

ANGLIA RUSKIN UNIVERSITY

FACULTY OF SCIENCE AND ENGINEERING

BIRDS IN THE NEANDERTHAL ECOLOGICAL NICHE – USING BIRDS  
FROM PLEISTOCENE CAVE ARCHIVES TO CHARACTERISE THE  
RELATIONSHIP BETWEEN NEANDERTHALS AND BIRDS

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requirements of Anglia Ruskin University  
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**To my sons Aiden and Tyler**

No matter how complicated life gets, always believe in yourselves. ... You can do it.

**To Mum and Dad**

For always believing in me, when everyone else gave up

## **Acknowledgements**

Back in 1989, when I was six years old, I first walked down with my parents to Gorham's Cave and explored this wonderful site that had been occupied by Neanderthals in Gibraltar for thousands of years. It was an abrupt introduction into this world of the Neanderthals. In parallel, my parents also introduced me to the magical world of birds and their migrations across the Strait of Gibraltar. When in 1993 I first stepped into the Biological Reserve of Doñana in Southern Spain, my life changed – it was like stepping into the world of the Neanderthals. Many of the animals and plants I knew from fossils in the caves, suddenly came to life. I must therefore start by thanking these Neanderthal people, and the birds for allowing me to peek into their world.

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**Abstract**

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Aspects of Neanderthal and modern human behaviour and ecology, particularly their relationship with birds are investigated. Birds are good indicators of climate and habitat and are frequently present in Neanderthal sites. This permitted the characterisation of Neanderthal habitats and climate, important given current questions about their ability to tolerate cold climates and tundra, which has implications when explaining their extinction as climate-caused. In addition, the inability of Neanderthals to catch birds has been used to support models of superior modern human cognitive capacity. Given recent published results showing Neanderthal exploitation of birds, a reassessment was considered necessary.

A database of hominin sites and associated bird species was created. Bird species were assigned to specific climatic and habitat categories which permitted analyses of the climates and habitats occupied by Neanderthals and modern humans during the last glacial cycle (125 – 10 thousand years ago), the period when the two hominin taxa came into contact in Eurasia. The principal bird species associated with Neanderthals were identified and their taxonomic, behavioural and ecological features recognised. Finally, a database of bird species known to have been processed by Neanderthals was created from published sources. Both multivariate and univariate statistics were used to analyse the data including novel applications of PCA in this area.

The results showed that Neanderthals were temperate climate hominins that rarely occupied extremely cold climates and open habitats. They occupied habitat mosaics where they regularly exploited a non-random suite of bird species, characterised by particular taxonomic, behavioural and ecological characteristics.

The evidence presented here shows that, in terms of climate tolerance, habitat occupation and bird species exploitation, Neanderthals overlapped broadly with modern humans. Neanderthals had skills and abilities capable of despatching a wide range of birds and they were selective in the species that they took. This evidence calls into question models of modern human superiority as the cause of the Neanderthal extinction, and appears to support climate factors instead.

**Keywords:** Neanderthal, Mousterian, Birds, Palaeartic, Pleistocene, Taphonomy

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BIRDS IN THE NEANDERTHAL ECOLOGICAL NICHE – USING BIRDS  
FROM PLEISTOCENE CAVE ARCHIVES TO CHARACTERISE THE  
RELATIONSHIP BETWEEN NEANDERTHALS AND BIRDS

STEWART FINLAYSON

A Thesis in partial fulfilment of the requirements of Anglia Ruskin University for the  
degree of Doctor of Philosophy

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## **1.1 Introduction**

This thesis is the result of a growing interest in the study of birds and their importance as a resource to the Neanderthals. Prior to 2009 (Blasco & Fernández Peris, 2009), no evidence that Neanderthals exploited birds had been published. The general consensus in the palaeoanthropological and zooarchaeological community was that Neanderthals did not catch birds, and this conclusion was reached because tell-tale signs of intervention (such as cut marks produced by stone tool implements) on bird bones recovered from Neanderthal sites were missing.

I have been formally involved, as project member, in excavations at the Neanderthal sites of Gorham's and Vanguard Caves (declared a World Heritage Site by UNESCO in 2016) for the past ten years although my interest in these caves goes back much further. It was from these caves that some of the early evidence of Neanderthal exploitation of birds was documented and published in 2012 (Finlayson *et al.*, 2012). My personal interest in birds started me off in the subject of Neanderthal-bird interactions and I was curious about the high number of remains of many bird species that were being excavated from Neanderthal contexts. To date 161 bird species have been recovered from these caves and they represent around a third of all the extant bird species of Europe, more than any other Pleistocene site anywhere. How were these birds getting into the caves? It was in trying to answer this question that I became involved, as team member, in contacting zooarchaeologists who could study these bird remains. Discussions with them, and observing them at work, helped me understand

the principles of taphonomy and what constituted clear evidence of anthropic activity on bones, those of birds included.

These studies established the Neanderthals as main agents bringing birds back to the caves (Blasco *et al.*, 2014; 2015). We then knew who was doing it, but I felt that there was a need to take this work beyond simply demonstrating that Neanderthals caught birds. Missing in all this was ecology. I was clearly aware of pioneering work that had been done by Finlayson in 2006 (Finlayson, 2006); she had quantified the habitat of Neanderthals outside the caves using birds as indicators. With the new evidence of Neanderthal exploitation (which had been unavailable to her in 2006), I became increasingly curious about which species were being taken and for what purpose. Work in 2011 and 2012 was showing that Neanderthals in Italy and in Gibraltar may have been catching large raptors for their feathers (Peresani *et al.*, 2011; Finlayson *et al.*, 2012). In 2015, colleagues in Zagreb (Croatia), with whom I had been in discussion, published that the talons of a white-tailed eagle (*Haliaeetus albicilla*) had apparently been used as jewellery by Neanderthals (Radovčić *et al.*, 2015). Of particular importance was the date associated with the find: 130,000 years ago (kya). The practice pre-dated the arrival of modern humans in Eurasia by at least 90,000 years (kyr) and could clearly not have been copied from them by the Neanderthals.

I was surprised at how little ecology was brought into the subject of Neanderthals, and especially their relationship with birds. I could see that patterns might emerge from the detailed study of the birds being taken by Neanderthals. One early example of what could be done was in a paper which I co-authored in 2016 (Finlayson & Finlayson, 2016) which suggested, not only that Neanderthals may have been targeting scavenging birds, but that they may have been doing so during the autumn and winter months. It is this approach which I have developed, and expanded, in this thesis. My

aim has been to use birds as indicators of Neanderthal climate and habitat (Chapter 3), before moving into questions related to which bird species were associated with the Neanderthals (Chapter 4), and which species (determined from direct taphonomic evidence) were taken (Chapter 5). In this respect, seeing this is a new field in its infancy in which many bird species and sites may not have been studied taphonomically, I felt that it would be useful to make predictions. I have attempted to identify which bird species and sites might be suitable candidates for taphonomic examination, and I have done this in Chapter 5.

## **1.2 Neanderthals and Models of Recent Human Evolution**

The Neanderthals were hominins who occupied large parts of Eurasia for approximately 300 kyr, between circa 300 kya and 32 kya (Mellars and Stringer, 1989; Stringer and Gamble, 1993; Klein, 1999; Finlayson, 2004; Finlayson *et al.*, 2006). They are given full species status – *Homo neanderthalensis* – by some authorities but are relegated to sub-species (*H. sapiens neanderthalensis*) by others (Stringer and Gamble, 1993). Recent evidence showing that interbreeding between Neanderthals, modern humans and Denisovans – the latter a new lineage discovered in the Altai Mountains in Siberia (Meyer *et al.*, 2012) – was frequent and widespread (Slon *et al.*, 2018), would appear to have resolved the discussion in favour of the single species model. In this scenario, all populations of *Homo* living across the Old World during the Late Pleistocene comprised a polytypic species (Mayr, 1942), Neanderthals and modern humans being of sub-specific taxonomic rank. Neanderthals represent a lineage that diverged from our own (Green *et al.*, 2010; Prufer *et al.*, 2013) around half-a-million years ago (mya). Neanderthals and modern humans evolved in relative isolation in Eurasia and tropical Africa respectively (Stringer & McKie, 1996). There

is evidence of contemporaneity of the two lineages in the Middle East around 100 kya (Akazawa *et al.*, 1998) although it is not clear if they actually met. The earliest presence of modern humans in the Middle East is now put at circa 180 kya (Hershkovitz *et al.*, 2018) and a recent paper has placed modern humans in Greece even earlier, at circa 210 kya (Havarti *et al.*, 2019). Yet it is only after 45 kya that modern humans appear to have expanded across Europe where they encountered the Neanderthals and supposedly caused their extinction (Bar-Yosef & Pilbeam, 2000; Higham *et al.*, 2011; Nigst *et al.*, 2014).

Two models of recent human evolution have dominated in the literature for several decades. The multi-regional evolution model (Wolpoff, 1989) proposed that, following an early expansion of the ancestral species *H. erectus* from Africa around 1.9 mya, lineages evolved in parallel in different parts of the Old World, with a degree of gene flow between them. Today's humans would, in this scenario, be the product of this process. In contrast, the Out-of-Africa 2 Model (Cann *et al.*, 1987; Stringer and Andrews, 1988; Stringer, 1989) postulated a second African expansion of humans around 100 kya. These humans were, biologically, modern and no different from present-day humans worldwide. This model is also known as the Replacement Model as it is implicit in it that modern humans replaced all existing human populations (known as archaic humans) including the Neanderthals. The Replacement Model had received the wide support of the palaeoanthropological community, but it now appears to have been overtaken by recent genetic evidence which clearly shows widespread interbreeding between Neanderthals and modern humans, and not an outright replacement of one by the other (Fu, *et al.*, 2015; Villanea and Schraiber, 2019).

Intermediate models, that had been proposed but received less attention than multi-regionalism and replacement, now seem particularly relevant. Among these, Brauer

(1992) proposed an African expansion of modern humans with a significant African genetic contribution to European and western Asian populations, in other words hybridisation. Smith (1992) offered a similar model, but reduced the importance of the African contribution to European and western Asian populations. Lahr and Foley (1994, 1998), and Foley and Lahr (1997) proposed multiple dispersals from Africa linked with genetic bottlenecks and replacements. The reality is that the complex processes involving the expansion and contraction of human lineages in the Pleistocene probably had an element of continuity and replacement of populations.

### **1.2.1 Behavioural Modernity and the Replacement Model**

It is not just the genetic evidence which has called the Replacement Model into question. An important element of this model is that modern humans achieved geographical expansion at the expense of archaic humans, because of behavioural features that enabled them to outcompete all other *Homo* which they encountered. According to Mellars (1991), the features that characterised the modern human behavioural package were:

- The production of standardised and economically-manufactured tools as exemplified by blades as opposed to flakes, together with an increase in their diversity and complexity, and the appearance of regional variations.
- The use of raw materials such as antlers and bone in addition to stone.
- The first known production of non-functional mobile symbolic objects such as beads.
- The first appearance of naturalistic rock art.
- Apparent changes in economic behaviour, exemplified by the targeting of particular prey species, and the strategic exploitation of resources in accordance with local or seasonal availability and abundance. The exploitation of coastal resources has been seen as a major component that enabled modern humans to expand out of Africa (Marean *et al.*, 2007). This argument has been based on Optimal Foraging Theory (Krebs, 1978).

The development of this modern behavioural package has been described as the Human Revolution (Mellars & Stringer, 1989). It has come under increasing scrutiny and criticism in recent years (McBrearty & Brooks, 2000). One major source of criticism has been that the modern behavioural package does not appear at once in a single place but emerges gradually over a long time frame across a wide geographical area (McBrearty, 2007). Many of the features which allegedly catapulted the modern human expansion appear thousands of years before, begging the question of the degree to which they were the cause of the geographical spread.

These views, also have important implications for the Neanderthals and their relationship with birds. These implications were: (a) Neanderthals were considered not to have the cognitive capacities, abilities or technologies for catching birds, and (b) birds were classified as fast-moving, difficult-to-catch, prey that were first exploited by modern humans with their advanced technology and know-how. Therefore, the entire question of bird-catching had become incorporated into views of what it meant to be modern and what constituted modern behaviour (e.g. Mellars, 1991; Stiner 1991; Stiner *et al.*, 2000; Klein, 1999, 2001), and such definitions excluded the Neanderthals.

### **1.3 Neanderthals and behavioural modernity**

In the past decade, and especially since the publication of the first draft Neanderthal genome (Green *et al.*, 2010), our view of the Neanderthals has begun to change. It has become clear from a number of publications (Zilhao *et al.*, 2010; Peresani *et al.*, 2011; Finlayson *et al.*, 2012; Rodriguez Vidal *et al.*, 2014) that they were intelligent humans capable of a wide range of activities that are comparable to those of our direct ancestors (referred to in this thesis as ‘modern humans’ - *H. s. sapiens*). An important



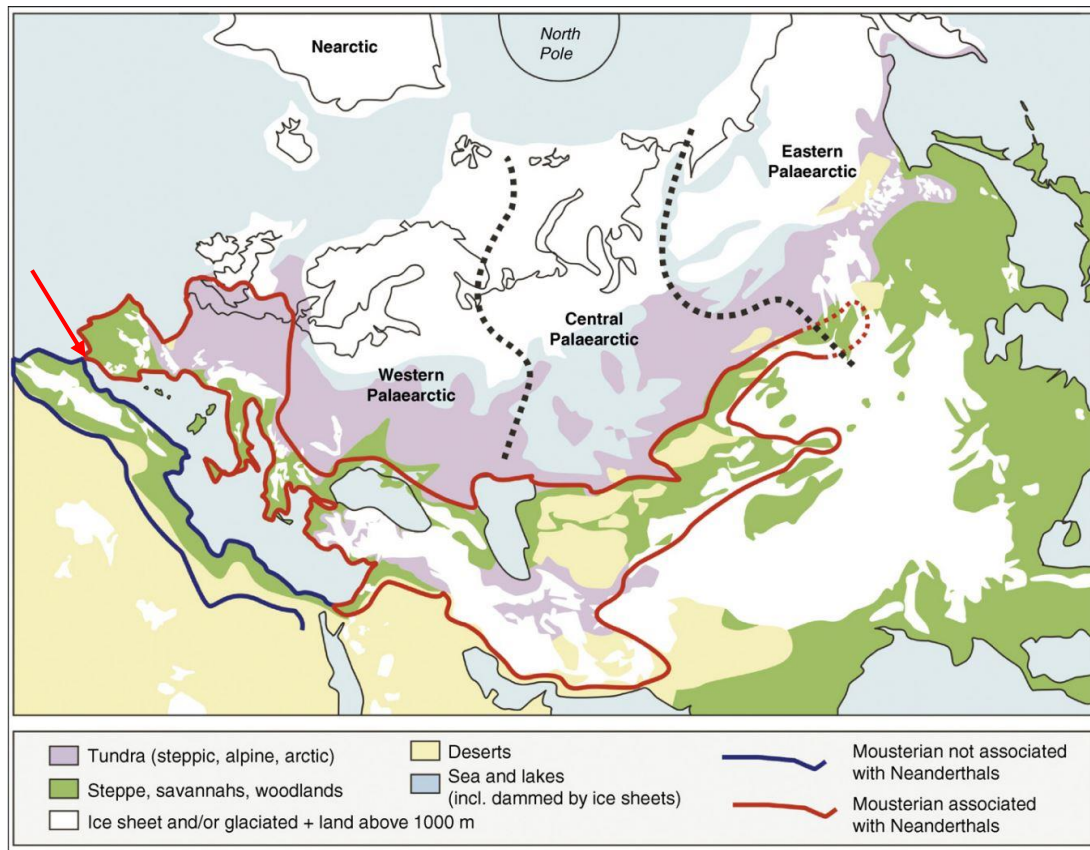
component of this new evidence is the relationship between Neanderthals and birds (Peresani *et al.*, 2011; Finlayson *et al.*, 2012; Blasco *et al.*, 2014).

It now also seems that the exploitation of birds was not limited to hunting for food; the evidence found in caves in Gibraltar, France, Italy and Croatia, has revealed that birds were also taken for their feathers and talons (Peresani *et al.*, 2011; Finlayson *et al.*, 2012; Moran and Laroulandie, 2012; Radovic *et al.*, 2015). This has been interpreted as evidence of the cognitive capacities of the Neanderthals, using feathers as signalling devices, and talons as jewellery. Recent evidence also suggests that Neanderthals were capable of executing symbols that could be equated to art. Shells with pigment that may have been used in painting have been found in south-eastern Spain (Zilhao, *et al.* 2010). Most recently the early age of cave art in the Iberian Peninsula, prior to the arrival of modern humans, has been attributed to the Neanderthals as the artists (Hoffmann *et al.*, 2018). These new discoveries are the tip of the iceberg and are opening up new areas of Neanderthal behavioural research.

