bearing evidence of non-human predators were recovered from a natural alcove within the rock. A further specimen bearing digestion traces also appeared at this depth, isolated from other avian remains.

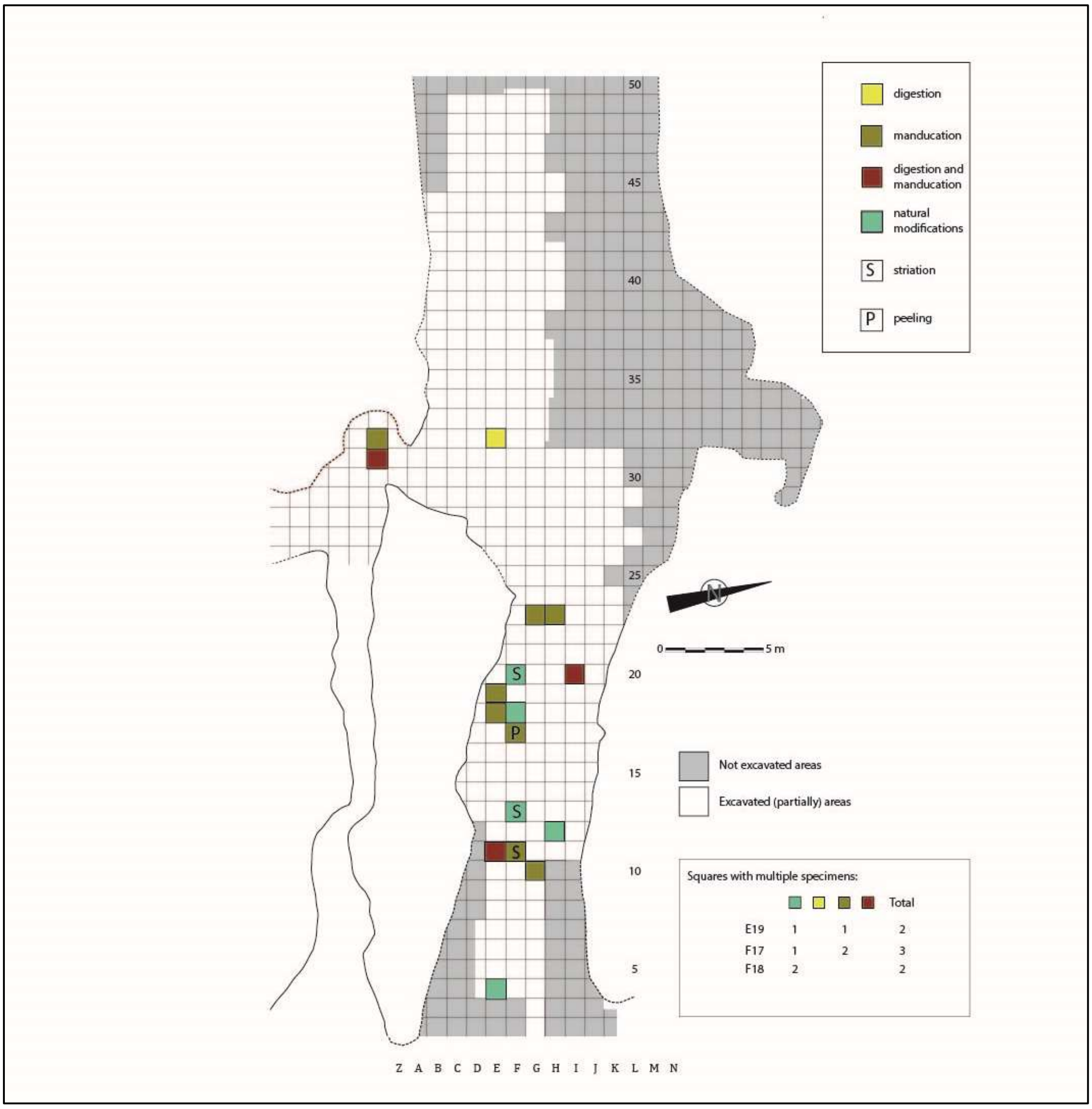
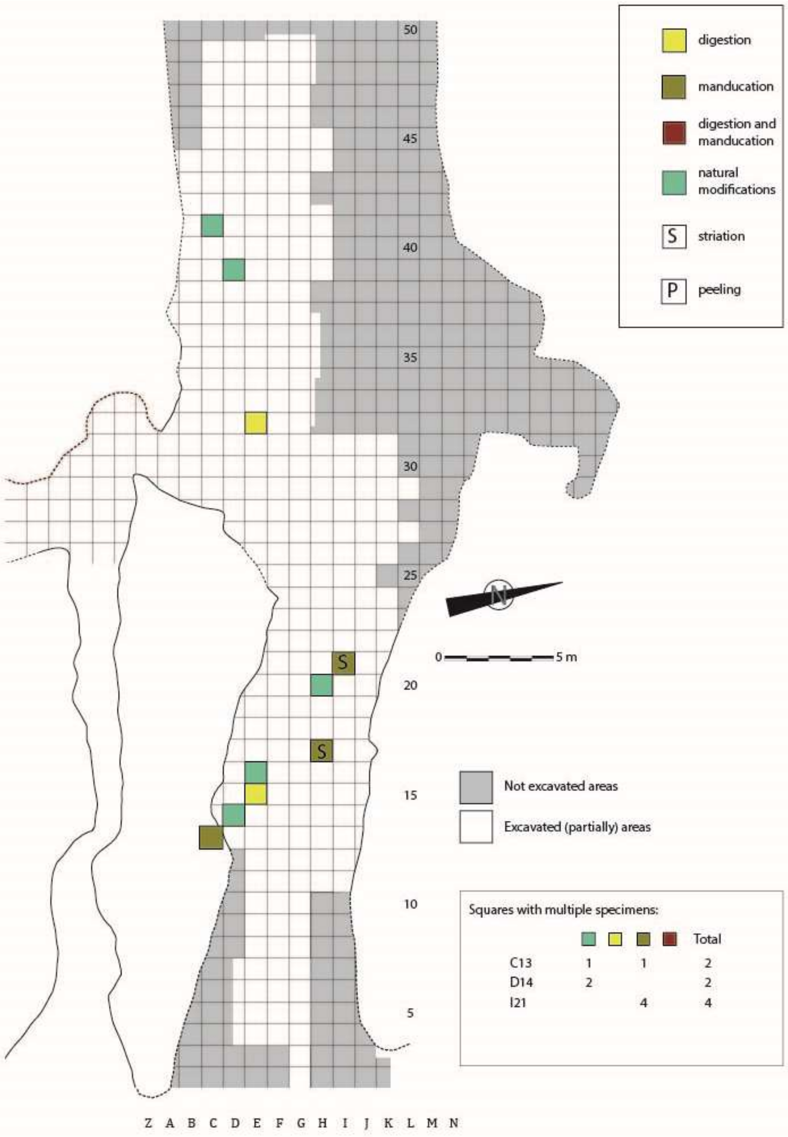


Figure 6.23 Spatial distribution of bird remains in context group MIS 5-5 showing the type of taphonomic traces identified on each specimen.The main occupation during MIS 5-5 was between 10 and 25 metres from the main entrance of the cave. Map base © Archéologie Andennaise.

Specimens bearing human modifications were located at 17 and 21 metres from the cave entrance in context group MIS 5-4 (Figure 6.24) along with the majority of remains at this level (n = 12). Three specimens appear farther back in the cave in the fill of what was once an erosional gulley (Pirson 2007; Pirson *et al.* 2008). Two isolated specimens showed digestion traces, while 7 showed traces of manducation. Those showing carnivore tooth marks were concentrated between 13 and 21 metres from the cave entrance.

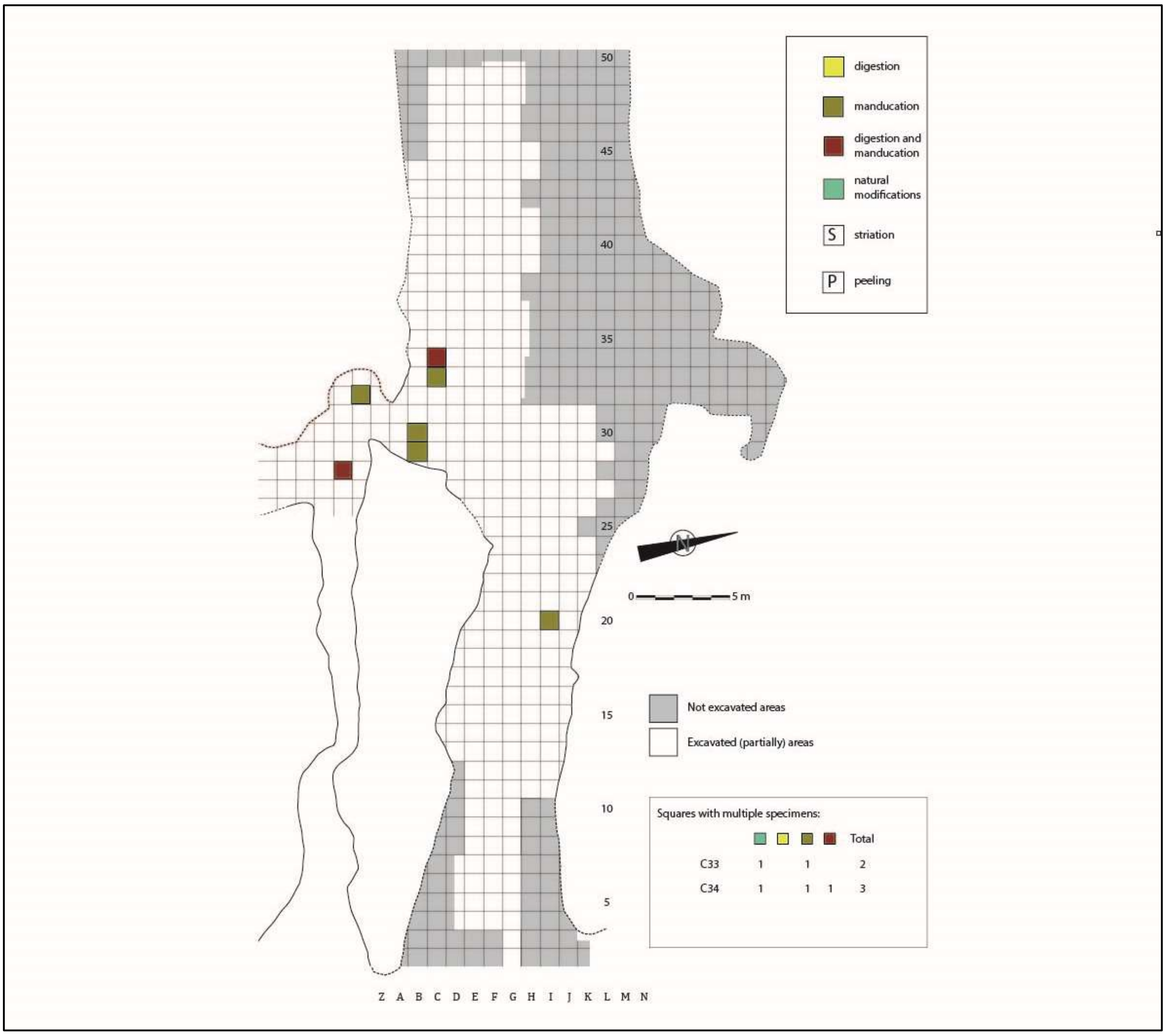


Squares with multiple specimens:

	🟩	🟨	🟫	🟥	Total
C13	1		1		2
D14	2				2
I21			4		4

Figure 6.24: Spatial distribution of bird remains from context group MIS5-4 showing the type of taphonomic traces identified on each specimen. Map base © Archéologie Andennaise.

All but one remain in context group MIS 5-3 was concentrated in the area where Scladina Cave joins with Saint Paul Cave (Figure 6.25). All but two remains display manducation traces, with some also showing evidence of digestion. This spatial distribution does not align with any anthropogenic agency in the cave, instead indicating a denning behaviour.

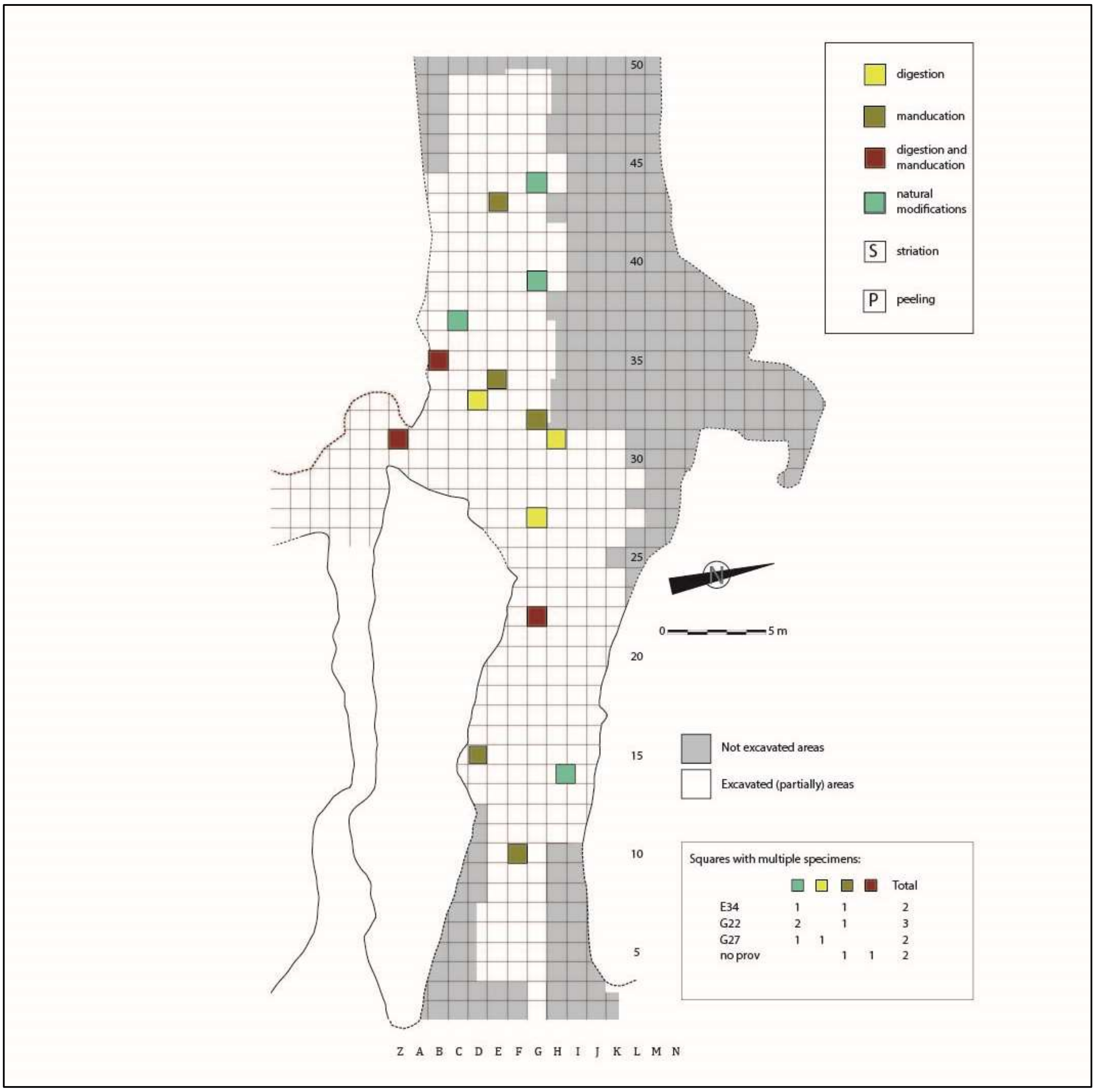


Squares with multiple specimens:

	🟩	🟨	🟫	🟥	Total
C33	1		1		2
C34	1		1	1	3

Figure 6.25: Spatial distribution of bird remains from context group MIS 5-3 showing the type of taphonomic traces identified on each specimen.Map base © Archéologie Andennaise.

The remains in context group MIS 3 appear more evenly distributed over a greater area of the cave than during MIS 5 (Figure 6.26). Predator modifications are present in all areas of the cave. Remains bearing only digestion traces are concentrated between 27 and 33 metres from the cave entrance.



Squares with multiple specimens:

	🟩	🟨	🟫	🟥	Total
E34	1		1		2
G22	2		1		3
G27	1	1			2
no prov			1	1	2

Figure 6.26 Spatial distribution of bird remains in context group MIS 3 showing the type of taphonomic traces identified on each specimen. no prov = specimens without spatial information beyond unit. Map base © Archéologie Andennaise.

6.8 Interpretation of the Scladina avifauna

6.8.1 Neanderthal behaviour

This investigation of the Scladina avifauna confirms Neanderthal exploitation of birds in both MIS 5 and MIS 3 in NW Europe. Most cut-marked specimens were game birds (Galliformes) and water fowl (Anseriformes) except one, a cormorant (*P. carbo*). Gamebirds and water fowl are well known for their palatable meat and have been exploited by Neanderthals at Bolomor Cave (Blasco and Peris 2009, 2012). The placement and orientation of cut marks present on the remains suggest butchery for subsistence purposes. Despite the small number of remains in total (n = 81), cutmarks appear on 8% (n = 7) of the sample with more than one modification often present on each bone. The high frequency of surviving remains with human modifications suggests that the exploitation of birds was a regular behaviour of the Neanderthals of Scladina and not a rare occurrence.

MIS 5-Layer 5, dated to 130 ka BP (Pirson *et al*. 2018), contains the clearest evidence of exploitation. A minimum of three birds were processed out of a total MNI of 17 (17.6%). A long bone fragment of a grouse-sized bird was especially informative as it suggested three types of Neanderthal behaviour. Firstly, cutmarks on the bone disarticulation indicated that the specimen was brought into the cave, defleshed, and eaten. Secondly, the bone was later discarded and trampled, shattering it into small fragments like the one recovered. Thirdly, the fragment was exposed to direct heat, likely in one of several hearths recorded in Unit 5 (Bonjean *et al.* 2014). This caused a uniform char across the entire bone surface, including the fracture edges. In terms of Neanderthal behaviour, this one specimen functions as a snapshot of Neanderthal life, informing us about their subsistence strategy, the presence of a hearth in their camp, and the organization of their living space. Thermal modification only appears on this single specimen. The scarcity of this modification in the sample studied can be attributed to the fragile nature of burned bones, and their almost complete destruction when trampled (Lev *et al.* 2020). Another grouse and a goose-sized bird were also consumed, implying that the Neanderthals on Unit 5 not only exploited birds found in the wooded areas in the direct vicinity of the cave, but also targeted species that frequented aquatic habitats.

Intrasite spatial analysis of the specimens with human modifications in MIS 5-5 revealed that they were concentrated between 10 and 25 metres from the cave entrance. This coincided with other anthropogenic lithic and faunal datasets, placing the cut-marked remains securely within the main occupation zone (Figure 6.23; Figure 6.4; Otte and Bonjean 1998; Abrams *et al.* 2014). The scattered remains between 30 and 36 metres from the entrance may indicate scavenger activity by carnivores. It is also possible this spread of artefacts is the result of post depositional processes which are evident throughout the sequence in Scladina Cave (Pirson *et al.* ibid.).

In the subdivisions of MIS 5-Layer 4, specimens bearing striations were also located towards the front of the cave (Figure 6.24). However, some material was distributed well into the back section of the cave. These specimens came from within sedimentary Unit 4A and had been washed from their original position through the same erosional melting gulley that caused the distribution of the skull fragments and teeth of the Scladina juvenile throughout Unit 4A. The origin of the avifaunal material in MIS 5-4 is not known beyond the fact that it was deposited after Unit 5 and before Unit 3 (Pirson 2007). It may represent material reworked from Unit 5 like the lithics examined by Di Modica and Bonjean (2004, 2005). Thus, while they represent clear evidence of Neanderthal exploitation of birds, their provenance is not certain.

Of the two species bearing cutmarks in MIS 5-4, one stands out as unusual. The great cormorant (*P. carbo*) is a relatively recent addition to the current ecosystem along the river Meuse. Its presence was first recorded in the early 1990's (Carss and Marzano 2005), but today both wintering and breeding populations can be found along the river and its tributaries. This bone signifies the first instance of a cormorant bone in sediments dating to MIS 5 in Belgium (Q. Goefette, *pers. comm.*). That it also had striations on the bone surface and was part of the Neanderthal diet at Scladina makes it an even more intriguing find. During my visit to Scladina Cave, I observed the cormorant groups roosting in trees on the islands along the river Meuse. The islands offer a greater degree of security and privacy than the riverbanks, and are therefore a preferred roosting site for some wetland birds (Cramp *et al.* 1977-1994). The identification of flint sources north of Scladina imply that crossing the Meuse would be a necessity in procurement of raw materials (Di Modica *et al.* 2010). Neanderthals might have combined their expeditions to procure flint with hunting trips, exploiting the food sources the river offered as they traversed it. At the very least, they could have observed the cormorants along the river while crossing it.

In MIS 3, the living space in the cave expanded into the inner cave (Bonjean *et al.* 2002). This was reflected in the distribution of bird remains (Figure 6.26). This expansion may be due to the collapse of the aven during the deposition of Unit 1B (Pirson 2007) which allowed light to filter into the living space below and made it easier to navigate the area without light from a hearth. Another possibility is that post depositional processes transported some of the avian material further into the cave (Pirson 2007; Pirson *et al.* 2008). There was some overlap between a cluster of bird remains and an area of lithic concentration (Figure 6.27), but the numbers of specimens are too low to provide a definitive relationship.

No remains from MIS 3 (Layers 1A and 40) showed evidence of human agency. This is also the case with the macrofauna of Unit 1A where the only evidence of human agency is 196 burned bones that were used for fuel (Abrams *et al.* 2010). On the other hand, the relationship between the NISP and MNI indicates that more birds were being introduced to the accumulation during this phase than in periods with no human occupation (MIS 5-3 and MIS 5-4). The contexts of MIS 3 also contained a greater variety of species (n = 11) than MIS 5-5 (n = 7) where bird exploitation is unambiguous.

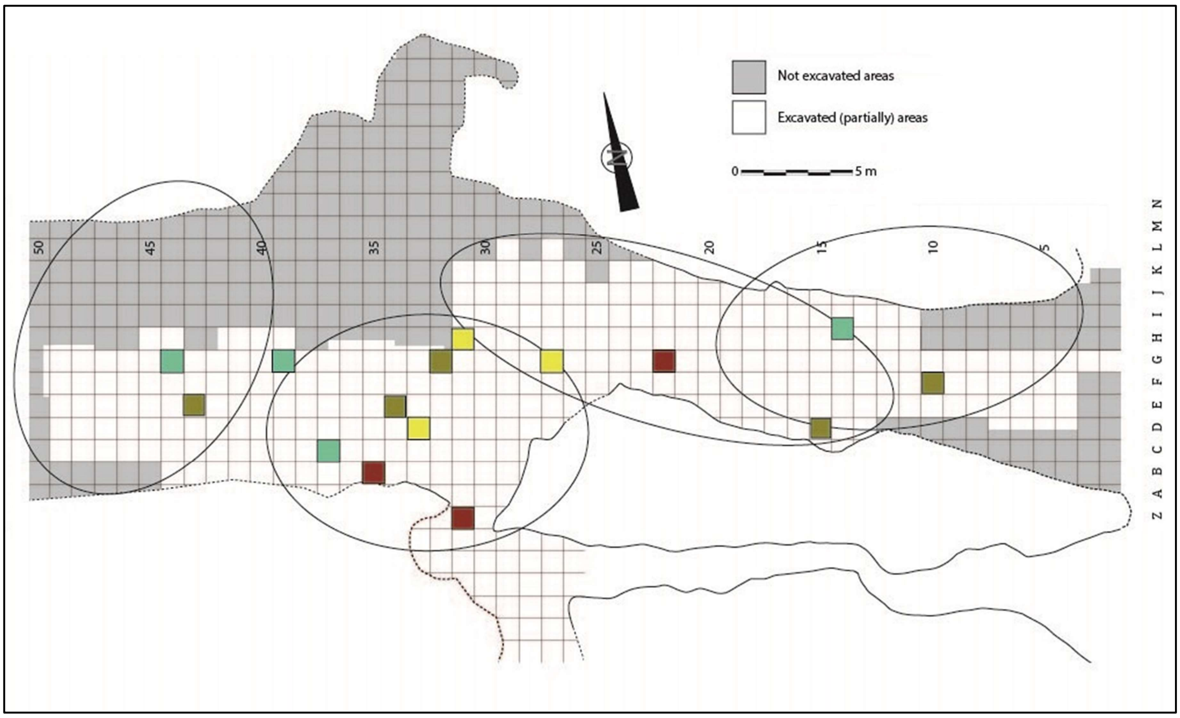


Figure 6.27: Distribution of bird remain in context group MIS 3 in relation to the flint distributions in Unit 1A (oval shapes).(Yellow signifies digestion traces, gold = manducation, red = digestion and manducation, green = natural taphonomic processes)Map base and flint distribution data © Archéologie Andennaise.

No exploitation of birds for symbolic purposes is evident in the Scladina avifauna, but cultural use of pigment in contemporary layers attests to the cognitive abilities of the Scladina Neanderthals (Bonjean *et al.* 2015).

6.8.2 Other agents contributing to the accumulation

All bird remains in the occupationally sterile MIS 5 Layer 3 displayed carnivore tooth marks. It is also the only context group where all types of carnivore modification were visible on the bone surfaces. The remains were of game birds (MNI = 2; a capercaillie and a black grouse-sized bird) that were likely predated close to the cave. The remains were limited to an area with an alcove at the point where Scladina and Saint-Paul caves merge (Figure 6.25, squares X/Y32/33). The NTAXA (n = 1) differs from the occupied units 1A and 5 (context groups MIS 3, n = 11 and MIS 5-5, n = 7). The bird remains from Layer 3 were accumulated by a small to medium carnivore and indicated denning behaviour through their distribution. The mammalian fauna is rich in carnivores, including large mammals such as cave bears (*U. spelaeus*), wolves (*C. lupus*), and cave hyenas (*C. c. spelea*) (Daujeard *et al* 2016; Table 6.3). However, taphonomy indicates that the carnivores responsible for the partial accumulation of bird remains in Scladina were smaller. The presence of dhole (*Cuon sp*.), red fox (*V. vulpes*), badger (*M. melis*), wild cat (*F. silvestris*), and mustelid remains are prime candidates for the agent behind the manducation and digestion traces identified on bone surfaces.

Though small carnivores hunted birds of their own accord, they may also have scavenged the discarded remains of human meals. This behaviour may be surmised from the presence of both cut marks and carnivore toothmarks on the bones of a cormorant and a capercaillie in MIS 5-4. In MIS 5-5 avian remains with carnivore traces accounted for 56.5% of the sample, but there was no evidence of carnivores scavenging Neanderthal leftover bird carcasses. Instead, rodent gnawing was present on the discarded bone of a large grouse-sized bird. In the natural alcove utilized by carnivores in MIS 5-3, a co-occurrence of bones suggests its use as a den at some point during MIS 5-5. The presence of remains modified both by human and non-human agents within the cave suggests that Neanderthals may have shared their living space with other species. The cavernous karstic structure that is Scladina has the potential for both human and non-humans to have brought in their prey simultaneously. However, based on present evidence, this must remain conjecture and the small carnivores cannot be considered commensal. The mammalian record shows the presence of canids and bears during this phase (Patou-Mathis 1998; Daujeard *et al.* 2016), but the bird bones do not reflect predation by large mammalian carnivores. This is not unexpected as larger carnivores would eat the whole carcass and digest all the bones (Andrews 1990).

The spatial distribution of owls (Strigiformes) under the main arch of the cave during MIS 5 (Figure 6.28) suggests that these were the result of attritional accumulation in connection to roosts and nests. They were unlikely to have roosted when the cave was occupied by Neanderthals (Bochenski 2005; Bochenski *et al*. 2018). There is no evidence of raptors catching birds in the recovered material, but a study of digestion traces on the molars of micromammals from MIS 5 and MIS 3 determined that two classes of Strigiform predator were responsible for their accumulation (Lopez-Garcia *et al.* 2017). Diurnal raptor remains in MIS 3 layers (n = 2) were found in an area between 35 and 40 metres from the cave entrance. Neither the *Gyps/Aquila*-sized raptor nor the sparrowhawk (*A. nisus*) specimen exhibited identifiable traces of human agency.

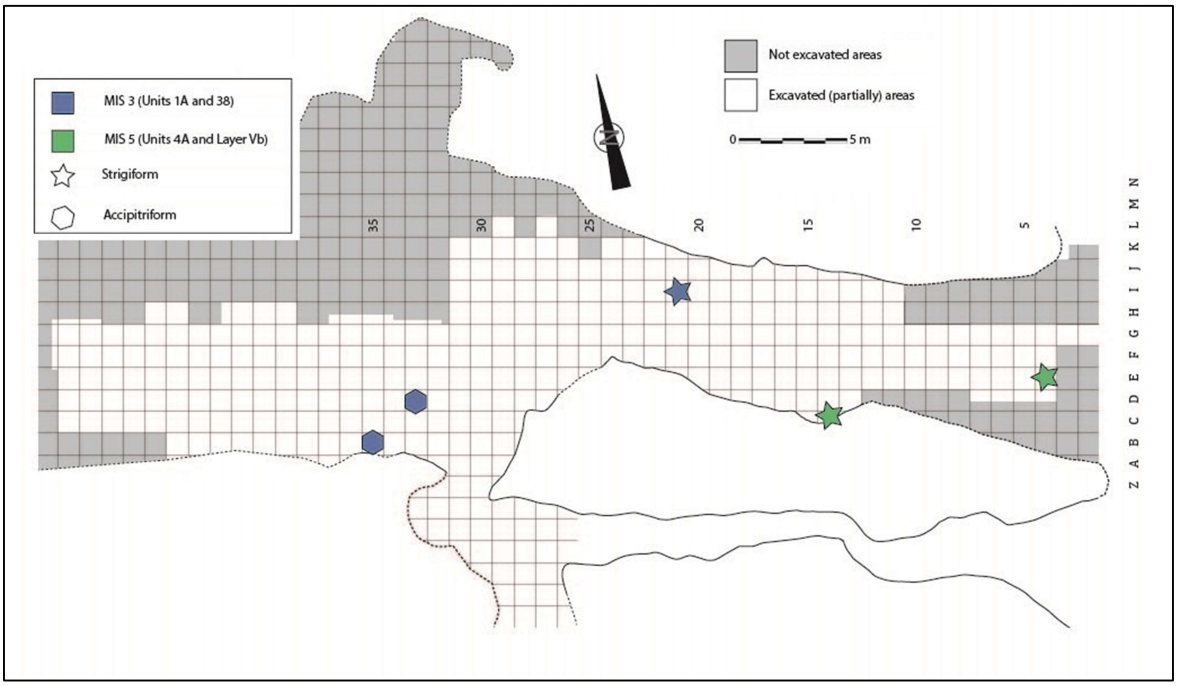


Figure 6.28: Distribution of raptor remains in Scladina Cave in MIS 3 and MIS 5.

6.8.3 Ecological interpretations

The avian species present in the sample point towards the presence of a landscape that featured both open and wooded areas in MIS 5 and MIS 3. This might have been in the form of a mosaic-type vegetation, or a dynamic shifting of habitats through time. Large Tetraonidae (capercaillie and black grouse) would have frequented boreal environments in the valleys around the cave, while the less arboreal *Lagopus* would have occupied a more open, tundra environment (Cramp *et al.* 1977-1994). Waterfowl such as the Mallard (*A.*

platyrhynchos) and geese (*Anser sp.)* could have exploited the nearby water bodies. Mallards are highly adaptable and readily exploit any water body available (Birdlife Datazone 2021). Geese however may have been drawn to the islands on the River Meuse for breeding and inland water bodies (Cramp *et al.* ibid). The islands along the Meuse also provide a nesting habitat for the Great Cormorant (*Phalacrocorax carbo*). This insular nesting behaviour is seen in the species in the today (Carss and Marzano 2005).

These observations are supported by pollen analyses (Court-Picon and Damblon; Pirson 2007) and in the small and large mammal studies of various authors (Cordy 1992; Simonet 1992; Moncel 1998; Patou Mathis 1998; Daujeard *et al.* 2016; Lopez *et al*. 2017). Herbs and forbs are most frequent, in both MIS 3 and MIS 5, signalling open areas. The presence of boreal conifers in both stages also alludes to patches of forest (Court and Damblon; Pirson 2007; Pirson *et al.* 2008). In MIS 5 however, malacophyll trees appear, signalling a warmer climate than in MIS 3 (Pirson *et al.* ibid.) Micromammals from MIS 3 (Unit 1A) indicate cold and dry conditions (*Lagurus lagurus, Lemmus lemmus, Dicrostonyx torquatus, Microtus arvalis and Chionomys nivalis*). In MIS 5 the species representation indicated sporadic peaks in aquatic local environments (*Microtus agrestis, Talpa europaea, Sorex gr. araneus, and Microtus gregalis*) (Lopez-Garcia *et al.* 2017).