### **1.3.1 Gibraltar, the Neanderthals and behavioural modernity**

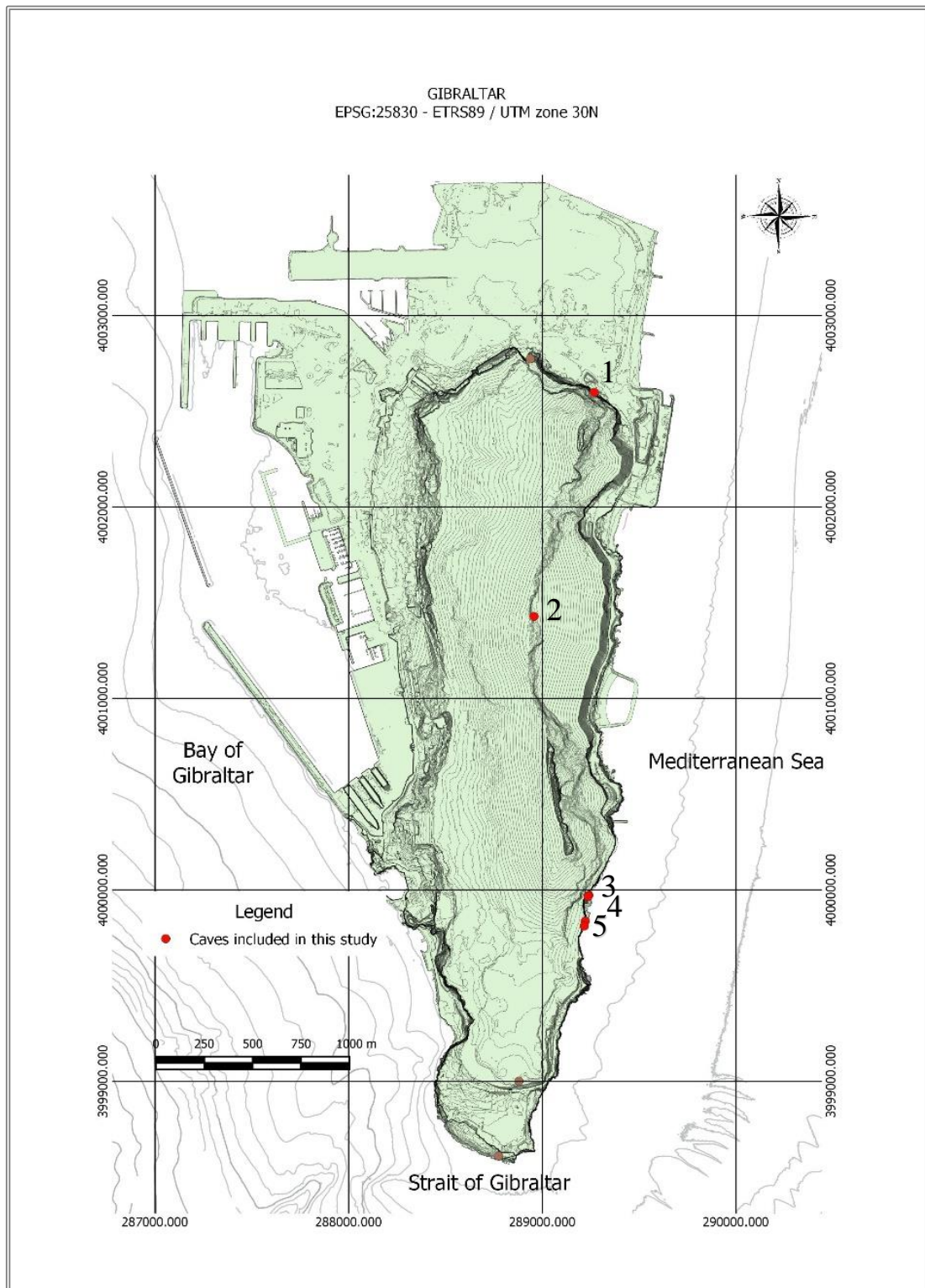
The evidence indicating that the Neanderthals had comparable behaviours to modern humans has come from a number of sites including Gorham's and Vanguard Caves in Gibraltar. A rock engraving found in Gorham's Cave indicates that Neanderthals were at least capable of intentionally executing abstract motifs (Rodriguez-Vidal *et al.*, 2014). Recent work in these caves has also shown that the Neanderthals were exploiting coastal biological resources (molluscs, seals and dolphins) as well as birds (Stringer *et al.*, 2008; Finlayson *et al.*, 2012; Blasco *et al.*, 2014; Fa *et al.*, 2016). In fact, evidence from a site just 100 km from Gibraltar has confirmed that the Neanderthal exploitation of coastal resources (intertidal molluscs) was happening as

early as the earliest modern human evidence from South Africa (Cortes-Sanchez, *et al.*, 2011).

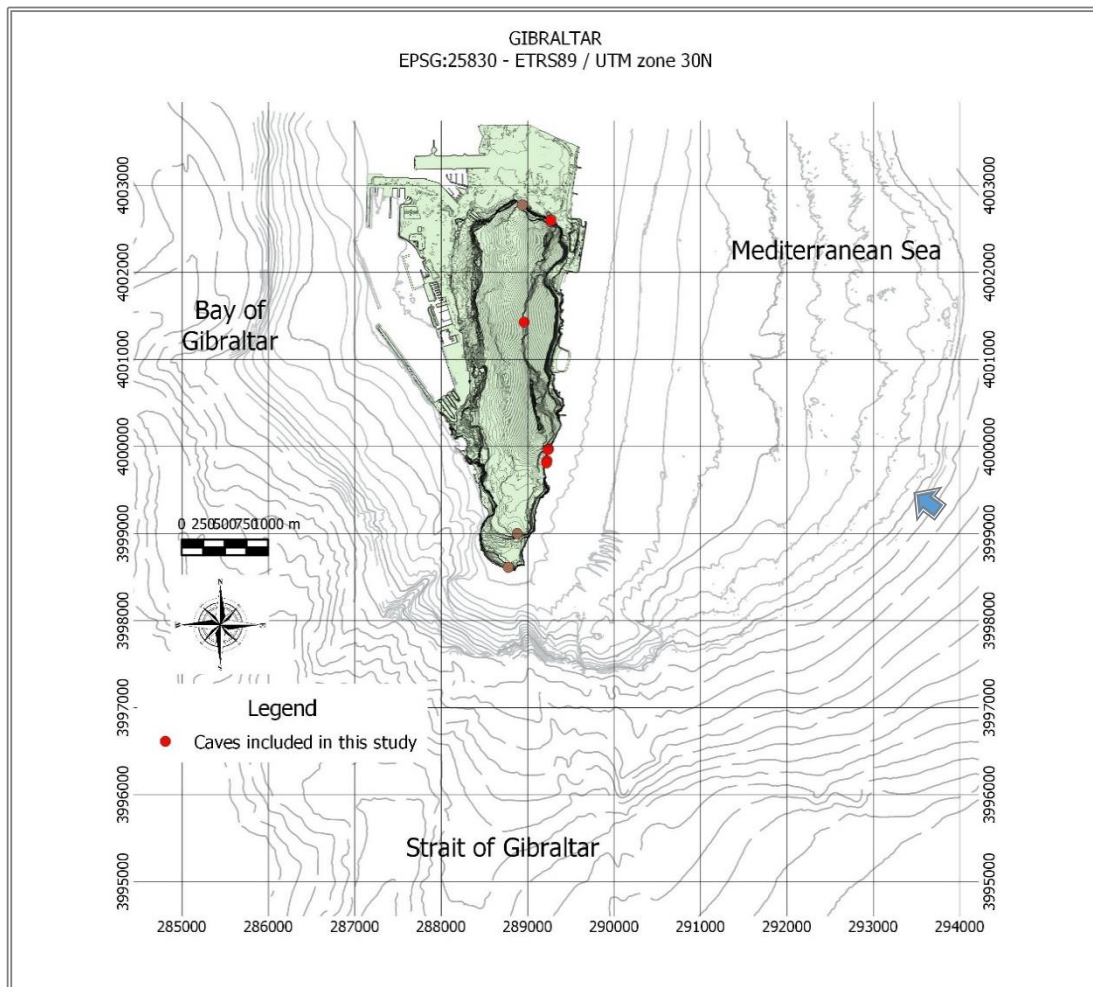


*Figure 1.1 Map of Neanderthal geographical range (in red). Location of Gibraltar, at extreme south-west of the range is indicated by a red arrow. From Finlayson and Carrión (2007).*

Gibraltar lies at the south-western extreme of Eurasia and of the Neanderthal range (Figure 1.1), and Gorham's and Vanguard Caves (Figure 1.2 to Figure 1.4) were occupied by Neanderthals for at least 100 kyr (Barton *et al.*, 2012). These caves have proved to be rich in bird remains that are contemporary with the Neanderthals and it seems that Neanderthals were largely responsible for the accumulation of the bird bones in the caves (Blasco *et al.*, 2014).



*Figure 1.2 Location of Gibraltar Neanderthal sites associated with birds and referred to in this study. 1 – Devil's Tower Rock Shelter; 2 – Ibex Cave; 3 – Hyaena Cave; 4 – Vanguard Cave; 5 – Gorham's Cave.*



*Figure 1.3 Location of the caves indicated in Figure 1.2 in relation to the bathymetry of the coastal shelf. During glacials and stadials, the sea level dropped by as much as 120m (Siddall et al., 2003) exposing a large surface of land. The blue arrow indicates the –100m contour beyond which a cliff exposed very little additional land.*

So far, 161 bird species have been identified in these caves, representing 31% of the present-day European avifauna. This is a globally important resource which offers an opportunity for a detailed understanding of the relationship between Neanderthals and birds. This is not a trivial question, as it strikes at the heart of our understanding of Neanderthal behavioural capabilities and their ability to have survived the glacial conditions of Eurasia.

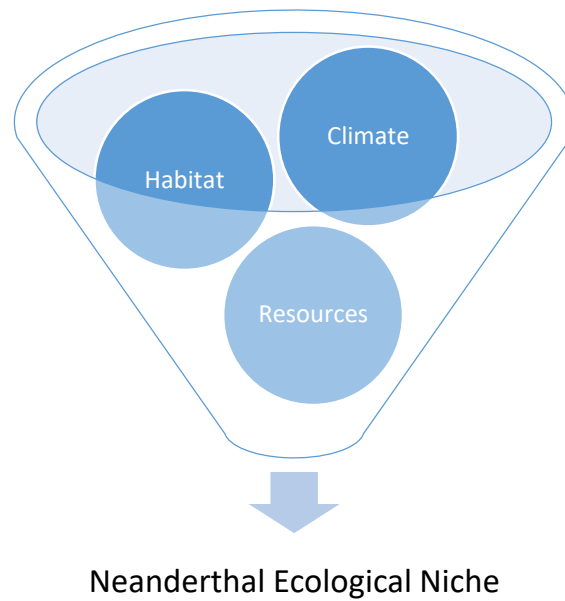




*Figure 1.4 Gorham's Cave (left) and Vanguard Cave (right) at the base of the Rock of Gibraltar.*

#### **1.4 Birds in the Neanderthal ecological niche**

In this section I provide the rationale for the approach taken in this thesis. It is an exploration into the Neanderthal ecological niche. In particular, I focus on three dimensions of this niche which operate at three scales (Figure 1.5). Climatic tolerance sets the limits of occupation at the geographical scale; habitat sets a local occupation scale which may be expanded to larger spatial scales as landscape; and resources (e.g. food) are key to ensuring survival and reproduction (Levin, 1992). The three scales are interconnected. Climate is a determining factor of landscape and habitat, which are in turn, factors which contribute to the presence or absence of species (Figure 1.6). Habitat and landscape are also important in providing conditions in which prey may be obtained.



*Figure 1.5 The three components of the Neanderthal Ecological Niche studied in this thesis.*

Climate, habitat and resources (in this case specifically, birds) will be the three components that will be discussed in this thesis. I will use birds as indicators of Neanderthal climate and habitat, and in turn, as resources exploited by the Neanderthals. A corollary of these analyses will be an examination of Neanderthal behaviour and how this contributed to their success as bird hunters.

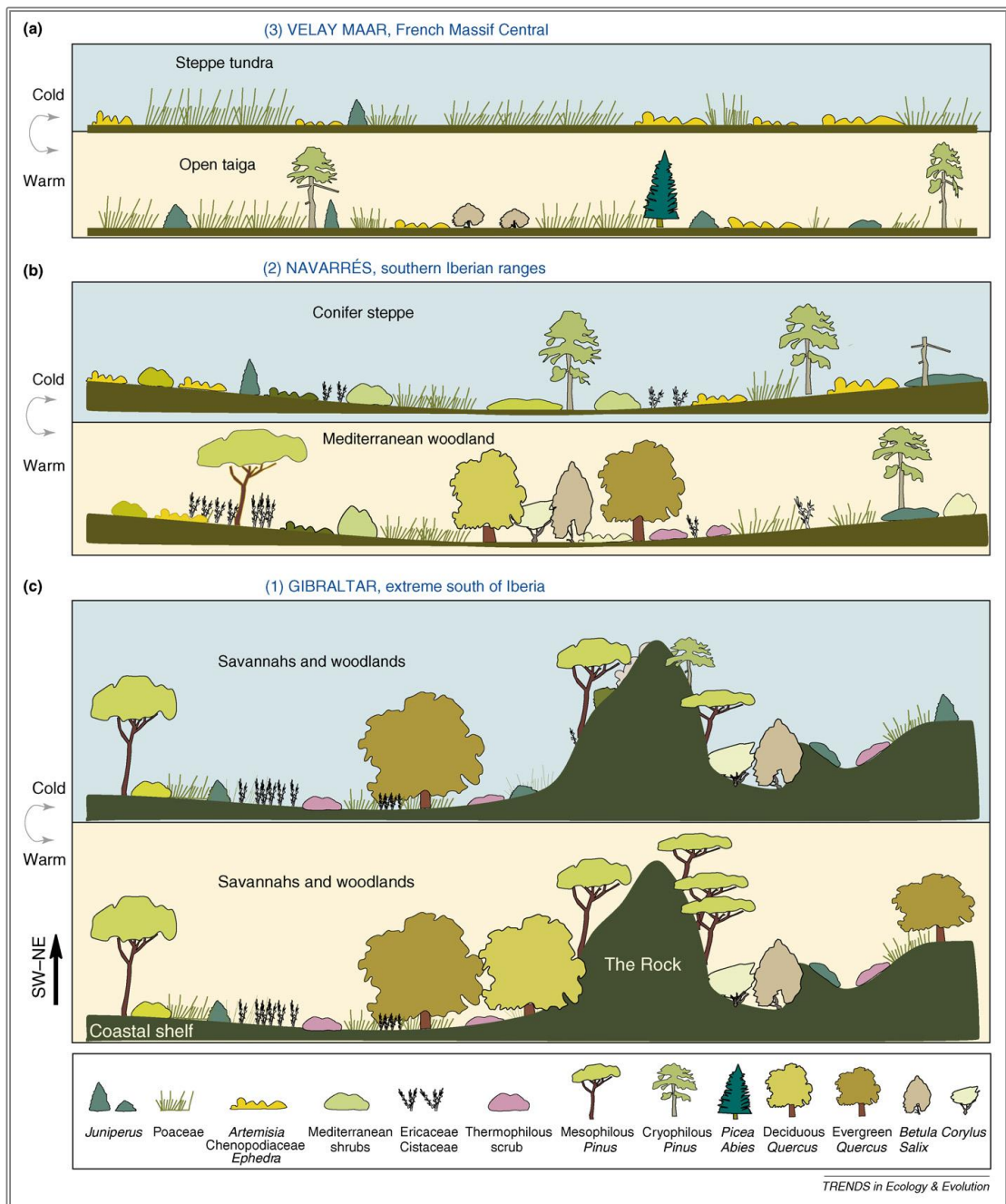


Figure 1.6 Effect of climate on vegetation at three different sites on a gradient from south-west France to Gibraltar. The sites are numbered in Figure 1.7. The figure shows how the vegetation response to climate change varies with latitude. The corresponding vegetation structure will, in turn, influence the presence or absence of birds and other animal species in any locality in any given point in time. In addition, vegetation structure will influence the tactics open to potential predators including humans. From Finlayson and Carrión (2007)

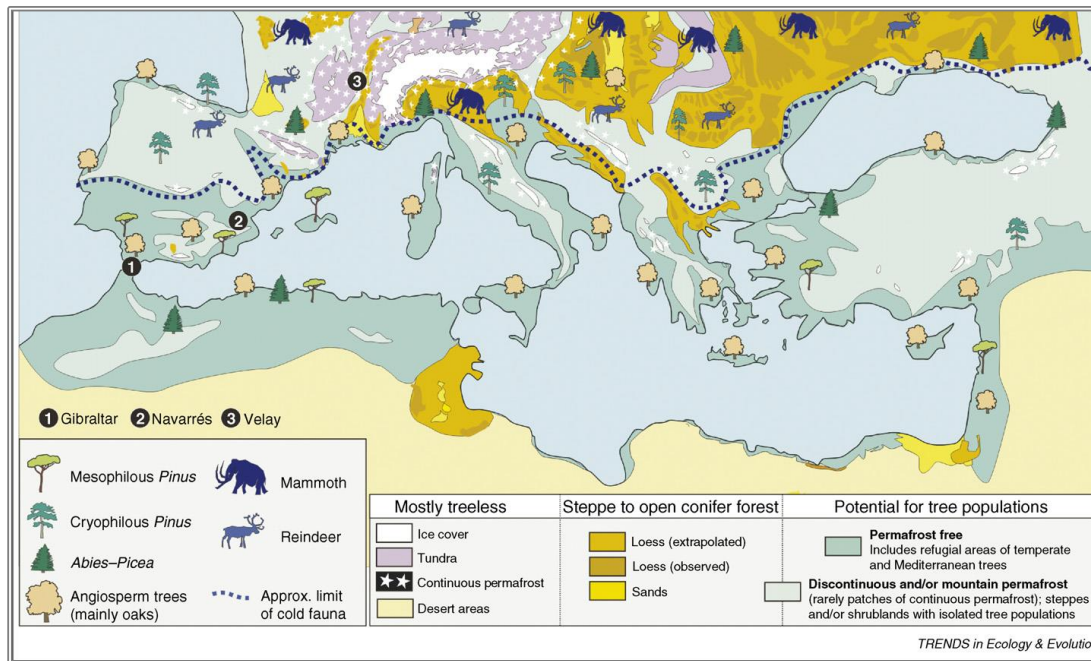


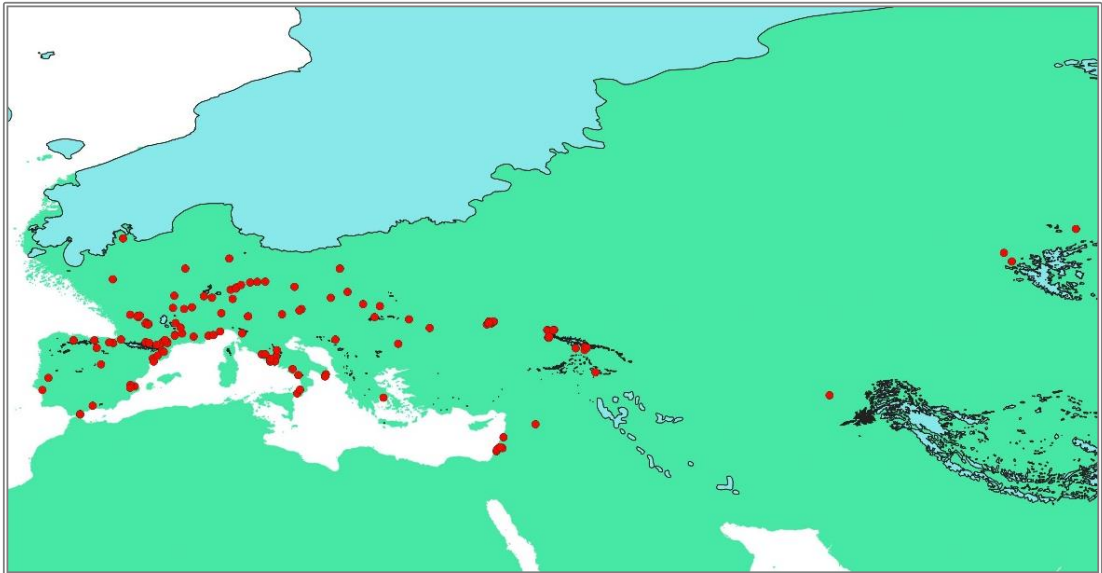
Figure 1.7. Location of sites in Figure 1.6 set against a map of central and southern Europe, and north Africa, at the last glacial maximum. From Finlayson and Carrión (2007).

#### 1.4.1 Birds as indicators

Most work on the fauna associated with Neanderthals (and indeed other hominins) has been carried out by palaeontologists and zooarchaeologists. Recent work in Gibraltar has shown that there is room for ecologists to enter into the discussion. Finlayson's (2006) thesis, quantifying the Neanderthal habitat by studying the living relatives of the species whose remains have been found in the caves, was a landmark study in this respect. The approach that I have taken in this thesis has evolved from that work. Using bird behavioural and ecological data collected today it is possible to provide insights into the nature of the Neanderthal-bird relationship, as exemplified in a recent paper (Finlayson & Finlayson, 2016). Such insights may prove to be critical in our interpretation of Neanderthal behavioural ecology.



The first step is to gain an understanding of the first two components of the Neanderthal niche: climate and habitat. This will allow us to then tackle critical questions of Neanderthal behaviour. I do this in this thesis, using birds as indicators of climate and habitat to address Research Question 1, in which I attempt to associate



*Figure 1.8 Location of Neanderthal sites with associated birds, used in this study. The sites are shown on a map representing a cold glacial, with ice sheets shown in light blue, and lowered sea levels.*

Neanderthals with particular climates and habitats across their entire geographic range or in particular parts of it using birds as indicators (Figure 1.8). I also seek differences in climate and habitat in the areas occupied by Neanderthals and modern humans.

### 1.4.2 Climate

One question which continues to be debated in the literature is that of cold-adaptation in Neanderthals. The argument goes back to the study of body size and proportions in Neanderthals and the application of ecogeographical rules (e.g. Bergmann's and Allen's Rules) to infer that they were adapted to the cold conditions of glacial Europe (Holliday, 1997). This assumption was highly significant for the Replacement Model. If Neanderthals were cold adapted, why did they disappear during the onset of the Last Glacial Maximum (LGM), in the period of highly variable and cooling climate of Marine Isotope Stage 3 (MIS 3; van Andel & Davies, 2004) when conditions would have favoured their body form over that of tropical-adapted modern humans arriving from Africa? The implication was a cognitive superiority on the part of modern humans that overrode the climatic adaptation.

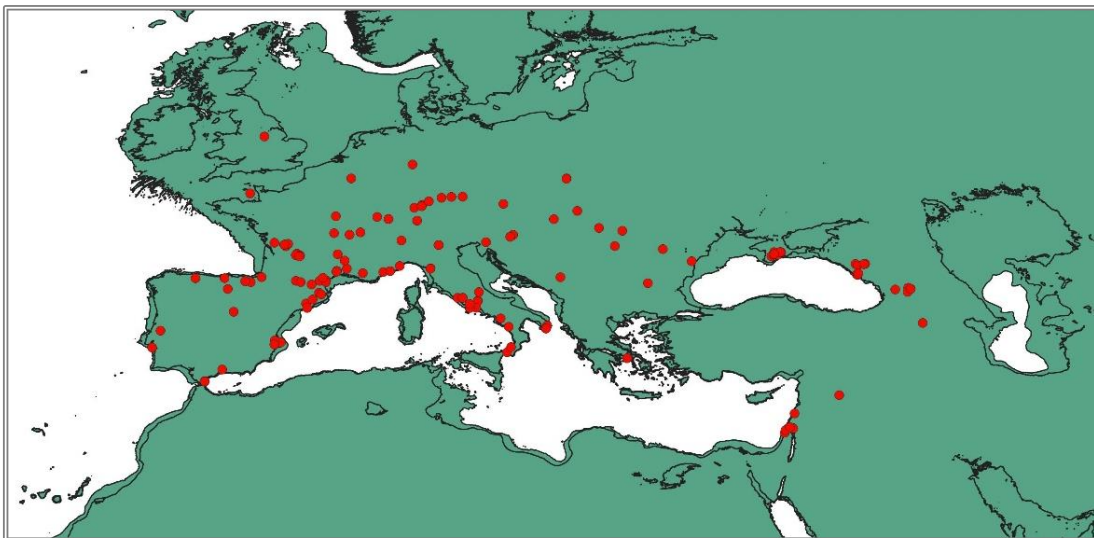


Figure 1.9 Detail of the European sites shown in Figure 1.8

Cold-adaptation in Neanderthals, who were known to have controlled fire and worn clothing (Goren-Inbar *et al.*, 2004; Gilligan, 2017), was questioned on the basis that Neanderthal sites in northern Europe were only found during warm interglacials and interstadials (Finlayson, 2004). Furthermore, physiological models revealed that the Neanderthal body features which had been attributed to cold adaptation (Ruff *et al.*,

1993; Ruff, 1994; Holliday, 1997 a & b) would have had a minimal effect on survival in the extreme cold of glacial Europe (Aiello & Wheeler, 2004). Once it was understood that the Neanderthal range contracted to southern regions (referred to as glacial refugia) during cold periods, the question of their population fragmentation and demise appeared to have been the result of climate change and the related loss of the wooded habitats which they inhabited. So the question of replacement by modern humans was put in doubt (Finlayson *et al.*, 2000).

The question of cold-adaptation has recently resurfaced (Churchill, 2014) with the argument that Neanderthals did, at times, endure very cold climates and that their morphological similarities with circumpolar modern humans represent a case of convergence and that, like modern peoples of the arctic, Neanderthals were cold-adapted. A recent article claims to have found the likelihood of molecular resemblance between suites of cold adaptation traits in Neanderthals and woolly mammoths (*Mammuthus primigenius*), (Kislev & Barkai, 2019). I will re-examine and review the evidence of the use of cold environments which birds can provide, given the importance of this question in defining the climate dimension of the Neanderthal niche, which ultimately has a bearing on their extinction.

### **1.4.3 Habitat**

In her thesis, Finlayson (2006) described the habitat conditions that typified the Neanderthals. This was based on a subset of all birds found in the Gibraltar caves – those associated with terrestrial vegetation – and amplified geographically with examples from other parts of the Neanderthal range. The model was later amplified in a comparison of 79 Palaeartic *Homo* occupation sites, including 34 associated with

Neanderthals (Finlayson *et al.*, 2011). These studies served as precursors to the habitat dimension of this thesis in which the number of Palaeartic sites occupied by humans and birds has been significantly amplified, particularly those associated with Neanderthals.

The main conclusions of Finlayson *et al.*'s (2011) paper were that there was an observable and close association between Pleistocene humans and wetlands, coastal habitats also being of importance. Almost all sites were associated with terrestrial vegetation indicating that human sites were consistently mosaics or ecotones where terrestrial vegetation habitats came into contact with wetlands. Single habitat sites were ignored by humans with a preference for sites with 3-5 distinct habitats represented.

This paper was not specifically about Neanderthals but it did show that Neanderthals, and other humans, consistently occupied habitats with intermediate vegetation structure between dense forest and open, treeless, plains. In this thesis I will examine these conclusions and look into the Neanderthal habitat in greater detail. I will also seek to establish if there were differences in habitat occupation with contemporary modern humans.

#### **1.4.4 Birds as Resources**

Having established the climatic and ecological context of the Neanderthals, we can predict which bird species they would have regularly come into contact with. These results will enable us to answer questions related to the exploitation of birds by Neanderthals, for economic or other (e.g. symbolic) purposes. This is the subject of Research Question 2 in which I examine the association between Neanderthals and

particular bird species across their range, including the features and characteristics of these species. Additionally, I examine differences between Neanderthals and modern humans in terms of bird species, their ecological characteristics and potential economic and symbolic value.

## **1.5 Neanderthal as bird hunters**

One aspect of particular importance in relation to the characteristics of birds associated with Neanderthals has to do with bird and Neanderthal behaviour. It is well established that the Neanderthals practised close-quarter hunting of animals, getting close and using heavy thrusting spears to dispatch large herbivores (Churchill, 2002). Large birds of prey and corvids may have been taken precisely by catching them as they fed on carrion, possibly by ambushing, rushing at the feeding frenzy, or hiding in pits (Finlayson and Finlayson, 2016). In this case the relationship between carrion-feeding birds taken by Neanderthals appears to be a strong one as it has crossed taxonomic boundaries: birds of prey belong to the order Accipitriformes and corvids to the order Passeriformes. So a common behaviour among distinct taxonomic bird lineages points to the behaviour as the key. In this thesis I will explore if such close-quarter hunting, possibly first developed by Neanderthals or their ancestors to catch large herbivores, was a common practice that enabled them to catch birds for food, feathers, talons or other, as yet undetermined, anatomical components. I will do so by comparing and contrasting the ecology and behaviour of the species which appear to have been exploited by the Neanderthals. If different species, particularly if they are taxonomically distinct, share similarities, then we may be able to detect patterns that inform us.

Behaviours that permitted hunting or collecting resources from predictable situations in space and time may have been selectively advantageous for humans, Neanderthals included, providing a direct link to optimal foraging theory (Krebs, 1978). Predictable resources could take different forms. For example, rabbits would have been available year round, intertidal molluscs during low tide, seals during breeding season, and fruit seasonally. Carcasses, on the other hand, would have been available year round in areas with large predators and large herds of herbivores (such as would have occurred in many areas of Pleistocene Europe). Although their occurrence would have been patchily distributed in space and time, the following of cues (such as vultures – obligate scavengers – descending rapidly) would have given an element of predictability in the finding of carcasses. Clumped resources are more easily defensible than widely dispersed ones, leading to short- or long-term territoriality. Being able to predict the location of such resources may have been a feature of Neanderthal life which opened up ways of concentrating effort and energy. It would also have exposed them to other species, hyaenas to vultures, with similar habits. In this thesis I will look at the bird groups which appear commonly associated with Neanderthal sites to see if they also show features that would allow the Neanderthals to concentrate their efforts in harvesting them, throughout the year, or in specific seasons. Among the groups that I will examine are:

- a) Lekking Birds. Species of game birds gather in patches of ground where males perform courtship displays. These leks are often, but not always, clearings in forests. The behaviour crosses taxonomic boundaries: occurring in game birds (Phasianidae) but also in the bustards (Otididae) and some wading birds (Scolopacidae).

- b) Seabirds. Many species of pelagic and coastal birds gather in colonies, often at high density numbering many thousands of birds, to breed. The species cross taxonomic boundaries and include auks (Alcidae), gulls (Laridae), shearwaters (Procellariidae) and cormorants (Phalacrocoracidae).
- c) Cave- and cliff-dwellers. Some species nest or roost in high density in caves or cliffs at specific times of the year and therefore constitute a predictable resource. The species come from diverse taxonomic groups and include doves (Columbidae), falcons (Falconidae), owls (Strigidae) and choughs (Corvidae).
- d) Aquatic birds. These are species which live around lakes, lagoons, pools and other wetlands where they often gather in large flocks. In semi-arid environments, they will gather in very large numbers during the dry season in receding pools of water and are then vulnerable. Such times would also be ideal moments for ambushing mammalian herbivores. In addition, ducks go into eclipse plumage after breeding and, for a short while, are unable to fly. The potential species cross taxonomic boundaries and include ducks (Anatidae), herons (Ardeidae) and ibises (Threskiornithidae).

In addition to these groups and the scavengers already mentioned, I will examine a further group of birds which *a priori* seem to appear frequently in Neanderthal sites. These are cryptically-coloured ground dwelling birds. Most are brown and streaked and will freeze on the ground when detected. Again, they cross taxonomic boundaries and include stone curlews (Burhinidae), larks (Alaudidae), snipe (Scolopacidae), nightjars (Caprimulgidae) and quail (Phasianidae). I will contrast these potentially vulnerable groups with the remaining groups which may not be so well represented in Neanderthal sites.

In a recent paper I suggested that the autumn and winter months may have been an important time for the Neanderthals to catch scavenging birds (Finlayson and Finlayson, 2016). I reached this conclusion on the basis of the times of year when some species, known to have been targeted by Neanderthals, come to carrion. Thus, golden (*Aquila chrysaetos*) and white-tailed eagles (*Haliaeetus albicilla*) will mainly scavenge in autumn and winter and could only have been caught by these means in these seasons. In addition, scavenging birds that might have been expected in Neanderthal sites but were poorly represented (e.g. Egyptian vulture, *Neophron percnopterus*), were those that migrated to winter in Africa (where there were no Neanderthals). It is of course possible, that year-round scavengers (e.g. griffon vulture, *Gyps fulvus*, or cinerous vulture *Aegypius monachus*) could have been taken at any time of year. I will use data gathered in the field, both for this thesis or part of earlier fieldwork, to establish when different groups of birds, such as seabirds, might have been available to the Neanderthals. Putting the various sources of information together I will seek to establish if bird catching was a seasonal practice and, if so, when this took place.

## **1.6 Direct Evidence of Neanderthal Exploitation of Birds and its significance**

The third data chapter of this thesis will examine the rapidly increasing direct evidence of Neanderthal intervention on bird bones. In the case of raptors, the evidence is usually in the form of cut marks made with stone tools in order to extract feathers (e.g. Romandini *et al.*, 2014), or talons and claws (e.g. Morin & Laroulandie, 2012). Other evidence may include incisions and scrapes and these have been found on all the main wing bones of raptors that are linked with the insertion of flight feathers: ulna, radius, coracoid, carpo-metacarpus (Finlayson *et al.*, 2012). These results have to be



interpreted with caution, in particular data from foot bones. This is because talons are hard and likely to preserve better than other anatomical parts. Also, following discoveries of use of raptor talons by Neanderthals, there may have been a biased examination of these parts by researchers looking at collections. Nevertheless, it is clear that Neanderthals are intervening on wing bones, which are likely for feather extraction given the almost complete absence of meat in these bones in raptors (Finlayson *et al.*, 2012), and leg and foot bones, which imply selection for talons and claws. In the case of birds being taken for consumption, the evidence from cut marks (particularly in bones supporting large muscle mass such as sternum and tibiotarsus) may be supplemented by other clear signals, such as burning that indicates roasting (Blasco *et al.*, 2014).

The results presented in the previous sections will be used to supplement this taphonomic data in order to answer Research Question 3 in which I look for links with particular bird species and seek to identify how many of these have taphonomic evidence linking them to Neanderthals.

## **1.7 Supporting sources of information**

The key material evidence that will allow us to interpret Neanderthal behaviour comes from taxonomy, the systematic identification and classification of the bones found in caves, and taphonomy, the study of the agents and processes leading to the accumulation of these bones. I will argue that this vital evidence is incomplete without an understanding of the behaviour of the species that formed the bone accumulations. Can we find alternative lines of enquiry, beyond those developed by palaeontologists and zooarchaeologists, which will allow us to add to this understanding of Neanderthal

behavioural ecology? This thesis will argue that an understanding of the ecology and behaviour of birds that were the contemporaries of the Neanderthals can make an important contribution that will supplement other lines of evidence. In doing so, careful attention will need to be exercised. For example, we will need to be satisfied that the birds themselves have not changed in habits; we will also need to exercise caution when considering bird responses to seasonality given the wide climatic oscillations of the last glacial cycle (LGC, 125-10 kyr), which includes the period when Neanderthals are known to have exploited birds.

Our strongest argument in favour of using the present to understand the past will come from common lines of evidence derived from unrelated bird taxa when these all point in the same direction. Our interpretations will gain further robustness if we observe the patterns that we detect in the Gibraltar caves also occur elsewhere within the Neanderthal geographical area. Furthermore, if we detect evidence from a single site over a long time frame, this could indicate that the observations are not indicative of casual, but rather of regular and systematic, behaviour.

In Chapter 6 (Discussion), I will review those aspects of the ethnographic literature on the use of birds by modern human cultures (Cocker, 2013) as relevant to the discussion of Neanderthal bird exploitation. The aim will be to understand the range of possible human bird-exploitation behaviours and the techniques employed. This will enable me to situate the Neanderthals within a framework to understand possible parallels with modern humans. I will focus particularly on the available literature on the exploitation of birds of prey for feathers by North American First Nations people (Wilson, 1928; Mails, 1972) given recent findings of raptor exploitation by Neanderthals.