Birds found in the cave sediments today occupy arctic to temperate latitude bands (categories A to C) with some species appearing in multiple latitude bands. This distribution is mirrored by temperature tolerances, which also trend towards cold to temperate climate ranges. The presence of arctic taxa (*B. scandiacus, A. albifrons/serrirostris*) in MIS 5-5 and MIS 5-4 suggested the climate was cooler than today, an observation made previously using other proxies: Cryoclastic sediments from Layer 5 (MIS 5-5) had a clear periglacial climatic signature , herbs and forbes in the pollen record indicated a steppe/tundra landscape with boreal inclusions in a cooling climate phase (Court-Picon and Damblon in Pirson 2007; Pirson *et al.* 2008), while magnetic susceptibility indicated a cooler period (Elwood *et al.* 2004)

The erosional channel that formed during the deposition of Layer 4 (MIS 5-4) is a melting gulley (Pirson 2007). This feature reflected a climatic improvement which was indicated by the presence of boreal to temperate forest, the appearance of macrophyll temperate species, and monolete fern spores (Court-Picon and Damblon in Pirson 2007). Micromammals in Layer 4 showed a return of forest species, bats and insectivores, and the disappearance of arctic taxa. (Cordy 1992; Lopez-Garcia *et al*. 2017) forest species, bats, insectivores. However, the birds show no environmental change from MIS 5-5 to MIS 5-4.

Occupationally sterile layer 3 (MIS 5-3) held few remains, making ecological trends impossible to establish. However, the presence of game birds (grouse) indicates that boreal and mixed (open and boreal) environments were present nearby. This is also visible in the small mammals studied by Cordy (1992) and Lopez-Garcia *et al.* (2017) and large mammals examined by Simonet (1992). Magnetic susceptibility and palynology indicated cooling with temperate pollens disappearing and being replaced by tundra species with some boreal trees (Bastin 1992; Pirson *et al.* 2008).

In Layer 1 (MIS 3) there is an increased number of cold tolerant bird species that are present in multiple latitudinal bands (Category F). There are also only species with moderate to generalist bioclimatic tolerances, reflecting an avian population capable of surviving changes in climate and environment. Palynology from MIS 3 shows a high herb count which reflects a hardy climate and an open tundra-type landscape (Pirson *et al*. 2008). Migratory species like the Whimbrel (*N. phaeopus*) and the cormorant (*P. carbo*) can inform us about the season of deposition. Whimbrels generally breed in the sub-arctic during summer, spending winters in the tropics (Cramp *et al.* 1977-1994). The presence of possible Whimbrel remains at Scladina may indicate deposition in the summer (Finlayson 2011). Two juvenile chamois in Layer 5, one killed in winter and the other between October and June, speak to a winter phase of occupation when Scladina functioned as a chamois 'hunting stop' (Patou-Mathis 1998). If the tentative identification is verified, the presence of the Whimbrel along with the chamois indicates that Scladina was occupied at different times throughout the year.

Overall, the avifaunal remains of Scladina suggest temperate to cold climatic conditions with diverse landscape-types available around the cave. Though there were periods of climatic improvement and cooling throughout the sequence, the ecological variables reflected by the bird species recovered from the cave sediments are generally homogeneous. The small mammals and palynological data provide a more detailed account of the climatic and environmental changes than the avifauna

6.8.4 Summary

- The Scladina avifauna has a NISP of 81 and an NTAXA of 12. The remains originate from 22 original layers which were grouped into six groups covering MIS 6 to MIS 1.
- Cutmarks identified on seven specimens from 4 layers reflect 6 species, including game birds, ducks and geese, and a cormorant. These show that Neanderthals included birds in their diet in MIS 5 (Layer 5 - MIS 5-5 and Layer 4 – MIS 5-4) and MIS 3 (Layer 39 – MP/UP transition). Cutmarks on a bone from MIS 2 shows that bird exploitation was also practiced by the Aurignacian inhabitants of the cave (Pirson 2007; Bonjean *et al.* 2014).
- The spatial distribution of remains reflects the single living area in MIS 5 and the division of living areas in MIS 3 after the aven began to open (Pirson 2007; Di Modica 2010; Abrams *et al.* 2010). In MIS 5-3 (Layer 3), a concentration of remains close to the alcove where Scladina Cave joins Saint Paul cave suggested a carnivore denning area.
- The bird species present in the sequence reflect an overall cold, dry to semi-humid environment in MIS 5 and MIS 3. Boreal, cold to temperate tolerant species exploited both forest and open habitats in the vicinity of the cave. Waterfowl frequented the rivers nearby.
- The ecological results from the Scladina avifauna align well with general traits defined by other researchers, but fall short of the high resolution achieved through the study of other proxies (Pirson 2007; Pirson et al. 2008; Lopez-Garcia et al. 2017).

7 Tabun Cave

This chapter presents the results of my taxonomic and taphonomic study of avifauna remains from Middle Palaeolithic occupation layers B and C at Tabun Cave, Israel. These remains were recovered from excavations undertaken by Jelinek from 1967 to 1972, and Ron Shimelmitz and Mina Weinstein-Evron of the Zinman Institute of Archaeology at the University of Haifa, from 2017 to present. The remains were made available to me to undertake my analyses, which is the first time this material has been investigated. The site is of great value to this thesis as it provides a perspective of Neanderthal behaviour in a different environmental setting from that of other sites under study. Tabun is located in an area that both Neanderthals and modern humans occupied in the Late Pleistocene (Kuhlwilm *et al.* 2016; Hershkovitz *et al.* 2018; Hubisz, Williams & Siepel 2020). Israel is also an avian migration bottleneck of three migration routes between Africa and Eurasia (Leshem and Yom-Tov 1998). This chapter focuses exclusively on the Middle Palaeolithic layers of Tabun Cave where the avian remains examined were recovered.

7.1 Physical setting

Tabun Cave (32°40’13.80”N 34°57’55.80”E) lies on the western border of Mount Carmel, ~15 km south of the city of Haifa in Israel (Figure 7.1). This karstic cave is set within limestone bedrock that forms the southern flank of the Wadi el-Mugharet (Valley of Caves). The cave is part of the Nahal Me’arot UNESCO World Heritage site along with the nearby caves of Gamal (Lower Palaeolithic), el-Wad (Middle-, Upper-, and Epi-Palaeolithic) and Skhul (Middle Palaeolithic) (Figure 7.2). Together, these caves provide the best continuous record of the Mid-Late Pleistocene in Southwest Asia presenting a total sequence of ~500,000 years (Ronen *et al*. 2011).

Tabun Cave is located 45 m above sea level and has a north-facing entrance. It is composed of three roughly circular chambers (Garrod and Bate 1937, Figure 7.1): The outer chamber measures 15 m by 18 m and opens out onto a steep terrace. The intermediate chamber, measuring 5 m by 5 m, is little more than a roofed constriction between the inner and outer chamber. Finally, the inner chamber, measuring approximately seven metres in diameter, has a natural chimney.

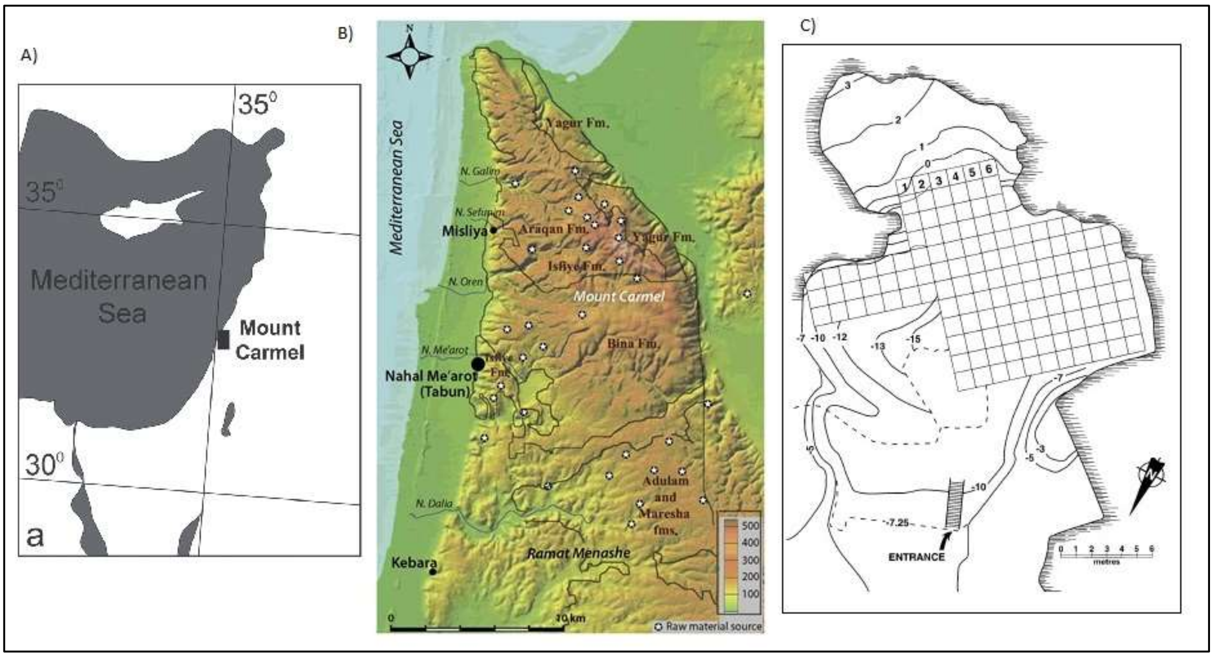


Figure 7.1 A) Location of Mount Carmel on the eastern coast of the Mediterranean Sea (Yeshurun 2016). B) Location of Tabun Cave (Shimelmitz et al.2020). C) Plan drawing of Tabun Cave (Albert et al. 1999)

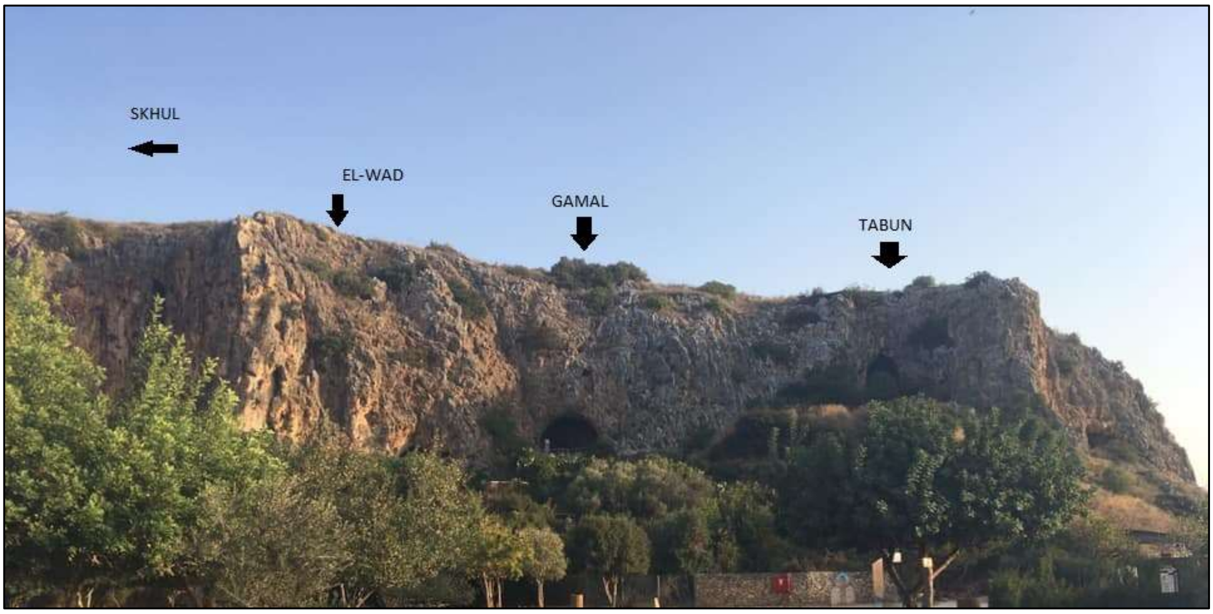


Figure 7.2: The archaeological sites of Tabun, Gamal, El-Wad, and Skhul make up the Nahal Me'arot Nature Reserve. Facing south. Photo: L. Amos 2019.

Tabun Cave overlooks a wide coastal plain that extends to the Mediterranean Sea. At present, the coastline is ~5 km away, but this distance varied during the Pleistocene due to fluctuations in sea level caused by glacial cycles (Sivan *et al*. 1999, Benjamin *et al*. 2017). To the east, Wadi el-Mugharet continues into the interior of Mount Carmel, an 8 km wide, 21 km long coastal mountain range that runs north - south in northern Israel. The wadi (valley) ecosystems at Mount Carmel support an impressive biodiversity of life. The heat of the sun on south facing slopes offers hot, arid habitats, while the north-facing inclines are cooler with a greater shrub cover. In the bottom of the wadis, water may flow at certain times of the year, and trees offer shade. These conditions allow diverse faunal and floral species with different ecological requirements to coexist within a limited geographical area (Nevo *et al*. 1999; Nevo 2009; Pavlíček *et al.* 2003).

7.2 Archaeological investigations

Three major excavations have taken place at Tabun Cave. The first was directed by Dorothy Garrod, from 1929 to 1934, who undertook large-scale excavations in all three chambers of the cave (Garrod and Bate 1937; McCown and Keith 1939: Zviely and Ronen 2004a). Garrod documented a 25-metre stratigraphic sequence containing Lower Palaeolithic, Middle Palaeolithic, Bronze Age, and recent occupation horizons (Layers A-G; Table 7.1; Figure 7.3; Figure 7.4). Jelinek directed the second excavation from 1967 to 1971 with the aim of further refining the geological and cultural history of the site. His team recorded a ten-metre deep stratigraphic profile in the intermediate chamber and divided the sequence up into 14 major geological units and 90 beds (Jelinek *et al*. 1973; Jelinek 1975, 1982ab, 1988, 1990). The third excavation from 1975 to 2003 was undertaken by Ronen and focused on Lower Palaeolithic levels (Goldberg and Nathan 1975; Ronen and Tsatskin 1995; Tsatskin 2000; Zviely and Ronen 2004 b; Ronen *et al.* 2011). A new phase of excavations is underway in the inner chamber, directed by Shimelmitz and Evron (UoH).

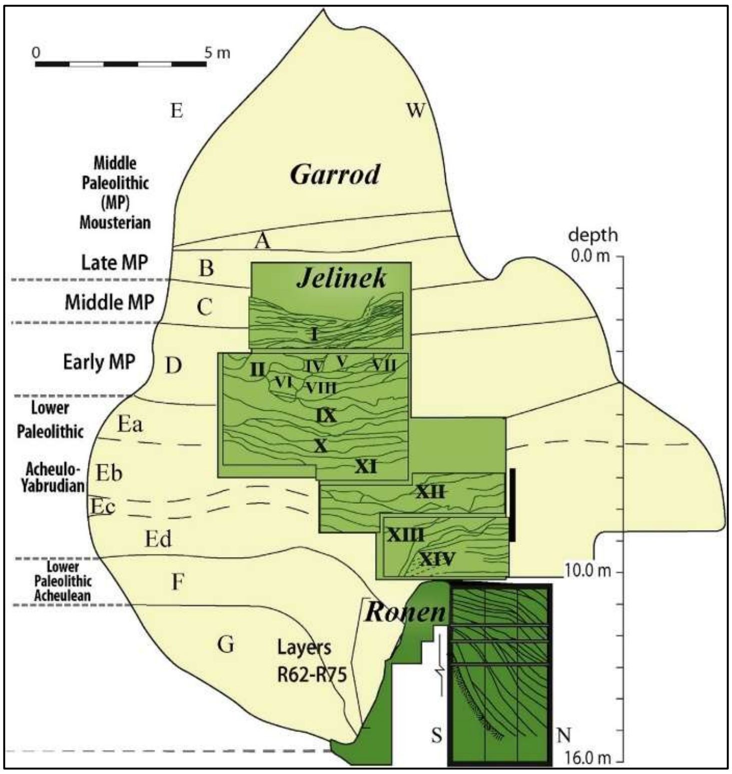


Figure 7.3: Stratigraphy of Tabun Cave (Shimelmitz et al. 2020).

Figure 7.4: Photograph of Tabun section of Garrod in the present day. Photo: L. Amos 2019.

Jelinek found reasonable agreement between Garrod's stratigraphic sequence and his own interpretation, equating Unit XIV to Layer G of Garrod, Unit XII roughly to Layer Eb, Unit XI roughly to Layer Ea, Unit IX to the lower part of Layer D, Units V-II to Layer D/C and Unit 1 to Layer C. However, recent studies have reassessed the correlations, instead equating Jelinek's XIV to Garrod's Layer Ed (Table 7.1; Figure 7.3; Figure 7.4; Jelinek *et al*. 1973; Jelinek 1982; Mercier and Valladis 2003; Ronen *et al*. 2011; Kuhn and Clark 2015; Shimelmitz *et al*. 2020). The avifaunal remains discussed in this chapter come from the excavations of Jelinek and the recent excavations of Shimelmitz and Evron. Specifically, the fauna was recovered from Unit I of Jelinek's sequence in beds 1-26 (Garrod's Layer C), as well as from material recovered from the inner chamber in the current campaign (Layer B of Garrod and an area not excavated by Jelinek). Information on these specific contexts now follows.

Table 7.1: The sedimentary sequence of Tabun Cave showing stratigraphic units as described by Garrod and Jelinek, including industry, sediment type, dating, climate interpretations, fauna, human remains, number of lithics, presence of hearths, and mode of occupation. After Garrod and Bate (1937), Jelinek et al. 1973, Jelinek 1982, Mercier and Valladas 2003, Coppa et al. 2005 & 2007, Ronen et al. 2011, Shimelmitz et al. 2020. TL = thermoluminescence, ka = thousand years. Layers B and C are highlighted in grey because this is where the avian remains come from.

Garrod Layer	**Chronology/ Industry**		**Sediment**	**Jelinek Bed**	**Jelinek Unit**	**Dating (TL)**	**Climate**	**Fauna**	**Human remains**	**nLithics tools/total**	**Hearths**	**Mode of occupation**
A	Bronze age to Modern		Contains lumps of breccia identical to Layer C					Hippo teeth in lump originating from Layer C	Human milk incisor in 'Layer C' lump; dry human remains (post Mousterian)			
Chimney			Division between I&II is arbitrary					Bones more complete here than inside lower cave layers	Fragmentary human remains in Chimney II, 4.50m above datum	369/1087		
B	Levantine Mousterian	Middle palaeolithic	Unit I: terra rossa washed in through chimney from plateau above; limestone blocks from chimney collapse; division between chimney and B is arbitrary	Not excavated	Not excavated	Undated; prob. 75-47 ka	Increased rainfall	Bate's great faunal break. Disputed by later studies. Higher frequency of *dama mesopotamica* than C	7 isolated teeth at various depths (tabun bc7); 29 scattered skull fragments at 3.20 above datum (associated with 5 deer phalanges in a heap); 9 milk teeth with fragments of maxilla at 2.20 above datum	475/955	Scattered hearths	Non-domestic. Possible butchery site and use of the chimney as a natural trap during game drives. Also, possible that the natural trap became a known source of game
C				1-17	I	165+/-16 ka	Climate grows drier, but perennial water is present. Dense vegetational cover with interruptions of grass and lower mediterranean type vegetation	Rich fauna with several distinct types. Hippopotamus and rhinoceros. Greater proportion of *gazella gazella* than B	Almost complete skeleton, 1.35 below datum, 0.35 below surface of C (Tabun 1); mandible on east of talus at 2.20 below datum (Tabun 2); right femur shaft, right *os hamatum*, left pisiform, terminal phalanx of left pollex, all from same individual (?) At 2m below datum; distal fourth of right radius	679/1907		Domestic occupation site. Frequently used in lower c, but less and less frequent into unit i as chimney collapses become more frequent and greater in volume
			Unit II: Thin alternating layers of varying concentrations of terra rossa, wood ash, charred materials, and baked soil; Increasing amount if limestone upwards; Chimney begins to open at beginning of this layer	18-26							Continuous hearths	
D				27-69	II-IX	196 +/-21 ka	Drier than previously	Bone found in red soils		1115/2133		

Garrod Layer	Chronology/ Industry		Sediment	Jelinek Bed	Jelinek Unit	Dating (TL)	Climate	Fauna	Human remains	nLithics tools/total	Hearths	Mode of occupation
			Unit III: eolian sand, increasingly silty upwards, the top part of iii is strongly disturbed by small erosional channels and slumping			222 +/-22 ka 256+/-26 ka						
E	Acheulo-yabrudian	Lower palaeolithic		70-90	X-XIV	267 +/- 22 ka 264 +/- 28 ka 324 +/- 31 ka 302 +/- 27 ka 415 +/- 27 ka	Warm, damp climate; perhaps tropical at the beginning, gradual approach to drier conditions in layer D	At 8.25 below datum, a mound of red earth against the south wall of the trench contained well preserved bird bones	5.60 below datum - right femur shaft, male (tabun e1); 6.50 below datum – lower right molar tooth, female (tabun e2)	36514/44634		
F	Acheulian			Excavated by Ronen (r64-r67)		Undated; prob >400 ka	Fauna suggests a warm, damp, probably tropical climate	Rodents, small birds, millipedes		3859/4370		
G	Acheulian (Tayacian)					Undated				75/464	Distinct hearths	

7.2.1 Stratigraphic Interpretations of Layer B and Layer C

I am highlighting Garrod's layers B and C because the avian remains studied in this thesis come from those contexts. Layers B and C differ somewhat in sedimentary composition. Both layers decrease in thickness from the inside towards the outside of the cave, indicating that the source of the sediment was the chimney where terra rossa from the plateau above had washed in. While Layer B contained mainly red clay or terra rossa sediments from the plateau above the cave, Layer C was comprised of a series of thin beds that vary in colour from red to black and white (Jelinek *et al.* 1973, 1982a). Both layers contained angular limestone blocks, which first appeared at the bottom of Layer C and increased in size and frequency upwards into Layer B. This was consistent with an increasingly rapid opening of the chimney above the site, leading to a change in deposition (Jelinek *et al.* ibid).

Garrod interpreted layers B and C as occupation deposits based on the presence of lithics, hearths, and cutmarks on animal bones. She noted a distinction between the two layers, with evidence of human agency on the fauna becoming sparser in layer B, while layer C contained a greater number of lithics, although the proportion of finished tools was higher in Layer B than in Layer C (Garrod and Bate 1937; Table 7.1). Jelinek (Jelinek *et al.* 1973; Jelinek 1975, 1977) also identified large concentrations of lithics, including manufacture debris, belonging to the Levantine Mousterian industry produced using a Levallois reduction sequence. He noted that these were more frequent in Layer C (equivalent beds 18-26 of Unit I) than in Layer B (equivalent upper beds 1-17) where only a small scatter of artefacts was found (Table 7.2; Jelinek 1982), and that the proportion of flakes and points differed significantly between Layers while the presence of blades was uniform throughout. Jelinek interpreted this as a change of mode from a residential, continuous occupation in Layer C to a butchering station for game in Layer B. He argued that game was driven towards the chimney, which would function as a natural trap (Jelinek *et al.* 1973, Jelinek 1982). Current excavations focus on the chimney area with the aim to examine the nature of sediment deposition more closely, and to determine whether there is in fact a change in the use of this space from Layer C to Layer B.

Garrod observed sediment disturbances between Layer C and Layer D (Garrod and Bate 1937), as did Jelinek in equivalent Units III-IV (Jelinek *et al.* 1973). This disturbance highlighted to both a possible discontinuity or hiatus, which was reflected in a change in the composition of faunal assemblages between the two layers (see section 7.2.3).

Table 7.2: Basic lithic categories, Tabun Unit I (Jelinek 1982b).

	Lithic categories		
Beds (Jelinek)	**Flakes**	**Cores**	**Tools**
1-17	272	52	54
18-26	2947	253	364

7.2.2 Human remains

Human remains were found in both Layer B and Layer C. The most well studied specimens relevant to this thesis are Tabun 1, Tabun 2 and Tabun BC7 (Table 7.3). Tabun 1 was a female Neanderthal of slight build, found close to the surface of Layer C. This led to the interpretation by some researchers (Garrod 1937, Bar-Yosef and Callander 1999) that the remains were from a burial from overlying Layer B. ESR dating on the remains produced results of 112+/-29 ka and 143+/-37 ka (Grün and Stringer 1991).

Tabun 2 was an individual of indeterminate taxon (Harvati and Lopez 2016), excavated from Layer C. Garrod noted that this individual had a chin and could therefore not be a Neanderthal (Garrod and Bate 1937). The jaw was found in 6 pieces, 0.9 m lower in the stratigraphy than Tabun 1. After reconstruction, it was determined to be that of an anatomically modern human based on the presence of the chin (Garrod 1937). This conclusion was supported by some researchers (Rak 1998).However, Stefan and Trinkaus (1998) proposed that the symphysis was not well enough preserved to properly assess the presence of a chin, and noted that dental metrics supported a Neanderthal assignation. Most recently Harvati and Lopez (2016) declined to categorize the affinity of the specimen after analysing it using geometric morphology, concluding that the individual was large and robust, likely male, and of an indeterminate taxon.

Tabun BC7 is a Neanderthal from the same population as Tabun 1 (Coppa *et al*. 2005, 2007). Seven human teeth from the upper arc were identified as part of the same individual based on preservation and wear. Through the analysis of sediment dose values, the teeth were determined to be from layer B, and a best dating estimate of 90+30/-16 ka was proposed (Coppa *et al*. 2005, 2007). This entails an overlap in the upper limit with the dates of Tabun 1.

The human remains from Tabun Cave are at the centre of discussions regarding the dispersal of modern humans from Africa because of the taxonomic classification of the remains. If Tabun 2 is anatomically modern human, Tabun shows a stratigraphy where anatomically modern humans underlie Neanderthals in the stratigraphy. This was of great importance to discussions of human dispersals in the late 20th century and showed that Neanderthals and anatomically modern humans inhabited the same geographical area, though not necessarily at the same time, in the Middle Palaeolithic Levant prompting a multitude of studies (Bar-Yosef *et al.* 1986; Bar-Yosef and Vandermeersch 1993; Shea 1998, 2008; Lieberman and Shea 1994; Kaufman 2001). Any evidence of human agency on the bird remains from Layer C cannot be assigned to either Neanderthals or modern humans because of the indeterminate classification of Tabun 2.

Table 7.3: Middle Palaeolithic human remains from Tabun Cave Layers B and C. After Howell & Fritz 1975 and McCown & Kieth 1939. Indet. = indeterminate.

Layer	Specimen no.	Elements	Sex	Taxon
B	B1	Maxilla, juvenile (10-11 years)	M	Neanderthal
	BC2	Upper left I2, M1, right P3, M1 (unworn)	Indet.	Neanderthal
	B3	Lower right I2 (unworn)	Indet.	Neanderthal
	B4	Upper felt I1, I2, lower left M1, right M3	Indet.	Neanderthal
	B5	Upper left M2, right M2 (milk teeth)	Indet.	Neanderthal
	BC6	Upper right I1, lower left M2 (milk teeth)	Indet.	Neanderthal
	BC7	7 teeth from upper dentition	Indet.	Neanderthal
C	C1 (Tabun 1)	Burial; almost complete	F	Neanderthal
	C2 (Tabun 2)	Mandibula	M	Indet.
	C3	Distal right femur diaphysis	F	"Archaic"
	C4	Distal right radius	F	Indet.
	C5	Right os hamatum	Indet.	"Archaic"
	C6	Right os pisiforme	Indet.	Indet.
	C7	Phalanx proximalis pollucis	Indet.	Indet.

7.2.3 Faunal analyses

Bate published the faunal report from Tabun in 1937 (Garrod and Bate 1937). In it, she forwarded the hypothesis of a ‘Great Faunal Break’ between Layer C, which she argued contained archaic species, and Layer B, which was of a more modern character. The argument was mainly based on a change in the frequency of gazelle (*Gazella gazella*) and Mesopotamian fallow deer (*Dama mesopotamica*) which shifted from a majority of the former in Layer C to an overwhelming majority of the latter in Layer B. To Bate, this reflected a sharp shift of environment and climate from a hot, dry steppe landscape to a cooler, more humid forested environment. In addition, she cited the extinction of some species present in layers C-G by the time Layer B was deposited (Garrod and Bate, *ibid.*).

Marín-Arroyo (2013) conducted a taphonomic evaluation of the mammal remains from Tabun, identifying a higher concentration of human agency and carnivore tooth marks in Layer C than in Layer B (Table 7.4). There was also evidence of human consumption of carnivores in both layers where leopard and bear respectively were exploited for meat, skins, and marrow. Marin-Arroyo's conclusions supported the interpretation of Layer C as an occupation horizon where the human inhabitants exploited animals that they brought to the cave. In Layer B, cutmarks on fallow deer suggested a particular use of the ungulate, along with charred remains of aurochs, fallow deer, and gazelle. Marín-Arroyo (*ibid.*) interpreted layer B as a natural trap known to humans who occasionally visited to exploit carcasses, which sometimes included carnivores.

Table 7.4: Mammals recorded at Tabun Cave, layers B and C. After Marin.Arroyo (2013)

Taxon	**Common name**	**Layer B**	**Layer C**
Stephanorhinus kirchbergensis	Merck's rhinoceros		26
Hippopotamus amphibius	hippopotamus		35
Bos primigenius	aurochs	49	100
Equus hydruntinus	European wild ass	39	
Equus hemionus	onager	4	4
Equus caballus	horse		11
Camelus sp.	camel		1
Cervus elaphus	red deer	17	21
Dama mesopotamica	fallow deer	1729	43
Capreolus capreolus	roe deer	3	
Capra sp	goat/ibex	21	15
Gazella	gazelle	332	187
Sus scrofa	wild boar	9	38
Lepus capensis	cape hare		2
Procavia capensis	rock hyrax	1	3
Hystrix indica	porcupine	13	
Hyaena	striped hyena	9	
Crocuta crocuta	spotted hyena		2
Panthera pardus	leopard	48	2
Felis cf. *silvestris*	wild cat	2	
Canis aureus	golden jackal	4	
Canis lupus	wolf	2	
Vulpes vulpes	red fox	42	6
Ursus arctos	brown bear		15
Martes foina	beech marten	3	
size=megafauna	Indeterminate		17
size=large mammal	Indeterminate		13
size=medium mammal	Indeterminate	3	3
size=small mammal	Indeterminate		10
Indet.	Indeterminate	3	1
	Total Ungulates	**2203**	**420**
	Total Carnivores	**110**	**25**
	Total	**2333**	**555**

Bate also found supporting evidence of the "Great Faunal Break" in the small mammals. She demonstrated that several species of micromammal disappeared from the sequence after Layer C, but were prolific in layers C-G. However, detailed recording and sieving of sediments in Jelinek's excavation indicated a likely admixture between layers C and D in the material Bate analysed. Jelinek *et al*. found that the species in question appeared in beds relating to layer D, but not C (1973), and concluded that the faunal break happened between layer C and layer D. In addition to small mammals, Jelinek *et al.* (1973) mentioned that birds and reptiles were found in the site, but that the preservation was very poor.

7.2.4 Plant macrofossils.

7.2.4.1 Palynology

Analysis of pollen in samples taken from Garrod's Layers C, D and G during Jelinek's excavation in 1970 revealed the presence of several tree species during the Late Middle Palaeolithic, including oak (*Quercus spp.*), Aleppo pine (*Pinus halepensis*), olive (*Olea europaea*), and Mediterranean cypress (*Cupressus sempervirens*). The lower beds of Layer C also contained traces of pistachio (*Pistacia sp.*). In addition to trees growing in the wadi, the presence of grasses (*Gramineae*), sedges (*Cyperaceae*), and flowering plants like daisies (*Asteraceae, Echinops*), goosefoot (*Chenopodieaceae*), asphodels (*Asphodelus*), mugwort (*Artemisia*) and the Carmel daisy (*Scabiosa prolifera*) suggested open areas, with sufficient water sources to sustain growth. These species reflected a more humid and cooler climate, which was in alignment with the climatic record from the Hula region (Horowitz 1971; Weinstein-Evron 1983; Jelinek *et al.* 1973). Jelinek's palynological results constituted a rare source of information from a Middle Palaeolithic sequence, complemented only recently by Aharonovich *et al*.'s study of the Nahal Mahanayeem Outlet (2014).

7.2.4.2 Charcoal and phytoliths

Albert *et al.* (1999) examined the phytoliths present in ash in the sediments of Layers B and C. While ash was rare in Layer B, in Layer C highly variable proportions of ash and terra rossa were found in the various beds. Rather than large-scale clearing fires as proposed by Jelinek *et al.* (1973), the black layers were found to be the products of a number of overlapping individual hearths (Albert *et al.* 1999). Though evidence of hearths was sparse in Layer B (Garrod and Bate 1937, Jelinek *et al.* 1973), thin sections of ash suggested that charcoal fragments were present in the stratigraphy. An examination of phytoliths from the charcoal in both layers returned results congruent with wood and bark fires, not grass fires. This demonstrated that the burned materials in Layer C were the product of hearths, while also highlighting the presence of fires lit in the cave during the deposition of Layer B, despite the mode of occupation in the site shifting from a domestic occupation to a more ephemeral butchery site (Albert *et al.* ibid; Marín-Arroyo 2013).

7.3 The avifauna of Tabun

Avifauna specimens from Jelinek's excavations were housed at the National Natural History Collections at the Hebrew University in Jerusalem (HUJ). Academic Curator Prof. Rivka Rabinovich granted me access to study these in November 2019 at the zooarchaeology laboratory of the Zinman Institute of Archaeology, University of Haifa (UoH).

Avifauna remains from the current excavations at Tabun were housed at UoH. These included materials retrieved from the sampling of Jelinek's stratigraphic profiles. Dr. Mina Weinstein-Evron granted me access to study these remains in September 2019. I separated the avian material from other vertebrate remains to complete this work, and assigned each specimen a unique number for use during this study (format LA-XXX).