## **1.8 Research Questions and Thesis Structure**

In this section I formalise my Research Questions based on the objectives stated above.

I then present the structure of this thesis by chapters and link these to the Research Questions.

### **1.8.1 Research Questions**

Research Question 1: Using birds as indicators of climate and habitat, do Neanderthals associate with particular climates and habitats across their entire geographic range or in particular parts of it? A corollary will be to Neanderthals and modern humans.

Research Question 2: Are Neanderthals associated with particular bird species across their range, and if so, what are the features and characteristics of these species? As with Research Question 1, I will compare Neanderthals and modern humans.

Research Question 3: If there are links with particular bird species, how many of these have taphonomic evidence linking them to Neanderthals? I then use this information to predict what other species could be found in the future with similar taphonomic evidence, and identify sites which, because of the type of bird species found, should be targeted for future taphonomic work.

### **1.8.2 Thesis Structure**

In Chapter 1, I review the relevant literature and develop the conceptual framework, outline the research objectives of the thesis and the approach that will be used to answer them. The structure of the thesis is delineated.

In Chapter 2, I describe the Gibraltar study sites and provide a summary of the other Eurasian sites to be included in the analysis. A detailed description of the database, the contents and construction is included. The statistical techniques to be applied will be described in each subsequent chapter as they are introduced.

In Chapter 3, the Neanderthal and modern human climate and habitat occupation is compared using birds as indicators of climate and habitat. I address Research Question 1 using a dataset to define the characteristics of Eurasian bird species in relation to climate and habitat characteristics. This dataset includes for each species, rankings and indices relating to climate, habitat as well as migratory behaviour and diet. Multivariate analyses are used in combination with univariate and bivariate statistics to define the climate and habitat boundaries of sites occupied by Neanderthals and modern humans and therefore their respective tolerances.

Chapter 4 describes Neanderthal and modern human associations with birds, addressing Research Question 2. Using the same dataset, but examining individual bird species rather than using them as climate and habitat proxies, I seek to establish which bird species Neanderthals and modern humans came into regular contact across their range. Univariate statistics are used to establish frequency distributions for each bird species in relation to the two hominins. Using indices of bird behaviour (e.g. lekking, cursorial versus arboreal, scavengers), plumage (e.g. cryptic) and ecological characteristics (e.g. colonial seabirds, aquatic birds, seasonal distribution patterns), I establish the characteristics of the main species associated with Neanderthals and modern humans. From this I seek patterns that will inform of how the bird species may have been obtained by the hominins.

Chapter 5 is dedicated to direct evidence of the use of birds by Neanderthals and modern humans. It addresses Research Question 3. I list the species known taphonomically to have been exploited by Neanderthals and modern humans with their corresponding characteristics (from Chapters 3 and 4). I then examine the remaining bird species from the dataset to establish which species share features with species already known to have been exploited. This will allow for predictions to be made as to which species may be identified in the future as having been exploited by Neanderthals and modern humans.

Chapter 6 is the General Discussion. In it I summarise from the data chapters (chapters 3 to 5) and discuss the implications of these findings for understanding the ecological and behavioural similarities and differences between Neanderthals and modern humans. This discussion then interprets the results in the context of the broader theory of Neanderthal extinction and modern human colonisation of Eurasia and in the context of our understanding of Neanderthal and modern human cognitive abilities. The limitations of the study are discussed and suggestions for future work are made.



## **2.1 Introduction to the main dataset**

This chapter covers the broad aspects of the methodology applied in this thesis. Further detail, as relevant, is provided in the subsequent data chapters (Chapters 3 to 5). This chapter is divided into four parts which cover the main elements that comprise the data used in this thesis. The first covers the study sites which are distributed across the Palaearctic Region; the sites located on the Rock of Gibraltar, which are those with the richest record of Neanderthals and their association with birds, are given special mention. The second unit describes the various human cultures known to have occupied the Palaearctic Region during the last glacial cycle (LGC, 125 – 10 kya). This is the time period for which most archaeological sites with bird remains have been reported and which form the basis of my dataset (see below). Most of the cultures relate to the presence of modern humans and the Mousterian culture is the main one associated with the Neanderthals. I then examine the range of bird species present in the Palaearctic Region during the LGC. These comprise the total range of bird species that would have been available and potentially co-shared habitats with Neanderthals and modern humans. Lastly, I describe those sites where taphonomic studies have provided direct evidence of bird exploitation by Neanderthals and modern humans.

Even though the number of publications demonstrating a direct intervention by Neanderthals on birds are relatively few, and span only the last decade, there is a large body of published material listing bird species present in Neanderthal and modern human Pleistocene sites across the Palaearctic, mostly western Palaearctic and Europe in particular where the tradition for excavation of Palaeolithic sites is strongest

(Gamble, 1986). The most comprehensive compilation of sites, and that which forms the spine of the main database that I have created (Appendix 1) is by Tyrberg (1998; 2008). Part of the work of this thesis has involved digitizing the information provided by Tyrberg and standardising it in terms of terminology and categories. I have supplemented the sites listed by Tyrberg with additional sites from the literature post 2008, and from my own study of the birds from five Gibraltar cave sites. Tyrberg's list was scrutinised in detail as part of the process of creating the database. Any sites outside the time range of the LGC (e.g. attributed to the Acheulian culture, made by Neanderthals or their predecessors – *Homo hiedelbergensis*), or of dubious attribution (for example, giving Neanderthal and modern human ascriptions for the same archaeological level) were removed as part of this data cleaning process. Additionally, palaeontological sites (i.e. with no cultural attribution) were also removed. Sites on islands known not to have been occupied by Neanderthals or their contemporaries (e.g. Iceland, Ireland) or which were within the Palaeartic Region, but outside the range of the Neanderthals (e.g. Morocco, Japan) were not included either. The same applied, though less frequently, to bird species. A case in point is the listing of red jungle fowl (*Gallus gallus*) or common pheasant (*Phasianus colchicus*) in some Pleistocene sites; these are introduced species into Europe in historical times and are therefore cases of mistaken identity or mixing of the Pleistocene levels with more recent archaeological contexts, as can happen as a result of bioturbation. For the reasons given above, in all, exactly 1,000 sites in the Tyrberg catalogue and supplement were not included in the study.

In spite of my attempt to remove sites for the reasons explained above, with a database compiled of so many different sites and excavated by different archaeologists over a wide time period, it is acknowledged that there may be the occasional incorrect



attribution. I feel that my data cleaning process has kept these to a minimum, and my own knowledge of the distribution of bird species and the ecology of bird communities has served to pick up obvious cases that have needed checking. In such cases, and where possible, I have referred to the original sources. On the other hand, the majority of sites have been worked by highly experienced and reputable bird taxonomists and are clearly correctly identified. The analysis of the database largely depends on the examination of the entire bird assemblage given for a particular archaeological context and this serves to minimise the impact of any remaining errors resulting from the misidentification of a particular species even further.

Some sites report bird species for more than one archaeological level. These may have been several contexts of Neanderthal occupation or a sequence including Neanderthals and modern humans. In such cases, and in order to prevent biasing in favour of such multi-context sites, I have taken the average presence of a bird species. For example, if a site contained five Neanderthal archaeological levels and only two of them contained a bird species, e.g. golden eagle (*Aquila chrysaetos*), then the presence/absence scores for the five levels would be 0, 0, 0, 1, 1; in this case the score for golden eagle at this site would be  $2/5=0.4$ . A site with only one archaeological level would score either 0 or 1 depending on whether golden eagle was present or absent.

Where I have found it useful to compare multi-level sites, I have done so and here I have treated each level as a unit of analysis. I have carried out these analyses with reference to the major multilevel sites (including those of Gibraltar) in Chapter 3. It should however be borne in mind that almost half (46%) of sites are single-level sites.

I have avoided including chronological attributions to archaeological levels as dating techniques have changed significantly during the time period when excavations were made as have been the calibration curves available for converting radiocarbon dates into calendrical dates (Wood, 2015). Not all sites had specific dates recorded either. The important aspect, which I have kept through throughout the generation of the database, is that all sites relate to the LGC, the period from 125 kya to 10 kya. This is the period which saw the transition from interglacial conditions to one of climatic turmoil that eventually led to the Last Glacial Maximum (LGM). It is the period of Neanderthal occupation of Eurasia, of their extinction, and of the arrival of modern humans from Africa (van Andel & Davies, 2004). This period allows us to test the limits of Neanderthal and modern human climatic tolerance, habitat occupation at a time of great environmental change. It also allows us to compare Neanderthal and modern human behaviour strategies as closely as possible within the same geographical area and timeframe.

The resulting dataset (Appendix I) is a digitization and extension of Tyrberg (1998; 2008) containing records of bird species found by site and context. It has 1169 columns and 432 rows and includes records from 431 bird species from covering 1143 contexts from 520 sites (Table 2.1). It also includes climatological, ecological, behavioural and other (edible, mass) attributes (Tables 2.2, 2.3, 2.4/5 and Table 2.6; Section 4.5.7) for each species. This data set is used in Chapters 3, 4 and 5.

## **2.2 The Study Sites**

The study region was the Palaearctic (Procheş & Ramdhani, 2012, and Figure 1.1) and the time frame used was the LGC (125-10 kya; Gibbard *et al.*, 2010). The reason for

the choice of region and time frame was that Neanderthals were confined to the Palaeartic and it is in this region that modern humans and Neanderthals met during the Late Pleistocene (Finlayson, 2004). The location of the study sites is shown in Figure 1.8 and Figure 1.9. The sites are shown against a backdrop of maximum advance of ice sheets and lowered sea levels. The sites spread across the Palaeartic from Portugal and the United Kingdom in the west to the Altai Mountains of Russia in the east. There is a clear predominance of sites within Europe, reflecting intensity of excavation effort.

### **2.2.1 The Gibraltar Study Sites**

Apart from being caves in which I have been directly involved in their excavation, the Gibraltar caves (Figure 1.2 and Figure 1.3) are the richest in bird species in the entire dataset (Appendix 1). Some data from these Gibraltar sites were included in Tyrberg (2008) but additional Gibraltar caves and a significant number of bird species have been added in this study.

Five sites contain evidence of Neanderthal activity and birds: Gorham's, Vanguard, Hyaena, Ibex Caves and Devil's Tower Rock Shelter (Gibraltar Museum, 2016). Gorham's Cave is the best known, having been excavated partly during the 1950s (Waechter, 1951; 1964) and the subject of ongoing excavations which commenced in 1989 (Gibraltar Museum, 2016). The importance of the bird remains from this cave were recognised by Eastham (1968) at an early date. Subsequently, drawing on new material Cooper (1999) added information on the avifauna of the Pleistocene levels of Gorham's Cave and, for the first time, data from Vanguard, Hyaena and Ibex Caves and from Devil's Tower Rock Shelter. Although a number of papers relating to the

exploitation of birds by Neanderthals at Gibraltar have recently been published (Finlayson *et al.*, 2012; Blasco *et al.*, 2014; Finlayson & Finlayson, 2016) and birds were also used in the quantitative reconstruction of the Pleistocene habitats outside these caves (Finlayson, 2006), this is the first time that a complete compilation of all the Late Pleistocene bird species found in Gibraltar has been undertaken.

Gorham's Cave is the longest studied cave and the best understood with an 18-metre deep stratigraphic sequence which includes the last-known Neanderthal occupation levels, dated to ~32 kya (Finlayson *et al.*, 2006). Work in Vanguard Cave and Hyaena Cave commenced in 1995 (Barton *et al.*, 2012). Vanguard Cave's stratigraphic sequence, 17-metres deep, is comparable to Gorham's Cave but recent dating has confirmed earlier work indicating that this cave has older deposits going back to the last interglacial (MIS 5e) at around 127 kya (Rhodes, 2012; Doerschner, 2018). Between them, Gorham's and Vanguard Caves cover the complete last glacial cycle (127-10 kya). Hyaena Cave is a small cave adjacent to Vanguard Cave and current dates put its levels within MIS 4 (65-61 kya). Ibex Cave was the subject of an excavation in 1994 and is dated by ESR to between 37 and 49 kya (Rhodes *et al.*, 2000). Devil's Tower Rock Shelter was completely excavated in 1926 (Garrod *et al.*, 1928) and has not been dated.

Neanderthal remains have been recovered in Gibraltar from Forbes' Quarry (1848), Devil's Tower Rock Shelter (1926) (Stringer, 2000) and from Vanguard Cave in 2017 (unpublished). The Forbes' Quarry find predated the Neander Valley discovery in Germany by eight years. The evidence of Neanderthals in Gorham's, Hyaena and Ibex Caves comes from stone tools, hearths and butchered animals. The evidence of Modern Humans in the Late Pleistocene of Gibraltar comes exclusively from Gorham's Cave and is associated with the Solutrean and Magdalenian cultures which

occupied the site during the Last Glacial Maximum (LGM) and the global warming thereafter (23-13 kya; Finlayson *et al.*, 2006).

In all, 85 archaeological contexts have been identified in the Gibraltar caves, 75 associated with Neanderthal occupation and ten with Modern Humans. Context refers to the place where an artefact or bone is found. It includes the layer that the item came from and all its contextual information. Contexts are discrete units and are treated as separate temporal events. Even though it is not possible to date all of these contexts, the overall dating framework places them within the Late Pleistocene (the period covering the last glacial cycle). For the purposes of this thesis, finding bird bones in contexts of Neanderthal or Modern Human occupation is sufficient to attempt to correlate the presence of these hominins with climatic and environmental features of each context. Direct taphonomic evidence of human intervention on bird bones adds a new dimension: one which directly implicates the hominins.

Of the 75 Neanderthal contexts with birds in the Gibraltar caves, 35 are from Gorham's, 17 from Vanguard, 11 from Ibex, six from Devil's Tower and another six from Hyæna Cave. The ten Modern Human contexts are from Gorham's Cave.

### **2.2.2 The Palaeartic Study Sites and Human Cultures**

The Palaeartic study sites, including the Gibraltar sites, are outlined in Table 2.1. They comprise a total of 520 sites and cover 1143 contexts (Appendix 1). Of these, 281 sites (54%) had more than one archaeological context while the remainder (239; 46%) only had a single context recorded. This is to be expected as some sites have long stratigraphic sequences (e.g. Gorham's Cave) while others do not. Short sequences would be found, for example, in small rock shelters which were not living

spaces but instead places where short-term visits took place, for example for hunting particular prey. Such differences in occupation have recently been used to compare site quality (Finlayson *et al.*, 2016).

*Table 2.1 Summary of the main dataset of Palaeolithic sites by cultural attribution (as used in Chapters 3 to 5). Chronology follows Finlayson & Carrión (2007) and Lengyel & Wilczynski (2017). Cultures corresponding with the height of the Last Glacial Maximum (LGM, 26.5 – 19 kya; Clark et al, 2009) are shaded in grey. Note: <sup>1</sup> The last Neanderthal dates are given at 32 kya by Finlayson et al (2006), but other authors place the date around 40 kya (Higham et al., 2014).*

<b>Cultural attribution</b>	<b>Hominin</b>	<b>Chronology (kya)</b>	<b>Number of contexts</b>	<b>Number of sites</b>	<b>Number of species</b>
<b>Mousterian (MOU)</b>	Neanderthal	125-32 <sup>1</sup>	421	154	288
<b>Aurignacian (AUR)</b>	Modern	43-36	142	55	169
<b>Gravettian (GRA)</b>	Modern	34-24	75	33	149
<b>Epigravettian (EPI)</b>	Modern	24-13	41	13	155
<b>Solutrean (SOL)</b>	Modern	22-17	40	22	116
<b>Magdalenian (MAG)</b>	Modern	20-13	330	176	132
<b>Azilian (AZI)</b>	Modern	12-8	48	38	142
<b>Mesolithic (MES)</b>	Modern	10-6	46	29	169
<b>Total</b>			1143	520	430

The sites with birds and hominins have been subdivided by cultural attribution. The majority of known sites are identified from stone tool technology as only a few have

fossils. This classification follows Finlayson & Carrión (2007) who highlighted the extent of uncertainties regarding the link between culture and biological attribution.

#### 2.2.2.(a) Mousterian

This is a widespread flake-based technology with a variety of retouched implement types. Bifacial tools (e.g. hand axes) are rare or absent. In Europe, and probably much of Asia, it is exclusively associated with the Neanderthals (Mellars, 1996; Klein, 1999). In the Middle East and North Africa, it is also associated with early Modern Humans. This association between Mousterian and Modern Humans in the Middle East and North Africa occurs early in the Late Pleistocene (MIS 5), a time when all hominins in Eurasia, the Middle East and North Africa appear to have made the Mousterian. After this time, particularly in the Palearctic Region and the time frame of this thesis, the Mousterian appears solely associated with Neanderthals. The Mousterian is therefore a good proxy for Neanderthal occupation.

#### 2.2.2.(b) Transitional Industries

A number of Middle-Upper Palaeolithic transitional industries have been identified by archaeologists (Mellars, 1989; Camps and Chauhan, 2009). There is uncertainty as to the makers of these industries which are spread across Europe and the Middle East. Given this uncertainty and the relative paucity of sites with such industries and bird remains, they have been omitted from this study. These have, nevertheless, been included in Table 2.1 in order to provide as complete a record of the cultural sequence as possible.

#### 2.2.2.(c) Aurignacian

The first European Upper Palaeolithic technology; characterized by blade-based tools that show a high degree of standardization, antler, ivory and bone projectile points, body ornamentation and cave art. The Aurignacian is attributed to the first Modern Humans in Europe and the Middle East (White, 1989; Klein, 1999) but the attribution is less firmly based than for the Mousterian (Conard *et al.*, 2004). The Aurignacian is attributed to Modern Humans in this thesis, but with a degree of caution.