I carried out taxonomic identifications at UoH using their comparative collections and complemented this with two visits to the Steinhardt Museum (SM) in Tel Aviv. Dr. Amos Belmaker granted me access to the collections at SM in November 2019. My taphonomic analysis was conducted at the UoH zooarchaeology laboratory.

7.3.1 Contexts in this study

While Jelinek interpreted beds 1-17 as 'Garrod's B' and 18-26 as 'Garrod's C', the deposition between layer B and C at this point was continuous (Jelinek *et al.*1973). Later researchers have allotted all of beds 1-26 as Garrod's Layer C (Shimelmitz *et al.* 2020). Based on this, I have chosen not to distinguish between B and C in Jelinek's sample. Instead, I separate the material by excavation phases, a distinction made in agreement with Schimelmitz and Evron (Table 7.5). In this thesis, Jelinek's beds 1-17 are referred to as 'Unit C-1', while beds 18-26 are grouped as 'Unit C-2'. Specimens from Jelinek's excavation with unclear provenance beyond layer will be analysed as 'C-G' (C – general) as a supplement to the other two 'C' - units. The material from recent excavations led by Shimelmitz and Evron in the chimney area of Garrod's Layer B is referred to as 'Layer B'. These excavations take place at a vertical elevation of several metres above the Jelinek's, making it more useful to separate from Jelinek's beds 1-17, regardless of whether these beds indeed represent the bottom of Garrod's Layer B.

Table 7.5: Unit and layer given to material in this study defined in agreement with Ron Schimelmitz of the Zinman Institute of Archaeology and the University of Haifa.

This Study	Jelinek's Beds	Garrod's Layers
Layer B	n/a	B/Chimney
Unit C-1	1-17	C (lowest B?)
Unit C-2	18-26	C
C-G	1-26	C

7.4 Taxonomic results

Of the 616 ($_{\text{NISP}}$B = 236, $_{\text{NISP}}$C = 380) specimens constituting the Tabun avifauna, 514 were identified beyond class (*Aves* sp.). Of these, 201 were identified to species, 38 to genus, 10 to family, and 267 to order (Table 7.6; Appendix 3; Appendix 4). Passeriformes dominated the NISP (n = 297, 50.2%), but only 14.5% (n = 33) could be identified beyond order. Columbiformes were the most frequent order in both layers, comprising 17% (n = 40) and 26.6% (n = 101) of the NISP in Layers B and C, respectively. Galliformes (n = 27) and Corvidae (n = 18) were the next most frequent taxa groups in the sequence. Twenty-four classifications were represented by a single specimen.

Two specimens of the Ardeidae family (order Pelicaniformes) were morphologically similar to the cattle egret (*Bulbicus ibis*) and the little bittern (*Ixobrychus minutus*). A third specimen belonged to the Threskiornithidae and was either of a Eurasian spoonbill (*P. leucocordia*) or a northern bald ibis (*G. eremita*).

Sixteen species of non-corvid Passeriformes were identified in the sequence. , but only three genera were represented by more than one element per layer. 264 Passeriform remains could not be identified beyond order.

The minimum number of individuals present in the avian remains from Tabun was 159 (Figure 7.5). 55 were from Layer B, and 104 were from Layer C ($_{\text{MNI}}$C-1 = 54, $_{\text{MNI}}$C-2 = 40, $_{\text{MNIC}}$-G = 10). A linear regression showed a positive relationship between NISP and MNI.

See (appendix) for detailed classification and taxonomic distribution beyond layer.

Table 7.6: Taxonomic breakdown of species at Tabun sorted into context groups.

	Layer	**B**	**%B**	**C**			**C-TOT**	**%C**	
	Unit			**C -1**	**C -2**	**C -G**			**TABUN**
Taxonomic identification									**TOTAL**
GALLIFORMES									
Alectoris	*chukar*			1			1	0.3%	1
Alectoris	*sp.*	1	0.4%	2			2	0.5%	3
Coturnix	*coturnix*	12	5.1%	5	5	1	11	2.9%	23
COLUMBIFORMES									
Columba	*livia/oenas*	37	15.7%	58	36	7	101	26.6%	138
Spilopelia	*senegalensis*	3	1.3%						3
CHARADRIIFORMES									
Scolopax	*rusticola*					1	1	0.3%	1
Larus	*sp.*	1	0.4%	1			1	0.3%	2
PELICANIFORMES									
Threskiornithidae	*(G.eremita/P.leucorodia)*					1	1	0.3%	1
Ardidae size	*Ixobrychus minutus*			1			1	0.3%	1
Ardidae size	*Bulbicus ibis*				1		1	0.3%	1
ACCIPITRIFORMES									
Aquila size	*nipalensis*	1	0.4%						1
Accipitriformes				1		2	3	0.8%	3
STRIGIFORMES									
Tyto	*alba*			1			1	0.3%	1
FALCONIFORMES									
Falco	*subbuteo*				3		3	0.8%	3
Falco	*sp.*	1	0.4%	3	3		6	1.6%	7
PASSERIFORMES									
Lanius	*sp.*	1	0.4%		1		1	0.3%	2
Garrulus	*glandarius*			1			1	0.3%	1
Coloeus	*cf. monedula*	1	0.4%		3		3	0.8%	4
Corvus	*corone*	1	0.4%					0.0%	1
Corvus	*sp.*	2	0.8%	2	4		6	1.6%	8
Corvidae		1	0.4%	2	1		3	0.8%	4
Parus	*major*				1		1	0.3%	1
Alauda	*arvensis*	1	0.4%		1		1	0.3%	2
Alauda	*sp.*			1			1	0.3%	1
Melanocorypha	*calandra*	1	0.4%					0.0%	1
Pycnonotus	*xanthopygos*				1		1	0.3%	1
Hirundo	*rustica*	3	1.3%	2	3		5	1.3%	8
Hirundo	*sp.*			5	2		7	1.8%	7
Phylloscopus	*collybita*	1	0.4%						1
Sylvia	*atricapilla*	1	0.4%						1
Sturnus	*sp.*				1		1	0.3%	1
Turdus	*sp.*			2	1		3	0.8%	3
Erithacus	*rubecula*	1	0.4%		1		1	0.3%	2
Passer	*domesticus*			1			1	0.3%	1
Passer	*sp.*	1	0.4%						1
Motacilla	*alba*			1			1	0.3%	1
Motacilla	*sp.*	2	0.8%					0.0%	2
Coccothraustes	*coccothraustes*				1		1	0.3%	1
Chloris	*chloris*	1	0.4%						1
Carduelis	*cf. carduelis*	1	0.4%	1			1	0.3%	2
Carduelis	*sp.*					1	1	0.3%	1
Emberiza	*calandra*	1	0.4%						1
Emberizidae		1	0.4%						1
Passeriformes		133	56.4%	56	72	3	131	34.5%	264
INDETERMINATE									
Aves	sp.	26	11.0%	39	26	11	76	20.0%	102
	NISP	**236**	**100%**	**186**	**167**	**27**	**380**	**100%**	**616**
	NTAXA	**21**		**16**	**15**	**6**	**24**		**31**
	MNI	**55**		**54**	**40**	**10**	**104**		**159**

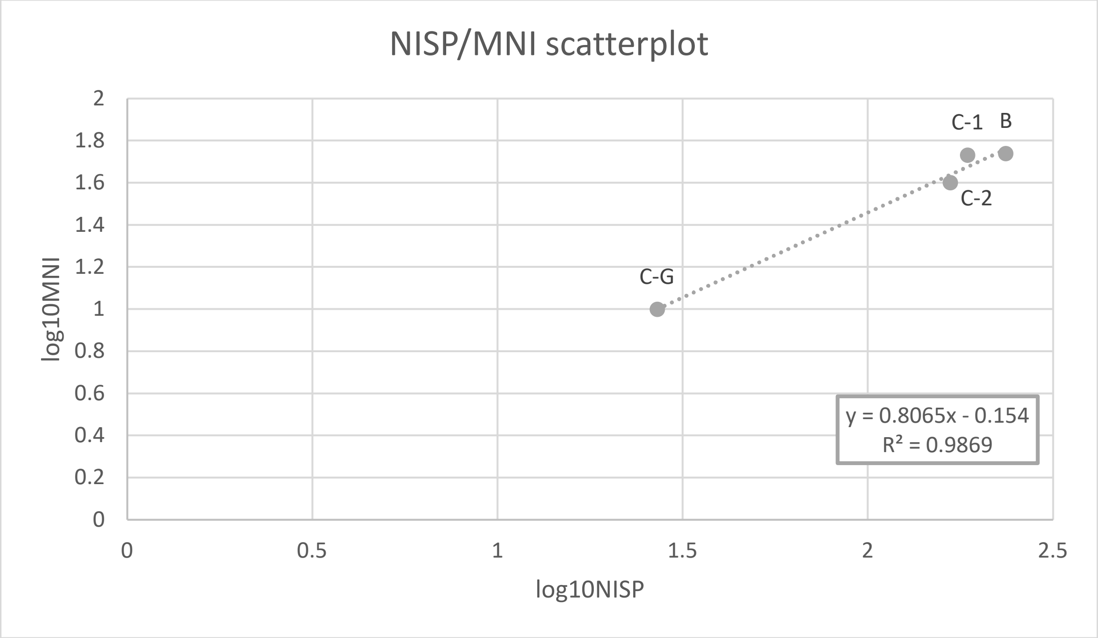


Figure 7.5: Scatterplot of logNISP and NISP/MNI showing that preservation is

7.4.1 Skeletal elements

Wing elements comprised the majority of elements in both layers B and C (n = 126 and n = 134, respectively; Figure 7.6;

Figure 7.7). Fragile elements such as the sternum and radius were rare, while skull fragments other than beak elements are completely absent. In Layer C, longbone shafts and fragments were the most frequent remain (n = 59). These corresponded largely to the specimens classified as *Aves* sp. and Passerine indet. (n = 57). A high frequency of talons (n=40) was observed in Layer C, 21 of which were rock/stock dove (*C. livia/oenas*). This was in stark contrast to the frequency of other pedal phalanges. Only 4 talons were identified in Layer B.

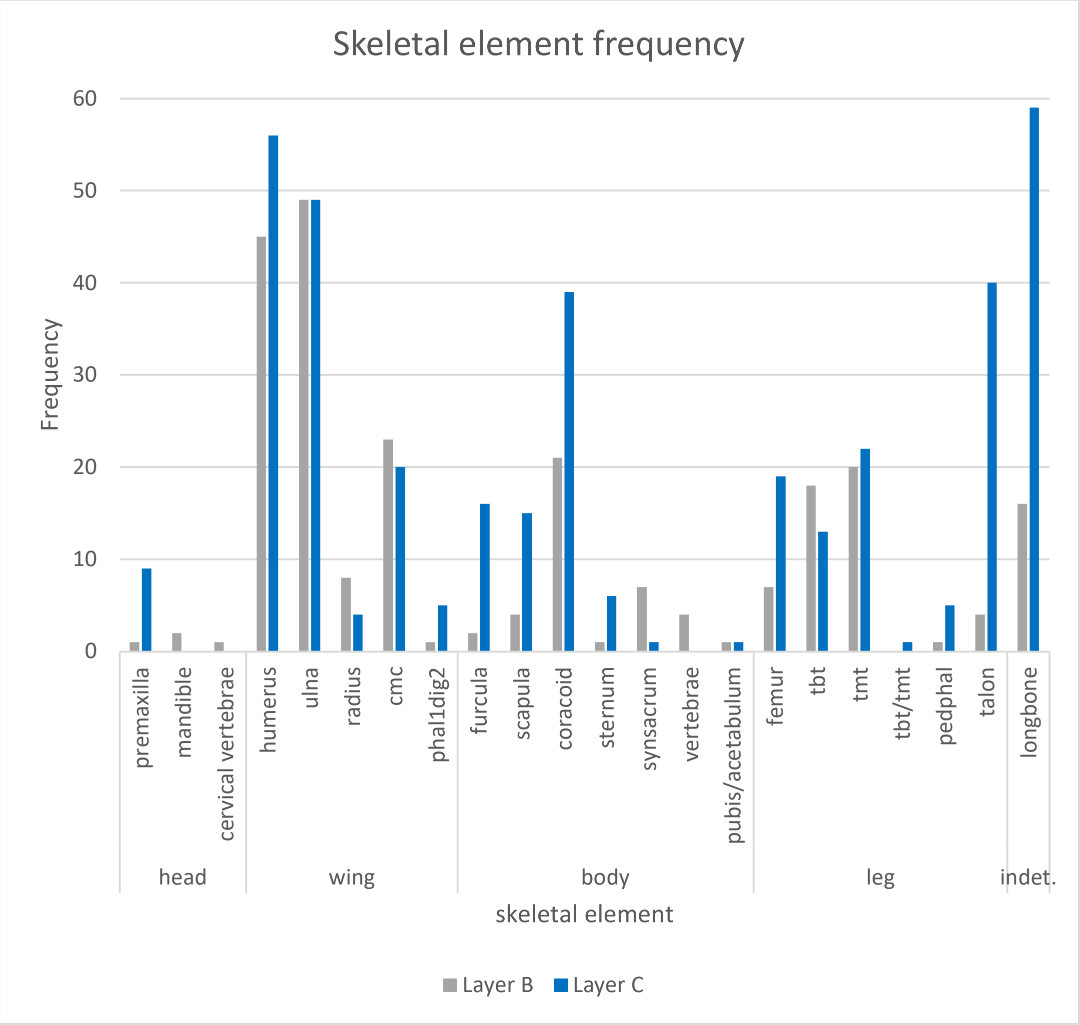


Figure 7.6: Skeletal element frequencies in layers B and C at Tabun Cave. Longbone shafts and fragments re the most common element in Layer C while humeri feature most frequently in Layer B.

A chi^2-test was performed to investigate differences in the observed and expected frequencies of wing, leg, body and longbone elements in layers B and C. Based on the assumption that preservation should be the same in both contexts, the expected values were calculated from the total NISP of each element multiplied by the proportion of remains in each context. There was a significant difference between the expected and observed frequencies of wing elements ($p = <0.001$, $df = 2$) and longbone fragments and shafts ($p = 0.002$, $df = 2$) relative to the expected values (Figure 7.7). There were more wing elements than expected in Layer B, and fewer long bone fragments in Layer B than C. There was no significant difference in the frequencies of body and leg elements.

CHI-SQUARE TEST

Observed

Body zone	Layer B	Layer C	TOTAL
wing	126	134	260
body	40	78	118
leg	50	100	150
longbone	16	59	75
	232	371	603
%remains	0.3847	0.6153	

Expected

Body zone	Layer B	Layer C	TOTAL
wing	100	160	260
body	45	73	118
leg	58	92	150
longbone	29	46	75
	232	371	603

Probability

Body zone	
wing	<0.001
body	0.307
leg	0.196
longbone	0.002

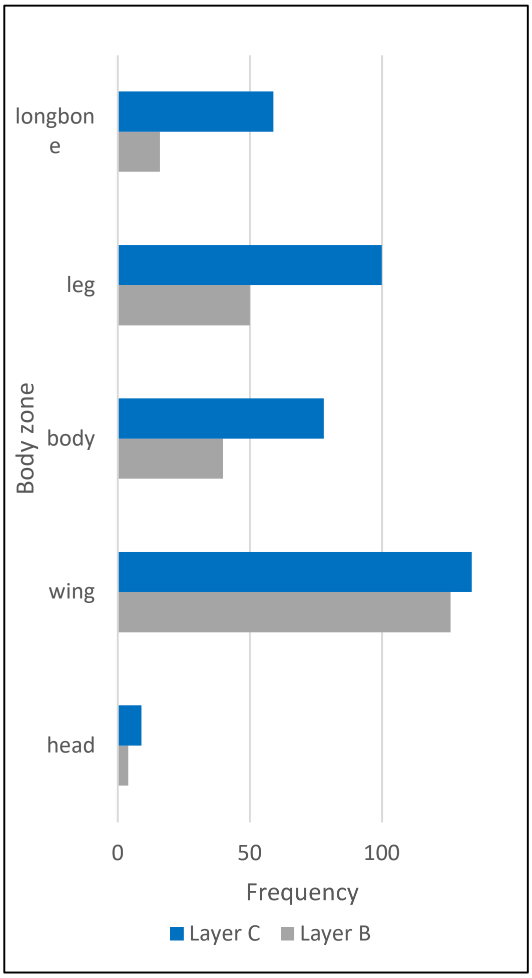


Figure 7.7: Chi^2-test and figure of the frequency of body zone elements in layers B and C. Expected values were calculated from the relative proportion of total remains recovered from each layer (Layer B = 0.3847, Layer C = 0.6153)Results are significant for wing elements and long bone shafts/fragments, most of which (n=57) cannot be identified.

7.5 Ecological results

In this section, I present the results of my ecological analysis of Tabun Cave. Specimens without secure species level identification were not included in the detailed analysis but are mentioned in relation to the distribution of higher taxa. Due to small sample sizes, it was not possible to test the results for statistical significance for the examined layers. C-G is not included as a context because the remains here come from either C-1 or C-2. However, a woodcock (*S. rusticola*) specimen in C-G has been allocated to C-2 so it may be included in the ecological analysis because it is the only marker of several important variable categories and therefore significant to the results.

Table 7.7: Ecological variables of bird species at Tabun Cave. After Finlayson (2011). TOL: bioclimatic tolerance (A= specialist, B= semi-specialist, C= moderate, D= semi-generalist, E= generalist), LAT: latitude range (A= arctic 70°N, B= boreal 60°N, C= temperate 50°N, D= mid-latitude belt (warm species) 40°N, E= subtropical 30°N, F= multilatitude – species occupies several latitude bands), TEM: temperature tolerance (A-E from cold to hot), HUM: humidity tolerance (A-E from arid to wet), Foraging and Nesting habitats (F= forest, O= open, M= mixed F/O, W= wetland, R= rocky, Ma= marine, A= aerial) , diet (E= endotherm, O= omnivore, I= insectivore, H= herbivore, N= necrophyte, M= mixed strategy carnivore, F= fish eater), and Migration behaviours (M= migratory, S= sedentary, P = partially migratory).

Common name	**Taxon**	**Order**	**TOL**	**LAT**	**TEM**	**HUM**	**HF**	**HN**	**D**	**M**
Chukar partridge	*Alectoris chukar*	Galliformes	B	D	E	A	M	M	O	S
Common quail	*Coturnix coturnix*	Galliformes	D	F	D	D	O	O	O	M
Rock dove	*Columba livia/oenas*	Columbiformes	D	F	D	D	M	R	*O*	*S*
Turtle dove	*Streptopelia senegalensis*	Columbiformes	D	F	C	C	M	M	O	M
Woodcock	*Scolopax rusticola*	Charadriiformes	E	C	B	D	F	F	M	M
Steppe eagle	*Aquila sp. (size=nipalensis)*	Accipitriformes	A	D	C	A	O	O	M	M
Barn owl	*Tyto alba*	Strigiformes	D	F	C	C	O	R	M	S
Hobby	*Falco subbuteo*	Falconiformes	E	F	B	D	A	M	M	M
Eurasian jay	*Garrulus glandarius*	Corvidae	D	F	C	D	F	F	O	S
Jackdaw	*Coloeus cf. monedula*	Corvidae	C	F	C	B	O	R	O	P
Carrion/hooded crow	*Corvus corone*	Corvidae	D	F	B	C	O	O	M	P
Skylark	*Alauda arvensis*	Passeriformes	D	F	C	D	O	O	O	P
Calandra lark	*Melanocophya calandra*	Passeriformes	A	D	E	A	O	O	O	S
Great tit	*Parus major*	Passeriformes	E	F	C	D	F	F	O	S
White-spectacled bulbul	*Pycnonotus xanthopoylos*	Passeriformes	A	E	E	A	M	M	O	S
Barn swallow	*Hirundo rustica*	Passeriformes	C	F	B	B	A	R	I	M
Common chiffchaff	*Phylloscopus collybita*	Passeriformes	C	F	C	B	F	F	O	P
Blackcap	*Sylvia atricapilla*	Passeriformes	D	F	C	C	F	F	O	P
Robin	*Erithracus rubecula*	Passeriformes	D	F	C	C	F	F	O	P
House sparrow	*Passer domesticus*	Passeriformes	D	F	C	C	M	M	O	P
Pied/white wagtail	*Motacilla alba*	Passeriformes	E	F	B	C	W	W	I	P
Hawfinch	*Coccothraustes coccothraustes*	Passeriformes	E	C	B	C	F	F	O	P
Greenfinch	*Chloris chloris*	Passeriformes	C	F	C	C	F	F	O	P
Goldfinch	*Carduelis cf. carduelis*	Passeriformes	D	F	C	C	O	O	O	P
Corn bunting	*Emberiza calandra*	Passeriformes	B	F	D	C	O	O	O	P

7.5.1 Bioclimatic tolerances

The range of bioclimatic tolerances reflected in avian species at Tabun remained largely constant throughout layers B and C (Table 7.8). This suggests that the landscape around Tabun was not only able to sustain bioclimatically resilient species generalist (E) and semi-generalist (D) species, but also provided niche habitats for specialist species. All five categories appeared in both layers B and C (total). Category E and D species were found in all layers, while specialist (A), semi-specialists (B), and moderate (C) species were only found in layer B and either C-1 (B) or C-2 (A and C).

Table 7.8: Bioclimatic tolerances by layer. A – Specialist, B – Semi-specialist, C – Moderate, D – Semi-generalist, E – Generalist. Table shows NTAXA of species which belong to each category and frequency of category in the sequence (FREQ and FREQ%). Layer C-G does not count towards the total frequency because these species originate in either C-1 or C-2. All bioclimatic tolerance categories are present at Tabun showing that the environment provided conditions that supported both specialist and generalist species.

	Layer (NTAXA)					
TOL	**B**	**C1**	**C2**	**CG**	**FREQ**	**FREQ%**
A	2		1		2	67
B	1	1			2	67
C	3		1		2	67
D	8	6	4	2	3	100
E	1	2	4	1	3	100

7.5.2 Latitude range, temperature tolerance, and humidity tolerance.

Multi-latitude species (F) were present in all examined layers at Tabun (Table 7.9). 73.7% (n = 14) of these species also have semi-generalist or generalist bioclimatic tolerances. No species from latitude ranges A, B and E were identified in the sequence. This absence can be explained by the geographical position of Tabun Cave at 32°N. Species from latitude range D were found in two contexts (B and C-1), and a single element of woodcock in unit C-2 was the only example of category C. The Woodcock is a migratory species, breeding in Scandinavia and wintering in south-western Europe in the current day. During the Middle Palaeolithic, advancing ice sheets in the north may have displaced woodcocks and other temperate species into ranges they do not frequent today (Finlayson 2004; 2011). Alternatively, they may have wintered in Israel in the Pleistocene. In the present day, the Woodcock is an infrequent winter visitor to Israel (BirdLife Israel, 2021).

Table 7.9: Latitude range by layer. A – Arctic 70°N, B – Boreal 60°N, C – Temperate 50°N, D - Mid-latitude belt, warm, 40°N, E – Subtropical 30°N, F - Multi-latitude (occupies several bands). Table shows NTAXA of species which belong to each category and frequency of category in the sequence (FREQ and FREQ%). Layer C-G does not count towards the total frequency because these species originate in either C-1 or C-2. Only temperate (C), midlatitude (D), and multilatitude (F) species are present in the sequence.

	Layer (NTAXA)					
LAT	**B**	**C1**	**C2**	**CG**	**FREQ**	**FREQ%**
A					0	-
B					0	-
B/D					0	-
C			1	1	1	33
D	2	1			2	67
E						-
F	13	8	8	2	3	100

No species preferring cold temperatures (A) were present in Tabun (Table 7.10), but all the examined layers contained species reflecting categories B-E (21-100% heat). The majority of the species in the ecological examination preferred a moderate to high temperature (n=19). Individually, Layer B and Units C-1 and C-2 showed the same pattern; a majority of category C species, and lesser values of categories D and E. The chukar partridge and calandra lark were both sedentary species belonging to category E, inhabiting areas with a high average temperature. The presence of category E species in all layers pointed towards a warm climate during the deposition of layers C and B.

Table 7.10 Temperature tolerances by layer. Scale from cold to hot, A – 1-20 %, B – 21-40 %, C – 41-60 %, D – 61-80 %, E – 81-100 %. Table shows NTAXA of species which belong to each category and frequency of category in the sequence (FREQ and FREQ%). Layer C-G does not count towards the total frequency because these species originate in either C-1 or C-2No cold species are present at Tabun Cave.

	Layer (NTAXA)					
TEM	**B**	**C1**	**C2**	**CG**	**FREQ**	**FREQ%**
A					0	0
B	2	2	3	1	3	100
C	9	4	4		3	100
D	3	2	2	2	3	100
E	1	1	1		3	100

No species of humidity category E (wet) were present in the sample (Table 7.11), corresponding well with the absence of temperature category A (cold). However, the presence of seven humidity category D species (woodcock, hobby, quail, rock dove, jay, skylark, and great tit) indicates some level of humidity, either in the form of seasonal rainfall, or wetland habitats available close to the site.

Table 7.11: Humidity tolerances by layer. Scale from arid to humid, A – 1-20%, B – 21-40%, C – 41-60%, D – 61-80%, E – 81-100%. Table shows NTAXA of species which belong to each category and frequency of category in the sequence (FREQ and FREQ%). Layer C-G does not count towards the total frequency because these species originate in either C-1 or C-2. No species with high humidity tolerance are present at Tabun.

	Layer (NTAXA)					
HUM	**B**	**C1**	**C2**	**CG**	**FREQ**	**FREQ%**
A	2	1	1		3	100
B	3	1	2		3	100
C	7	4	2		3	100
D	3	3	5	3	3	100
E					0	-

7.5.3 Foraging and nesting habitats

Five foraging habitats were reflected in the avian species at Tabun (Table 7.12). The majority of species foraged in Mixed and Open habitats. Forest foragers featured in Layer B and both units of Layer C, indicating that tree-cover in the Wadi el-Mugharet was also present in the Middle Palaeolithic. Aerial foragers also featured in both layers. Wetland feeders (*Motacilla alba*) only appeared in unit C-2 in the form of the pied/white wagtail. This species also constituted the sole occurrence of a wetland nester. Four other nesting habitats, forest, open, mixed and rocky, were present in all contexts (Table 7.13). The high occurrences of rock dove (*C. livia*) in the sample were echoed here alongside other species that were attracted to the rocky cliff face on the western border of Mount Carmel. Forest nesters were well-represented by the few identified species of Passeriformes, the woodcock, and the Eurasian jay. The hobby, chukar partridge and turtle dove exploited an array of nesting habitats depending on what was readily available to them.

Table 7.12: Frequency of foraging habitats per layer. Table shows NTAXA of species which belong to each category and frequency of category in the sequence (FREQ and FREQ%). Layer C-G does not count towards the total frequency because these species originate in either C-1 or C-2. Marine and rocky foragers are absent, and wetland foragers are rare.

	Layer (NTAXA)					
HF	**B**	**C1**	**C2**	**CG**	**FREQ**	**FREQ%**
A	1	1	2		3	100
F	4	1	3	1	3	100
M	2	3	2	1	3	100
Ma					0	-
O	8	3	3	1	3	100
R					0	-
W		1			1	33

Table 7.13: Frequency of nesting habitats per layer. Table shows NTAXA of species which belong to each category and frequency of category in the sequence (FREQ and FREQ%). Layer C-G does not count towards the total frequency because these species originate in either C-1 or C-2. A variety of nesting habitats were available close to the cave.

	Layer (NTAXA)					
HN	**B**	**C1**	**C2**	**CG**	**FREQ**	**FREQ%**
F	4	1	3	1	3	100
M	1	2	1	2	3	100
O	7	2	2	2	3	100
R	3	3	3	1	3	100
W		1			1	33

7.5.4 Higher Taxa Groups

The specimens that could not be identified beyond order, family, or genus, and therefore could not be included in the ecological analyses, were included an analysis of higher taxa groups. At Order level, game birds, shore birds, water birds, diurnal raptors, and falcons all featured in more layers than was obvious from species-level consideration alone (Table 7.14; Figure 7.8).

The addition of indeterminate partridges (*Alectoris* sp.) enhanced the ecological results. These were likely also chukar partridges based on the exclusive distribution pattern of partridges in the Palearctic (Randi 1996). The reclassification to species level added to the frequency of heat and humidity tolerant semi-specialist species present in the sequence. It was clear from the relative abundance of the higher taxa groups that pigeons and game birds appeared more frequently than other taxa groups at Tabun. Along with corvids, which were also present in both layers at Tabun, these taxa groups were known food resources for Neanderthals (Finlayson *et al*. 2012; Blasco *et al.* 2014, 2016; Romero *et al.* 2017). In a study of the palatability of bird species, Cott described these birds as among the most flavourful (1946).

Within shorebirds, the inclusion of two gull (*Larus* sp.) specimens along with the Woodcock (*S. rusticola*) expanded the frequency of this order from one context to all contexts, highlighting the coastal and wetland environments near the cave. Though gulls are rocky nesters, they are mostly aquatic and littoral scavengers, staying close to the coast (Birdlife Datazone 2021). The inclusion of these two specimens in the dataset widens the spectrum of habitats reflected in the avifauna of Tabun Cave, but such low numbers entail a risk of having found a bird species that was not in its natural habitat. Gulls may also have been introduced as food as Cott described some species as palatable (1946), but without knowing the exact species of gull it is difficult to assess the possibility that they were introduced to the site as human food.

The order Pelecaniformes was present in the form of two members of the heron (Ardidae) family and one Threskiornithidae (ibises and spoonbills). The presence of these families reflected open and wetland habitats of the coastal plain to the west of Tabun. The remains were only found in Layer C (Ardidae size *Bulbicus ibis*: C-1, Ardidae size *Ixobrychus minutus*: C-2, *G. eremita/P. leucorodia*; C-G). The presence of these species only in Layer C was interesting as they are not usual inhabitants of the direct surroundings. Layer C is also the most densely occupied layer. It was possible that these birds were brought to the site by humans who collected them from the coastal plain and wetlands. These species also widened the frequency of Lat range D to all three units of Layer C.

In terms of birds of prey, both falcons and diurnal raptors were present in both Layers B and C. As only a single specimen represented owls, there was no difference in the frequency of higher taxa. In total, birds of prey accounted for 3.7 % of the NISP (n = 23) and 8.2 % of the MNI (n = 13).

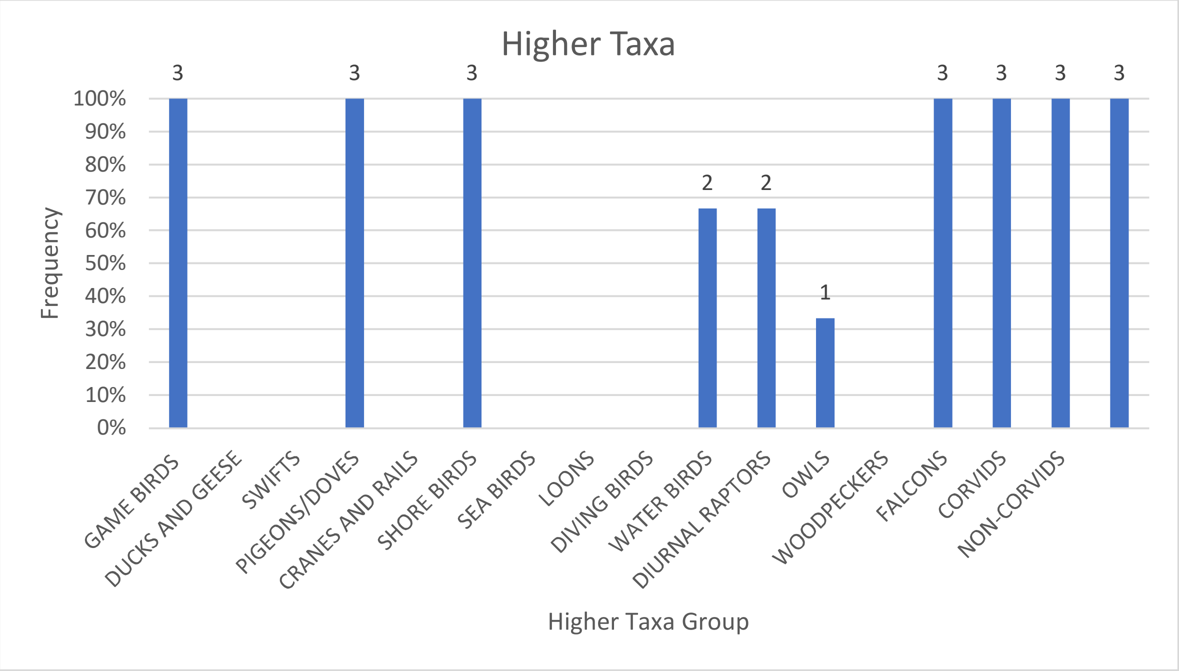


Figure 7.8: Frequencies of higher taxa groups at Tabun Cave.

Table 7.14: NISP of higher taxa elements in the layers and units of Tabun. Pigeons and gamebirds are the most well represented groups.

		Layer	**B**	**C**			
		Unit		**C -1**	**C -2**	**C -G**	
Common name	**Order**	**Family**					**TOTAL**
GAME BIRDS	GALLIFORMES	ALL	13	8	5	1	27
DUCKS AND GEESE	ANSERIFORMES	ALL					
SWIFTS	APODIFORMES	ALL					
PIGEONS/DOVES	COLUMBIFORMES	ALL	40	58	36	7	141
CRANES AND RAILS	GRUIFORMES	ALL					
SHORE BIRDS	CHARADRIIFORMES	ALL	1	1	1	**	3
SEA BIRDS	PROCELLARIIFORMES	ALL					
LOONS	GAVIIFORMES	ALL					
DIVING BIRDS	SULIFORMES	ALL					
WATER BIRDS	PELICANIFORMES	ALL		1	1	1	3
DIURNAL RAPTORS	ACCIPITRIFORMES	ALL	1	1		2	4
OWLS	STRIGIFORMES	ALL		1			1
WOODPECKERS	PICIFORMES	ALL					
FALCONS	FALCONIFORMES	ALL	1	3	6		10
CORVIDS	PASSERIFORMES	CORVIDAE	5	5	8		18
NON-CORVIDS	PASSERIFORMES	NON-CORVIDS	149	69	85	4	307
	INDETERMINATE	ALL	26	39	26	11	102
		NISP	236	186	168	26	616
		NTAXA	21	16	15	6	58

7.6 Taphonomic results

This section presents the results of the taphonomic examination of the avian remains from Tabun Layers B and C (Table 7.15). Over 60 % of the material (n = 444) had a lisibility rank of 1 (Figure 7.9). Allocation to higher ranks was due in part to other taphonomic processes obscuring the bone surface, and in part to fragmentation. The distribution of lisibility ranks was stable throughout the sequence. Few specimens (n = 11) were completely unreadable (rank 4).

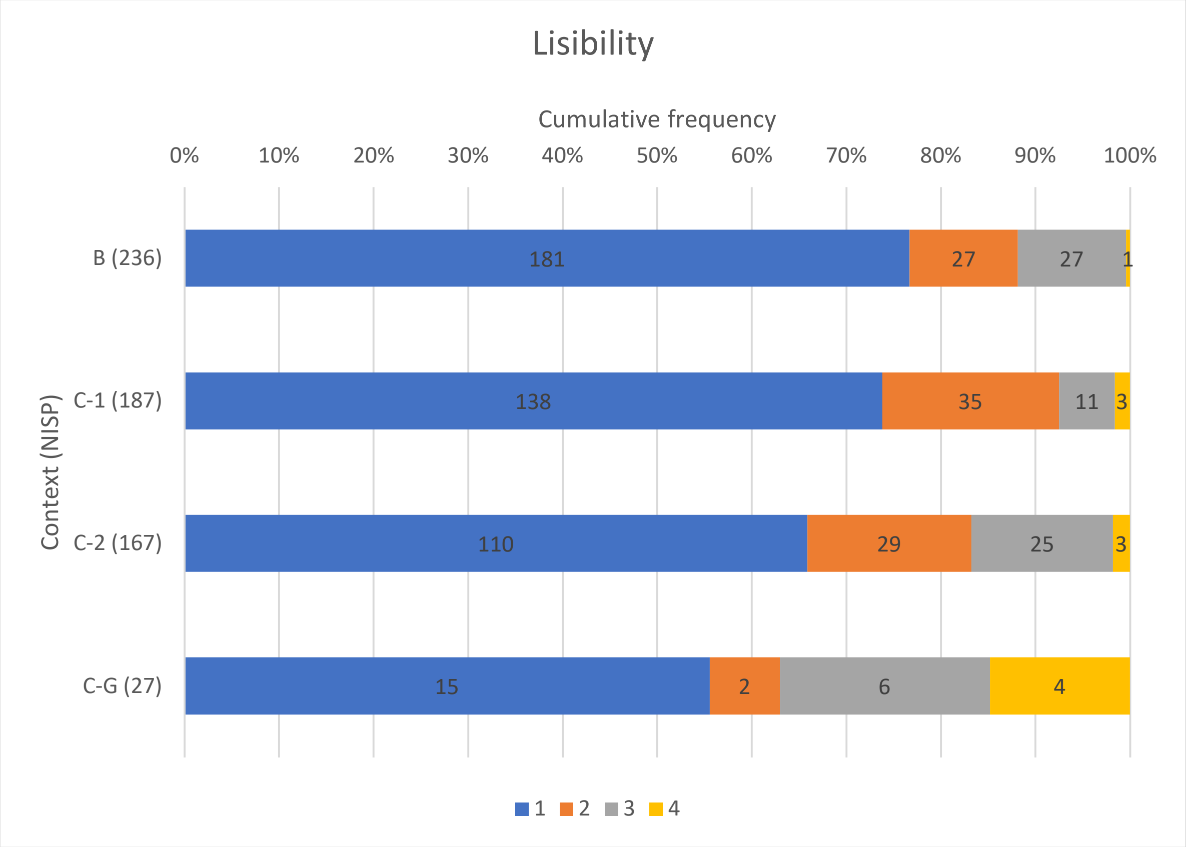


Figure 7.9: Lisibility ranking by layer/unit on a scale from clear (1) to unreadable (4).

Table 7.15: Presence of taphonomic modifications by context.

	B	**%**	**C-1**	**%**	**C-2**	**%**	**C-G**	**%**
Concretions	152	64.4%	107	57.2%	108	64.7%	18	66.7%
Manganese staining	131	55.5%	86	46.0%	82	49.1%	14	51.9%
Trample	2	0.8%	4	2.1%	5	3.0%	3	11.1%
Root etching	4	1.7%	9	4.8%	13	7.8%	5	18.5%
Weathering	110	46.6%	53	28.3%	46	27.5%	13	48.1%
Human? tooth mark								
Carnivore tooth mark	22	9.3%	31	16.6%	13	7.8%	1	3.7%
Rodent gnaw	1	0.4%	1	0.5%	0			
Bird of Prey beak mark	13	5.5%			5	3.0%		
Indeterminate tooth mark	2	0.8%					1	3.7%
Digestion	200	84.7%	110	58.8%	82	49.1%	10	37.0%
Cut mark								
Thermal modification	2	0.8%	83	44.4%	89	53.3%	15	55.6%
Peeling			1	0.5%				

7.6.1 Natural modifications

7.6.1.1 Concretions, Manganese staining and Root etching.

Some degree of concretion was present on 62.5% of the material (n = 386), and all levels of modification were present in all layers (Figure 7.10). The concretions generally contained ‘terra rossa’ sediment that originated on the plateau above (Jelinek *et al.* 1973). Water percolating through the limestone bedrock left deposits on the bone and sediment, binding them together (Fernandez-Javlo and Andrews 2016). Manganese oxide staining was present on 314 specimens (50.8 %) (Figure 7.11). Rank 4 modifications were limited to a single specimen in Layer B.

Acid etching from rooting was infrequent in the sample (n = 31) (Figure 7.12). Arid conditions may have been responsible for retarding plant growth in Layer C (Table 7.1). In Layer B, the lack of plant growth is connected to the nature of the chimney, which does not allow sun to penetrate.

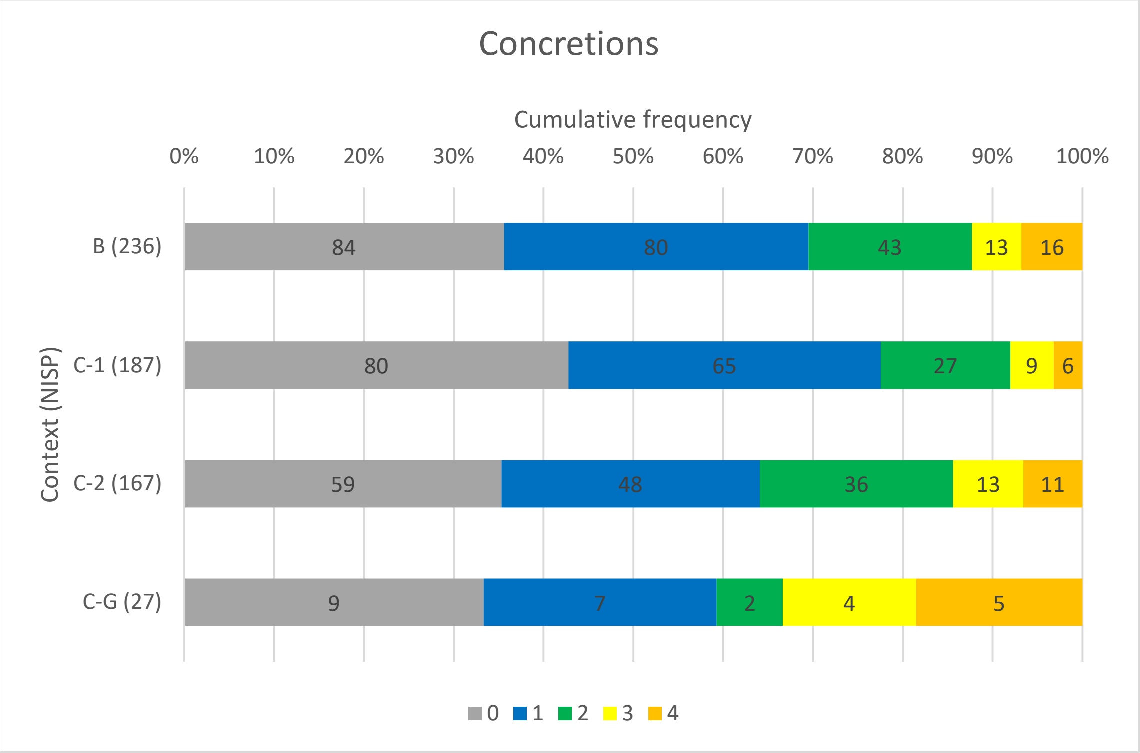


Figure 7.10: Degree of concretions present by layer. 1= 0-25 %, 2= 26-5 0%, 3= 51-75 %, 4= 76-100 %, 0= no concretions.

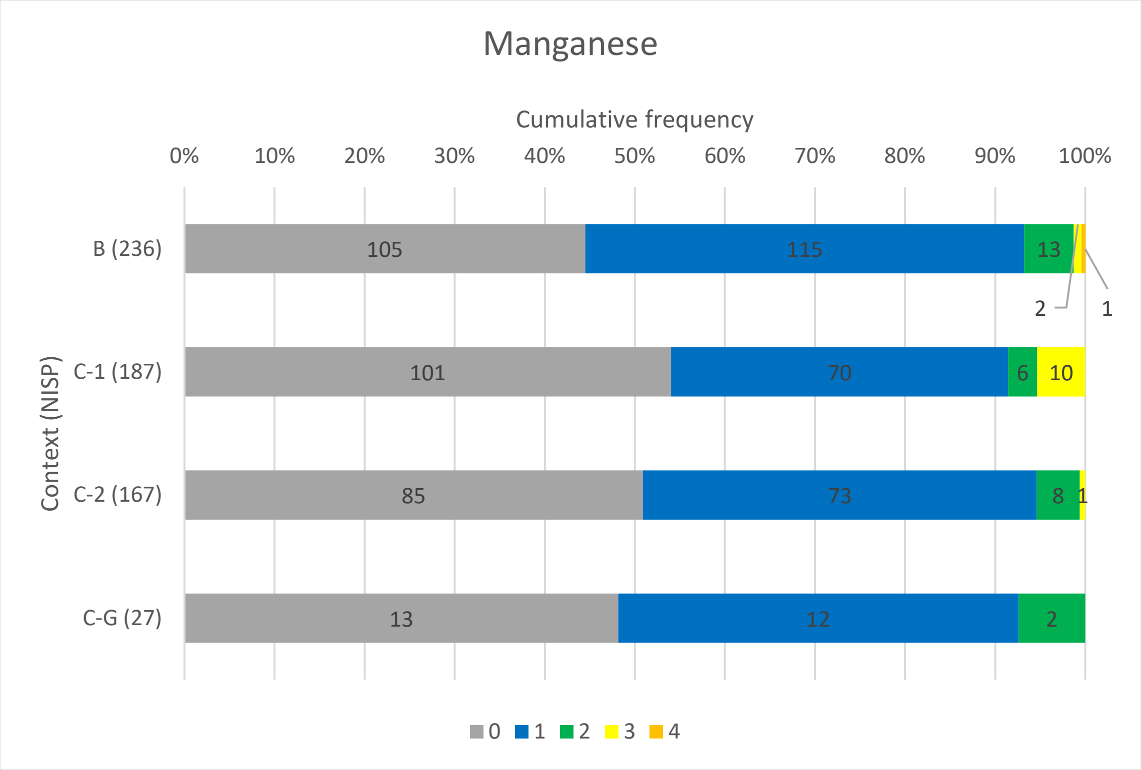


Figure 7.11: Degree of manganese oxide staining by layer. 1= 0-25 %, 2= 26-50 %, 3= 51-75 %, 4= 76-100 %, 0=no manganese oxide.

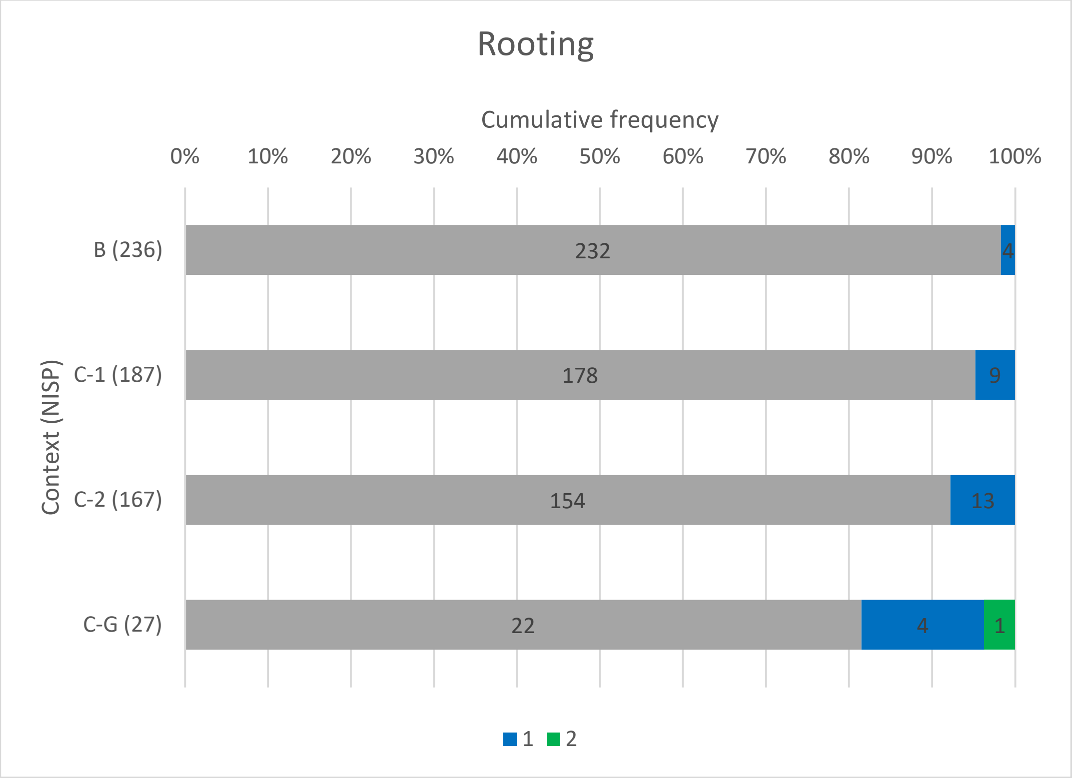


Figure 7.12: Degree of rooting present by layer. 1= low level of rooting, 2= moderate level of rooting.

7.6.1.2 Weathering and Trample

A total of 46.6% (n = 110) of specimens in Layer B displayed some degree of weathering. This contrasted with Units C-1 and C-2 where 28.3 % and 26.5 % were weathered, respectively. This disparity may have several causes. During the occupation phases in Units C-1 and C-2, trample and efforts to keep the floor of the site clean may have led to lower survival of more weathered pieces. Jelinek's excavations of beds 1-26 (Layer C) were undertaken as cuts into the section left by Garrod. Garrod's original section in itself would have exposed the material within the sediment to additional erosional processes such as heat and aridity, potentially leading to the rapid degradation of already fragile weathered materials within the sediment.

Trample modifications were extremely low in the sequence (n = 14; Figure 7.14). However, large amounts of long bone fragments in Layer C may indicate a higher degree of trample than the surface modifications alone (see:7.6.4).

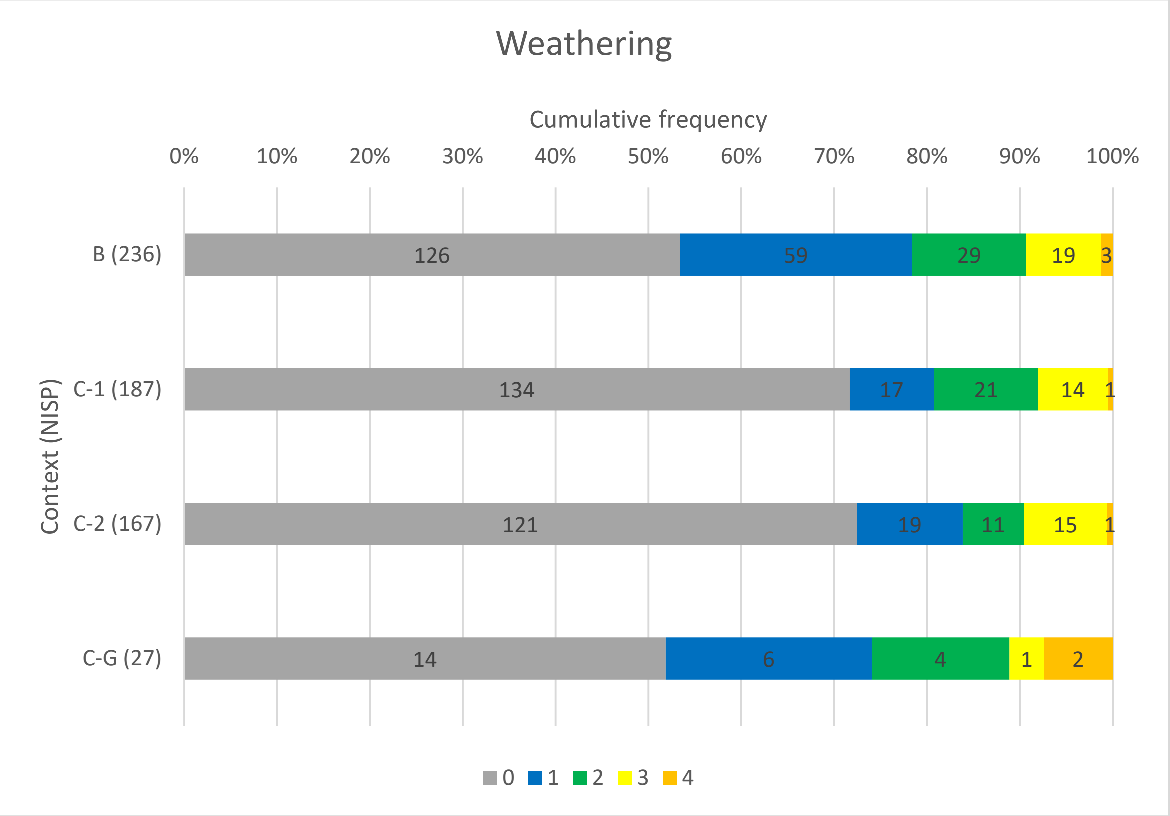


Figure 7.13: Degrees of Weathering modifications by layer where 0 = no modification and 5 = highest degree of modification. Weatherig was present on a higher proportion of the paterial in Layer B than in Layer C contexts.

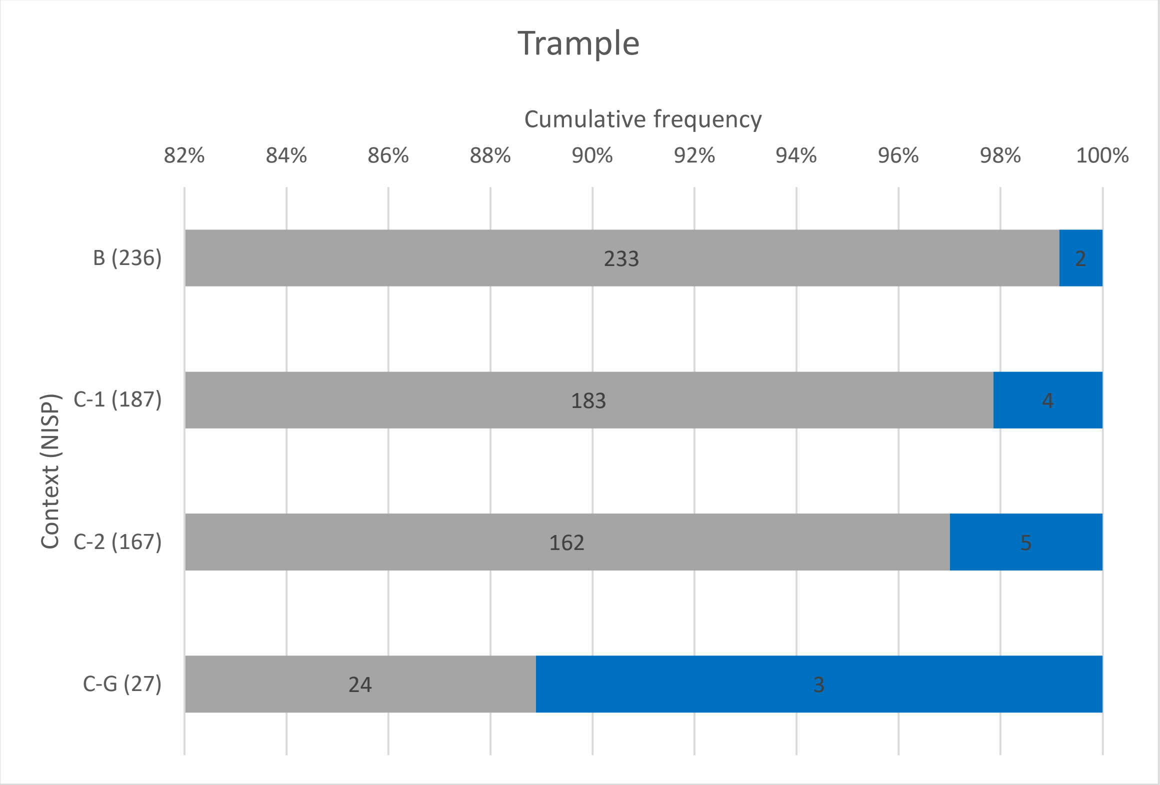


Figure 7.14: Frequency of trampling modifications present by context. 1= trample present, 0= no trample present. Trample frequencies were very low throughout the sequence.

7.6.2 Predator modifications

In total, 14.4 % (n = 89) of the sample displayed signs of manducation (Table 7.16). Though Layer B had a higher number of modified specimens (n = 37), Unit C-1 displayed a higher relative frequency of modified specimens (17.1%, n=32). Only 10.2 % of specimens (n = 18) in Unit C-2 presented with manducation traces.

Table 7.16: Presence and type of manducation modification present by context. NISPmod = number of specimens with modifications, %mod = proportion of modified remains in the context, total mod = number of modifications, cren = crenulated edges.

	NISPmod	%mod	Total mod	Pit	Score	Notch	Puncture	Cren	Gnaw
B	37	15.7 %	46	1	0	2	31	10	1
C-1	32	17.1 %	38	1	2	5	12	17	1
C-2	18	10.8 %	22	1	4	2	9	6	0
C-G	2	7.4 %	2	0	0	0	2	0	0

Small carnivores were responsible for most of the manducation traces throughout the sequence (n = 67) and are found in all contexts. Rodent gnaw and traces of an indeterminate nature were present in small numbers (n = 5). Manducation traces produced by birds of prey were only present in Layer B (n = 13) and unit C-2 (n = 5). Layer B was the only context where all three identified agents were active, in addition to the indeterminate agent. The presence of birds of prey roosting and feeding in the site suggested an intermittent absence of humans during the deposition of C-2, and to the complete absence of occupation during the deposition of Layer B (Bochenski *et al.* 2018).

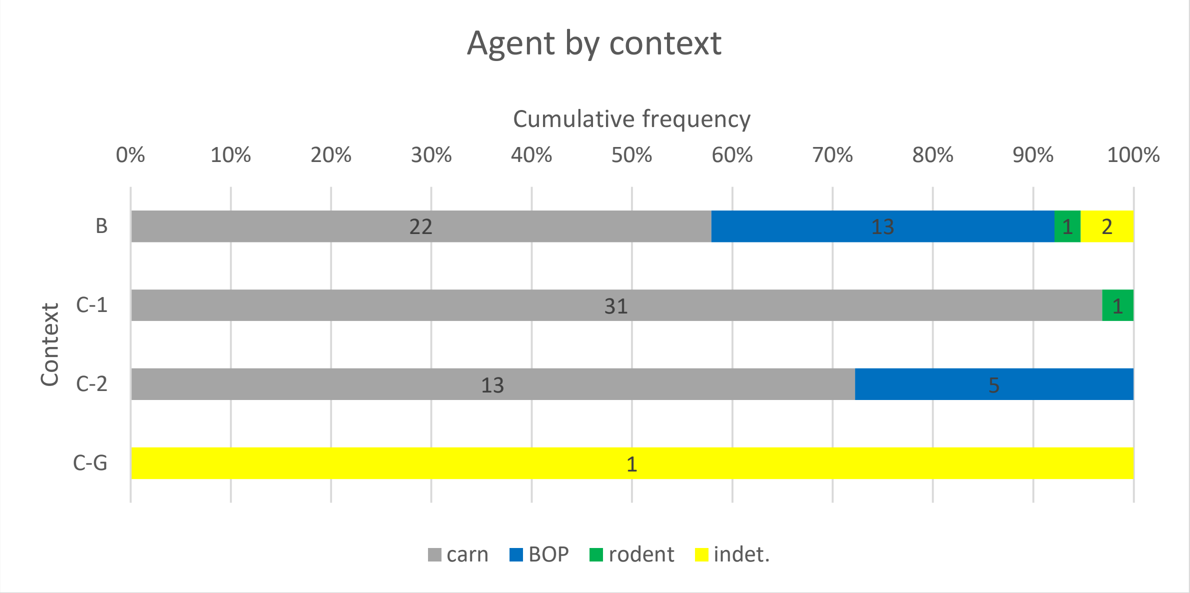


Figure 7.15: Agency as reflected by manducation modifications per context.

A total of 65.3 % (n = 403) of the specimens displayed digestion modifications. However, a chi^2-test revealed that there was a significant difference between the frequency of digested specimens in Layer B (n = 197, 84.7 %) and those in Layer C (n = 116, 58.5 % of C-1; n = 82, 49.1 % of of C-2) (p = <0.001, df = 1; Table 7.17). While units C-1 and C-2 displayed the same distribution of digestion modification ranks, Layer B deviated with a low number of undigested remains and a high proportion of low-level acid etching. (Figure 7.16).

Table 7.17: Chi^{2}test showing the significance of the frequencies of digested and non-digested elements in layer B, unit C-1, and unit C-2. Based on the assumption that the distribution should be uniform, expected values were calculated from the NISP of the modified/unmodified specimens multiplied by the proportion of the total NISP in each context. Context group C-G was not included in the test as it was not an independent context. The result was highly significant (p= <0.001, df = 1).

CHI^2 TEST				
Observed	B	C-1	C-2	sum
dig	200	110	83	393
no dig	36	77	85	198
sum	236	187	168	591
%NISP	0.399	0.316	0.284	
Expected	B	C-1	C-2	sum
dig	157	124	112	393
no dig	79	63	56	198
sum	236	187	168	591
Probability				
dig	<0.001			
no dig	<0.001			

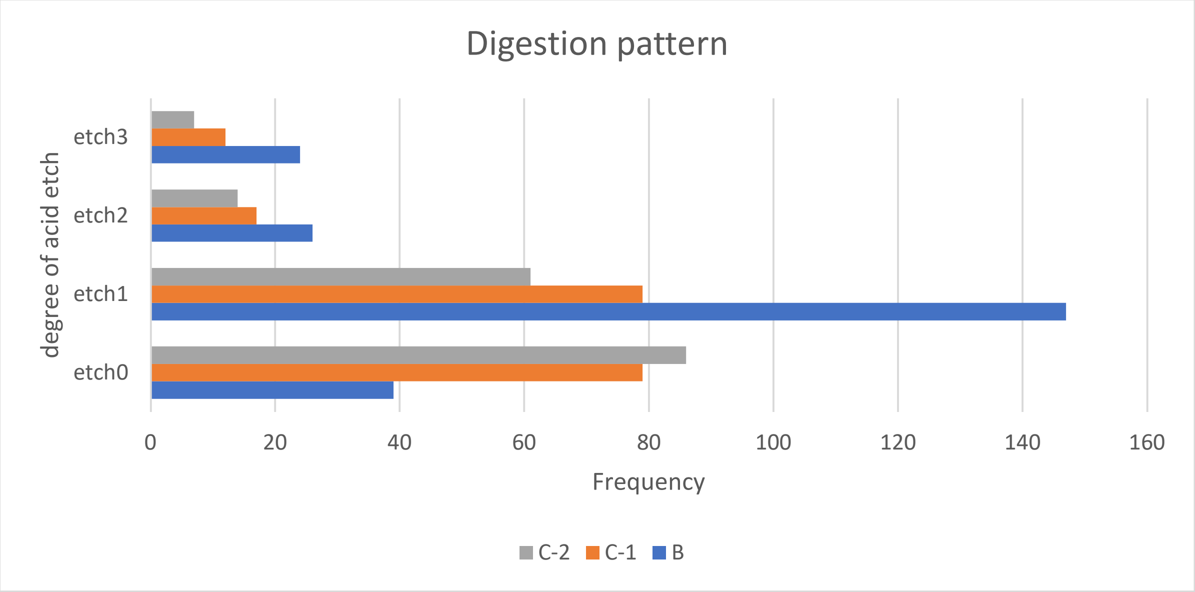


Figure 7.16: Variation of digestion trace ranks by context. High levels of low-degree etch in Layer B suggested that nocturnal birds of prey were contributing to the accumulation. etch0 = no etch, etch 3 = heavy etching.

Low-degree etching is often attributed to nocturnal birds of prey (Andrews 1990), which were found in the sequence in Unit C-1 (*Tyto alba*). However, no beak punctures were visible on samples from Unit C-1. This may either reflect owls' practice of swallowing their prey whole, or that human occupation of the site drove the nocturnal birds of prey from their roosts and the low-level digestion in that unit is the product of small carnivore agency (Bochenski 2005). Upon investigating the prevalence of digestion traces on bones with manducation modifications (Figure 7.17), 48 % of bones (n = 32) with evidence of carnivore agency also had digestion traces. In Layer B and Unit C-2, bird of prey agency was visible on the avian remains, 78 % of which had digestion traces.

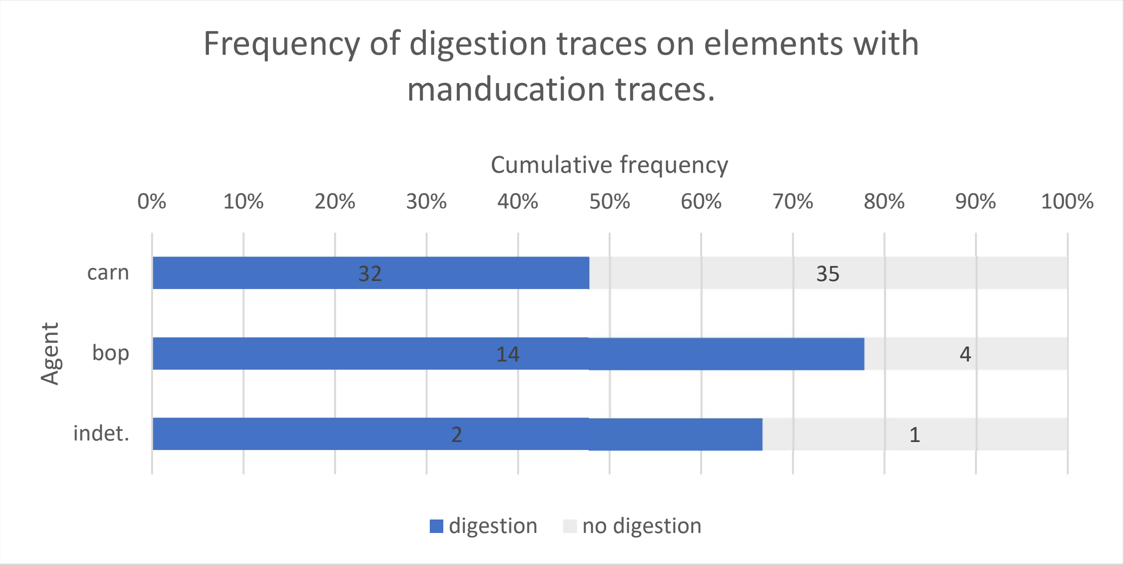


Figure 7.17: Stacked bar chart showing the relative frequencies of digested elements on bones exhibiting identifiable manducation modifications. Carn = carnivore, bop = bird of prey, indet. = indeterminate. 78% of bones modified by birds of prey also exhibited digestion modifications.