#### 2.2.2.(d) Gravettian

The first technology of the steppes; characterized by small pointed bladelets with blunt but straight backs. This culture is associated with Venus figurines, construction of large skin tents on mammoth bone frames in Eastern Europe, the first large and semi-permanent camps, and the first atlatls (spear throwers) and eyed needles. There is good evidence linking this culture with the westward advance of Modern Humans across Eurasia and into Western Europe (Roebroeks *et al.*, 1999; Otte, 2013)).

#### 2.2.2.(e) Epigravettian

This Modern Human technology is characteristic of Eastern Europe and evolved from the Gravettian (Klein, 1999). It is characterized by the reduction (microlithization) of stone tools. The use of bone is rare. Given the localised nature and the relative paucity of sites with such industries and bird remains, they have been omitted from this study.

#### 2.2.2.(f) Solutrean

This is an advanced Upper Palaeolithic technology of south-western Europe with associated cave art and body ornamentation and is firmly associated with Modern Humans (Straus, 1990a). A characteristic is the production of fine bifacial leaf points made by a high pressure flaking technique, light projectiles, tanged and barbed



arrowheads. The bow-and-arrow probably originates with this culture. Given the localised nature and the relative paucity of sites with such industries and bird remains, they have been left out of this study.

#### 2.2.2.(g) Magdalenian

The Magdalenian culture, characteristic of post-glacial Western Europe, emerges from the Solutrean and represents the cultural explosion associated with the end of the LGM and the expansion of humans into north-western Europe from Iberia. (Weniger, 1990; Klein, 1999). It is firmly linked with Modern Humans.

#### 2.2.2.(h) Azilian

The Azilian is a regional development of the Magdalenian in northern Spain and southern France and is associated with the global warming leading to the start of the Holocene (Straus, 1985). It is firmly linked with Modern Humans. Given the localised nature and the relative paucity of sites with such industries and bird remains, they have been omitted from this study.

#### 2.2.2.(i) Mesolithic

Also referred to as the Epipalaeolithic, this culture is firmly associated with Modern Humans and marks the last hunter-gatherers prior to the onset of agriculture in the Neolithic (Bailey and Spikins, 2008). Given the relative paucity of sites with such industries and bird remains, they have been omitted from this study.

### **2.3 The Birds**

In this section, I describe the species of birds used in this study and the climatological and ecological attributes ascribed to each as will be used in Chapter 3. In addition, I

describe the categorisation of bird species into taxonomic categories as will be used in Chapters 4 and 5.

### **2.3.1 Bird species**

The number of breeding species in the Palearctic today is 863 (Finlayson, 2011). The number would have been similar in the Late Pleistocene except for the presence of the great auk *Pinguinus impennis* which became extinct in the 19<sup>th</sup> Century (Birkhead, 1993). A total of 430 bird species, for which Late Pleistocene remains have been found and present day information was available, were included in the database (Appendix 1). In addition, the presence of the great auk was included where data were available. Nevertheless, the great auk has been left out of the main analyses as we have no present day climatic or ecological information on this species. Its presence in sites will, however, be included in the final discussion. This dataset represents 50% of the Palearctic avifauna. The underrepresented species are largely those from the easternmost Palearctic where there are few archaeological or palaeontological sites with birds.

Following the criteria in Finlayson (2011), each bird species was allocated climatological and behavioural characteristics (Tables 2.2 - 2.5;). For climate, the reference point of 36°N was selected as it indicates the most southerly latitude of Europe and coincides with that of Gibraltar. As most bird displacements during the Pleistocene were from latitudes to the north of 36°N southwards, this reference point covers the range of displacements that took place. On the other hand, there was very little, or no, northward displacement from latitudes south of 36°N. Each species was allocated a climate rank in accordance with Table 2.2. Species from ranks with similar

climatic characteristics were lumped into climate categories (Table 2.3). The frequency of species in each climate category (Figure 2.1) shows a decreasing species trend from warm to cold/extreme cold. The decline towards hot probably reflects a real species impoverishment in the extreme south of the Palaearctic, much of which is dominated by vast (Saharan, Arabian) deserts. As expected the category with fewest species is montane, as mountain climates are relatively localised and proportionately small in area.

### **2.3.2 Taxonomic categories**

Some bird species may be geographical replacements of each other, but from the perspective of a predator (including human) the taxonomic position of, for example, the three *Alectoris* partridges, would not appear to be important. For this reason, in Chapters 4 and 5 groups of birds are clumped into loose taxonomic categories viewed from the perspective of a human predator. These categories are described in further detail in Chapters 4 and 5.

*Table 2.2 Climate ranks used to classify bird species found in Neanderthal and Modern Human sites. In addition to the ranks listed some had populations falling under two categories as follows: F/E2 n=1; F/E3 n=22; G1/D1 n=2; G1/E1 n=4; G2/E2 n=1; H/E3 n=8; J/E3 n=1. Note: a vagrant bird occurs outside its normal geographical range; a scarce visitor occurs in very low numbers on a regular basis within its normal geographical range (Alerstam, 1982).*

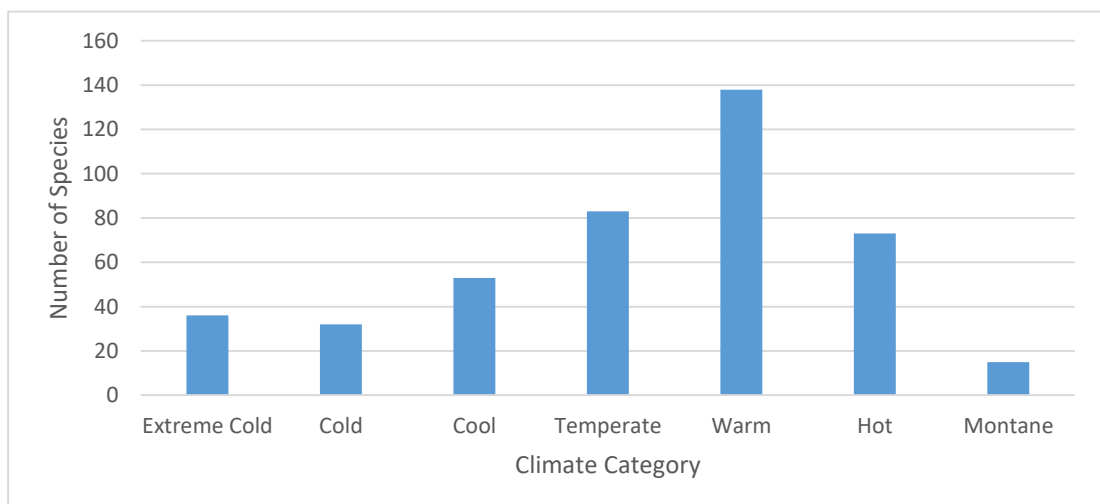
<b>Climate Rank (C)</b>	<b>Definition</b>	<b>Climate Category (K)</b>	<b>Number of Species</b>
<b>A1</b>	Resident species with breeding range centred in Arctic belt (70°N) which do not reach 36°N today	EXTREME COLD	2
<b>A2</b>	Migratory species with breeding range centred in Arctic belt (70°N) which do not reach 36°N today	EXTREME COLD	12
<b>A3</b>	Resident species with breeding range centred in Boreal belt (60°N) which do not reach 36°N today	EXTREME COLD	17
<b>B1</b>	Migratory species with breeding range centred in Boreal belt (60°N) which do not reach 36°N today	EXTREME COLD	5
<b>B2</b>	Resident species with breeding range centred in Temperate belt (50°N) which do not reach 36°N today	COLD	9
<b>B3</b>	Migratory species with breeding range centred in Temperate belt (50°N) which do not reach 36°N today	COLD	1
<b>C1</b>	Migratory species with breeding range centred in Arctic belt (70°N) which are winter vagrants to 36°N today	COLD	9

<b>Climate Rank (C)</b>	<b>Definition</b>	<b>Climate Category (K)</b>	<b>Number of Species</b>
<b>C2</b>	Migratory species with breeding range centred in Boreal belt (60°N) which are winter vagrants to 36°N today	COLD	11
<b>C3</b>	Migratory species with breeding range centred in Temperate belt (50°N) which are winter vagrants to 36°N today	COLD	1
<b>D1</b>	Migratory species with breeding range centred in Arctic belt (70°N) which are scarce winter visitors to 36°N today	COLD	1
<b>D2</b>	Migratory species with breeding range centred in Boreal belt (60°N) which are scarce winter visitors to 36°N today	COOL	13
<b>D3</b>	Migratory species with breeding range centred in Temperate belt (50°N) which are scarce winter visitors to 36°N today	COOL	4
<b>E1</b>	Migratory species with breeding range centred in Arctic belt (70°N) which are regular winter visitors to 36°N today	COOL	2
<b>E2</b>	Migratory species with breeding range centred in Boreal belt (60°N) which are regular winter visitors to 36°N today	COOL	22
<b>E3</b>	Migratory species with breeding range centred in Temperate belt (50°N) which are regular winter visitors to 36°N today	COOL	12
<b>F</b>	Resident species with breeding range centred in the Temperate belt (50°N) or with broad ranges spanning several latitude belts which have resident populations in 36°N today	TEMPERATE	44
<b>G1</b>	Migratory species with breeding range centred in Arctic belt (70°N) which migrate to the	WARM	15

<b>Climate Rank (C)</b>	<b>Definition</b>	<b>Climate Category (K)</b>	<b>Number of Species</b>
	tropics and are regular passage migrants to 36°N today		
<b>G2</b>	Migratory species with breeding range centred in Boreal belt (60°N) which migrate to the tropics and are regular passage migrants to the 36°N today	WARM	15
<b>H</b>	Migratory species with breeding range centred in the Temperate belt (50°N) or with broad ranges spanning several latitude belts which migrate to the tropics and are regular passage migrants to 36°N today	WARM	59
<b>I</b>	Resident species with breeding range centred in the Mid-latitude belt (40°N) but confined to high altitude mountains and are regular in 36°N today	MONTANE	12
<b>J</b>	Migratory species with breeding range centred in the Mid-latitude belt (40°N) but confined to high altitude mountains which migrate to the tropics and are regular in 36°N today	MONTANE	3
<b>K</b>	Resident species of the Mid-latitude belt (40°N) which are regular in 36°N today	WARM	49
<b>L</b>	Migratory species of the Mid-latitude belt (40°N) which migrate to the tropics and are regular in 36°N today	HOT	46
<b>M</b>	Resident and migratory species of the Sub-tropical belt (30°N) which do not reach the 36°N today from the south	HOT	27

*Table 2.3 Climate Ranks (from Table 2.2) lumped into Climate Categories and used in Chapter 3.*

<b>Climate Category</b>	<b>Climate Ranks-</b>	<b>Number of Species</b>
<b>Extreme Cold</b>	A1, A2, A3, B1	36
<b>Cold</b>	B2, B3,C1, C2, C3, D1	32
<b>Cool</b>	D2, D3, E1, E2, E3,	53
<b>Temperate</b>	F, F/E2, F/E3, G1/D1, G1/E1, G2/E2, H/E3, J/E3	83
<b>Warm</b>	G1, G2, H, K	138
<b>Montane</b>	I, J	15
<b>Hot</b>	L, M	73



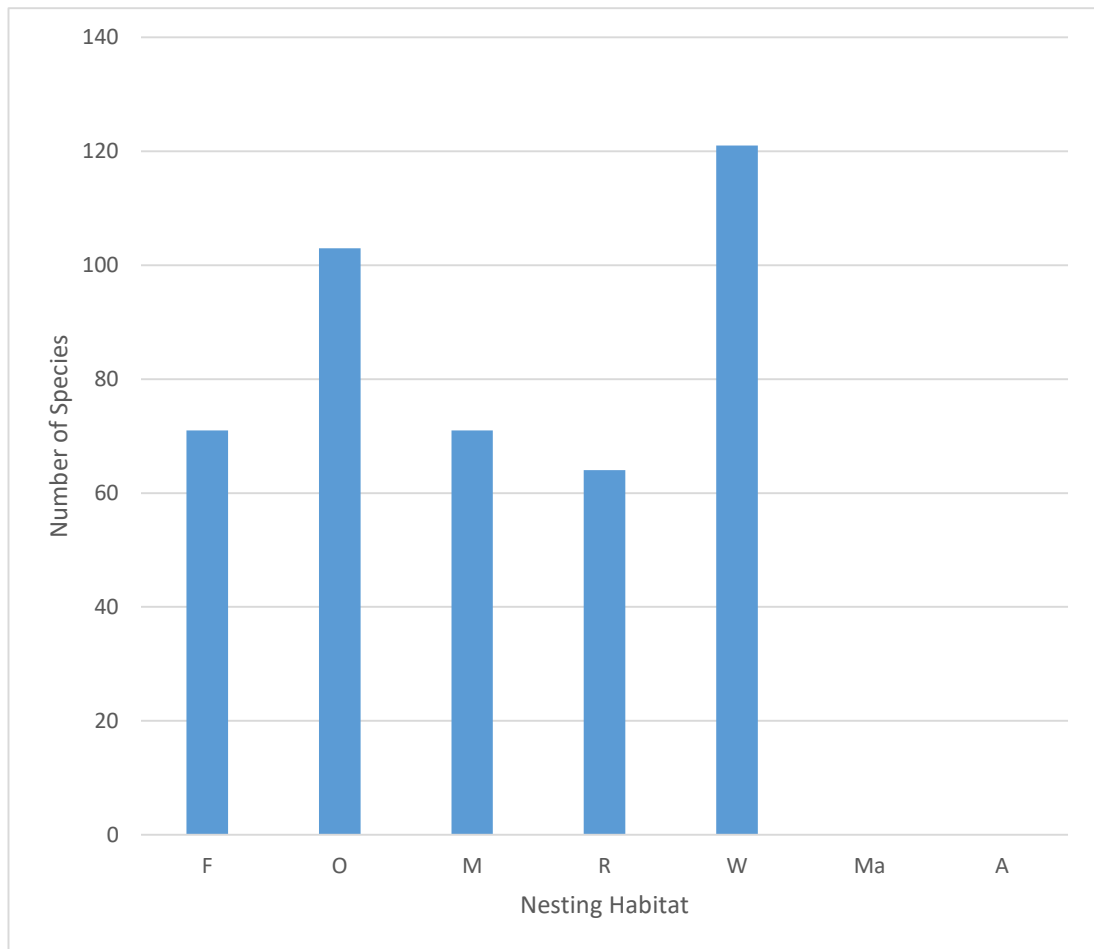
*Figure 2.1 Frequency distribution of 430 Palaearctic Bird Species used in this thesis by Climate Category (data from Table 2.3).*

In the definition of bird habitats, bird nesting and foraging habitats were distinguished as they may yield different signals. For example, few birds forage in rocky habitats but many use these for nesting. Thus the presence of a species in an archaeological context could give a different signal if it was nesting or simply foraging. In the case of the open sea (Ma) and the air (A), these are clearly habitats only used for foraging. Examples include swifts (*Apus* spp.) breed in rocky habitat and forage in the air; gannets (*Morus bassanus*) breed in rocky habitats and forage in the sea. The habitat categories and the number of bird species in each category in Table 2.4 and the distribution of species illustrated in Figure 2.2 and Figure 2.3. These show a marked tendency for birds to occupy open and wetland habitats more than mixed and forest habitats. The rocky habitat is insignificant as a foraging habitat but is very important as a nesting habitat. The majority of aerial and marine foragers are species which nest in rocky habitats.