7.6.3 Human modifications

7.6.3.1 Striations

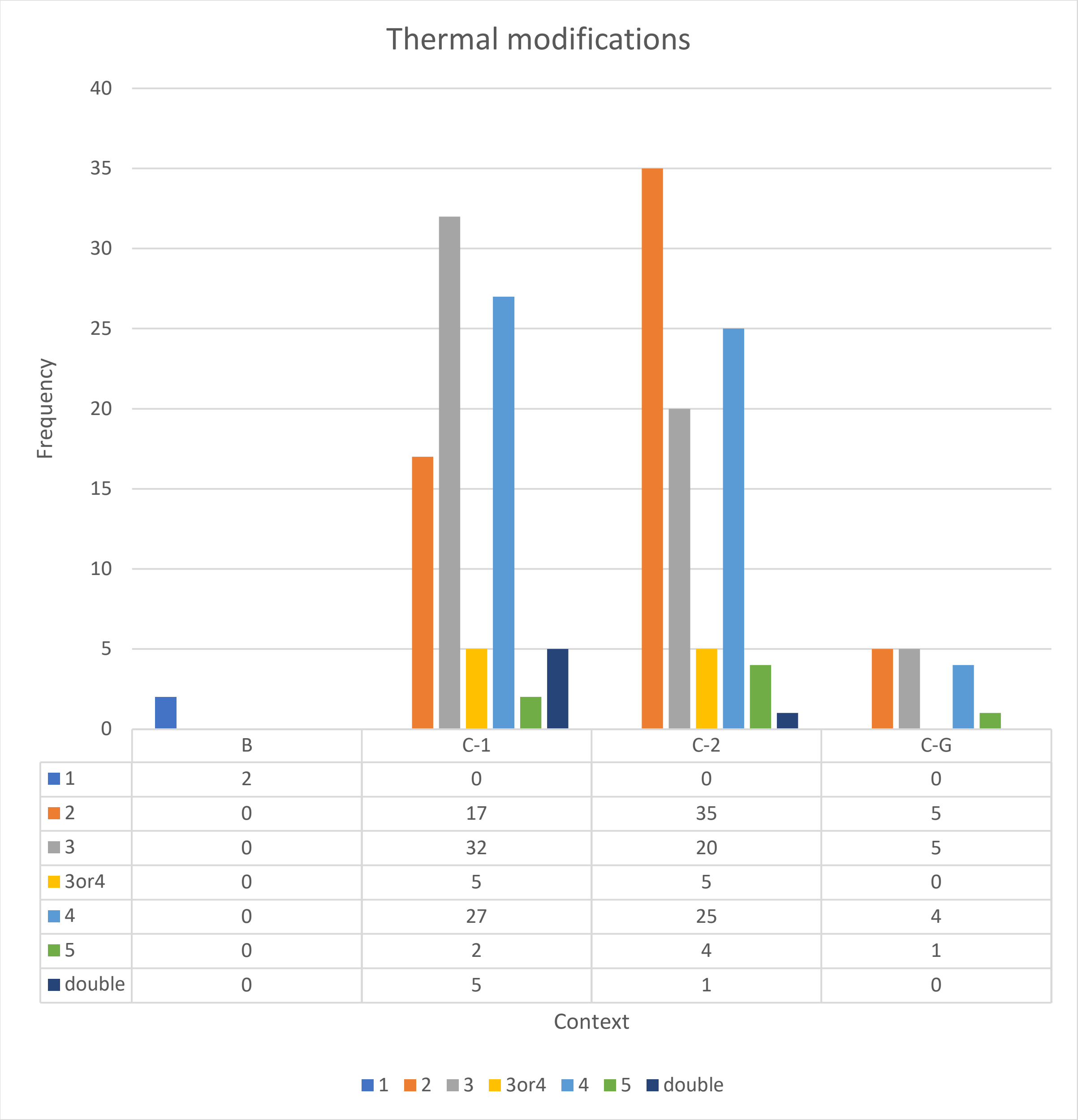
No specimens in the Tabun sample displayed striations that were the product of human agency.

7.6.3.2 Peeling

The proximal right coracoid of a Common Quail (*Coturnix coturnix*) from Unit C-1 (LA-645) showed indications of peeling of the bone surface near the fracture. This specimen also presented with thermal modification with double colouration, indicating a differential exposure to flame.

7.6.3.3 *Thermal modifications*

Two specimens from Layer B showed speckling indicative of thermal modification (Figure 7.18). In contrast, units C-1 and C-2 showed a diversity of higher ranks of thermal modification. This variation in exposure, along with evidence of frequent hearths in layer C (Albert *et al.* 1999) suggested an intentional exposure of bird carcasses to fire. Six elements exhibited double colouration, indicating a differential exposure to heat caused by the presence of flesh on the bone (Blasco and Peris 2009) (Figure 7.20; Figure 7.19).



	B	C-1	C-2	C-G
1	2	0	0	0
2	0	17	35	5
3	0	32	20	5
3or4	0	5	5	0
4	0	27	25	4
5	0	2	4	1
double	0	5	1	0

Figure 7.18: Thermal modifications by context, ranging from 1 (speckling) to 5 (calcined). 'double' reflects two degrees of modification found on the same specimen.

Passeriformes (n = 76) were most frequently exposed to fire followed by Columbiformes (n = 54) and the collective remains of indeterminate taxa (n = 43) (Table 7.18). These groups were complemented by gamebirds, water birds, and corvids. In addition, fire damage was noted on falcons (n = 4) and the remains of a diurnal raptor (n = 2).

Table 7.18 Thermal modifications by higher taxa group.

Order	Family	C-1	C-2	C-G	C-TOTAL
Galliformes	All	2	2	0	4
Columbiformes	All	27	23	4	54
Pelicaniformes	Ardeidae	1	0	0	1
Accipitriformes	All	0	0	2	2
Falconiformes	All	1	3	0	4
Passeriformes	Corvidae	0	3	0	3
Passeriformes	Non-corvids	29	45	2	76
Indeterminate		23	13	7	43
Total		83	89	15	187

Figure 7.19: LA-593 – A rock dove (C. livia) femur showing thermal modification to the proximal articulation.

Figure 7.20: LA420 – A longbone fragment of 'Aves sp. (size = columba)' showing thermal modifications to the right side due to direct exposure to heat, while the left side was not directly exposed

7.6.4 Fragmentation

A total of 300 fractures were found to be completely, or partially, made on fresh bone, or made close to the time of deposition (Table 7.19). Of these, 49 were of mixed character. Recent flaking and flaking of fracture surfaces made these unsuitable for further examination. Of 251 fractures of 'old' character, 76 displayed an irregular or jagged fracture outline. 48 specimens showing a transverse outline were likely the result of trampling activities close to the time of deposition. Seven specimens were too obscured by concretions to accurately discern the character of the fracture.

A total of 81 specimens displayed a spiral fracture outline, of which 34 exhibited an oblique fracture angle. Sixteen of the spiral-oblique fractures also presented with a smooth fracture surface. However, six of those 16 specimens were in Layer B where there is no evidence of human occupation except sporadic visits. It is noted by Bochenski (in O'Connor 2002) that birds of prey may leave spiral fractures on avian remains. The remaining 10 were found in the occupational deposits in units C-1 (n=3) and C-2 (n=7). It cannot be ruled out that these specimens were the result of human butchery and dismemberment practices.

Table 7.19: Fractures of 'mix' and 'old' character sorted by context and outline.

	Context									
	B		**C-1**		**C-2**		**C-G**		**Total**	
Outline	old	mix	old	mix	old	mix	old	mix	old	mix
Spiral	34	7	17	3	29	5	1	0	81	15
Transverse	18	0	9	0	21	4	0	1	48	5
Mix	9	4	13	4	5	1	2	0	29	9
Irregular	20	4	32	5	12	3	1	1	65	13
Jagged	5	3	6	0	8	4	2	0	21	7
Longitudinal	0	0	0	0	0	0	0	0	0	0
Obscured	4	0	1	0	2	0	0	0	7	0
Total	**90**	**18**	**78**	**12**	**77**	**17**	**6**	**2**	**300**	

In addition to the fractures on identifiable elements, there were a large number of longbone shaft fragments in the Tabun material that cannot be securely identified beyond class (n = 75). The fractures were the result of trampling, either by humans or by other mammals.

7.7 Spatial distribution

Spatial data available from the excavation archives allows for an examination of the distribution of avian remains across the excavated area (Figure 7.21; Figure 7.22). The NISP for each square (Jelinek *et al.* 1973) was calculated per defined unit. Depth information within the units of Layer C was available, but the sample size in each individual bed was so low it did not produce meaningful results.

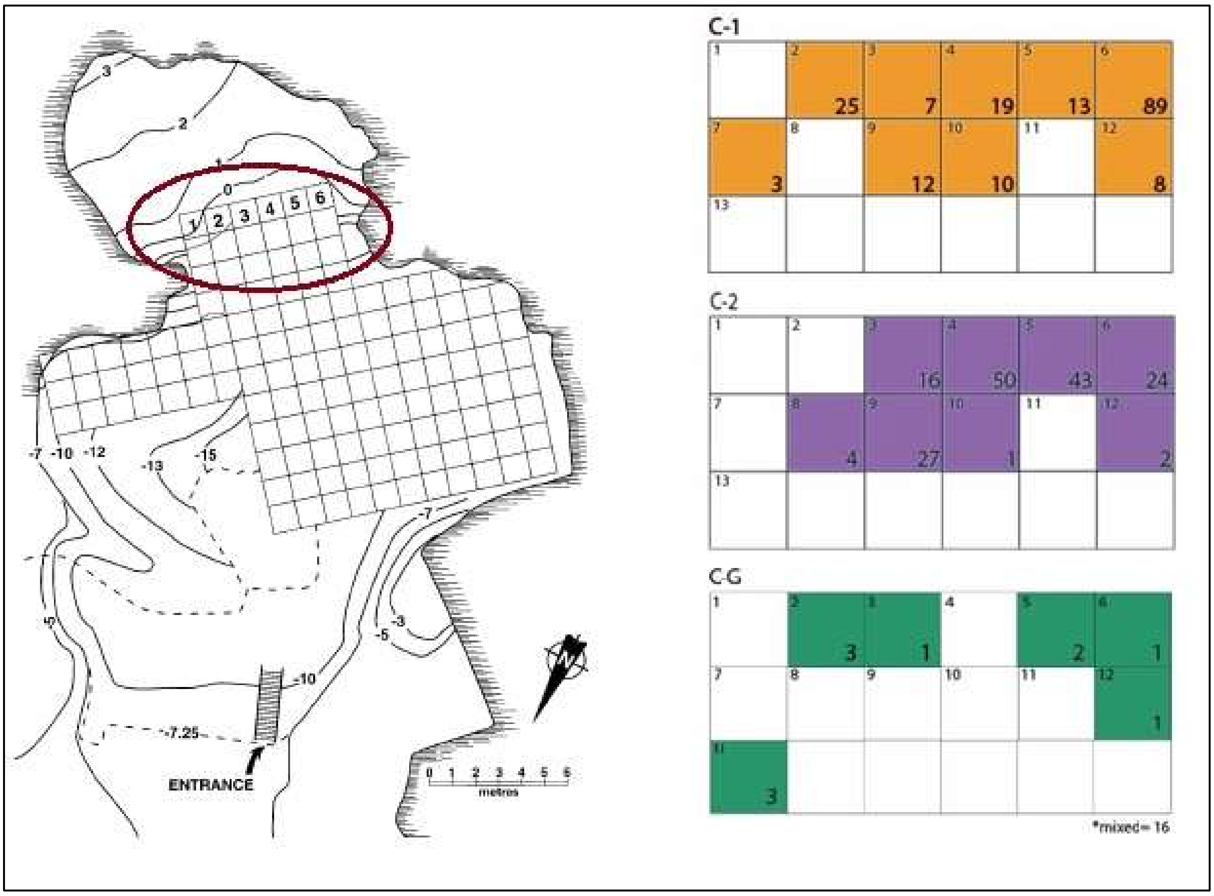


Figure 7.21: Spatial distribution of bird remains in contexts C-1, C-2 and C-G. Small numbers in the top left hand corner of the squares are Jelinek's grid numbers, large numbers at the bottom right of each square is the number of bird remains in each square. Plan drawing of Tabun Cave is after Albert et al. 1999.

The spatial distribution of avian remains in Layer C was confined to the horizontal plan of Jelinek's cut into Garrod's section (Figure 7.21). In addition to the remains recovered by Jelinek's team, these NISPs included bird material from section samples processed by Ph.D. candidate Tal Fried (UoH) who is currently studying the micromammal sequence of Tabun. The recent samples embellished Jelinek's original material (Table 7.20) and accounted for all of the material assigned to Square 6 in Unit C-2. Square 6 was the richest in bird remains (n = 113). In Unit C-1, the 89 remains included rock dove (*C. livia*), partridge (*Alectoris* sp.), quail (*Coturnix* sp.), falcons (*Falco* sp.), and a gull (*Larus* sp.). Seven rock dove (*C. livia*) and rock dove-sized bones from this concentration of remains displayed varying degrees of thermal modification.

Table 7.20: Origin of avian remains in squares 3, 5, and 6 in Tabun layer C.

Unit	Square	Jelinek's NISP	Recent sample NISP	Total NISP
C-1	3	2	5	7
C-1	6	65	17	89
C-2	5	23	20	43
C-2	6	0	24	24

In unit C-2, if recent samples are excluded, the remains were concentrated towards the middle of the excavated area, within the living area during occupied phases. 62.4 % (n= 58) of the remains in squares 4 and 5 exhibit varying degrees of thermal exposure. Few remains from C-G have reliable contextual data (n = 11). However, it was interesting that the Accipitriformes in this layer came from the same square as the remains from C-1.

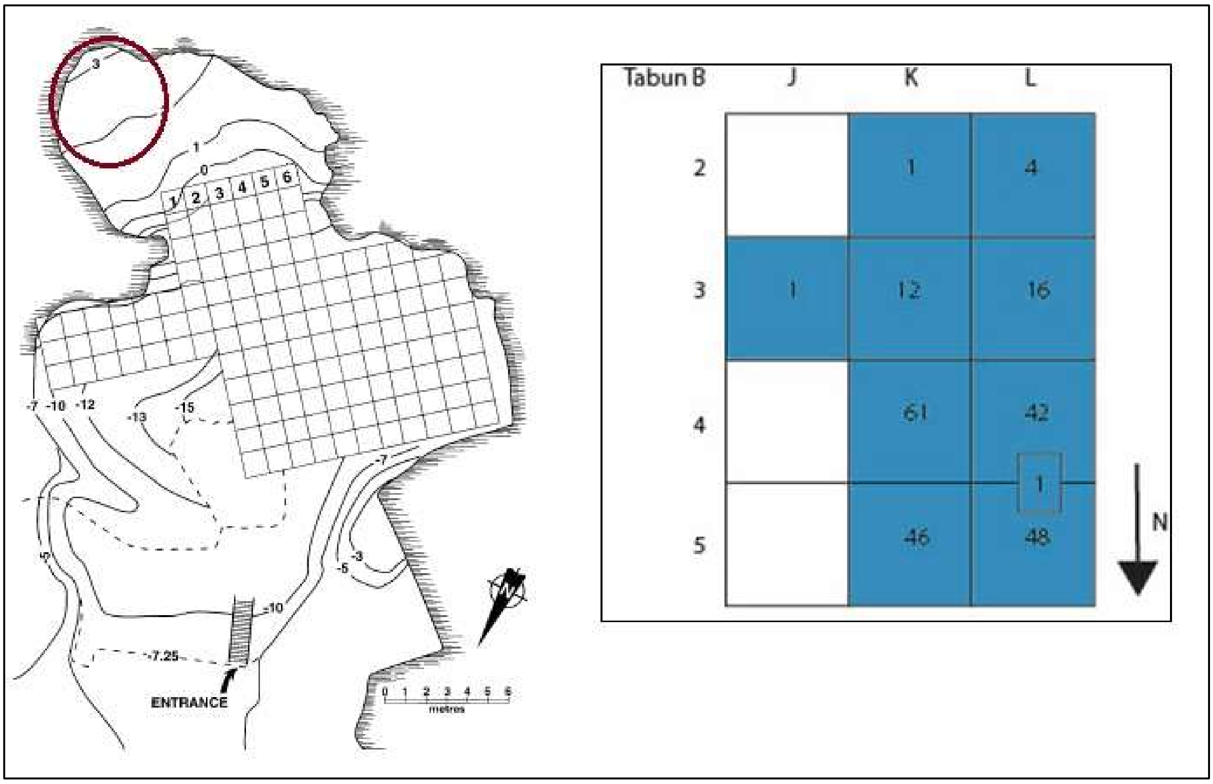


Figure 7.22: Spatial distribution of birds from recent excavations in Layer B. The area of the chimney under investigation is marked in red. Plan drawing of Tabun Cave after Albert et al.1999.

In Layer B, few remains were recovered from squares J3, K2, and L2 close to the chimney wall. The density of remains rose towards the middle of the chimney and were highest in squares K4 to L5. These were also the squares in which the greatest depths had been reached (Figure 7.23). The largest concentration of bird bones was between 2 and 2.5 metres above the datum.

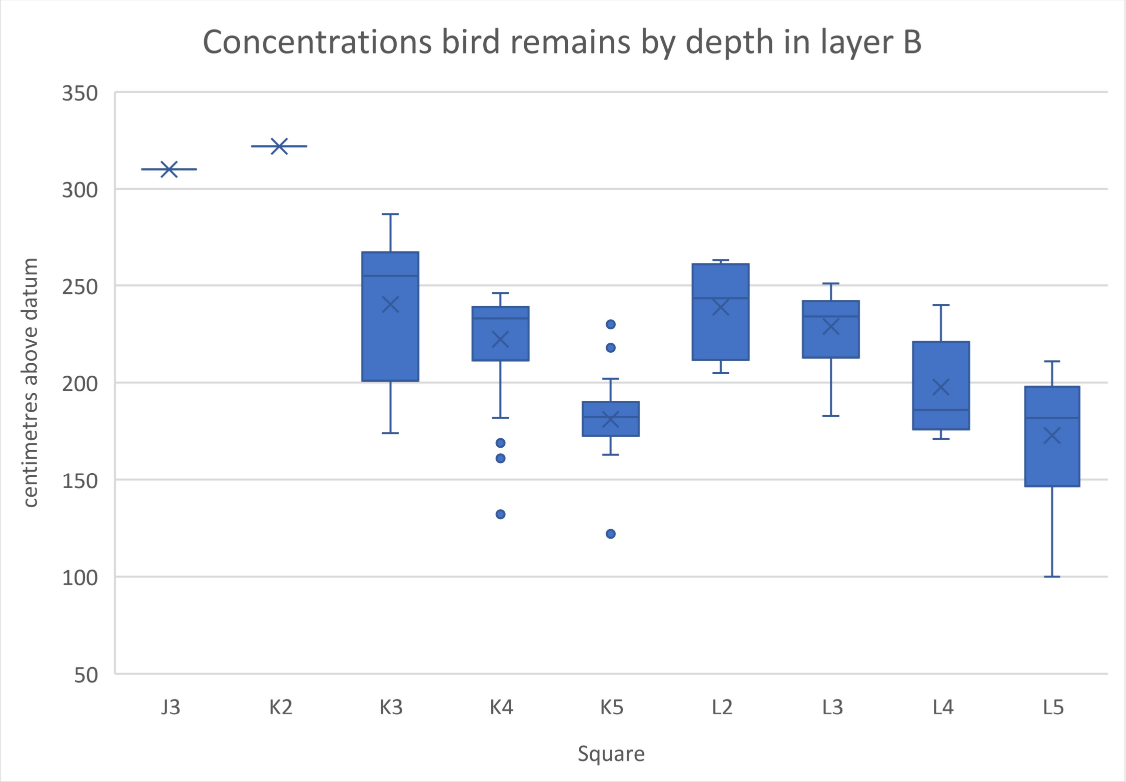


Figure 7.23: Concentration of bird remains per square, measured in centimetres above site datum. Depths increase towards the centre of the site.

7.8 Interpretation of the Tabun avifauna

7.8.1 Human behaviour

Neanderthals frequenting Tabun Cave in layer B and the indeterminate hominid taxon in layer C show markedly different modes of occupation at Tabun Cave (Garrod and Bate 1937, Jelinek *et al.* 1973, add more recent references here). However, as the sequence of deposition is continuous from C to lower B (Jelinek 1982), and no absolute identification can be made of the humans present in C (Harvati 2016), no distinction will be made between human taxa in the following discussion.

The composition of avian species in layers B and C inform us about the catchments of the humans who frequented Tabun Cave, and the variety of habitats they exploited (Finlayson *et al.* 2016; Finlayson 2011). Wetland foragers and/or nesters like the Pelicaniformes and the shore birds in layer C would not naturally appear in a cave environment (Cramp *et al.* 1977-1994; Finlayson 2011; Laroulandie 2000). An external agent must have introduced them to the site from their natural habitat, presumably on the coastal plain to the west (Shirihai 1996). The habitual transportation of food resources from the open plains was supported by the mammalian remains recovered at Tabun in Layer C, including the semi-aquatic hippopotamus (*Hippopotamus* sp.) and the grassland gazelle (*G. gazella*). Indications of indeterminate remains with waterfowl affinities suggested the exploitation of waterbirds and shore birds alongside pigeons and game birds. After the chimney collapse (Garrod and Bate 1937; Jelinek *et al.* 1973), humans no longer transported species from the surrounding landscape into the site (Jelinek *et al.* 1973, Marin-Arroyo 2013). In the bird remains, this change was visible in the absence of wetland and shore birds in layer B, as well as the absence of thermal modifications on the remains (Table 7.6; Figure 7.18).

No cut marks were identified on avian remains from my study. However, this does not mean that birds did not feature in the human diet at the site. A range of thermal modifications on specimens in both units of layer C strongly suggested human exploitation. Unit C-1 and C-2 showed thermal modifications on 44.4 % and 53.7 % of the remains, respectively. Including context C-G, 49.1 % (n = 187) of bones in layer C exhibit modifications. The variety of degrees of burning along with the presence of elements exhibiting double colouration points towards non-uniform exposure to fire. Localised charring and double colouration suggest cooking practices (Blasco and Peris 2009). The articular ends of bones exposed during disarticulation, were more directly exposed to fire while flesh partially or completely protected the rest of the bone (Rosell 2001). Therefore, even in the absence of cutmarks, the thermal modification of avian remains indicates human exploitation of birds at Tabun Cave. In Unit C-1 the remains were most highly concentrated in one area (Square 6), while remains in C-2 were spread throughout squares in the centre of the living floor. This can be aligned with the hearths observed throughout C-2 (Jelinek *et al.* 1973, Albert *et al.* 1999), and the change from the middle to the margin of the cave floor may reflect the changing use of the site in C-1 as the chimney collapses accelerated.

At species level, rock doves constituted the majority of the thermally modified remains (n = 52), and the NISP in general (n = 138; 26.3%). This indicated that the rock doves native to the cliffs around Tabun were a known source of subsistence and were consumed *in situ* both when the site was a residential site in Unit C-2, and in Unit C-1 when occupational episodes were less frequent. Remains of game birds (n = 4), and corvids (n = 3) were also thermally modified, alongside two charred raptor remains and 4 charred remains of a falcon. A heron (Ardeidae), one of the wetland species that are not native to cave sites, also had thermal modifications of the bone surface, indicating that the bird was brought to the site for cooking and consumption (Blasco and Peris 2009; Fernandez-Javlo and Andrews 2016). In Layer B, rock doves still dominated the sample numerically, but they accounted for a smaller percentage of the NISP (n = 37; 15.7 %) indicating that more individuals were introduced to the accumulation when humans occupied the site in Layer C than in Layer B when no human agency is visible on the bird remains.

7.8.2 Other agents contributing to the accumulation

Taphonomic analysis has shown that parts of the avifauna accumulation in Layer B was due to avian predators and small carnivores. Non-human predator agency was evident in carnivore tooth marks (n = 67) and digestion traces (403) on the surface of remains. As well as feeding on the birds present in the area, small carnivores and larger birds of prey would have been attracted to the nourishment present in the accumulation of mammal remains. In Layer B the avifauna accumulation was attritional and natural in character. In layer B, Tabun was a non- domestic, wild site (Jelinek *et al.* 1973; Jelinek 1982; Marin-Arroyo 2013)

High frequencies of low-level digestion indicate the presence of roosting owls within the site (Andrews 1990). No direct evidence of their presence has been found so far in this context. However, birds of prey are known to roost in the open chimney to this day (*pers* *comm* R. Yeshurun). Remains of what was likely a steppe eagle (*A. nipalensis*) and a small falcon were recovered in the sediment alongside micromammals. Some of these remains likely washed in with sediment from the plateau above, but others are part of the natural accumulation at this level of the deposit. Passerines inhabiting the wadi environments would have provided prey for both diurnal and nocturnal raptors, like falcons and owls.

The presence of predatory species was also evident in both units in layer C. In C-2, where there was an almost continuous accumulation of residential deposits, birds of prey and small and large carnivores all frequented the site. Whether these agents visited the site during intervals between human occupations, or openly shared the site with the humans living there, they left bite marks and digestion traces on material in the deposits. The remains of falcons and an indeterminate larger raptor, along with spotted hyena (*C. crocuta*), large felines and red foxes (*V. vulpes*) demonstrated the multitude of agents that may have contributed to the primary or secondary (scavenging) deposition of avian remains in the unit (Marin-Arroyo 2013; Yeshurun 2016).

In C-1, there were no manducation traces that directly identify avian predators as the agent behind the accumulation. This was likely due to the increased instability of the cave roof making the cave less attractive as a roost. On the other hand, this was the only context to produce remains of a nocturnal raptor (barn owl *Tyto alba*). However, this context also contained the remains of wild cats, which also produce low-level digestion traces along with red foxes (*V. vulpes*), and beech martens (*M. foina*) (Marin-Arroyo 2011; Yeshurun 2016). All of these small carnivores would have been attracted to the accumulation of fallow deer in C-1.

In Layer C, Tabun slowly evolved from an occupied site to a more sporadically visited butchery site (Garrod and Bate 1937; Jelinek *et al.* 1973; Jelinek 1982; Albert *et al.* 1999, Marin-Arroyo 2013). Throughout both modes of occupation, the humans utilising the site shared their space with birds of prey and carnivores, both of which contributed to accumulation and modification of avian remains.

7.8.3 Ecological interpretations

Bioclimatic tolerances indicated an ecosystem more appropriate for moderate to generalist species, with few specialists appearing throughout the sequence and none in Unit C-1. The variety of ecosystems available in the landscape close to the cave, as suggested by the avian remains, could have provided a variety of food sources for birds on all levels of the trophic chain. The avian species at Tabun reflected a generally warm, dry environment with a few wetland species appearing in the deposits of Layer C. Palynological analysis placed Layer C in the Würm Pluvial. This data aligns with the Hula sequence (Jelinek *et al.* 1973) and places the deposition of Layer C during a cooler, wetter climate than at present when ice sheets in the north were advancing, binding seawater in ice, and displacing some temperate species into warmer areas outside their current distribution (Finlayson 2011). The temperate woodcock in context C- G may have been result of this displacement, though it is possible that the woodcock wintered in Israel during the Pleistocene (Birdlife Israel 2021).

Wetland marshes featured on the fertile coastal plain between the cliffs of Mount Carmel and the Mediterranean in the Middle Palaeolithic and would have supported populations of water birds and shore birds alongside mammals like the hippopotamus (Marin Arroyo 2011; Yeshurun *et al.* 2016). The unique wadi environment of Mount Carmel offered conditions similar to the present day (Nevo *et al*. 1999; Nevo 2009; Pavlíček *et al.* 2003), supporting a variety of Passeriformes (n = 307, NTAXA ≥ 15), from aerial insectivores like the swallow (*Hirundo* spp.) to the carnivorous shrike (*Lanius* sp.). The presence of fallow deer and other woodland species, along with the pollen of several tree taxa point to more extensive tree cover than at present (Jelinek *et al.* 1973; Weinstein- Evron 1983; Albert *et al.* 1999; Aharonovich *et al.* 2014). An absence of arctic and boreal species is not unexpected given latitude position of Tabun (32°N). However, the presence of unidentified specimens with Anseriform affinities may indicate the presence of wintering taxa on the coastal plain wetland marshes.

Migratory species enhance the sedentary bird populations, indicating the seasonality of the site. While pied wagtails (*M. alba*) winter in the Middle East in the present day (Shirihai 1996), the woodcock (*S. rusticola*) is not frequently found in Israel in the winter (Shirihai 1996). The hobby (*F. subbuteo)* on the other hand, visits Israel during summer months to breed (Cramp *et al.* 1977-1994; Shirihai 1996; Finlayson 2011). The appearance of these species within Tabun's Layer C could suggest that deposition happened in both summer and winter. This would be in line with interpretations of Layer C as a domestic residential site in continuous use (Jelinek *et al.* 1973). However, the southern displacement of species by advancing northern ice sheets may have led to pied wagtails (*M. alba*) and woodcocks (*S. rusticola*) breeding at this latitude during the Middle Palaeolithic (Eynaud *et al.* 2009;

Finlayson 2011). Given this ambiguity, the bird remains alone could not securely inform us about seasonality at the site.

Overall, the limited avian remains at Tabun appear to indicate stable environmental and climatic conditions and a broad range of available habitats while people occupied the site. Changes in the taxa present in layers B and C were most likely due to a change in the agent behind the accumulation of avian remains, not climatic changes. Further study of the indeterminate Passerines will contribute to a more detailed understanding of the environment and any changes in species representation between contexts.

7.8.4 Summary

- The avian remains from Tabun Cave layers B and C reflected the rich biodiversity of the ecosystem surrounding the site. Species which today inhabit forest, open, and wetland habitats appeared in the sediments, reflecting the breadth of the catchment area in Layer C.
- Breeding birds of prey contributed to the accumulation in Layer B by bringing prey back to their roosts in the chimney.
- In Layer C, humans inhabited the site, making hearths and exploiting birds as part of their diet. This is evident in thermal modifications attributable to cooking practices (n = 187). The rock dove was most intensively exploited species, complemented by game birds and sometimes corvids.
- Spatial analysis shows a difference in the distribution of bird remains between unit C-2 where the bird remains are concentrated in the middle of the living floor, and unit C-1 where the main concentration of remains is adjacent to the cave wall.
- Furthermore, throughout the entire depositional history of layers B and C, the site remained largely open to the sky, allowing a natural attritional deposition of local species to form in the site. The potential natural accumulation of species from the surrounding ecosystem sets the site apart from roofed cave sites where species not native to a cave environment must be introduced by an external agent.

8 Synthesis and Conclusion

In this chapter, I synthesise the collective results from chapters 3-7 and examine Neanderthal ecology and behaviour in order to address the research questions set out in Chapter 1 and summarised below.

1. Based on the avian taxonomic assemblages, how do the ecological parameters of the five Neanderthal sites compare between different geographical regions and through time? (Section 8.1)
2. How much evidence for human exploitation of birds exists at each site? (Sections 8.2.1, 8.2.2, and 8.2.4)
3. How does bird exploitation at the five sites inform us about Neanderthal subsistence strategies? (Section 8.2.3)
4. What is the temporal depth and geographic range of bird exploitation by Neanderthals? (Section 8.2.4)

8.1 Neanderthal ecology

The frequencies of four climate variables (bioclimatic tolerances, latitude ranges, temperature tolerances, and humidity tolerances) and two habitat variables (foraging and nesting habitats) represented by bird species were examined to see whether there were significant differences in climate and habitats in space and time at my five Neanderthal study sites. As explained in Chapters 3-7, sample sizes were generally too small to produce reliable results through chi^2-testing without grouping variables. Thus, to compare between the sites, Monte Carlo simulations of 10,000 random samples were run in SPSS27 to find the p-values using Fisher-Freeman-Halton Exact tests. The results are discussed below in relation to the Neanderthal bioclimatic and habitat niches. Categorical Principal Component Analyses (CATPCA) were run in SPSS27 on ecological variable frequency data from each site.

8.1.1 The Neanderthal climatic niche

The results of the Monte Carlo simulations were not significant for bioclimatic tolerances (p = 0.765, Fisher-Freeman-Halton exact test; Table 8.1), latitude ranges (p = 0.057, Fisher-Freeman-Halton exact test; Table 8.2), temperature tolerances (p = 0.085, Fisher-Freeman-Halton exact test; Table 8.3)or humidity tolerances (p = 0.076, Fisher-Freeman-

Halton exact test;Table 8.4). This lack of significance in all categories indicated that the Neanderthal bioclimatic niche did not vary across the geographical range represented by the sites in this study, or through the time span recorded at the sites (MIS 8 – MIS 3).

Table 8.1: Observed and expected (in brackets) frequencies of bioclimatic tolerances across five Neanderthal sites. A Monte Carlo sig. (2-sided) simulation based on 10,000 sampled tables produced a non-significant Fisher-Freeman-Halton Exact Test result (p = 0.765).

		Site										Total
		Cova Negra		Devil's Tower		Gorham's Cave		Scladina		Tabun		
Bioclimatic Tolerance	A	0	(1.2)	2	(1.2)	0	(1.1)	1	(0.5)	2	(0.5)	5
	B	9	(8.3)	8	(5.9)	4	(5.3)	1	(2.2)	2	(2.4)	24
	C	10	(10.0	6	(7.1)	7	(6.4)	4	(2.6)	2	(2.9)	29
	D	12	(11.4	8	(8.1)	8	(7.3)	2	(3.0)	3	(3.2)	33
	E	11	(10.7	6	(7.6)	8	(6.9)	3	(2.8)	3	(3.0)	31
		42		30		27		11		12		122

Table 8.2: Observed and expected (in brackets) frequencies of latitude ranges across five Neanderthal sites. A Monte Carlo sig. (2-sided) simulation based on 10,000 sampled tables produced a non-significant Fisher-Freeman-Halton Exact Test result (p = 0.057).