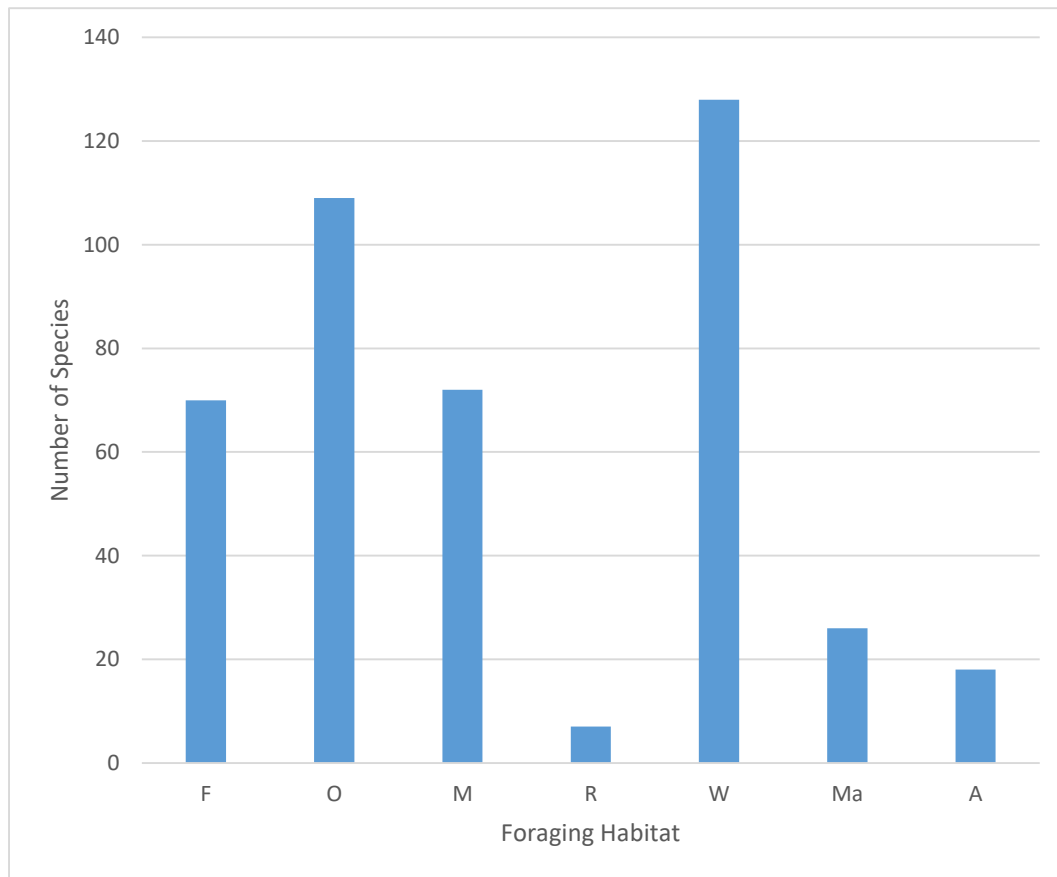
*Table 2.4 Habitat categories (after Finlayson, 2011) and number of bird species in habitat categories (from Appendix 1) used in Chapter 3.*

<b>Habitat</b>	<b>Code</b>	<b>Nesting</b>	<b>Foraging</b>
<b>Forest, habitats with a high density of trees</b>	F	71	70
<b>Open, habitats without trees</b>	O	103	109
<b>Mixed, habitats between F and O, including savannah, shrubland and mosaics</b>	M	71	72
<b>Rocky</b>	R	64	7
<b>Wetland, including all kinds of water habitats, including coastal ones, except marine</b>	W	121	128
<b>Marine</b>	Ma	0	26
<b>Aerial</b>	A	0	18





*Figure 2.2 Distribution of 430 Palearctic Bird Species used in this thesis by nesting habitat. F - Forest; O - Open; M - Mixed; R - Rocky; W - Wetland; Ma - Marine; A - Aerial. (Data from Table 2.4).*



*Figure 2.3 Distribution of 430 Palaearctic Bird Species used in this thesis by foraging habitat. Habitat categories as Figure 2.2 (data from Table 2.4)*

For each bird species a number of additional variables were recorded as being present or absent in each case (Table 2.5). These were behavioural or ecological variables thought to have potential meaning in the context of bird exploitation by humans. I could find nothing in the literature regarding the ecological properties of species exploited by Neanderthals or other Palaeolithic humans. I therefore devised these categories using a combination of personal experience in the field, interviews and discussions with gamekeepers and hunters, supplemented by summary texts on bird exploitation in historical times (Cocker, 2013; Shrubbs, 2013). My aim has been to seek patterns in these categories which would confirm their relevance from the perspective of the human hunter (Chapter 4), which would then be contrasted with taphonomic evidence of direct exploitation (Chapter 5).

*Table 2.5 Behavioural characteristics entered for each bird species (Chapters 4 and 5). The categories are not mutually exclusive.*

<b>Variable Name</b>	<b>Description</b>	<b>Potential</b>	<b>Number of Species</b>
<b>flocking</b>	Gather in large flocks at specific times of year or throughout the year	May provide opportunities for ambush hunting	198
<b>commensal</b>	Species associated with human activities and benefitting from these	May provide opportunities for ambush hunting or chance collecting	81
<b>large scavenger</b>	Species with mass >3 Kg and which feed on carcasses of large animals	May provide opportunities for ambush hunting	6
<b>partial scavenger</b>	Species which scavenge but are not wholly dependent on carcasses for food	May provide opportunities for ambush hunting	33
<b>cliff nester</b>	Species which nest on cliffs, often colonially	May provide opportunities for surprise stalking or egg collecting	44

<b>Variable Name</b>	<b>Description</b>	<b>Potential</b>	<b>Number of Species</b>
<b>ground nester</b>	Species which nest on the ground, sometimes colonially	May provide opportunities for surprise stalking or egg collecting	137
<b>wetland ground nester</b>	Species which nest on the ground, usually colonially	May provide opportunities for surprise stalking or egg collecting	64
<b>ground cryptic</b>	Ground dwelling species with camouflage plumage and tendency to freeze when threatened	May provide opportunities for stalking	168
<b>lekking</b>	Species that gather at fixed points in the spring to perform elaborate breeding displays	May provide opportunities for ambush hunting	10
<b>arboreal</b>	Tree or bush dwellers	Would require technology such as netting	170
<b>edible</b>	Species potentially edible by humans	Multiple opportunities depending on species characteristics	81
<b>weight class</b>	Species sorted by weight	May indicate preference for species of particular sizes	430

## 2.4 Sites of known Bird Exploitation

Sites with direct evidence of human exploitation of birds are rare, particularly for Neanderthals. New sites are now being added with some regularity following the published evidence of Neanderthal exploitation of birds. These have been identified (Appendix 2) and will be used in a detailed analysis of direct evidence of Neanderthal exploitation of birds in Chapter 5. For comparison, Late Pleistocene Modern Human sites with evidence of bird exploitation by Magdalenians (for which the most information is available) have been added in Appendix 3. Evidence from other modern human cultures are scarcer than for the Magdalenians and are listed in Table 2.6. The data in Appendices 2 and 3 were generated in the form of species (in rows) and sites

with published taphonomic evidence (in columns). For the Mousterian there were 71 taxa (52 species and 19 at genus level) in 19 sites, and for the Magdalenian 45 taxa (36 species and 9 at genus level) in 28 sites.

**Table 2.6** *Published sites of Modern Human exploitation of birds. Magdalenian sites are not included as they are presented in Appendix 3.*

Grotta Romanelli, Italy/EPI (Cassolli, 1997)
Geisenklosterle, Germany/AUR (Conard, 2013)
Geisenklosterle, Germany/GRA (Conard, 2013)
Hohle Fels, Germany/AUR (Conard, 2013)
Hohle Fels, Germany/GRA (Conard, 2013)
Djukhtai Cave, Russia/UPAL (Zelenkov, 2008)
Grotta della Madonna, Italy/MES (Gala, 2016)
Grotta della Madonna, Italy/EPI (Tagliacozzo, 2002)
Pavlov I, Czech/GRA (Bochenski, 2009)
Gorham's Cave, Gibraltar/SOL (Finlayson <i>et al.</i> , 2012; Blasco <i>et al.</i> , 2014)
Pair-non-Pair, France/EUP (In Laroulandie, 2003)
Combe Sauniere, France/SOL (Castel, 2002)
Brassempuoy, France/UPAL (In Laroulandie, 2016)
Crouzade, France/UPAL (In Laroulandie, 2016)
Le Piage, France/UPAL (In Laroulandie, 2016)

## 2.5 Data analyses

In each of the data chapters (3 to 5), I present the methodology used in data analysis. Briefly, Chapter 3 uses multi-variate methodology, particularly principal components

analysis (PCA) (Jolliffe, 2002), and also cluster analysis. In this chapter, birds are used as climate and habitat proxies at sites of Neanderthal and modern human occupation and PCA is used to tease out the main explanatory variables. Multivariate statistical package, (MVSP, Kovach Computing Services, 2011) has been used for these analyses. Comparative analyses of data in Chapters 4 and 5 largely follows non-parametric statistics with an emphasis on the use of Chi Square analysis (Sokal and Rohlf, 1981; Hawkins, 2009). SPSS (IBM, 2017) has been the package used for these latter analyses.

### **3.1 Introduction**

The aim of this chapter is to characterise the climatic conditions and habitats occupied by Neanderthals and to compare these with those of modern humans. The results will enable me to answer questions related to the capabilities of human groups to survive the glacial conditions of Late Pleistocene Europe. They will also be informative when coming to discuss the association and exploitation of birds by different human groups, and particularly the Neanderthals, in Chapters 4 and 5.

There has been considerable discussion in the literature regarding the ability of Neanderthals to live in cold glacial climates (Ruff, 1993; Stringer & Gamble, 1993; 1994; Holliday, 1997a & b; Klein, 1999; Finlayson *et al.*, 2000; Aiello & Wheeler, 2004; Finlayson, 2004; Churchill, 2014). This question has a bearing on the overall climatic tolerance of Neanderthals, and indeed other human groups, occupying the Palaeartic region during the late Pleistocene. Other than the question of cold adaptation however, there appears to be an absence of discussion on the wider climatic tolerance of the Neanderthals.

Linked to the climate question is the use of habitats by Neanderthals. One suggestion is that Neanderthals occupied areas which would always have had vegetation cover but not necessarily dense forest (Finlayson, 2006; Finlayson *et al.*, 2011). Cover would have been a requirement for ambush hunting, particularly for getting close to prey (Churchill, 2002). Stalking, followed by a rapid approach to prey, and then overpowering it by force, was considered the probable method of Neanderthal hunting

(Berger & Trinkaus, 1995). A recent paper (Stewart *et al.*, 2018) reinforces the view that the Neanderthal body form was indeed related to power-based locomotion (and by implication, close-quarter hunting) rather than thermoregulation. Other authors have suggested that Neanderthals also occupied open tundra (Slimak *et al.*, 2011) and exploited tundra animals, particularly reindeer (*Rangifer tarandus*) (Gaudzinski and Roebroeks 2000; Costamagno *et al.* 2006; Niven *et al.* 2012; Discamps and Faivre 2017). Occupation of such habitats implies living in cold climates (where thermoregulation may have played a more important role) and would have required alternative hunting methods, since ambushing in such open terrain would not have been possible.

Linked to these questions has been the significance of climate refugia to the survival of Neanderthals (Carrion *et al.*, 2008). Gibraltar has been highlighted, in particular, as a site of late Neanderthal survival (Finlayson *et al.*, 2006) on account of its particular climatic and ecological characteristics (Finlayson, 2008). This is, therefore, a site that is critical to our understanding of the Neanderthals and to their extinction (Muñiz Guinea *et al.*, 2019).

To advance these questions, this chapter addresses Research Question 1:

Using birds as indicators of climate and habitat, do Neanderthals associate with particular climates and habitats across their entire geographic range or in particular parts of it? A corollary will be to Neanderthals and modern humans.



### 3.2 Methods

The main dataset is used to examine the relationship between Neanderthal and modern humans, climate and habitat as summarised in Table 2.1 to Table 2.4. For each site examined, each species of bird present was recorded at each archaeological level (also referred to as context). The database allocates climatological (Table 2.3) and ecological (Table 2.4) categories to 430 species.

The dataset of Neanderthal and modern human sites (Chapter 2) yielded a list of bird species associated with Neanderthals and modern humans and their respective cultures (Table 2.1) for each site. Each bird species had a climate rank attributed (Chapter 2, Section 2.3 and Table 2.2). When a species was present in a site, it was given a presence score (P) of 1; when it was absent it was given a score of 0. This constituted the database at Appendix 1. The number of occasions that a species occurred in sites related to a particular culture was calculated by summing P for all sites associated with that culture.

$$P_s = \sum n \dots\dots\dots (1)$$

Where S is the bird species and n is the number of sites for a particular culture in which S has been detected.

Each species has a climate rank (C in Table 2.2), which allows us to convert  $S_x$  into a climatic categorisation and use the birds as climate proxies so:

$$S_x = C_x \dots\dots\dots (2)$$

So it follows that

$$C_x = \sum n \dots\dots\dots (3)$$

The first bird species in the database  $S_1$ , has a climate rank ( $C_1$ ), so for example, in the case of the species golden eagle (*Aquila chrysaetos*) with a climate rank of F, the species name is replaced by the climate rank F; the species snowy owl (*Bubo scandiacus*) with a climate rank of A2, the species name is replaced by climate rank A2, and so on.

The next step is the summation of all species with the same climate rank ( $\sum C_x$ ). Because some climate ranks are associated with more species than others, the summed score was then divided by the number of species ( $r$ ) in that climate rank,

$$C_{sum} = \sum C_x / r \dots\dots\dots (4)$$

The next stage was to combine climate ranks ( $C$ ) into the climate categories ( $K$  in Table 2.2). This would, for example, combine species in the extreme cold category (A1 – B1) together:

$$K_x = \sum C_{sum1} \dots C_{sum n} \dots\dots\dots (5)$$

Thus, the allocation for each site would be the number of cases in each climate category. For example, if a site had three species of bird that fell under the *Extreme Cold* category, then that site would score 3 for *Extreme Cold*. If it also had seven species in the *Temperate* category, then it would score 7 for *Temperate*, and so on. Some sites would have more climate categories than others represented, and the proportion of bird species in each climate category at that site would be a measure of the intensity of the climate signal at that site. To illustrate this further, a site with ten species in the *Extreme Cold* category, and no species in any of the other categories, would give a very strong signal of *Extreme Cold* (there is no other climate category represented). A second site with three species in the *Cool* category, ten in *Temperate*, and five in *Warm*, would show as a much milder climate signal, and so on. It is the

matrix of number of species in each climate category per site that is then used to generate the Principal Components Analysis. The same procedure was applied in respect of habitat categories. The above methodology was applied to sites with only one archaeological context represented.

Some archaeological sites were represented by more than one archaeological context (Table 2.1). For example, a site might have ten archaeological contexts, and if a bird species were present in all ten contexts, then the sum score of P for that site would be 10. On another site, with ten levels, the species might only be present in five contexts. In a single level site, if the species were present it would score 1. Clearly, a comparison of these three examples would bias the results: in the first case the P for that species at that site would be 10, in the second 5, and in the third 1. In order to avoid biasing the results in favour of these multi-context sites, the average score was taken. In our case, the first example P would be 1 (i.e. present in 10 out of 10 contexts), the second P would be 0.5 (i.e. present in 5 out of 10 contexts), and for the third, P would be 1 (i.e. present in 1 out of 1 contexts). As above, P is then converted into the climate rank score for at the site (Chapter 2).

As an example, a single context site with three species in the *Extreme Cold* category would give a score of 3 for that category. A second site with three contexts and these same three species in all the three contexts would also score 3 (Species 1  $3/3 = 1$ ; PLUS Species 2  $3/3 = 1$ ; PLUS Species 3  $3/3 = 1$ ; TOTAL SCORE = 3). A third site in which one of the species is only represented in one of the contexts would score 2.33 (Species 1  $1/3 = 0.33$ ; PLUS Species 2  $3/3 = 1$ ; PLUS Species 3  $3/3 = 1$ ; TOTAL SCORE = 2.33). In the particular example of the comparison of the few sites with a large number of contexts (Gibraltar, Combe Grenal and Riparo Fumane) Section 3.5, an additional analysis was carried out treating each archaeological context

individually. In these specific cases, archaeological contexts were treated as individual sites, the aim being to look at variability within the sites.

Similarly, the bird species present were used to assign a habitat category each site using the habitat categories attributed to each species as explained in Chapter 2, Sections 2.3, Table 2.4. The habitat analyses follow the same sequence and logic used for the climate analyses. In the case of habitat, two analyses were carried out for each comparison. One uses bird nesting habitat and the other bird foraging habitat. These are the equivalent of the climatic attribution, in this case the birds become habitat proxies. Bird remains from archaeological sites cannot inform us whether the birds at these sites were breeding there or simply foraging close to the site. In the latter, we cannot easily distinguish if the birds were present during the breeding season or at another time of the year. Nesting and foraging habitat, for some species, may be quite different as explained in Chapter 2 (see also Table 2.3). In the absence of this detailed information, the analysis is carried out twice. The first assumes the birds were in nesting habitat, and the second that they were in foraging habitat. My results will be interpreted with this in mind. If both point consistently in the same direction, this will corroborate my interpretation.

Using the climatic ranks and habitat categories from Appendix 1 (see also Tables 2.2 and 2.4), I then proceeded to analyse the sites of occupation by different cultures using principal component analysis (Jolliffe, 2002) and the programme MVSP (Kovach Computing Services, 2011). A covariance matrix was calculated for the variables. No transformations were performed on the data. This method has been previously applied in an eco-palaeontological context by Finlayson (2006).

### **3.3 Climate**

In this section I analyse the relationship of Neanderthal and modern human cultures to climate.

#### **3.3.1 Comparing Neanderthals with Aurignacians (early modern humans, 43-36 kya)**

I compared the Mousterian sites (ascribed to Neanderthals) with Aurignacian sites (ascribed to the earliest modern humans in Eurasia; Table 2.1), to provide the broadest possible, ‘like with like’ comparison. I explored the temporal/geographic overlap between Neanderthals and modern humans via a principal component analysis of all Mousterian and Aurignacian sites using birds as climate indicators. Three Norwegian palaeontological sites, which have bird species but no human remains associated with them, were included in the analysis. They represent extreme cold climatic conditions which are presumed inhospitable for humans and so form proxy ‘controls’ in the figures by delimiting the boundary of extreme cold, as defined by the bird species at these sites.

The first two principal component axes explained 73.4% of the variance: Axis 1 – 41.7%; Axis 2 – 31.7%; (Figure 3.1). Two sites which appeared as outliers (the Mousterian site RO40: Ust'-Kanskaya Peschera, Gorno-Altai, Russia; and the Aurignacian site UR24: Syuren 1, Krim, former Ukraine and now Russia) were removed from the figures in order to clarify the main trends. Both sites scored very highly on the first PCA axis which has a strong signal associated with cold and montane conditions and which I interpret to reflect the continental conditions experienced in eastern European sites at particular points of the Late Pleistocene. The

outliers, which showed little separation on the other two PCA axes, represent the limits of human occupation for either Neanderthals or modern humans, though not both. These conditions are nevertheless not comparable to the extreme cold conditions represented by the three Norwegian control sites, for which there is only one inhabited analogue (Figure 3.1) and that is another Russian site from the Altai (Mousterian site RO64: Sibiryachikha Cave). This is clearly an exceptional case.