		Site										Total
		Cova Negra		Devil's Tower		Gorham's Cave		Scladina		Tabun		
Latitude range	A	0	(2.1)	2	(2.0)	3	(1.6)	2	(0.9)	0	(0.9)	7
	B	4	(3.9)	6	(3.8)	2	(3.0)	1	(1.6)	0	(0.8)	13
	B/D	1	(2.1)	1	(2.0)	1	(1.6)	4	(0.9)	0	(0.4)	7
	C	2	(3.6)	5	(3.5)	1	(2.8)	3	(1.5)	1	(0.7)	12
	D	12	(8.6)	8	(8.4)	7	(6.7)	0	(3.6)	2	(1.7)	29
	F	12	(10.7	8	(10.4	10	(8.3)	3	(4.5)	3	(2.1)	36
		31		30		27		11		12		104

Table 8.3: Observed and expected (in brackets) frequencies of temperature tolerances across five Neanderthal sites. A Monte Carlo sig. (2-sided) simulation based on 10,000 sampled tables produced a non-significant Fisher-Freeman-Halton Exact Test result (p = 0.085).

		Site										Total
		Cova Negra		Devil's Tower		Gorham's Cave		Scladina		Tabun		
Temperature tolerance	A	0	(2.9)	4	(2.4)	3	(2.1)	2	(0.7)	0	(1.0)	9
	B	10	(10.3	7	(8.5)	8	(7.3)	4	(2.3)	3	(3.5)	32
	C	12	(9.3)	6	(7.7)	6	(6.7)	2	(2.1)	3	(3.2)	29
	D	12	(10.0	8	(8.2)	8	(7.1)	0	(2.3)	3	(3.4)	31
	E	1	(2.6)	4	(2.1)	0	(1.8)	0	(0.6)	3	(0.9)	8
		35		29		25		8		12		109

Table 8.4: Observed and expected (in brackets) frequencies of humidity tolerances across five Neanderthal sites. A Monte Carlo sig. (2-sided) simulation based on 10,000 sampled tables produced a non-significant Fisher-Freeman-Halton Exact Test result (p = 0.076).

		Site										Total
		Cova Negra		**Devil's Tower**		**Gorham's Cave**		**Scladina**		**Tabun**		
Humidity tolerance	A	0	(3.0)	5	(2.2)	0	(2.1)	1	(0.8)	3	(0.9)	9
	B	5	(8.3)	6	(6.1)	7	(5.7)	4	(2.2)	3	(2.6)	25
	C	12	(10.0	5	(7.4)	7	(6.8)	3	(2.6)	3	(3.2)	30
	D	12	(10.3	6	(7.6)	8	(7.1)	2	(2.7)	3	(3.3)	31
	E	9	(6.3)	6	(4.7)	4	(4.3)	0	(1.7)	0	(2.0)	19
		38		28		26		10		12		114

CATPCA showed that 2 dimensions were sufficient to explain 95.78% of the variance in the ecological variables pertaining to climate (Cronbach's Alpha .998; total Eigenvalue 20.114; Figure 8.1; Appendix 6). While Dimension 1 was primarily defined by the latitude position of the site and the bioclimatic tolerance of avian species, Dimension 2 was primarily defined by temperature and humidity tolerances. In contrast to the generalised results produced by the Fisher-Freeman-Halton tests, CATPCA placed the individual sites into a biplot positioning them more closely to the variables which were most important at each individual location. The results echo those from the individual chapters (chapters 3-7) and produced a visual aide to interpret the relationship between the climatic variables in the five study sites.

The climatic variables associated with Gorham's Cave, Devil's Tower, and Cova Negra were closely related to each other, creating an Iberian cluster which was related to mid- and multi-latitudinal ranges, moderate to high humidity levels, and moderate temperatures. Within the Iberian cluster, Gorham's Cave and Devil's Tower were also influenced by low temperature, and more northerly latitude bands. Meanwhile, Scladina and Tabun were not related to each other, nor to the Iberian group. Tabun alone showed a close relationship to high temperatures and low to moderate humidity despite species with these tolerances beign present in other sites. However, Tabun featured on the positive side of Dimension 1 with the Iberian group. Scladina featured alone on the negative side of Dimension 1, closely associated with low temperatures and more northerly latitude bands. However, like the Iberian sites, Scladina was more affected by moderate to high humidity levels.

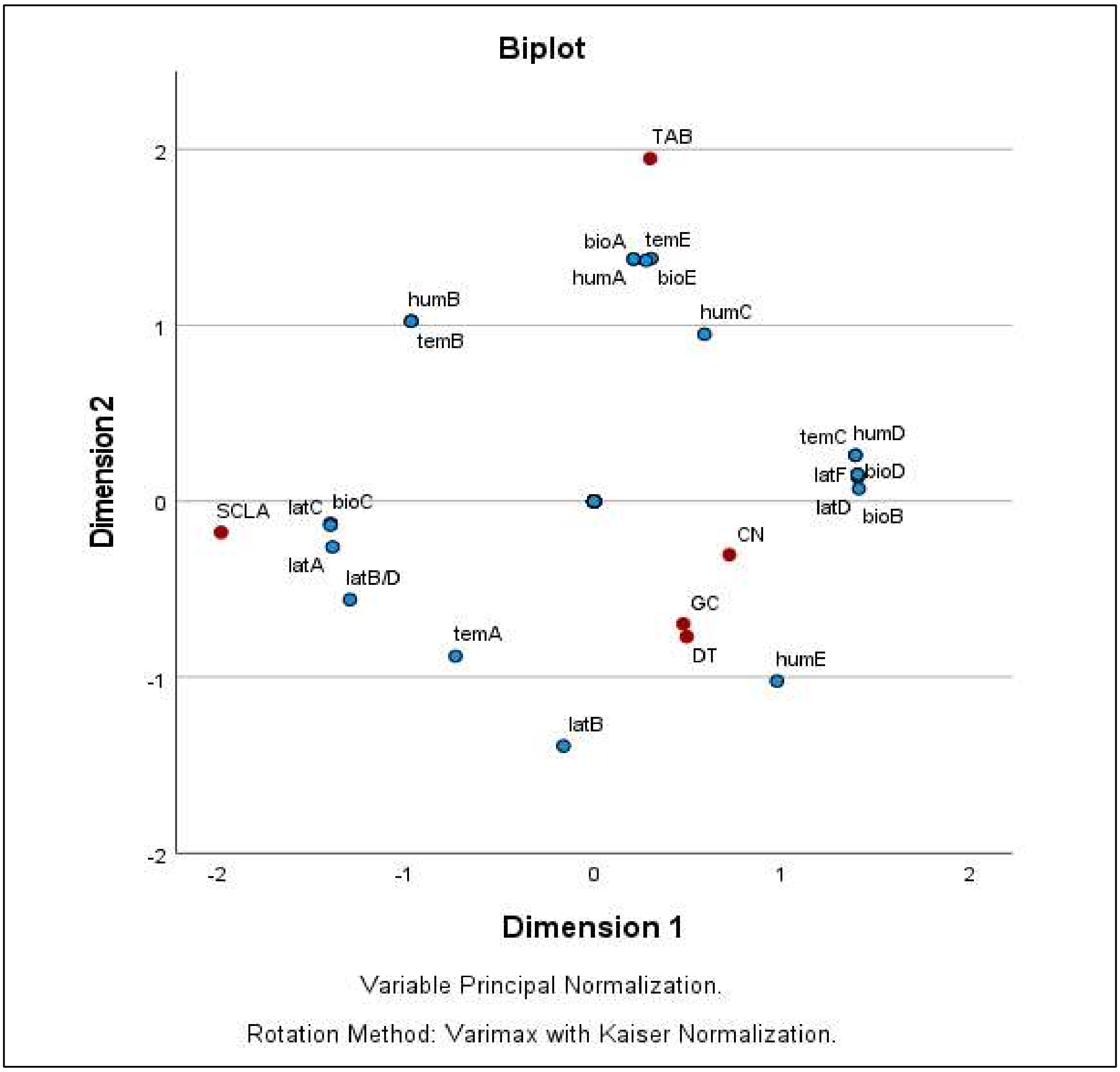


Figure 8.1: Biplot of results of CATPCA of climate variables at five Middle Palaeolithic sites. GC = Gorham's Cave, DT = Devil's Tower Rockshelter, CN = Cova Negra, SCLA = Scladina, TAB = Tabun. The Iberian sites cluster together while Scladina and Tabun are isolated. Three clusters of variables are visible, one reflecting medium to high latitude (lat A, C) and moderate bioclimatic tolerances (bioC), another connecting bioclimatic extremities (bio A, E), low to moderate humidity (hum A, C) and high temperatures (temE), and one showing a strong relationship between mid reange temperatures (temC), moderate bioclimatic tolerances (bioB, D), moderate to high rainfall (hum D) and mid- and multi-latitudinal ranges (latD, F).

Geographically, the sites were concentrated within the known Neanderthal home-range of temperate to mid-latitude western Eurasia. The northern signal (LAT A and LAT B) of Scladina Cave was eclipsed in the results by the presence of arctic and boreal species in Gibraltar. This was due, in part, to the small sample size from Scladina, but also to the southerly displacement of northern species into the mid-latitude belt during glaciations (Carrion *et al.* 2008; Eynaud *et al.* 2009). Subtropical species were not present in any of the examined sites, probably because the Sahara Desert acts as an ecological barrier that restricted the movement of subtropical species northwards (Finlayson 2004). A considerable wetting of this arid desert belt would be required to allow sub-tropical species to cross into the mid-latitude belt (Finlayson pers. comm.). The bioclimatic tolerances of each site trended towards generalists, capable of adapting to the fluctuating climatic conditions of the Middle Palaeolithic (Holm and Svenning 2014).

The temperature tolerances at all sites centred on moderate to warm temperatures with rare occurrences of hot-tolerant species at the Mediterranean sites. This distribution mirrored the latitude positions of the respective sites. Cold tolerant species (TEM A) congruent with the Arctic species (LAT A) were unsurprisingly present at Scladina due to its northerly position, but they also featured in Gorham's Cave, which comprised signs of a non-analogue refugium community (Rodriguez-Vidal *et al.* 2013). It must be noted that the frequency of moderate-to-warm species in the Waechter avifauna of Gorham's Cave did not reflect the diversity of species found in the more recent phase of excavations undertaken since the 1990s (Cooper 1999; Finlayson 2006; Finlayson *et al.* 2016; Finlayson 2019) – a discrepancy that likely arose from the sub-standard collection methods of the Waechter excavations (Collcutt and Currant 2012).

The temperature tolerance data derived the avifaunal evidence supports what is known about the Neanderthal range. The sites in my analysis alone show that they inhabited a range of temperature zones from cool conditions at Scladina in the north to mid-latitude heat at Tabun in the Middle East. Direct evidence from areas as diverse as the mountainous Russian Altai (Slon *et al.* 2019), the European Plains (Picin *et al.* 2020) and coastal sites on the Atlantic coast of Portugal (Zilhao *et al.* 2020), show that Neanderthals inhabited a wide range of landscapes. No available data supports long-term occupation of either extreme cold or extreme heat, although Neanderthals may have ventured closer to the ice front on occasion (Slimak *et al.* 2011; White and Pettitt 2011).

Humidity tolerances of the birds showed that Neanderthals occupied areas where there were varying levels of rainfall. Jennings *et al.* (2011) found that a majority of Neanderthal sites in southern Iberia were found in areas with a mean annual rainfall between 400 and 600 mm indicating that rainfall was a key factor in Neanderthal distribution patterns. In general, there was a lack of extreme wet and a lack of extreme dry (HUM A and HUM E), and sub-humid to dry tolerances were most frequent regardless of the site's geographic position. This intermediate, fluctuating rainfall has been linked to habitat diversity and underlines the importance of humidity in human habitat (Finlayson 2006, 2014; Jennings 2007; Jennings *et al.* 2011; Frumkin *et al.* 2011; Finlayson *et al.* 2013).

8.1.2 The Neanderthal habitat niche

The results of the Fisher-Freeman-Halton tests were not significant for foraging habitat (p = 0.583; Table 8.5), but were for nesting habitat (p = 0.020; Table 8.6). At all five sites, the bird species suggested diverse foraging and nesting opportunities. The apparent differences signalled by a significant p-value for nesting habitat is due to the under representation of mixed-habitat nesters, and the over representation of rocky nesters. However, avian foraging habitat frequencies indicate that mixed habitats were present across the Neanderthal range. Minor differences between sites reflect the exact location of the site in the landscape.

Table 8.5: Observed and expected (in brackets) frequencies of foraging habitats across five Neanderthal sites. A Monte Carlo sig. (2-sided) simulation based on 10,000 sampled tables produced a non-significant Fisher-Freeman-Halton Exact Test result (p = 0.583).

		Site										**Total**
		Cova Negra		**Devil's Tower**		**Gorham's Cave**		**Scladina**		**Tabun**		
Foraging Habitat	A	9	(7.2)	7	(5.2)	1	(4.0)	0	(1.7)	3	(1.9)	20
	F	7	(7.9)	5	(5.7)	3	(4.4)	4	(1.9)	3	(2.1)	22
	M	12	(12.6)	7	(9.1)	10	(7.1)	3	(3.0)	3	(3.3)	35
	Ma	1	(2.9)	5	(2.1)	2	(1.6)	0	(0.7)	0	(0.7)	8
	O	12	(10.8)	6	(7.8)	7	(6.0)	2	(2.6)	3	(2.8)	30
	R	2	(0.7)	0	(0.5)	0	(0.4)	0	(0.2)	0	(0.2)	2
	W	7	(7.9)	6	(5.7)	5	(4.4)	3	(1.9)	1	(2.1)	22
		50		36		28		12		13		139

Table 8.6: Observed and expected (in brackets) frequencies of nesting habitats across five Neanderthal sites. A Monte Carlo sig. (2-sided) simulation based on 10,000 sampled tables produced a significant Fisher-Freeman-Halton Exact Test result (p = 0.020).

		Site										**Total**
		Cova Negra		**Devil's Tower**		**Gorham's Cave**		**Scladina**		**Tabun**		
Nesting Habitat	F	7	(7.3)	5	(5.2)	3	(4.8)	4	(2.3)	3	(2.5)	22
	M	1	(6.6)	6	(4.7)	7	(4.3)	3	(2.1)	3	(2.3)	20
	O	11	(6.3)	3	(4.5)	0	(4.3)	2	(2.0)	3	(2.1)	19
	R	12	(10.9)	8	(7.7)	10	(7.2)	0	(3.4)	3	(3.7)	33
	W	7	(6.9)	5	(4.9)	5	(4.6)	3	(2.2)	1	(2.4)	21
		38		27		25		12		13		115

These minor differences are visible in the biplot resulting from CATPCA. Analysis showed that 2 dimensions were sufficient to explain 93.512% of the variance (Cronbach's Alpha .994; total Eigenvalue 11.221; Figure 8.2; Appendix 6). While Dimension 1 was primarily defined by Aerial feeders, open and mixed nesters, and species which feed and nest by water, Dimension 2 was defined by the presence of woodland habitats, marine foragers, and rocky nesters. The resulting biplot placed the sites in relation to the most important variables at each location.

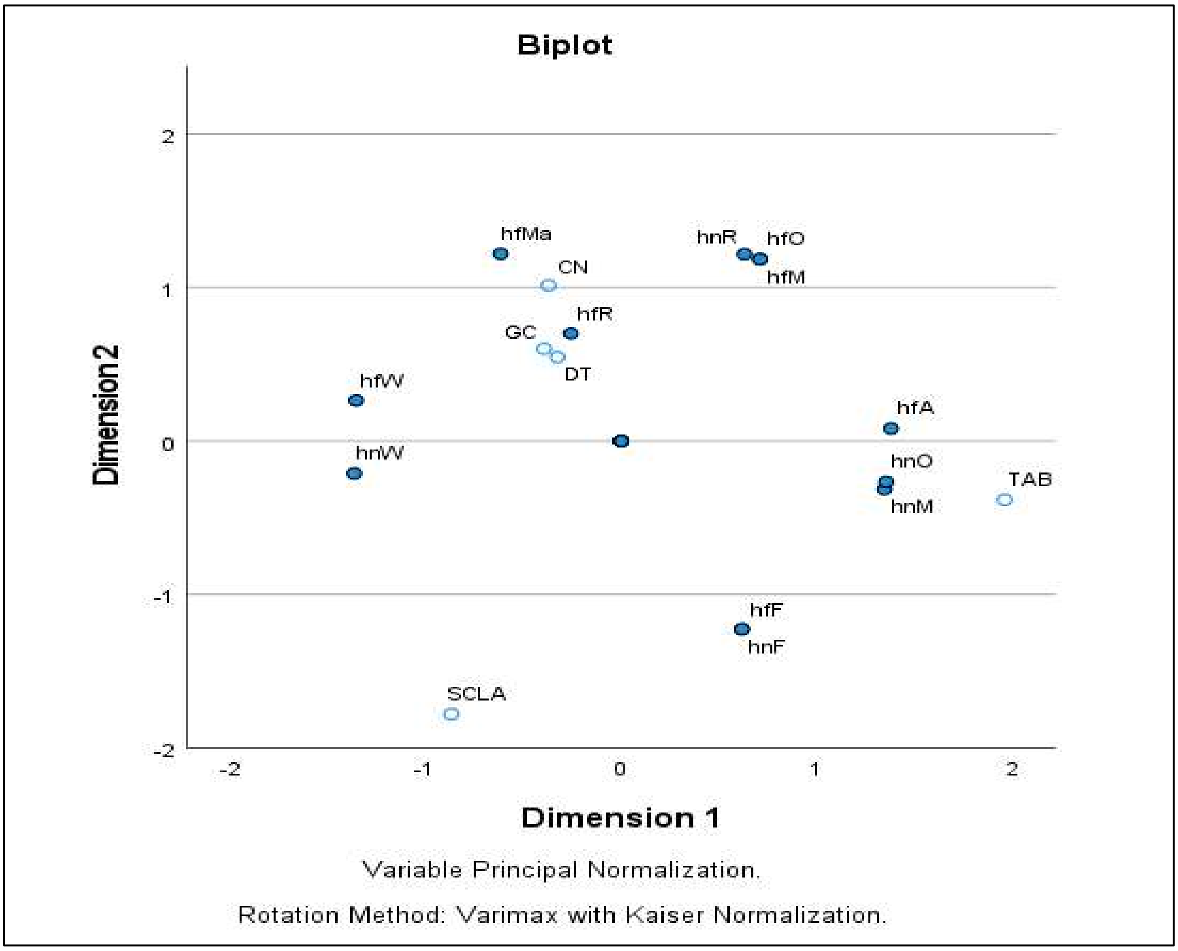


Figure 8.2: Biplot of CATPCA results for habitat variables at five Middle Palaeolithic sites. GC = Gorham's Cave, DT = Devil's Tower Rockshelter, CN = Cova Negra, SCLA = Scladina, TAB = Tabun. The Iberian sites cluster together while Scladina and Tabun are isolated. The Iberian sites are closely related to rocky, mixed, and marine habitats. Tabun shows an affinity to open and mixed habitat nesters and aerial foragers. Scladina is positioned between wetland and forest habitats.

As with the climatic variables, the Iberian sites clustered, showing strong relationships to rocky, marine, and wetland habitats. Forest habitats were more important at Scladina and Tabun, but while Tabun also was influenced by open and mixed habitats, Scladina was more influenced by wetland habitats. These results aligned well with the chi^2-tests in the individual chapters, the and the topographical positions of the sites.

The Fisher-Freeman-Halton tests indicated that Open, Forest, and Mixed habitats were present in all areas. Mixed savannah and shrubland habitats appeared in the intermediate region between open and forest habitats, forming a mosaic type, heterogenous landscape. This type of varied habitat is dependent on varied rainfall patterns (Finlayson *et al.* 2011). Open habitats varied in character along with climatic conditions. In cold, dry conditions like at Scladina, open habitat manifested as tundra-steppe landscape (Pirson 2007; Pirson *et al.* 2008), while around the Mediterranean coast, sunken sea-levels exposed coastal plains around Gibraltar west of Tabun Cave in Israel. These habitats were savannah-type warm, open habitats (Finlayson 2006; Finlayson 2019; Carrion *et al.* 2008; 2018; Figure 8.3).

Woodland habitats appeared as riparian gallery forests. In Gibraltar, these woodland features appeared in clusters on the coastal plain and close to fresh water sources (Finlayson 2004; Finlayson *et al*. 2006; Finlayson *et al*. 2008; Carrion 2003, 2008, 2018). Meanwhile at Cova Negra, woodlands were limited to the banks of the Albaida river (Fumanal 1986). Riparian trees also grow in the wadi near Tabun where water runs in the wet season (Jelinek *et al.* 1973). At Scladina, the presence of the capercaillie and black grouse speak to the presence of a well-developed woodland (Holm and Svenning 2014) along the river Meuse and the Rue de Pontaine. Along with the other tributaries of the river Meuse, these gallery forests may have functioned as cryptic refugia for forest species in the vast expanse of the steppe tundra which dominated in MIS 3 (Stewart and Lister 2001; Pirson 2007; Pirson *et al.* 2008; Stewart *et al.* 2010).

Wetland species presence at all sites highlighted the importance of fresh water sources for human habitation (Finlayson 2011). Again, there is a diversity in the type of wetland habitat available at each site. At Scladina, fresh water appeared as rivers, while in Gibraltar and at Tabun, the fresh water sources were on the coastal plains (Finlayson 2006; Jelinek *et al*. 1973; Yeshurun 2016). Though there is a river in the direct vicinity of Cova Negra, the wetland birds present in the sample prefer larger bodies of water (Madge and Burn 1987). The closest such body of water present in the area today is Lake Bellus, ~5 km to the south.

Marine foragers in Gibraltar exploited the rocky habitats on offer to nest while feeding off the edges of the coastal plain. At Devil's Tower, arctic marine ducks suggest the presence of a no longer extant estuarine environment to the north of the site (Finlayson 2006; Finlayson *et al.* 2008; Cooper 1999). At present, the coast is 30 km to the east of Cova Negra, a distance that would have increased in the Pleistocene when sea-levels were lower.

The marine shag would not appear naturally this far inland (Cramp *et al.* 1977-1994). Conversely, despite the relative proximity of the coastline at Tabun, no marine species were present in the avifaunal sample. It is possible that human activity at the site deterred seabirds from nesting close to the site. Another possibility is that the more sheer west-facing cliffs along the margins of Mount Carmel offered more suitable nesting opportunities.

The rocky habitats were important to nesting species at all of the southern sites. Rocky feeders only appeared at Cova Negra. Rocky nesters at Cova Negra and at Devil's Tower centred around the presence of breeding swift colonies in the summers. Conversely, there were no swifts in the sample at Gorham's Cave. The difference may lie in the sheer cliff face above Devil's Tower, which was also attractive to pelagic species (HF Ma, HN R). This was unusual because aerial insectivores are frequent visitors to Gibraltar today and have been identified in Middle Palaeolithic layers of Gorham's Cave during recent excavations (Cooper 1999, 2000, 2005, 2012). As an inland site, Cova Negra had no nesting seabirds, but like the other mid-latitude belt sites there was a strong presence of rock/stock dove (*C. livia/oenas*). It is possible that the importance of rocky habitats was overrepresented in this study because all the study sites were cave sites (Finlayson 2019).

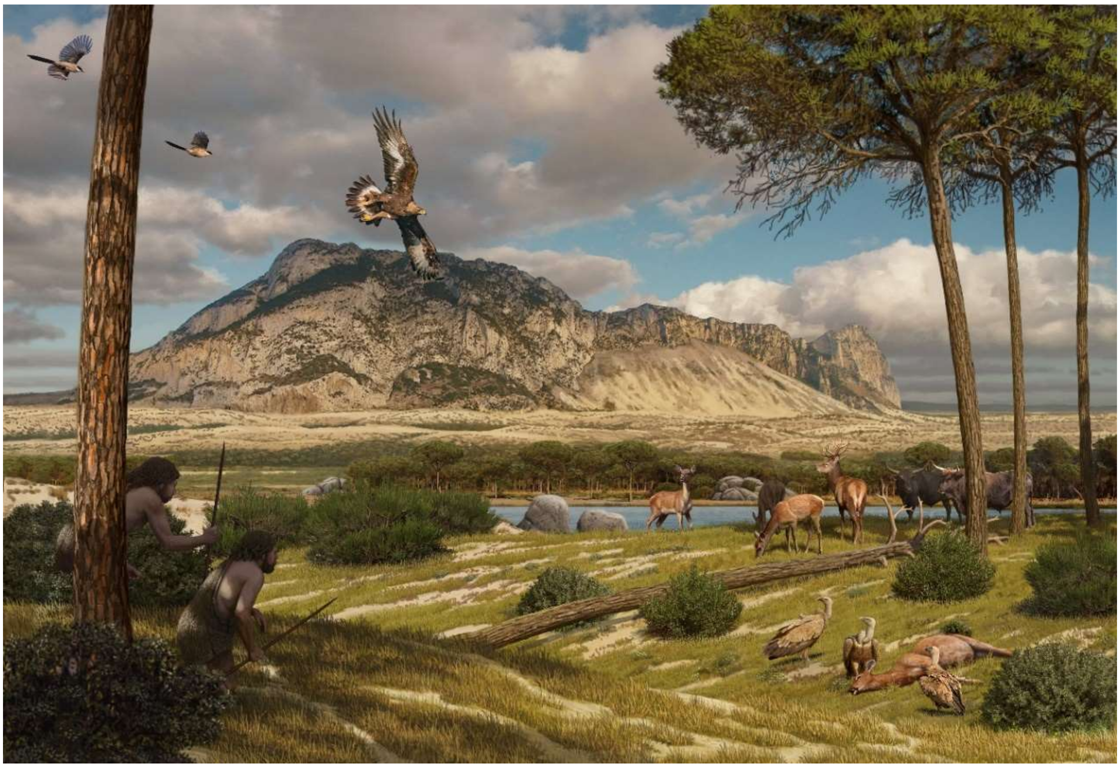


Figure 8.3: A recreation of the landscape of the coastal plain surrounding Gibraltar in the Middle Palaeolithic showing the mosaic-type habitat distribution. In the foreground, Neanderthals observe vultures gathering around a carcass ©Gibraltar National Museum/Mauricio Anton.

The uniformity seen across the five study sites, indicates that the Neanderthal habitat of choice was largely homogeneous across their range, regardless of geographical position. Neanderthals chose to inhabit mosaic-type landscapes with multiple hunting and foraging opportunities. Neanderthal ability to adapt to and exploit a variety of habitats was recently highlighted by Banks *et al.* in an examination of the changing landscape in Western Europe in MIS 4 (2021). Whether in Belgium, Israel, Spain, or Gibraltar, Neanderthals did the same thing ecologically, occupying areas with a high habitat heterogeneity where they had access to a rich diversity of potential prey. These results echo the conclusions of previous studies of the human habitat niche (Finlayson 2006, Finlayson *et al.* 2011; Carrión, Rose and Stringer 2011; Finlayson 2019; Amoros *et al.* 2021).

8.2 Neanderthal behaviour

In this section, I consider the combined evidence of Neanderthal behaviour in the bird collections from the five study sites. First, I look at the collective taphonomic results in relation to human exploitation and how these contribute to the current known material. I then focus on what the results say about Neanderthal hunting strategies. Finally, I evaluate the contribution of this study to our knowledge of the geographic and temporal spread of bird exploitation.

8.2.1 Neanderthal bird consumption

Cutmarks were identified on 17 of the 106 species appearing in this study, 11 of which represented the first direct evidence of exploitation of the particular species in Neanderthal contexts (cf. Blasco *et al.* 2019; Finlayson 2019; Table 8.7; Figure 8.5; Figure 8.7). These were the capercaillie (*T. urogallus*), a ptarmigan (*Lagopus* sp.) the red-legged partridge (*A. rufa*), the common scoter (M. *nigra*), the wigeon (*M. penelope*), a merganser (*M. merganser/serrator*), the great auk (*P. impennis*), the great cormorant (*P. carbo*), the shag (*P. aristotelis*), the Eurasian jay (*G. glandarius*), and the carrion crow (*C. corone*). In total, this study adds 53 bird bones with cutmarks to the 353 already known making the total number of currently known bird bones with cutmarks 406 over 39 species (Appendix 1), an increase of 15% (Figure 8.4). Preliminary results from the Gorham's Cave Complex indicate that Neanderthals took full advantage of the range of the birds available to them in Gibraltar where signs of exploitation were visible on 49 species (Finlayson 2019). However, these results are unpublished, and the type of traces identified are not described.

Bird remains belonging to 31 species from 11 higher taxa groups across all sites showed thermal modifications congruent with cooking practices (Table 8.8; Appendix 2). Evidence of heat exposure was especially important at Tabun where thermal and spatial distribution of remains strongly supported human consumption of birds. In total, 38 species (35.8%) showed evidence of human agency. Peeling was visible on 15 bones from 7 species, all of which also exhibited other human modifications (Table 8.9). With the inclusion of Devil's Tower, Tabun and Scladina, the number of sites with confirmed Neanderthal bird exploitation is now 30 (Appendix 1).

The bird species that were exploited by Neanderthals were also those that featured most frequently in the deposits. Finlayson also noted that the species which occur most frequently in Neanderthal sites across Europe were those which most frequently show taphonomic traces of human intervention (2019). The exception to this was Devil's Tower where a dominance of swifts overshadowed the counts of all other species. In other sites, pigeons, corvids, game birds, and ducks were most frequent. The MNI counts at all sites also showed a greater number of individuals represented in the occupied levels (Figure 8.6). Taphonomic evidence of exploitation suggests this increase in birds in the accumulation during periods of human occupation was connected to the Neanderthal diet breadth.

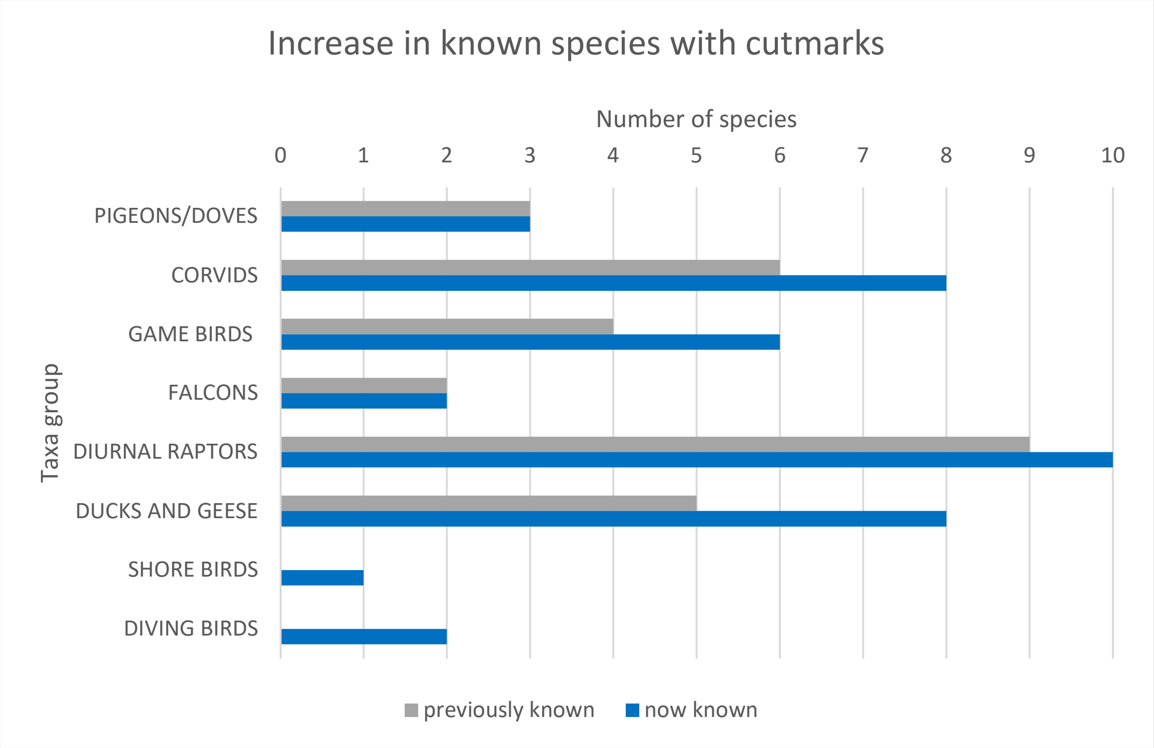


Figure 8.4: Barchart showing the contribution of this thesis to the number of bird species recorded with cutmarks. 11 unique species were added to the known record.

Table 8.7: Cut marks on specimens by site. 17 unique species displayed cutmarks, 11 of which had not previously been confirmed as Neanderthal prey. GC = Gorham's Cave, DT = Devil's Tower, CN = Cova Negra, SCLA = Scladian, TAB = Tabun.

	Site					
Species	**GC**	**DT**	**CN**	**SCLA**	**TAB**	**Total**
Tetrao urogallus				1		**1**
Lyrurus tetrix				1		**1**
Lagopus sp.				1		**1**
Alectoris rufa			3			**3**
Alectoris sp.		2				**2**
Melanitta nigra		1				**1**
Mareca penelope			1			**1**
Mergus merganser/serrator				1		**1**
Columba livia/oenas	4	2	17			**23**
Pinguinus impennis	1					**1**
Accipiter nisus		1				**1**
Pyrrhocorax pyrrhocorax		2	2			**4**
Pyrrhocorax graculus	1	1				**2**
Corvidae (medium)		2				**2**
Phalacrocorax aristotelis	1		1			**2**
Phalacrocorax carbo				1		**1**
Garrulus glandarius			1			**1**
Corvus corone			1			**1**
Corvus corax	2					**2**
Aves size *Tetrao* sp.				1		**1**
Aves size *Anser* sp.				1		**1**
Total	**9**	**11**	**26**	**7**	**0**	**53**

Table 8.8: Higher Taxa Groups with thermal modifications by site. . GC = Gorham's Cave, DT = Devil's Tower, CN = Cova Negra, SCLA = Scladian, TAB = Tabun.