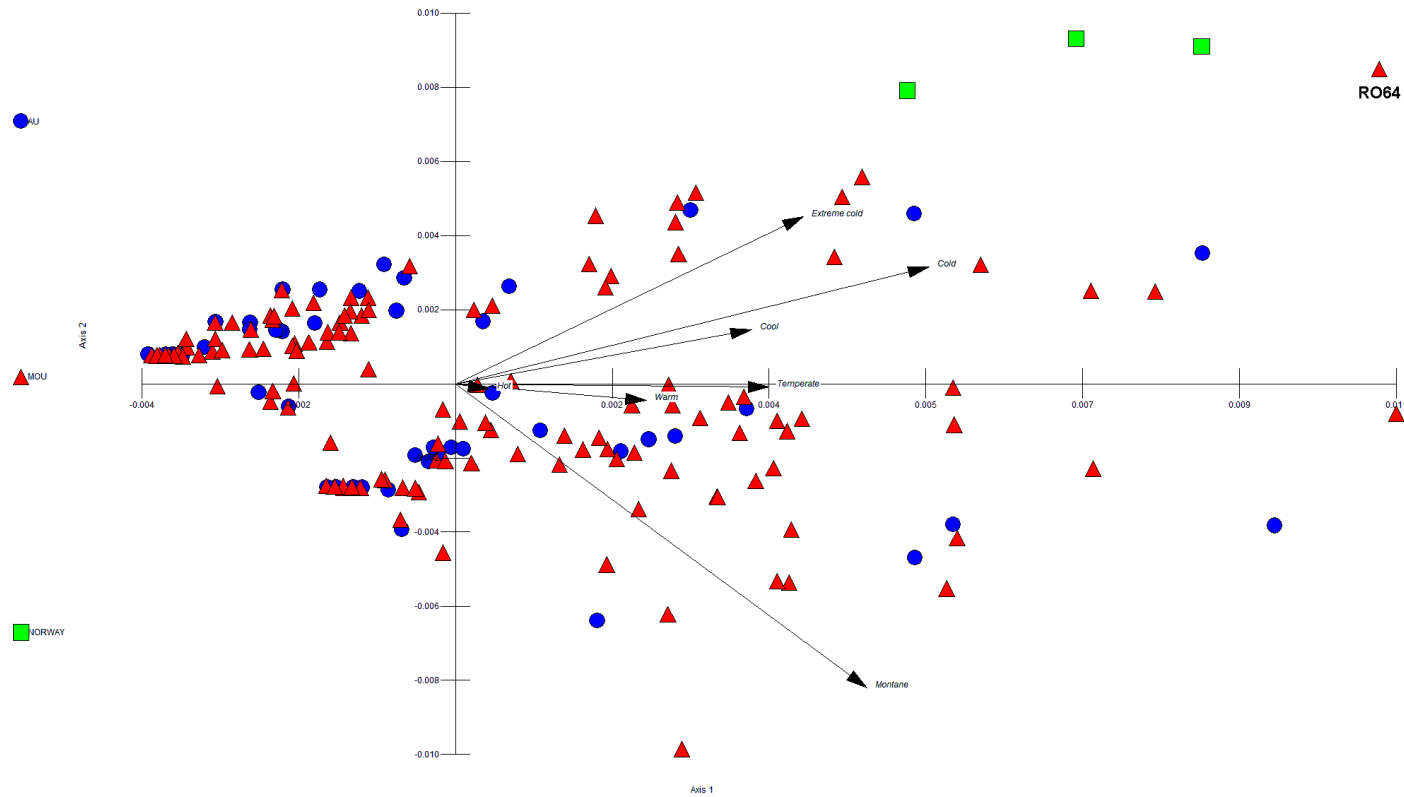


Figure 3.1 Euclidean biplot of Mousterian and Aurignacian sites on PCA axes 1 and 2 showing climatic conditions as labelled stress vectors. Red triangles = Mousterian; blue circles = Aurignacian; green squares = Norwegian sites. RO64: Sibiryachikha Cave in the Russian Altai, is highlighted as it is exceptional in climatic terms and the only cultural site comparable to the Norwegian palaeontological sites as explained in the text (see also Figure 1.).

PCA was repeated but excluding the montane climate variable to examine climate effects without the interference of altitude (Figure 3.2). The first two principal component axes explained 77.3% of the variance: Axis 1 – 57.6%; Axis 2 – 19.7%. In addition to the Russian site RO64, an Aurignacian site appears close to the extreme cold Norwegian sites. This is site HU20 (Istállóskő, Bükk, Hungary). These results confirm that removal of ‘montane’ clarifies the extreme cold-hot gradient along axis 2, but show significant overlap between Mousterian and Aurignacian sites with some indication that more Mousterian sites are more ‘warm-hot’ than Aurignacian ones and corroborates the almost complete absence of Neanderthals from extreme cold sites.

The PCA results are interpreted as follows:

- (a) There is large-scale climatic overlap in the Eurasian sites occupied by Neanderthals and the earliest modern humans;
- (b) most sites cluster around the warm-temperate-cool part of the climatic gradient, suggesting that this was the preferred part of the climatic spectrum for both Neanderthals and early modern humans;
- (c) some Mousterian and Aurignacian sites appear to be associated with cold but very rarely extreme cold climates;
- (d) some Mousterian and Aurignacian sites appear to be associated with a hot climate; and
- (e) some Mousterian sites and Aurignacian sites appear to be associated with a montane climate, which here relates to the mid-latitude belt conditions (e.g. Pyrenees, Alps, etc.) and not the northern mountains (e.g. Scandinavia) which were ice-bound and inaccessible for much of the Late Pleistocene.



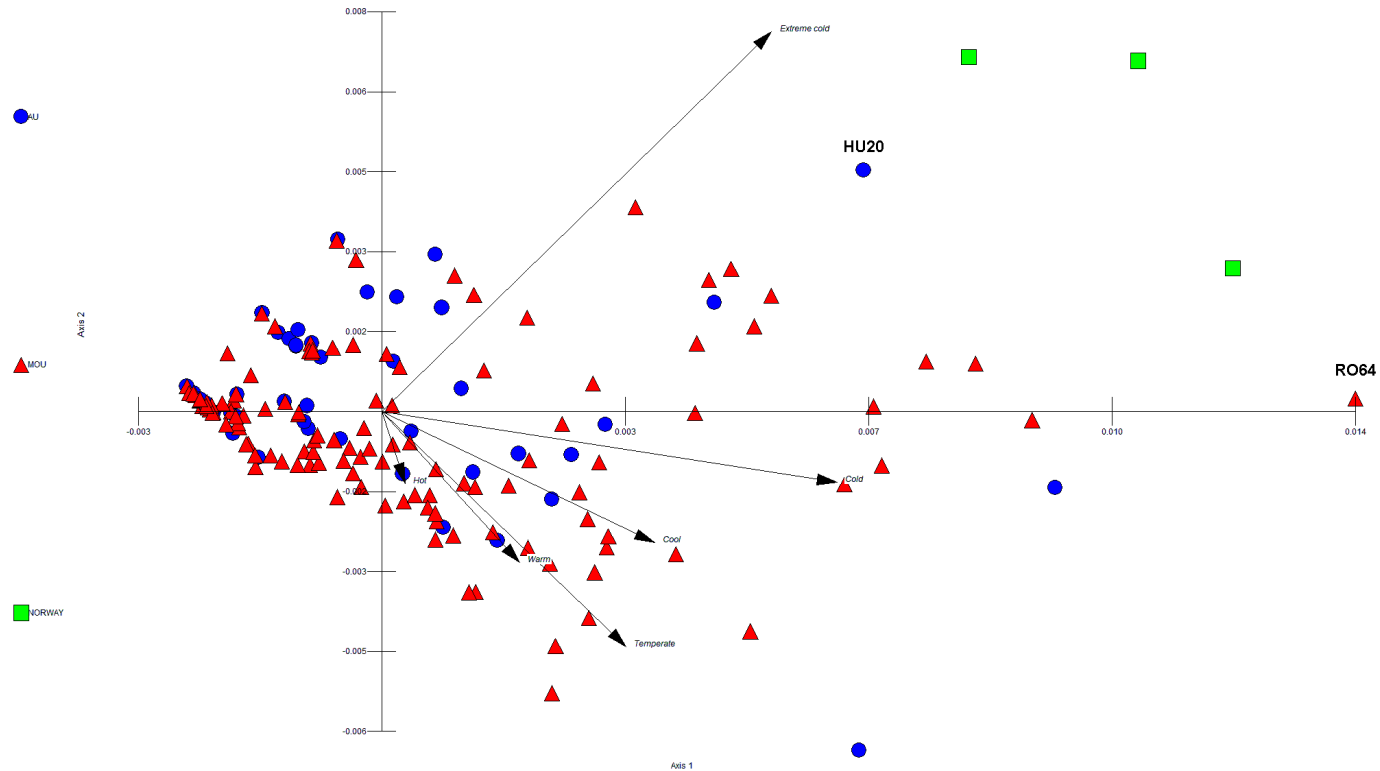


Figure 3.2 Euclidean biplot of Mousterian and Aurignacian sites on PCA axes 1 and 2 showing climatic conditions as labelled stress vectors. Montane climate indicators withdrawn from analysis. Red triangles = Mousterian; blue circles = Aurignacian; green squares = Norwegian sites. RO64: Sibiryachikha Cave in the Russian Altai, is highlighted as it is exceptional in climatic terms and the only cultural site comparable to the Norwegian palaeontological sites. In addition, the Aurignacian site of Istállóskő, Bükk, Hungary is added for similar reasons as explained in the text.

### **3.3.2 Comparing Neanderthals with Gravettians (later modern humans, 34-24kya)**

The Gravettians are distinctly modern human and appear to have arrived in Europe from the plains of Eurasia to the east. They succeeded the Aurignacians and did not show temporal overlap with Neanderthals (Table 2.1). Their arrival appears to have been linked with the spread of the steppe-tundra at the onset of the last glacial maximum (LGM). The Gravettians would have experienced colder climatic conditions than either their predecessors or the last Neanderthals. PCA was repeated by including Gravettian sites to the Mousterian and Aurignacian ones. There were no additional outliers to those from the previous analyses. The first two principal component axes explained 72.2% of the variance: Axis 1 - 43%; Axis 2 – 29.2% (Figure 3.3). The PCA results show significant overlap between Gravettians and Mousterians/Aurignacians, a pattern which is enhanced by removal of the montane climate when the first two axes account for 76.7% of net variance (Axis 1 – 56.9%, Axis 2 – 19.8%; Figure 3.4). There is no indication of an increase in occupation of extreme cold sites by the Gravettians, in spite of the cooling at the time of their presence in Eurasia. In fact, only site BU9 (Kozarnika Cave, Bulgaria) approaches the Norwegian sites (Figure 3.4). These results suggest that the climatic cooling at the time of the Gravettians was not met by a response to occupy colder sites and, instead, it seems that there may have been a degree of compression of sites within the narrowing zones of climatic tolerance.

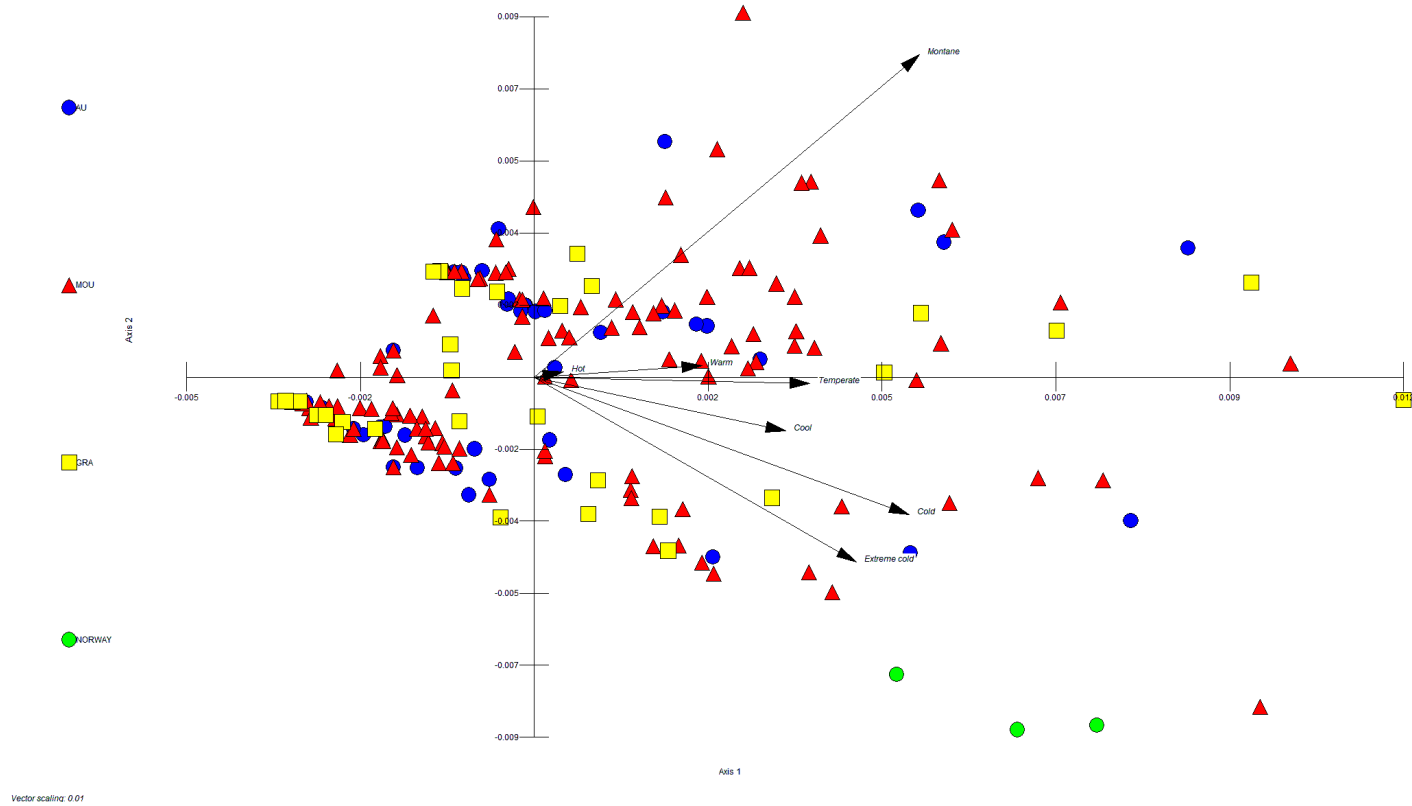


Figure 3.3 Euclidean biplot of Mousterian, Aurignacian and Gravettian sites on PCA axes 1 and 2 showing climatic conditions as labelled stress vectors. Red triangles = Mousterian; blue circles = Aurignacian; yellow squares = Gravettian; green circles = Norwegian sites

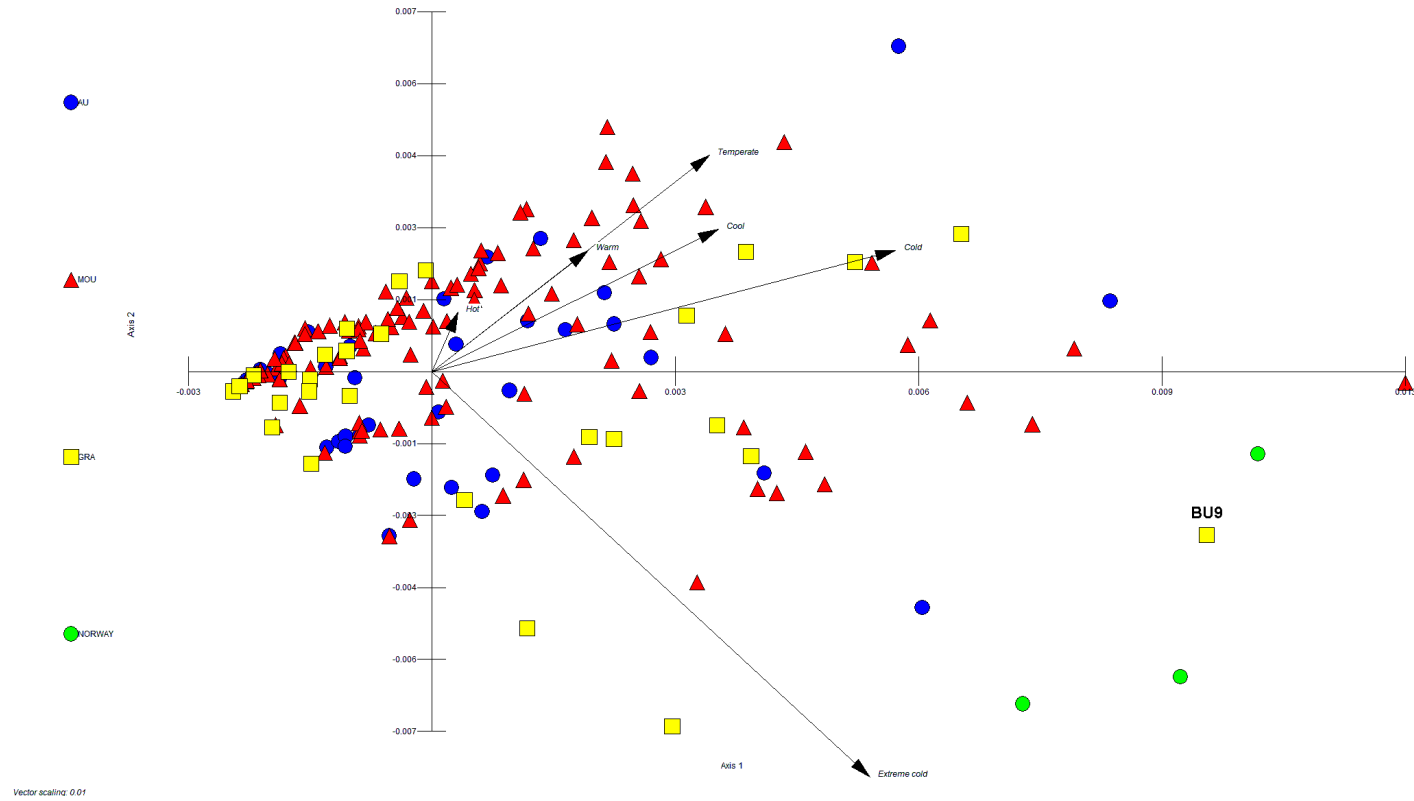


Figure 3.4 Euclidean biplot of Mousterian, Aurignacian and Gravettian sites on PCA axes 1 and 2 with climatic conditions as labelled stress vectors. Montane climate indicators withdrawn from analysis. Red triangles = Mousterian; blue circles = Aurignacian; yellow squares = Gravettian; green circles = Norwegian sites. BU9: Kozarnika Cave in Bulgaria, is highlighted as it is exceptional in climatic terms, comparable to the Norwegian palaeontological sites as explained in the text.