	Sites					
Taxa group	**GC**	**DT**	**CN**	**SCLA**	**TAB**	**Total**
Galliformes	4	6	9	1	4	**24**
Anseriformes	2	3	5			**10**
Columbiformes	18	16	52		54	**140**
Gruiformes	2					**2**
Charadriiformes	1	1				**2**
Ardeidae					1	**1**
Suliformes	2					**2**
Accipitriformes		4			2	**6**
Falconiformes		3			4	**7**
Corvidae	8	17	20		3	**48**
Passeriformes			1		76	**77**
Indeterminate	1		3		43	**47**
Total	**38**	**50**	**90**	**1**	**187**	**366**

Table 8.9: Peeling on specimens by site. Other evidence of human exploitation was visible on all seven species that displayed peeling.

	Sites					
Species	**GC**	**DT**	**CN**	**SCLA**	**TAB**	**Total**
Tetrao urogallus				1		**1**
Alectoris rufa	1		1			**2**
Alectoris sp.		1				**1**
Coturnix coturnix					1	**1**
Pyrrhocorax pyrrhocorax		2				**2**
Columba livia/oenas	3	1	2			**6**
Pinguinus impennis	1					**1**
Corvus corax	1					**1**
Total	**6**	**4**	**3**	**1**	**1**	**15**

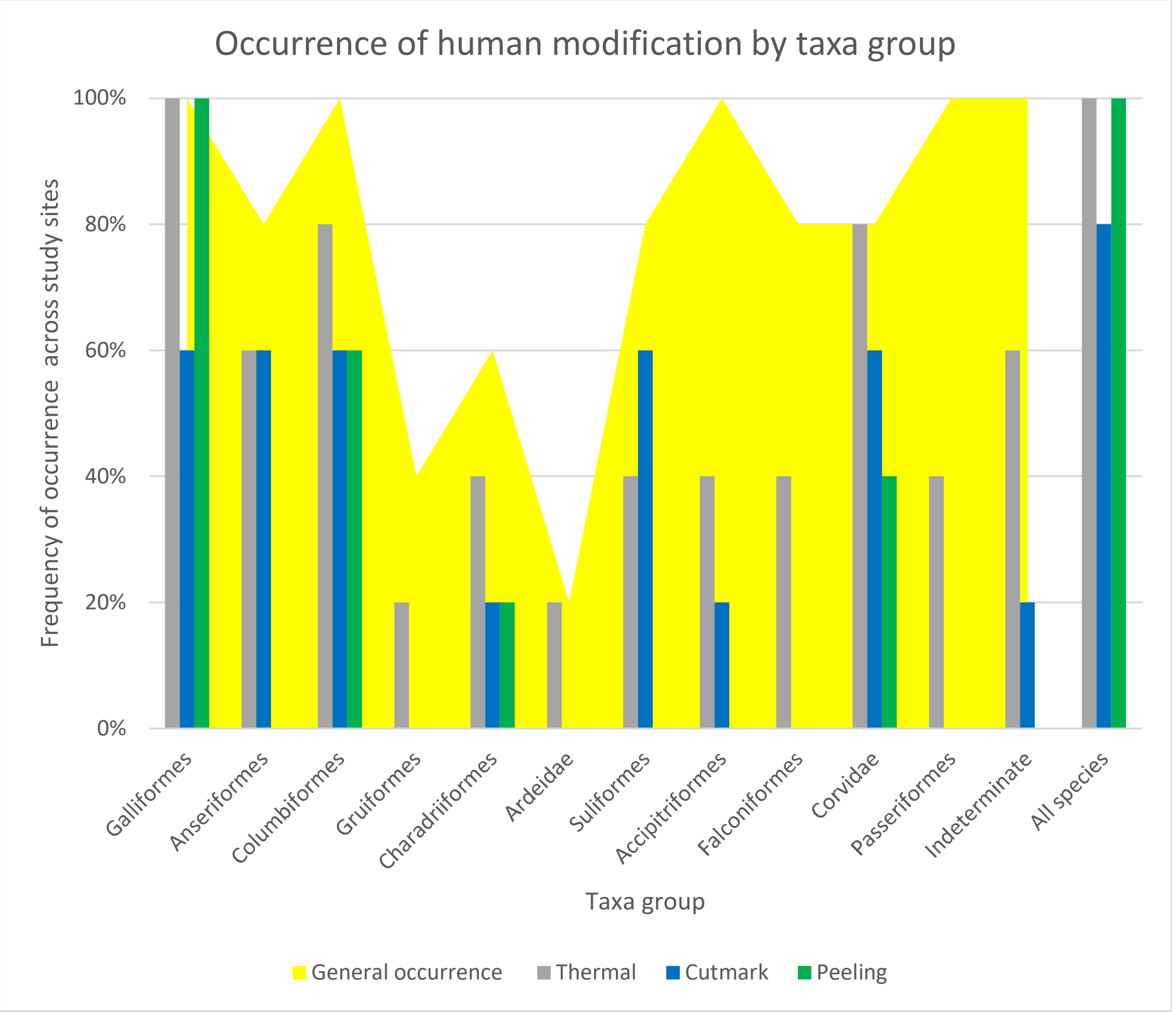


Figure 8.5: Frequency of occurrence of human modifications on species of each taxa group identified at the study sites. Galliformes, Columbiformes, corvidae and suliformes are exploited at at least 3 sites. Thermal modifications are most frequent across all taxa groups..

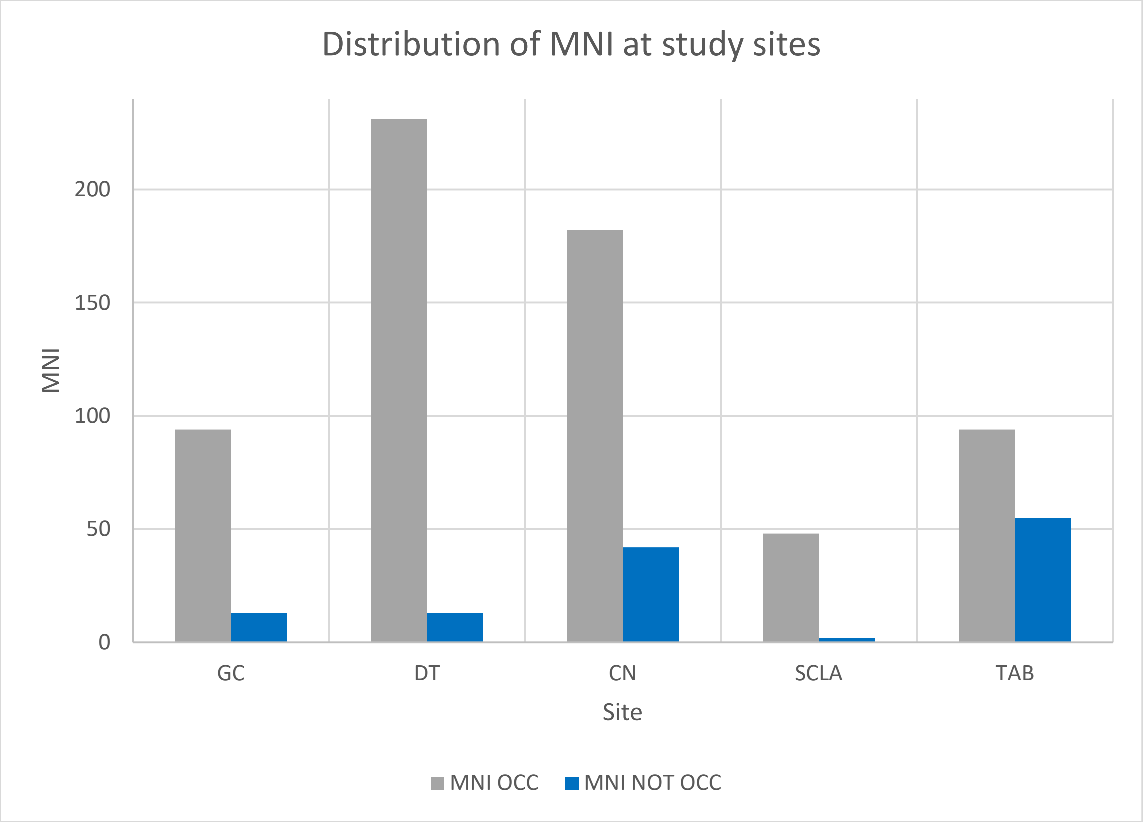


Figure 8.6: Barchart showing the distribution of MNI at each of the study sites. MNI OCC = MNI of collective occupied layers. MNI NOT OCC = MNI of collective unoccupied layers.

Figure 8.7: Neanderthals gathered by the hearth in Gorham's Cave. Two great auks (P. impennis) are hung against the cave wall (©Gibraltar National Museum/Mauricio Anton).

Layers with evidence of human occupation also produced the most diverse accumulations in all sites, indicating that fewer bird species were introduced to the cave accumulations during periods with no human occupation. This observation presents an important limitation to the use of birds from cave sites as an environmental marker. While caves serve as excellent catalogues for the preservation of accumulations (Finlayson 2006; Finlayson *et al*. 2008), an external agent must first introduce the carcasses to the cave environment for bird remains to accrue (Andrews 1990). Whether this agent was human, carnivore or bird of prey, the selection of birds in the cave was dependent on the hunter. Low NTAXA and NISP values in contexts without human occupation evidence does not reflect a deterioration of the ecosystem, but it does seem to show an absence of humans. In layers where only non-human predators were present, the avian species identified in the sample were restricted to those that frequent habitats very close to the sites. Neanderthals, on the other hand, appeared to exploit a wider range of birds than the local carnivores.

8.2.2 Non-utilitarian exploitation

Neanderthals visiting Devil's Tower Rockshelter extracted feathers from the wings of a sparrowhawk (*A. nisus*) and a red-billed chough (*P. pyrrhocorax*). The exploitation of feathers from Gibraltarian sites was first documented by Finlayson *et al.* (2012) who pinpointed raptors and corvids as especially targeted for symbolic exploitation. Cutmarks on hind limb bones of a red-billed chough (*P. pyrrhocorax*; distal tmt) at Devil's Tower, and a raven (*C. corax*; distal tbt) in Layer P of Gorham's Cave also indicated a non-utilitarian purpose because bird feet did not carry any nutritional value (ref). The removal of the toes from the tarsometatarsal of a raven in the Magdalenien contexts at Trou de Chaleux was interpreted as non-utilitarian (Goefette *et al.* 2020), and raven feet have been known to be used as amulets (Oosten and Laugrand 2006; Driver 2011). In Layer P at Gorham's Cave (> 67 ka BP) the implied symbolism was of a different character. Cut marks on the distal tibiotarsus of a raven indicated skinning. Finlayson and Finlayson (2016) have highlighted the relationship between Neanderthals and scavenging birds, among them the raven. Raven skin is well-documented ethnologically and is used in the Inuit tradition in the first garments of children along with other birds with dark plumage (Nakashema 2002; Oosten and Laugrand 2006). It has been suggested that the iridescent jet-black feathers were also attractive to Neanderthals (Finlayson *et al.* 2012). Collectively, the results from Gibraltar suggest that Neanderthals were exploiting birds for feathers and skins from MIS 4. It is unclear whether there was significant difference between the occupation mode of Gorham's Cave in Layer P and Devil's Tower because the extent of the excavation of Layer P was very restricted and this layer has not yet been reached in current excavations (Barton *et al*. 2012).

Elements of a sparrowhawk and an eagle/vulture sized raptor were deposited within the limits of the Unit 1A working floor deep in Scladina cave (DiModica 2010). These elements are the only known remains of diurnal raptor recovered from Scladina and are not species which would be found naturally in a cave. They must therefore have been introduced by an external agent. Raptors are known to have been exploited by humans for feathers and talons (Peresani *et al.* 2011; Finlayson *et al.* 2012; Morin and Laroulandie 2012; Romandini *et al.* 2014, 2016; Majkić *et al*. 2017; Julien *et al.* in press; Vanhaeren *et al.* in press; this thesis). Without direct evidence of exploitation, any assumption of symbolic activities based on their presence is speculative, but cut marks have not been identified on any faunal remains in this context despite clear evidence of Neanderthal occupation (Abrams *et al.* 2010).

8.2.3 Neanderthal hunting strategies

Based on the species that show cut marks and thermal modifications across the study sites, pigeons (C. livia/oenas) were the most frequently exploited bird. Cutmarks were identified on 23 pigeon elements, while 140 elements showed exposure to a heat source. Their modified remains were found at three sites in Iberia and at Tabun. These sites all lie within the mid-latitude belt which is the home range of the rock dove (*C. livia*). Pigeons made an excellent food choice for Neanderthals because they reproduced rapidly making them a sustainable and renewable resource found (Blasco *et al.* 2014). They were also readily available near caves because they nested in rocky habitats (*Figure 8.8*). It is possible that pigeons were over-represented in this study because the sites were all caves. Further examination of open-air sites may highlight any bias. Along with pigeons, corvids are important the mid-latitude belt, and especially choughs. However, corvids were better represented by thermally modified elements than by cutmarks in this study, unlike previous reports which identified cutmarks on corvid remains at several sites (Blasco *et al*. 2014; 2016; Peresani *et al*. 2011; Romero *et al.* 2017).

Gamebirds were the only taxa group exploited by humans at all five study sites. In the south, Neanderthals focussed on partridges and quail. At the northern site of Scladina, Neanderthals exploited ptarmigan, black grouse, and the Capercaillie. Finlayson (2019) analysed the exploitation of birds at Magdalenian and Neanderthal sites in Europe and proposed that mild-climate Neanderthals were exploiting partridges while Magdalenian cultures in cold tundra environments exploited grouse. The results from Scladina contradict this conclusion and instead indicate that the perceived difference between Neanderthals and Magdalenian AMH in the avian species they exploited is the result of skewed data due to the geographical positions of the examined sites. What is clear is that Neanderthals did not differentiate between species and genera. Gamebirds as a group, and not specific species or genuses were the focus of Neanderthal subsistence behaviours. My results indicate that Neanderthals merely exploited the species which were available to them in the landscape and latitude band they inhabited.

Figure 8.8: A colony of nesting seabirds populate the dunes close to where a group of Neanderthals are approaching a leopard with a kill ©Gibraltar National Museum/Mauricio Anton.

My results indicate that ducks were also frequently exploited across the Neanderthal range, suggesting that they were a recognized food source. The presence of duck bones with cut marks supports the observations Blasco and Peris (2009) made at Bolomor Cave where Neanderthals exploited at least two species of duck. Furthermore, ducks were regularly sourced from sites not in the direct vicinity of the habitation sites, implying that

Neanderthals specifically sought out wetland habitats to hunt for ducks. Wetland species in general were exploited across the Neanderthal range, highlighting the importance of freshwater habitats close to human occupations (Finlayson *et al.* 2011). In this sense, wetlands presented a combined resource as both a source of drinking water and of avian prey. Incidences of other water birds, such as the heron at Tabun, likely represent episodes where Neanderthals have encountered other water birds while specifically looking for ducks.

Members of the cormorant family were exploited at three sites, one specimen appearing ~30 km from the coastline. These birds, like the ducks, were recognised as food regardless of the species, merely by shape. Cormorants were known to have been exploited by First Nations peoples in Canada (Ashwell 1978; Damas 1984; Suttles 1990; Vaughan 1992), and there is currently an annual hunting season for shags in Norway (Carss and Marzano 2005; Orta 2016). In addition to the shag, other marine birds were specifically harvested. Pelagic species, such as great auk underscore the importance of the coastal habitat (Finlayson 2008; Benito *et al.* 2017). The great auk, though graceful in the water, was flightless and clumsy on land and would not have been difficult to capture if caught off guard. Many sea birds nest in colonies on cliff faces (Figure 8.8). Such gatherings of birds would represent a seasonal opportunity for Neanderthals to not only collect adult birds on the nest, but also to collect eggs (Serjeantson 1997; Finlayson 2019).

In this thesis, I have shown that Neanderthals at five sites across Eurasia exploited a wide range of birds that were available to them in the landscapes they inhabited (Figure 8.9). This new data joins the results of other studies from Neanderthal sites where birds were exploited (Appendix 1). The collective results stand in contrast to the conclusions of Stiner *et al.* (Stiner 1991abc, 1993, 1994, 2001; Stiner and Kuhn 1992, 2006; Stiner Munro, and Surovell 2000; Stiner and Munro 2002) that Neanderthals were not capable of hunting small, fast game. Instead, in addition to expertly exploiting large game (Gaudzinski-Weinhauser and Roebroeks 2000; de los Terreros *et al.* 2014), Neanderthals appeared as skilled, selective small game hunters (Morin *et al.* 2019; this thesis). They maintained a detailed awareness of the hunting opportunities available to them in the landscapes they inhabited, not only focussing hunting efforts on highly available pigeons and choughs, but also specifically targeting game birds, seabirds, and ducks. Other bird species were exploited as occasional bounties acquired while seeking specific food birds. The breadth of diet, with cutmarks now identified on at least 39 species, implies that Neanderthals carried the knowledge, and possessed the strategic prowess necessary to effectively locate and hunt bird populations in the Middle Palaeolithic landscape. Wherever they roamed, whether it be in the cold of north-western Europe, or in the warmth of the mid-latitude belt, Neanderthals knew what they wanted and, quite often, what they wanted was birds.

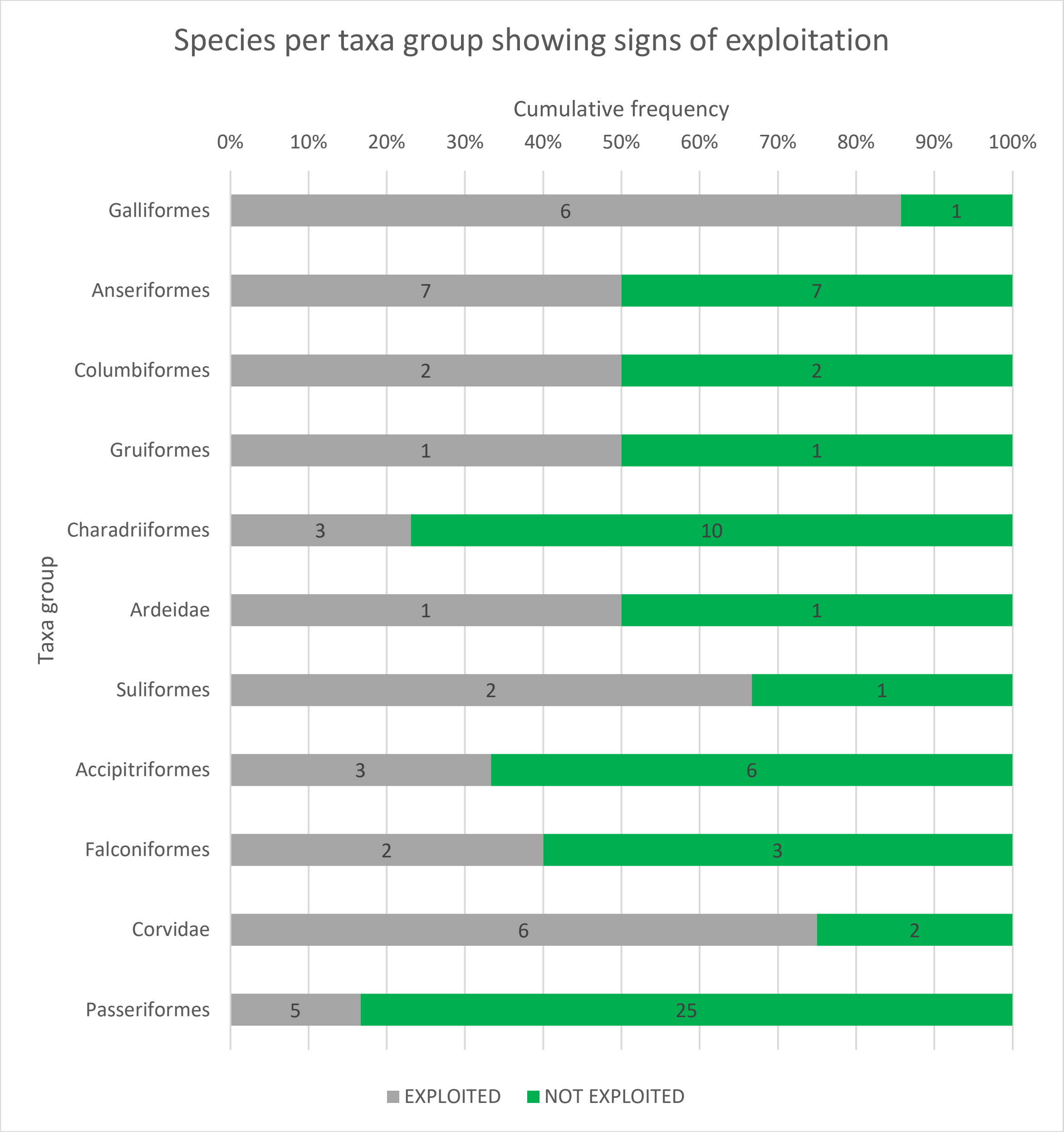


Figure 8.9: Barchart showing the cumulative frequency of bird species per taxa group featured in this thesis. NTAXA of non-exploited species are shown in green. More than 70% of corvid and galliform species found at the sites showed evidence of human exploitation. Anseriformes, columbifformes, and suliformes also showed exploitation of ≥50% of species. Non-traditional food species such as falconiformes, accipitriformes and small passerinesshowed exploitation on few species.

8.2.4 The temporal and geographical spread of bird exploitation

While four of the sites presented in this study do not greatly expand the known geographic or temporal horizons of bird exploitation in the Middle Palaeolithic (Appendix 1; Figure 8.10; Table 8.10), the presence of birds exploitation at Scladina Cave during MIS 5 broadens the known geographical range of this Neanderthal behaviour into north-western Europe. Scladina lies 413 km west of the reindeer hunting camp at Salzglitter-Lebenstadt where the cutmarked bones of a duck and a swan suggest sporadic exploitation of birds in MIS 3 (Gaudsinski-Windheuser 2009), and 320 km north of Grotte du Renne and Grotte d'Hyene at Arcy-sur-cure where current evidence predominantly reflects the exploitation of raptors, also in MIS 3 . Scladina offered a snapshot of bird exploitation at this latitude within the climatic parameters of MIS 5 and informed us about the breadth of the Neanderthal diet this far north. Alongside birds, Neanderthals exploited chamois and hare (Patou-Mathis 1998). The exploitation of northern gamebirds like grouse and capercaillie by Neanderthals at this latitude where partridges are not native, highlights the importance of gathering data from all areas of the Neanderthal range if we are to avoid bias in using birds to address human behavioural ecology.

At the Rock of Gibraltar, the results of the two study sites are in agreement with the comprehensive studies of more recently recovered avifaunal assemblages (Cooper 1999; Finlayson *et al.* 2016). While my analysis of the Devil's Tower enabled a detailed account of the immediate environment to be made, the Waechter avifauna from Gorham's Cave read as a flawed and biased collection. It was undoubtedly a subset of the greater Gorham's sample, but lacked the detailed diversity that the cave has become known for in recent times (Blasco *et al.* 2014; 2016; Finlayson *et al.* 2012, 2016). Bird exploitation was practiced by Neanderthals at two additional sites in Gibraltar that date to the late Pleistocene. At Ibex Cave, Neanderthals consumed choughs, while human tooth marks indicated that birds were consumed at Vanguard Cave (Finlayson *et al*. 2012). The disparity between Waechter's avifauna and the avifaunal remains discovered during modern investigations at Gorham's Cave highlights the significance of well-executed collection methods, which were not always practised in the past

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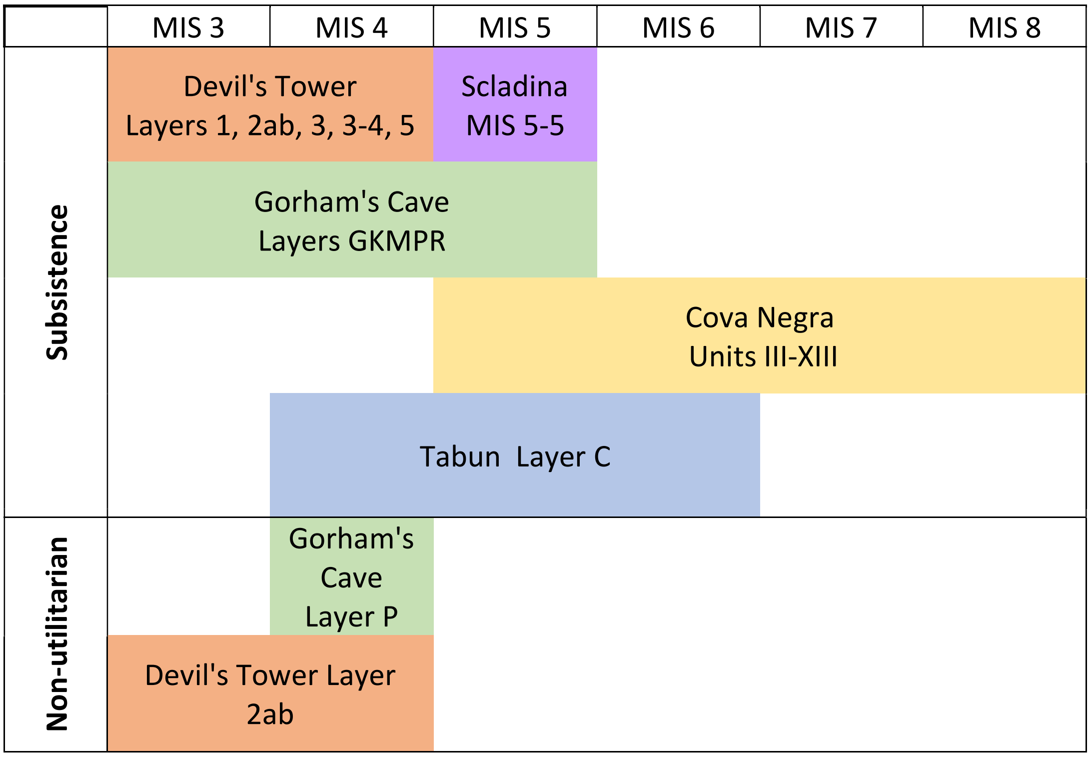
Source: US National Park Service

Figure 8.10: The current geographic extent of Neanderthal bird exploitation. Red triangles mark sites where this thesis has contributed new data (see also Appendix 1)

Elsewhere in the Iberian peninsula, Cova Negra is located only ~19 km north of Cova Beneito and ~23 km west of Bolomor Cave, two important sites with bird exploitation evidence (Blasco *et al.* 2013; Villaverde *et al.* 2014). Cova Beneito (MIS 3) produced a partridge (*Alectoris* sp.) element with cutmarks (Martinez *et al*. 1993) and avian remains from Bolomor Cave displayed cutmarks and thermal modifications indicating that Neanderthals in this area regularly exploited ducks (*Aythya* sp*.* *Anas* sp.), gamebirds (Phasanidae, Galliformes), pigeons (*Columba* sp.) and corvids (Corvidae) between MIS 7 and MIS 5e (Blasco *et al*. 2010, 2013: Blasco and Peris 2009, 2012). The dating of Cova Negra (MIS 8 – 5; Richards *et al*. 2019) indicates that some of the sporadic occupation episodes were potentially contemporary with Neanderthal occupation at Bolomor Cave, although much greater refinement of the chronology is required to test this hypothesis. There is exploitation of birds throughout the studied sequence at Cova Negra, and the same breadth of species was also exploited (ducks, gamebirds, pigeons, and corvids). The presence of shag (*P. aristotelis*) remains at Cova Negra implied that the Neanderthals visiting the site also exploited bird resource of the Mediterranean coast. It is thus intriguing to consider whether the same Neanderthals populations exploited both sites on a seasonal basis, or whether they were inhabited by distinct populations.

Table 8.10: The temporal span of bird exploitation for subsistence and non-utilitarian purposes at the study sites. Measures in Marine Isotope Stages (MIS).



<table>
<tr><th></th><th>MIS 3</th><th>MIS 4</th><th>MIS 5</th><th>MIS 6</th><th>MIS 7</th><th>MIS 8</th></tr>
<tr><td rowspan="4">Subsistence</td><td colspan="2">Devil's Tower
Layers 1, 2ab, 3, 3-4, 5</td><td>Scladina
MIS 5-5</td><td></td><td></td><td></td></tr>
<tr><td colspan="3">Gorham's Cave
Layers GKMPR</td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td colspan="4">Cova Negra
Units III-XIII</td></tr>
<tr><td></td><td colspan="3">Tabun Layer C</td><td></td><td></td></tr>
<tr><td rowspan="2">Non-utilitarian</td><td></td><td>Gorham's Cave Layer P</td><td></td><td></td><td></td><td></td></tr>
<tr><td colspan="2">Devil's Tower Layer 2ab</td><td></td><td></td><td></td><td></td></tr>
</table>

In SW Asia, data collected from Tabun Cave joins previously published data from the Neanderthal site of Qesem Cave, where cutmarks on three bones suggested human exploitation of swan (Cygnus sp.), pigeon (Columba sp), and brown-necked raven (C. ruficollis). At Tabun, thermal modification (n = 189) suggested pigeons, game birds and a heron were cooked, indicating that the inhabitants of both sites incorporated birds from similar habitats into their diets. While Qesem provided evidence of sporadic inclusion of birds in the diet between MIS 11 and MIS 6 (Blasco *et al.* 2016, 2019), evidence from Tabun suggested that birds were a regular inclusion in the Neanderthal diet from MIS 6 to MIS 4.

8.3 Conclusion

8.3.1 Key Findings

This study has contributed new data to the debate on Neanderthal ecology and new information regarding the nature of bird exploitation across the Neanderthal range. The key findings are summarised below.

- The combination of avian taphonomy and taxonomy is a successful methodological approach that effectively looks at birds in an integrated manner at multiple scales of analysis, allowing fresh insights to be made about Neanderthal ecology and behaviour. Its a truly holistic approach that cements bird bones as a key proxy in Neanderthal research.
- By using avian remains to identify a homogeneity in Neanderthal habitat choice and climate preferences across their range, my data adds further support to the conclusions of previous researchers (Finlayson 2006; Finlayson et al. 2011; Finlayson 2019). Neanderthals, like other members of the *Homo* genus, chose to live in areas of moderate to warm temperature ranges with fluctuating rainfall across their geographic range where a mixture of habitat types created a mosaic-type landscape. Within these diverse habitats they actively hunted birds, focussing especially on game birds, pigeons, and ducks.
- Geographically, the range of bird exploitation now extends into the north-west of Europe at Scladina Cave where Neanderthals hunted gamebirds during MIS 5. In MIS 3 there are indications of exploitation of raptors, though no cutmarks have been identified on material from this occupation. Neanderthal exploitation of boreal, cool-tolerant game birds expands our knowledge of the Neanderthal diet,

indicating that they did not differentiate between species within a taxa group. Gamebirds were food sources, regardless of the geographical position of a site.

- In coastal areas, like Gibraltar, marine species were also targeted. Neanderthals here hunted a wide range of species, including pigeons, gamebirds, corvids, arctic ducks, and rocky-nesting seabirds within the non-analogue community of species that were compressed into the southern Iberian glacial refugium. Neanderthals here also practiced non-utilitarian exploitation, harvesting feathers and skin from raptors and corvids. A Neanderthal group passing through Cova Negra consumed a shag, transported from the coast 30 km to the east. Migratory ducks were also targeted by Neanderthals here, likely from Lake Bellus, 5 km to the south, indicating that Neanderthals understood the rhythm of migration and knew when these species would be available.
- In the four sites in the mid-latitude belt, pigeons and game birds were the most important avifaunal sources of nutrition. At Tabun Cave, Israel, thermal modifications (n = 187) were the only evidence of human exploitation in Layer C, highlighting the degree to which birds can be processed and consumed without the use of tools. At Tabun, consumption of birds was a regular addition to the Neanderthal diet, while bird exploitation at nearby Qesem only indicated sporadic consumption of avian prey.
- New evidence of non-utilitarian exploitation of raptors and corvids at Gorham's Cave and Devil's Tower rock shelter furthers the idea that Neanderthals in Gibraltar targeted these birds for their feathers (Finlayson *et al*. 2012; Finlayson and Finlayson 2016). In a wider perspective, these results contribute to the debate regarding Neanderthal cultural complexity by forwarding the concept of feathers as objects of status and personal adornment and status.(Peresani *et al.* 2011; Fiore *et al*. 2016; Majkic *et al.* 2017; Finlayson 2019)

In summary, from the study of five new avifaunal collections from sites across the Neanderthal range, Neanderthals emerge as effective hunters of birds, targeting specific taxa groups from a variety of habitats within the mosaic-type landscapes, which they occupied, and decorating themselves with their feathers.

8.3.2 Limitations of this research

In Chapter 1, I presented a number of issues which could limit the usefulness of birds in Neanderthal research. During the course of my research, I encountered the following constraints to my interpretations.

The most obvious limitation I encountered was collection bias. The Waechter Avifauna from Gorham's Cave was an example of a collection where a lack of fine mesh sieving and the original researchers' focus on larger, whole pieces had resulted in the loss of information. Evidence of this loss was clear when the species richness of the studied sample was compared to that of Devil's Tower, and even more so when compared to the extensive array of birds from current Gorham's Cave excavation results. The remains I examined from Devil's Tower were mostly whole elements, or those elements which were easily identified. This in itself indicates that many broken or unidentifiable pieces were discarded. At Tabun and Scladina, however, the avian material was collected using sieving methods. At Tabun, where I sorted the bird bones from the other mammalian remains, there was a much higher frequency of both broken bones and bones of smaller species. At Scladina, despite the low number of remains, I was still able to verify the presence of diverse habitats due to the recovery methods not missing any bird bones.

Bias also affected the manner bird remains had been stored. Because birds were previously assumed uninformative, some collections had not been well curated. There was ample evidence that damage inflicted on remains during cleaning efforts, which may have obscured useful taphonomic information (Devil's Tower). Other types of post-excavation damage came from unsuitable storage in large bulk bags which caused the material to be crushed (Cova Negra). It is imperative to take the peri- and post-excavation practices into consideration when examining bird remains from older excavations, and to whether they may have influenced the results. However, these biases are not a consideration that is unique to the study of birds, and should not be used as an argument against the use of birds as a source of information.

An issue that is unique to birds, and that cannot be easily overcome was the lack of access to suitable comparative collections. When analysing the bird remains from Tabun Cave, I was unable to identify many of the non-corvid Passeriform species beyond class because extensive comparative material was not readily available. Even large museums may have limited collections, and those that do have comprehensive collections, may only have species that are native to a given geographical region. Future efforts in avian taxonomy to develop a 3-D database of comparative material could offer a useful alternative. Though there is potential in the use of photogrammetry to construct 3-D digital database of bird remains which could aide some identification, the interspecific similarities and intraspecific variations in birds currently make it necessary to have ample access to a well-stocked collection to confidently identify specimens.

8.3.3 Direction of future work

The future of ornitho-archaeology is bright. Birds remain a largely unexplored proxy. Though the volume of articles about bird taphonomy and studies has grown over the past few years, we are still only seeing the tip of the iceberg. There are hundreds of Middle Palaeolithic sites with bird remains which have yet to be examined taphonomically (Tyrberg 1998). Finlayson (2019) compiled a list of sites which warrant investigation. However, many sites which have evidence of exploitation feature far down on the list. It is my opinion that all excavated bird material ought to be examined in order to fully understand the extent of bird exploitation the Palaeolithic. Though this practice once seemed to be a rare occurrence, I believe that further research will show that birds were a regular resource in the human diet in the Middle Palaeolithic.

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Appendices

Appendix 1: Bird species with cut marks. Yellow highlight denotes new data contributed by this study (4 pages).

Site	**Location**	**Date**	***Tetrao urogallus***	*Lyrurus tetrix*	***Lagopus sp.***	*Alectoris graeca*	***Alectoris rufa***	*Alectoris sp.*	Phasanidae	Galliform	*Cygnus olor*	*Cygnus cygnus*
Sima del Elefante,	Spain	1.2 ma										
Durnsunlu	Turkey	0.9 ma										
Qesem Cave	Israel	420-200 ka										
Gran Dolina TD10 2	Spain	ca. 400 ka										
Gran Dolina TD10 1	Spain	MIS 9										
Bolomor Cave, XVII	Spain	> 350 ka							4	1		
Bolomor Cave, XII	Spain	MIS 6 - MIS									1	
Bolomor Cave, XI	Spain	MIS 6										
Bolomor Cave, IV	Spain	ca MIS 5e							2	2		
Lazaret UA25, CII	France	190 - 150										
Pie Lombard	France	ca. 140 - 70				6						
Krapina	Croatia	130 ka										
Scladina, MIS 5 - 3	Belgium	MIS 5	1	1	1							
Pech de l'Aze IV, 8	France	100 ka										
Pech de l'Aze I, 4	France	MIS 3										
Combe Grenal, S2	France	90 ka										
Salzglitter Lebenstadt	German	ca. 50 ka										
Les Fieux, G5 G6 G7	France	MIS 3										
Les Fieux, I/J	France	60 - 40 ka										
Les Fieux, Jbase	France	60 - 40 ka										
Les Fieus, K	France	MIS 3										
Noisetier	France	MIS 3										
Baume de Gigny, XV	France	ca. 50 ka?										1
Grotte de l'Hyene,	France	MIS 3?										
Axlor, IV	Spain	> 49 ka										
Axlor, V	Spain	> 47.5 ka										
Gorham's Cave	Gibraltar	MIS 5 - MIS										
Gorham's Cave, G-T	Gibraltar	MIS 5 - MIS										
Vanguard Cave	Gibraltar	MIS 5 - MIS										
Ibex Cave	Gibraltar	MIS 5?										
Devil's Tower	Gibraltar	MIS 4- MIS						2				
Cova Negra, IIIb	Spain	MIS 5 - MIS						1				
Cova Negra, Sector C	Spain	MIS 8- MIS					3					
Cova Foradada	Spain	ca. 80 ka										
Mandrin, E	France	52 - 56 ka										
Fumane, A12	Italy	MIS 3										
Fumane, A9	Italy	48 - 49 ka		4								
Fumane, A6 A5	Italy	40 - 45 ka										
Fumane, A4 A3	Italy	37 ka										
Castelcivita, cgr	Italy	41 - 47 ka										
Arbreda, MP1	Spain	40 - 45 ka				1						
Cova Beneito, D1	Spain	MIS 3						1				
Grotte du Renne, Xb	France	42 - 44 ka										1
Grotte du Renne, Xc	France	42 - 44 ka										
Grotte du Renne, VIII	France	42 - 44 ka										
Grotte du Renne, Ixb	France	42 - 44 ka										
Grotte du Renne, Xa	France	42 - 44 ka										
Grotte du Renne, IX	France	42 - 44 ka										
Grotte du Renne, IX X	France	42 - 44 ka										
Rio Secco, 7	Italy	48 - 49 ka										
Zaskalnaya, IV	Crimea	38 - 43 ka										
			1	**5**	**1**	**7**	**3**	**4**	**6**	**3**	**1**	**2**

Cygnus sp.	*Anas* sp.	*Aythya* sp.	***Melanitta nigra***	***Mareca penelope***	***Mergus merganser/serrator***	Anatidae	*Columba livia*	*Columba livia/oenas*	*Columba palumbus*	*Columba* sp.	***P. impennis***	***P. aristotelis***	***P. carbo***	cf. *Gypaetus barbatus*	*Gypaetus* cf. *barbatus*	*Gyps fulvus*	*Gyps fulvus/melitensis*	*Aegypius monachus*	cf. *Aegypius monachus*	*Clanga clanga*	*Aquila adalberti*	*Aquila chrysaetos*	***Accipiter nisus***
1										1													
	2					1																	
		18																					
	5	8								7													
							1																
							23																
					1								1										
																						2	
																						1	
1	1																						
																		1				1	
																						1	
																						1	
																						1	
								22									1					1	
								4			1	1											
										28						2							
			1					2															1
								29															
				1				17				1											
																					1		
																						1	
																						1	
														1					2	1			
									1						1								
																						1	
																2							
																1							
																1							
																1							
																1							
																						1	
2	**8**	**26**	**1**	**1**	**1**	**1**	**24**	**74**	**1**	**36**	**1**	**2**	**1**	**1**	**1**	**8**	**1**	**1**	**2**	**1**	**1**	**12**	**1**

Milvus milvus	*Milvus migrans*	*Haliaeetus albicilla*	medium-sized raptor	*Bubo bubo*	*Coracias garrulus*	*Falco naumanni*	*Falco vespertinus*	*Falco* sp.	***G. glandarius***	*Pica pica*	*Pyrrhocorax pyrrhocorax*	*Pyrrhocorax graculus*	*Pyrrhocorax* sp.	*Coloeus monedula*	***Corvus corone***	*Corvus ruficollis*	*Corvus corax*	*Corvus*	*Corvus/Pica*	small corvid	***Corvidae medium***
																1					
																				2	
													26								
		5																			
			1																		
		2																			
		1																			
		1																			
		1															1				
								1													
																	1				
5	1												19						1		
												1					2				
											1										
											4										
											2	1									2
					1	1					22							3			
									1		2				1						
										1		10									
							1					2									
										1											
													3	2							
		1		1																	
																	1				
5	**1**	**11**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**31**	**14**	**48**	**2**	**1**	**1**	**5**	**3**	**1**	**2**	**2**

Corvidae	Passeriform	small passeriformes	*Aves* indet.	*Aves* size *Tetrao* sp.	*Aves* size *Anser* sp.	medium-sized bird	large-sized bird	**References**
							1	Huguet *et al*. 2013
							1	Guleç *et al*. 2009
								Blasco *et al.* 2019
						1		Rodriguez Hidalgo *et al*. 2017
	1		1					Blasco *et al*. 2013
	2							Blasco *et al.* 2013
								Blasco *et al.* 2010; Blasco and Peris 2012a
								Blasco and Peris 2009
4			4					Blasco *et al.* 2013; Blasco and Peris 2012a, 2012b;
								Roger 2004
								Romero *et al*. 2017
								Radovčic *et al.* 2015
								this thesis
								Dibble *et al.* 2009
								Soressi *et al.* 2008
								Morin and Laroulandie 2012
								Gaudzinski-Windheuser and Niven 2009
								Laroulandie *et al*. 2016
								Morin and Laroulandie 2012; Laroulandie *et al.* 2016;
								Morin and Laroulandie 2012; Laroulandie *et al*. 2016;
								Morin and Laroulandie 2012; Gerbe *et al.* 2014; Laroulandie *et al.* 2016
								Morin and Laroulandie 2012
								Mourer Chauviré 1989
								Mourer Chauviré, pers. comm. In Fiore et al. 2004
								Gómez Oliviencia *et al.* 2018
								Gómez Oliviencia *et al.* 2018
1								Finlayson *et al.* 2012; Blasco *et al.* 2014, 2016
								this thesis
								Finlayson *et al.* 2012
								Finlayson *et al.* 2012
								this thesis
		7	1					Martinez-Valle *et al*. 2016
				1	1			this thesis
								Rodriguez-Hidalgo *et al.* 2019
								Romandini *et al.* 2014
								Fiore *et al*. 2004; Romandini *et al.* 2014, 2016
								Romandini *et al.* 2016; Fiore *et al.* 2016
								Peresani *et al.* 2011
								Romandini *et al*. 2016
								Fiore *et al*. 2020
								Lloveras *et al.* 2018
								Martinez *et al*. 1993
								Leroi Gourhan 1964; d'Errico *et al.* 1998; Majkić *et al.* 2017; Julien *et al.* in press; Vanhaeren *et al*. in press
			1					Majkić *et al.* 2017; Julien *et al*. in press; Vanhaeren *et al*. in press
			1					Majkić *et al*. 2017; Julien *et al*. in press; Vanhaeren *et al*. in press
			1					Majkić *et al*. 2017; Julien *et al.* in press; Vanhaeren *et al*. in press
								Majkić *et al*. 2017; Julien *et al.* in press; Vanhaeren *et al.* in press
								Majkić *et al*. 2017; Julien *et al.* in press; Vanhaeren *et al*. in press
								Majkić *et al*. 2017; Julien *et al.* in press; Vanhaeren *et al*. in press
								Romandini *et al*. 2014
								Majkić *et al.* 2017
5	**3**	**7**	**9**	**1**	**1**	**1**	**2**	

Appendix 2: Bird species in this thesis modified by Neanderthals

Order	Scientific name		Cutmarks	Burning	Peeling
GALLIFORMES					
	Tetrao	*urogallus*	x	x	x
	Lyrurus	*tetrix*	x		
	Lagopus	sp.	x		
	Alectoris	*barbara*		x	
	Alectoris	*rufa*	x	x	x
	Alectoris	sp.	x	x	x
	Coturnix	*coturnix*		x	x
ANSERIFORMES					
	Mareca	*penelope*	x	x	
	Anas	*platyrhynchos*		x	
	Anas	*crecca*		x	
	Aythya	*fuligula*		x	
	Melanitta	*nigra*	x	x	
	Clangula	*hyemalis*		x	
	Mergus	*merganser*	x		
	Anatidae			x	
COLUMBIFORMES					
	Columba	*livia/oenas*	x	x	x
	Streptopelia	*turtur*		x	
	Streptopelia	sp.		x	
GRUIFORMES					
	Fulica	*atra*		x	
CHARADRIIFORMES					
	Haematopus	*ostralegus*		x	
	Scolopax	*rusticola*		x	
	Pinguinus †	*impennis* †	x		x
SULIFORMES					
	Phalacrocorax	*carbo*	x		
	Phalacrocorax	*aristotelis*	x	x	
PELICANIFORMES					
	Ardea	sp.		x	
ACCIPITRIFORMES					
	Gyps	*fulvus*		x	
	Accipiter	*nisus*	x		
	Haliaeetus	*albicilla*		x	
FALCONIFORMES					
	Falco	*naumanni*		x	
	Falco	*subbuteo*		x	
	Falco	sp.		x	
PASSERIFORMES					
	Garrulus	*glandarius*	x		
	Pyrrhocorax	*pyrrhocorax*	x	x	x
	Pyrrhocorax	*graculus*	x	x	
	Pyrrhocorax	sp.	x	x	
	Coloeus	*monedula*		x	
	Corvus	*corone*	x	x	
	Corvus	*corax*	x	x	
	Corvus	sp.		x	
	Corvidae			x	
	Parus	*major*		x	
	Alauda	*arvensis*		x	
	Hirundo	*rustica*		x	
	Hirundo	sp.		x	
	Turdus	*viscivorus*		x	
	Turdus	sp.		x	
	Erithacus	*rubecula*		x	
	Passeriformes			x	
INDETERMINATE					
	Aves	sp.	x	x	

Appendix 3: Classification of remains from Tabun Cave.

Galliformes

Alectoris chukar

Jelinek: LA-433

Alectoris sp.

Evron/Shimelmitz: LA-006
Jelinek: LA-516, LA-517

Coturnix sp.

Evron/Shimelmitz: LA-055, LA-056, LA-159, LA-160, LA-161, LA-162, LA-166, LA-190, LA-167, LA-120
Jelinek: LA-343, LA-370, LA-439, LA-448, LA-454, LA-546, LA-552, LA-653, LA-665, LA-440, LA-645.

Columbiformes

Columba livia/oenas

Evron/Shimelmitz: LA-096 (col/cor vert.), LA-001, LA-002, LA-008, LA-012, LA-013, LA-015, LA-024, LA-025, LA-035, LA-040, LA-047, LA-052, LA-057, LA-058, LA-079, LA-082, LA-087, LA-095, LA-102, LA-103, LA-107, LA-116, LA-168, LA-170, LA-173, LA-174, LA-175, LA-186, LA-188, LA-193, LA-215, LA-216, LA-219, LA-106, LA054, LA-222

Jelinek: LA-301, LA-306, LA-307, LA-309, LA-310, LA-313, LA-314, LA-315, LA-316, LA-317, LA-318, LA-320, LA-321, LA-328, LA-335, LA-338, LA-345, LA-351, LA-371, LA-375, LA-376, LA-377, LA-380, LA-385, LA-388, LA-389, LA-397, LA-411, LA-427, LA-428, LA-429, LA-432, LA-446, LA-447, LA-449, LA-450, LA-452, LA-456, LA-466, LA-468, LA-484, LA-487, LA-488, LA-490, LA-492, LA-495, LA-496, LA-501, LA-502, LA-503, LA-506, LA-508, LA-510, LA-511, LA-514, LA-519, LA-520, LA-524, LA-526, LA-527, LA-540, LA-542, LA-543, LA-544, LA-545, LA-553, LA-563, LA-569, LA-570, LA-571, LA-572, LA-574, LA-575, LA-576, LA-577, LA-581, LA-593, LA-598, LA-607, LA-609, LA-610, LA-611, LA-612, LA-613, LA-619, LA-623, LA-640, LA-646, LA-647, LA-650, LA-651, LA-655, LA-656, LA-658, LA-659, LA-660, LA-662, LA-666, LA-668, LA-670, LA-681, LA-312

Spilopelia senegalensis

Evron/Shimelmitz: LA-179, LA-101, LA-154

Charadriiformes

Larus sp.

Evron/Shimelmitz: LA-123

Jelinek: LA-518

Scolopax rusticola

Jelinek: LA-478

Pelicaniformes

Ardeidae (ixobrychus?)

Jelinek: LA-507

Ardeidae (size *Bulbulcus ibis*)

Jelinek: LA-381

Threskiornitidae (*Geronticus eremita/Platlea leucocordia*)

Jelinek: LA-667

Accipitriformes

Aquila sp. (size nipalensis)

Evron/Shimelmitz: LA-108

Accipitriformes indet.

Jelinek: LA-305, LA-326, LA327

Strigiformes

Tyto alba

Jelinek: LA-639

Falconiformes

Falco subbuteo

Jelinek: LA-374, LA-419, LA-618

Falco sp.

Evron/Shimelmitz: LA-140
Jelinek: LA-674, LA-410, LA-554, LA-633

Passeriformes

Lanius sp.

Evron/Shimelmitz: LA-030

Jelinek: LA-344

Garrulus glandarius

Jelinek:LA-358

Coloeus monedula

Evron/Shimelmitz: LA-062, LA-016, LA-128
Jelinek: LA-386, LA-443, LA-599

Corvus corone

Evron/Shimelmitz: LA-048

Corvus sp.

Jelinek: LA-455, LA-485, LA-390, LA-451, LA-604, LA-620

Corvidae indet.

Evron/Shimelmitz: LA-134

Jelinek: LA-408, LA-308

Parus major

Jelinek: LA-373

Alauda arvensis

Evron/Shimelmitz: LA-171
Jelinek: LA-614

Alauda sp.

Jelinek: LA-551

Melanocorphya calandra

Evron/Shimelmitz: LA-164

Pycnonotus xanthopoylos

Jelinek: LA-392

Hirundo rustica

Evron/Shimelmitz: LA-023, LA-021, LA-060
Jelinek: LA-347, LA-467, LA-474, LA-479, LA-595, LA-425, LA-539, LA-550, LA-621, LA-636, LA-643, LA-652

Phylloscopus collybita

Evron/Shimelmitz: LA-139

Sylvia atricapilla

Evron/Shimelmitz: LA-038

Sturnus sp.

Jelinek: LA-465

Turdus sp. (size *merula*)

Jelinek: LA-302, LA-398, LA-596

Erithracus rubecula

Evron/Shimelmitz: LA-083
Jelinek: LA-404

Passer domesticus

Jelinek: LA-548

Passer sp.

Evron/Shimelmitz: LA-090

Motacilla alba

Jelinek: LA-606

Motacilla sp.

Evron/Shimelmitz: LA-077, LA-088

Coccothraustes coccothraustes

Jelinek: LA-459

Chloris chloris

Evron/Shimelmitz: LA-194

Carduelis carduelis

Evron/Shimelmitz: LA-041
Jelinek: LA-549

Carduelis sp.

Jelinek: LA-672

Emberiza calandra

Evron/Shimelmitz: LA-026

Emberizidae

Evron/Shimelmitz: LA-177

Passeriformes

Evron/Shimelmitz: LA-089, LA-004, LA-005, LA-007, LA-010, LA-011, LA-017, LA-018, LA-019, LA-027, LA-029, LA-031, LA-032, LA-034, LA-036, LA-039, LA-042, LA-043, LA-044, LA-045, LA-049, LA-050, LA-051, LA-053, LA-059, LA-061, LA-063, LA-064, LA-065, LA-066, LA-067, LA-068, LA-069, LA-070, LA-071, LA-074, LA-075, LA-076, LA-078, LA-080, LA-081, LA-

084, LA-085 LA-086, LA-091, LA-094, LA-097, LA-098, LA-099, LA-100, LA-105, LA-109, LA-110, LA-111, LA-112, LA-113, LA-114, LA-115, LA-117, LA-118, LA-119, LA-121, LA-122, LA-126, LA-127, LA-129, LA-130, LA-131, LA-132, LA-133, LA-135, LA-137, LA-138, LA-143, LA-144, LA-145, LA-146, LA-147, LA-148, LA-149, LA-150, LA-151, LA-153, LA-155, LA-156, LA-157, LA-158, LA-165, LA-169, LA-172, LA-176, LA-181, LA-182, LA-183, LA-184, LA-187, LA-189, LA-195, LA-197, LA-198, LA-199, LA-201, LA-202, LA-203, LA-204, LA-205, LA-206, LA-207, LA-210, LA-211, LA-212, LA-213, LA-214, LA-217, LA-220, LA-221, LA-223, LA-224, LA-225, LA-226, LA-227, LA-232, LA-234, LA-235, LA-236, LA-237, LA-238, LA-092, LA-093, LA-152, LA-180, LA-163, LA-218, LA141

Jelinek: LA-300, LA-303, LA-304, LA-311, LA-319, LA-324, LA-333, LA-334, LA-336, LA-337, LA-340, LA-341, LA-342, LA-346, LA-348, LA-350, LA-352, LA-353, LA-354, LA-355, LA-356, LA-357, LA-361, LA-366, LA-367, LA-368, LA-369, LA-379, LA-382, LA-383, LA-387, LA-391, LA-394, LA-395, LA-396, LA-399, LA-401, LA-402, LA-405, LA-406, LA-407, LA-409, LA-412, LA-413, LA-414, LA-415, LA-416, LA-417, LA-426, LA-430, LA-431, LA-435, LA-436, LA-438, LA-441, LA-442, LA-444, LA-453, LA-457, LA-458, LA-462, LA-463, LA-464, LA-469, LA-470, LA-475, LA-476, LA-477, LA-480, LA-481, LA-482, LA-483, LA-486, LA-491, LA-498, LA-499, LA-500, LA-512, LA-513, LA-521, LA-522, LA-528, LA-541, LA-547, LA-556, LA-557, LA-558, LA-559, LA-561, LA-564, LA-565, LA-566, LA-580, LA-582, LA-583, LA-584, LA-585, LA-586, LA-587, LA-588, LA-589, LA-590, LA-591, LA-592, LA-597, LA-600, LA-601, LA-602, LA-603, LA-608, LA-616, LA-617, LA-624, LA-625, LA-626, LA-627, LA-628, LA-629, LA-630, LA-635, LA-642, LA-644, LA-648, LA-649, LA-663, LA-664, LA-673, LA-677, LA-555, LA-615, LA-509, LA-641, LA-403

Aves indeterminate

Aves indeterminate.

Evron/Shimelmitz: LA-142, LA-192, LA-208, LA-009, LA-022, LA-033, LA-072, LA-228, LA-229, LA-230, LA-231, LA-191

Jelinek: LA-322, LA-323, LA-329, LA-330, LA-331, LA-360, LA-384, LA-393, LA-400, LA-418, LA-421, LA-422, LA-423, LA-424, LA-445, LA-460, LA-461, LA-471, LA-472, LA-473, LA-494, LA-525, LA-529, LA-530, LA-531, LA-532, LA-533, LA-534, LA-535, LA-536, LA-537, LA-538, LA-560, LA-562, LA-567, LA-568, LA-578, LA-579, LA-657, LA-675, LA-676, LA-637, LA-638, LA-678, LA-679, LA-680, LA-682, LA-683, LA-684, LA-685, LA-686, LA-687, LA-497, LA-349, LA-671, LA-339, LA-654, LA-372, LA-378

Aves indet. size large anatid

Evron/Shimelmitz: LA-003

Aves indet. size *Anser anser*

Jelinek: LA-489

Aves indet. size *Columba*

Evron/Shimelmitz: LA-020, LA-028, LA-046, LA-104, LA-124, LA-178, LA-185, LA-196, LA-200, LA-209, LA-233

Jelinek: LA-325, LA-332, LA-359, LA-362, LA-363, LA-364, LA-365, LA-420, LA-434, LA-437, LA-504, LA-505, LA-523, LA-573, LA-594, LA-631, LA-632, LA-661, LA-669

Appendix 4: NISP frequency of avian remains at Tabun Cave distributed for each analysed bed.

	Layer	B	C																								C- TOTAL	TABUN
	Unit		C -1									C -2								C - GENERAL								
Taxonomic identification	**Square**		**2**	**3**	**4**	**5**	**6**	**7**	**9**	**10**	**12**	**3**	**4**	**5**	**6**	**8**	**9**	**10**	**12**	**2**	**3**	**5**	**6**	**12**	**13**	**MIX**		TOTAL
GALLIFORMES																												
Alectoris	***chukar***					1																					1	1
Alectoris	***sp.***	1					2																				2	3
Coturnix	***coturnix***	12			1		2			1	1	1		4												1	11	23
COLUMBIFORMES																												
Columba	***livia/oenas***	37	13	1		4	27		5	3	5	3	10	8	9	1	3		2		1		1		1	4	101	138
Spilopelia	***senegalensis***	3																										3
CHARADRIIFORMES																												
Scolopax	***rusticola***																					1					1	1
Larus	***sp.***	1					1																				1	2
PELICANIFORMES																												
Threskiornithidae	***(G.eremita/P.leucorodia)***																									1	1	1
Ardeidae size	***Ixobrychus minutus***						1																				1	1
Ardeidae size	***Bulbicus ibis***												1														1	1
ACCIPITRIFORMES																												
Aquila size	***nipalensis***	1																										1
Accipitriformes			1																	2							3	3
STRIGIFORMES																												
Tyto	***alba***									1																	1	1
FALCONIFORMES																												
Falco	***subbuteo***												2				1										3	3
Falco	***sp.***	1					2		1				1				2										6	7

	Layer	**B**	**C**																								**C-TOTAL**	**TABUN**
	Unit		**C -1**									**C -2**								**C - GENERAL**								
Taxonomic identification	**Square**		**2**	**3**	**4**	**5**	**6**	**7**	**9**	**10**	**12**	**3**	**4**	**5**	**6**	**8**	**9**	**10**	**12**	**2**	**3**	**5**	**6**	**12**	**13**	**MIX**		**TOTAL**
PASSERIFORMES																												
Lanius	*sp.*	1										1															1	2
Garrulus	*glandarius*				1																						1	1
Coloeus	*cf. monedula*	1											1	1		1											3	4
Corvus	*corone*	1																										1
Corvus	*sp.*	2					1		1				1	2			1										6	8
Corvidae		1	2										1														3	4
Parus	*major*												1														1	1
Alauda	*arvensis*	1															1										1	2
Alauda	*sp.*						1																				1	1
Melanocorypha	*calandra*	1																										1
Pycnonotus	*xanthopygos*												1														1	1
Hirundo	*rustica*	3					1	1				1		2													5	8
Hirundo	*sp.*					1	2			1	1						2										7	7
Phylloscopus	*collybita*	1																										1
Sylvia	*atricapilla*	1																										1
Sturnus	*sp.*													1													1	1
Turdus	*sp.*		1					1					1														3	3
Erithacus	*rubecula*	1											1														1	2
Passer	*domesticus*						1																				1	1
Passer	*sp.*	1																										1
Motacilla	*alba*								1																		1	1
Motacilla	*sp.*	2																										2
Coccothraustes	*coccothraustes*													1													1	1
Chloris	*chloris*	1																										1
Carduelis	*cf. carduelis*	1					1																				1	2
Carduelis	*sp.*																									1	1	1
Emberiza	*calandra*	1																										1
Emberizidae		1																										1
Passeriformes		133	6	2	11	3	26		4	4		8	21	16	12	2	12	1				1			1	1	131	264
INDETERMINATE																												
Aves	sp.	26	2	4	6	4	21	1			1	2	8	8	3		5			1				1	1	8	76	102
NISP		**236**	**25**	**7**	**19**	**13**	**89**	**3**	**12**	**10**	**8**	**16**	**50**	**43**	**24**	**4**	**27**	**1**	**2**	**3**	**1**	**2**	**1**	**1**	**3**	**16**	**380**	**616**
NTAXA		**21**	**4**	**2**	**2**	**3**	**11**	**2**	**4**	**4**	**3**	**4**	**8**	**6**	**2**	**2**	**5**	**1**	**1**	**1**	**1**	**2**	**1**	**1**	**2**	**4**	**24**	**31**

Appendix 5: NISP frequency of avian remains at Scladina Cave distributed for each analysed layer.

	MIS 3 group						MIS 5 group								MIS 6	Aven collapse					?	
Taxonomical identification	**38**	**39**	**T-GN**	**40**	**1A**	**1B**	**3**	**4**	**4A**	**4A-GR**	**4A-GX1**	**5**	**Vb**	**5+6**	**Via**	**Z1**	**Z1 à Z3**	**Z1-TE**	**Z3-4**	**2004AT55**	**no layer**	**TOTAL**
Galliformes																						
Gallus gallus cf. *domestica*																1						**1**
Tetrao urogallus						1	8	4			1			2							1	**17**
Lyrurus tetrix					2				2			2			1							**7**
Lagopus sp.		1			1			1										1				**4**
Lagopus sp./*Lyrurus tetrix*												1										**1**
Galliformes size *Tetrao urogallus*																1						**1**
Galliformes size *Tetrao* sp.								1														**1**
Galliformes size *Lyrurus tetrix*					1		2															**3**
Galliformes size *Lagopus* sp.												2	1								1	**4**
Anseriformes																						
Mergus merganser/serrator																				1	1	**2**
Anser albifrons/serrirostris												1										**1**
Anser sp.														1			1					**2**
Anatidae size *Anas acuta*					1																	**1**
Anseriformes size *Anser anser*		1																				**1**
Anseriformes size *Anas platyrhynchos*			1		1			1				1										**4**
Columbiformes																						
Columba cf. *palumbus*					1																	**1**
Suliformes																						
Phalacrocorax carbo								1														**1**
Accipitriformes																						
Accipiter nisus					1																	**1**
Accipitriformes size *Aquila/Gyps*					1																	**1**
Strigiformes																						
Bubo scandiacus	1								1													**2**
Asio otus/flammeus													1									**1**

Taxonomical identification	MIS 3 group						MIS 5 group								MIS 6	Aven collapse					?	
	38	**39**	**T-GN**	**40**	**1A**	**1B**	**3**	**4**	**4A**	**4A-GR**	**4A-GX1**	**5**	**Vb**	**5+6**	**Via**	**Z1**	**Z1 à Z3**	**Z1-TE**	**Z3-4**	**2004AT55**	**no layer**	**TOTAL**
Passeriformes																						
Passeriformes small size					2																	**2**
Passeriformes size Emberiza citrinella					1																	**1**
Aves indet.																						
Aves size *Tetrao urogallus*					1			1		1		2										**5**
Aves size *Tetrao*sp.												2										**2**
Aves size *Lyrurus tetrix*												2										**2**
Aves size *Lagopus* sp.				1																		**1**
Aves size *Anser*sp.												1							1			**2**
Aves size *Columba livia*					1																	**1**
Aves size *Numenius phaeopus*												1										**1**
Aves middle												1										**1**
Aves middle/large					3																	**3**
Aves sp.					1				1			1										**3**
NISP	**1**	**2**	**1**	**1**	**18**	**1**	**10**	**9**	**4**	**1**	**1**	**17**	**2**	**3**	**1**	**2**	**1**	**1**	**1**	**1**	**3**	**81**
NTAXA	**1**	**2**	**1**	**1**	**9**	**1**	**2**	**4**	**2**	**1**	**1**	**3**	**2**	**2**	**1**	**2**	**1**	**1**	**1**	**1**	**3**	**12**

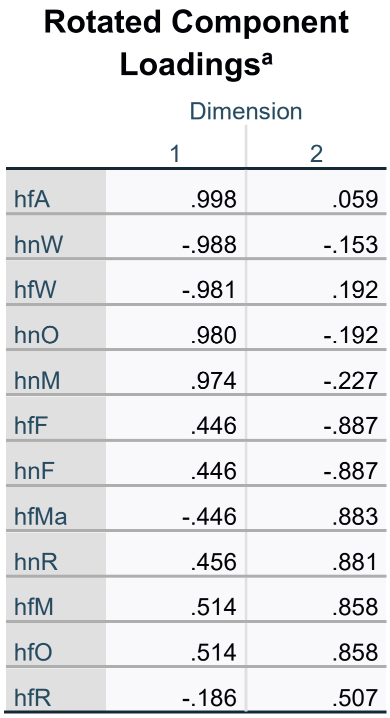
Appendix 6: CATPCA Rotated Loading Components.

a) Rotated Loading Components for climatic variables (figure 8.1)

Rotated Component Loadings[a]

	Dimension	
	1	2
latD	.996	.050
bioB	.992	.096
latC	-.991	-.097
bioC	-.991	-.088
bioD	.990	.108
latF	.990	.108
temD	.990	.108
latA	-.983	-.184
temC	.983	.184
humD	.983	.184
latB/D	-.918	-.396
latB	-.115	-.984
bioE	.215	.976
bioA	.149	.974
humA	.149	.974
temE	.195	.968
temB	-.687	.724
humB	-.688	.723
humE	.688	-.723
humC	.415	.671
temA	-.521	-.623

b) Rotated Component Loadings for habitat variables (figure 8.2)



Rotated Component Loadings[a]

	Dimension	
	1	2
hfA	.998	.059
hnW	-.988	-.153
hfW	-.981	.192
hnO	.980	-.192
hnM	.974	-.227
hfF	.446	-.887
hnF	.446	-.887
hfMa	-.446	.883
hnR	.456	.881
hfM	.514	.858
hfO	.514	.858
hfR	-.186	.507