### **3.3.3 Comparing Neanderthals with Magdalenians (LGM modern humans, 20-13 kya)**

The Magdalenians were modern humans who occupied large areas of Europe at the height of the LGM and who spread northwards with the start of the warming after the LGM. They have been traditionally, but not exclusively, associated with the exploitation of tundra as it spread northwards. They were separated from the Neanderthals, who occupied a similar geographical area, by at least 12 kyr (Table 2.1). The Magdalenians therefore represent the human extreme adaptation to glacial conditions. A comparison with the Neanderthals is therefore pertinent.

PCA was carried out for Mousterian and Magdalenian sites. Two Magdalenian outliers were removed in addition to the Mousterian RO40 outlier: CZ6 (Certova Dira, Moravia, Czech Republic) and IT46 (Grotta dei Colombi, Liguria, Italy). These two sites show a signal towards cold but not extreme cold. The first two principal component axes explained 72.4% of the variance: Axis 1 – 42.4%; Axis 2 – 30%.

The results (Figure 3.5) again show a large overlap with a focus around the more temperate climates, with a suggestion that Magdalenian sites tend more towards cool/cold and even extreme cold than Mousterian ones. At least one Magdalenian site (CZ37, Sipka, Moravia, Czech Republic) is comparable with the Norwegian sites, which could reflect the adaptation to tundra conditions. Again, the pattern is enhanced by removal of the montane climate and the tendency of Magdalenian towards cold when compared to Mousterian becomes very evident (Figure 3.6).

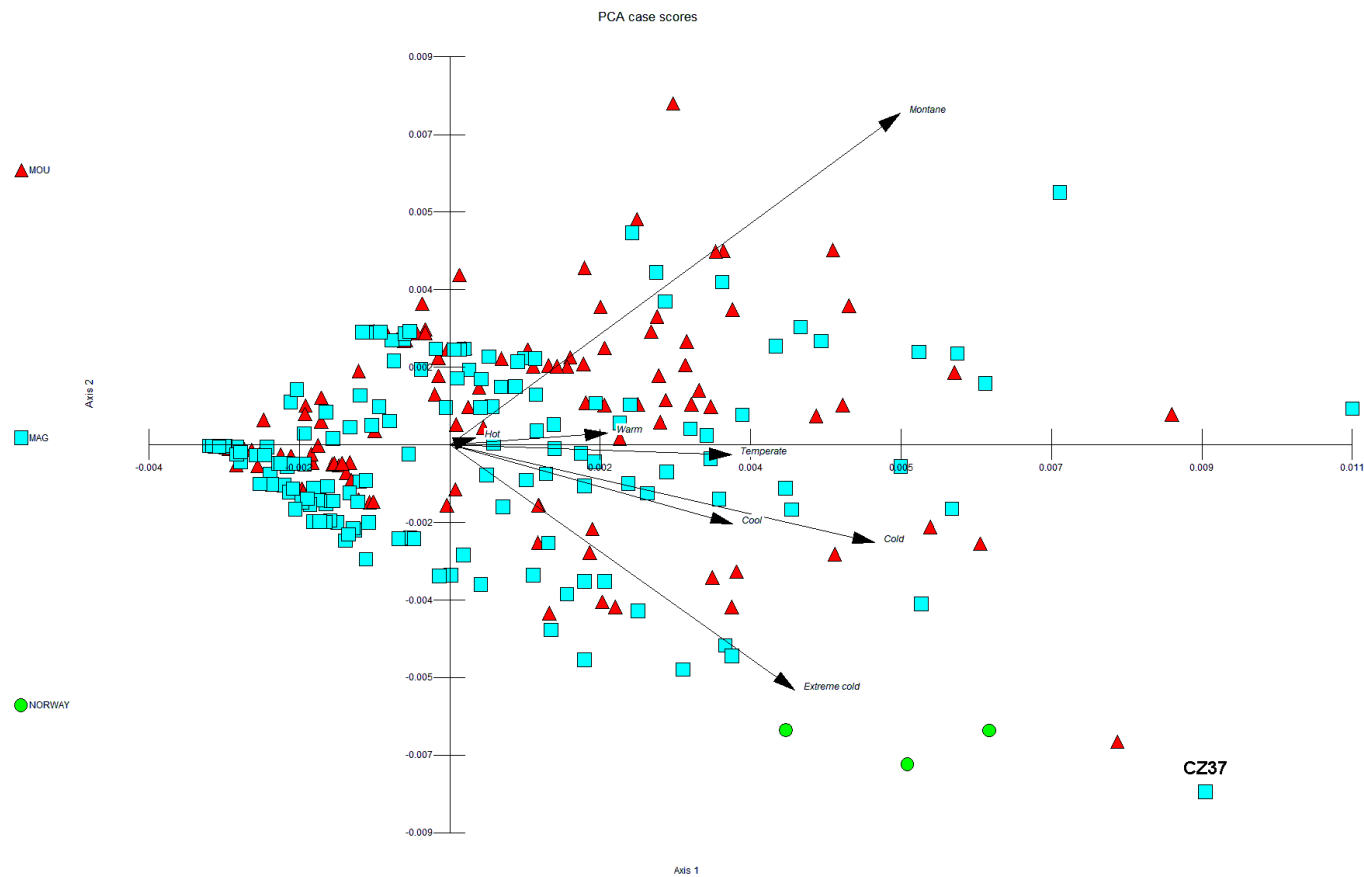


Figure 3.5 Euclidean biplot of Mousterian and Magdalenian sites on PCA axes 1 and 2 with climatic conditions as labelled stress vectors. Red triangles = Mousterian; light blue squares = Magdalenian; green circles = Norwegian sites. CZ37: Sipka, Moravia, Czech Republic, is highlighted as it is exceptional in climatic terms and comparable to the Norwegian palaeontological sites as explained in the text.

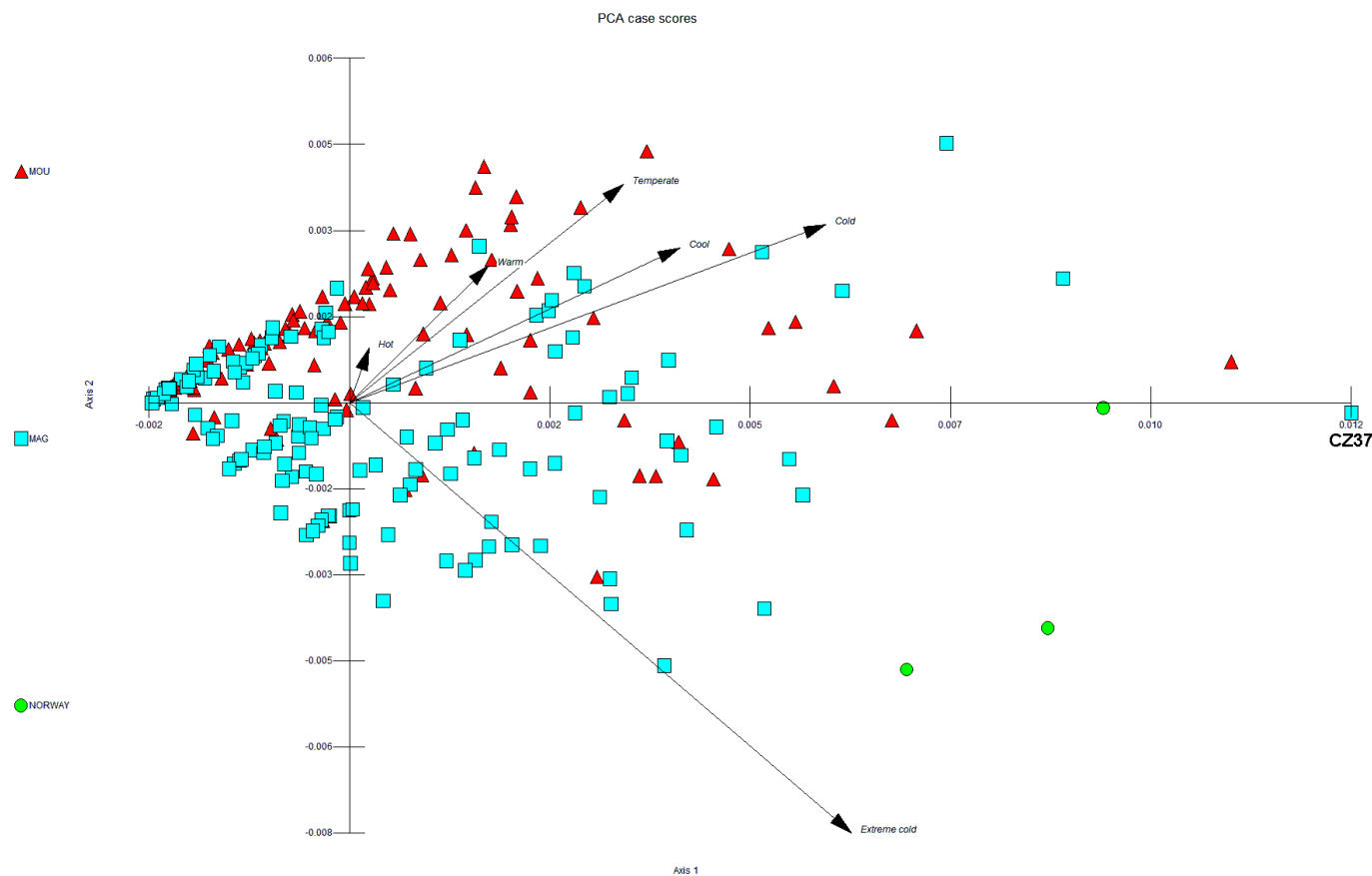


Figure 3.6 Euclidean biplot of Mousterian and Magdalenian sites on PCA axes 1 and 2 with climatic conditions as labelled stress vectors. Montane climate indicators withdrawn from analysis. Red triangles = Mousterian; light blue squares = Magdalenian; green circles = Norwegian sites CZ37: Sipka, Moravia, Czech Republic, is highlighted as it is exceptional in climatic terms and comparable to the Norwegian palaeontological sites as explained in the text.

### **3.4 Habitat**

In this section I analyse the relationship of Neanderthal and modern human cultures to habitat. I have followed the same approach as for climate, in this case using habitat in place of climate categories.

#### **3.4.1 Comparing Neanderthals and Aurignacians (early modern humans, 43-36 kya)**

##### **3.4.1.(a) Comparison of Nesting Habitat**

Four outliers, all tending strongly towards open and rocky habitats, were removed from the analysis. These were Mousterian sites RO 40 and RO 64, Aurignacian site UR24 (referred to in Section 3.3.1) and SP7 (Arbreda, Girona, Spain). PCA of estimated habitat at Neanderthal and Aurignacian sites based on nesting habitat categories explained 83% of the variance in the first two axes: Axis 1 – 66.3% and Axis 2 – 16.7% (Figure 3.7). These results indicate that Mousterian sites are associated with a wide range of habitats. Aurignacian sites, embedded within the Mousterian pattern, show weaker associations suggesting that individual Mousterian sites are associated with specific habitats or combinations of habitats, for example ‘forest’ with ‘rocky’; ‘wetland’ with ‘mixed’ or ‘open’ with either ‘forest/rocky’ or ‘wetland/mixed’. The weak Aurignacian signal suggests no particular preference for specific habitats and probably occupation of mixed habitats where the strong signal of one habitat is absent. Aurignacians and Neanderthals overlap in this part of the habitat sequence.

##### **3.4.1.(b) Comparison of Foraging Habitat**

Mousterian sites RO 40 and RO 64 and Aurignacian site UR24 (Section 3.2.1) were again removed as outliers (SP7 was not an outlier for foraging habitats). PCA based



on foraging habitat explained 70.5% of the variance in the first two axes: Axis 1 – 47.5%; Axis 2 – 23%. The most significant aspect of these results is a clear separation between Mousterian (associated with rocky and, particularly, aerial habitats) and Aurignacian sites (Figure 3.8). Aerial foragers are birds (e.g. swifts and swallows) that typically nest on cliffs so the strong tendency to show up on Mousterian sites reinforces the rocky habitat connection. Furthermore, these aerial foragers are largely summer visitors from tropical Africa so this may reflect a seasonal component in Neanderthal sites which is not as evident in the Aurignacian. As with nesting habitat, Mousterian sites are associated with a wider range of habitats than Aurignacian ones.

Combining foraging and nesting habitat, PCA results are interpreted as follows:

- (a) Mousterian sites were associated with a wide range of habitats, often with specific combinations of two or more habitats, suggesting mosaic landscapes.
- (b) The Aurignacian sites, associated with the earliest modern humans, were embedded within the range of Mousterian sites and showed no particular preference for specific habitats.
- (c) Mousterian sites differed from Aurignacian sites in having a presence of rocky habitat. The strong presence of aerial insect-feeding birds in Mousterian sites not only supports the rocky habitat connection (these birds nest preferentially on cliffs), but also a marked seasonal component, as they are summer visitors from tropical Africa. In contrast, a connection with aerial insect feeding birds is not observable in Aurignacian sites.

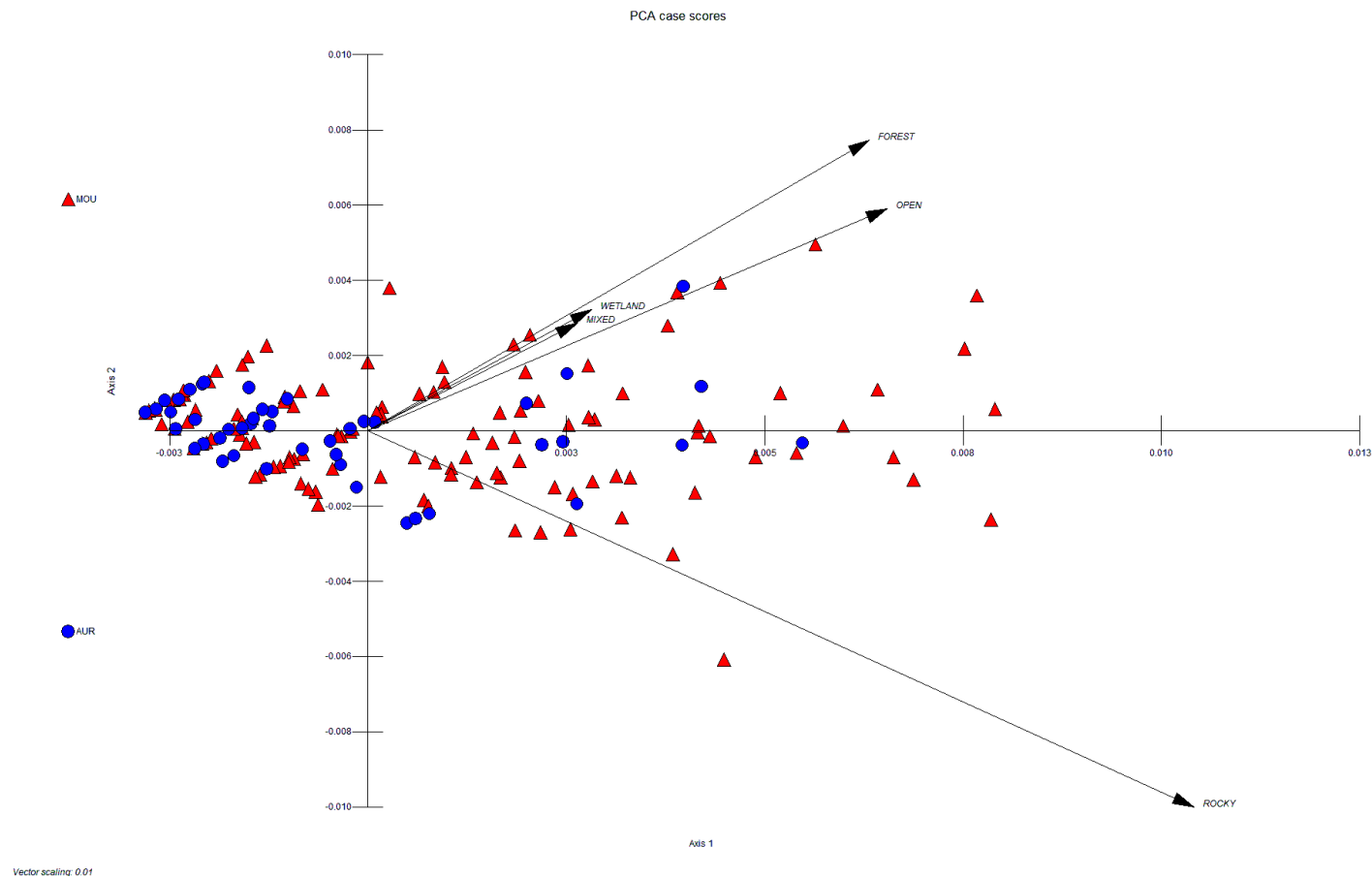


Figure 3.7 Euclidean biplot of Mousterian and Aurignacian sites based on nesting habitat on PCA axes 1 and 2 with nesting habitat as labelled stress vectors. Red triangles = Mousterian; blue circles = Aurignacian

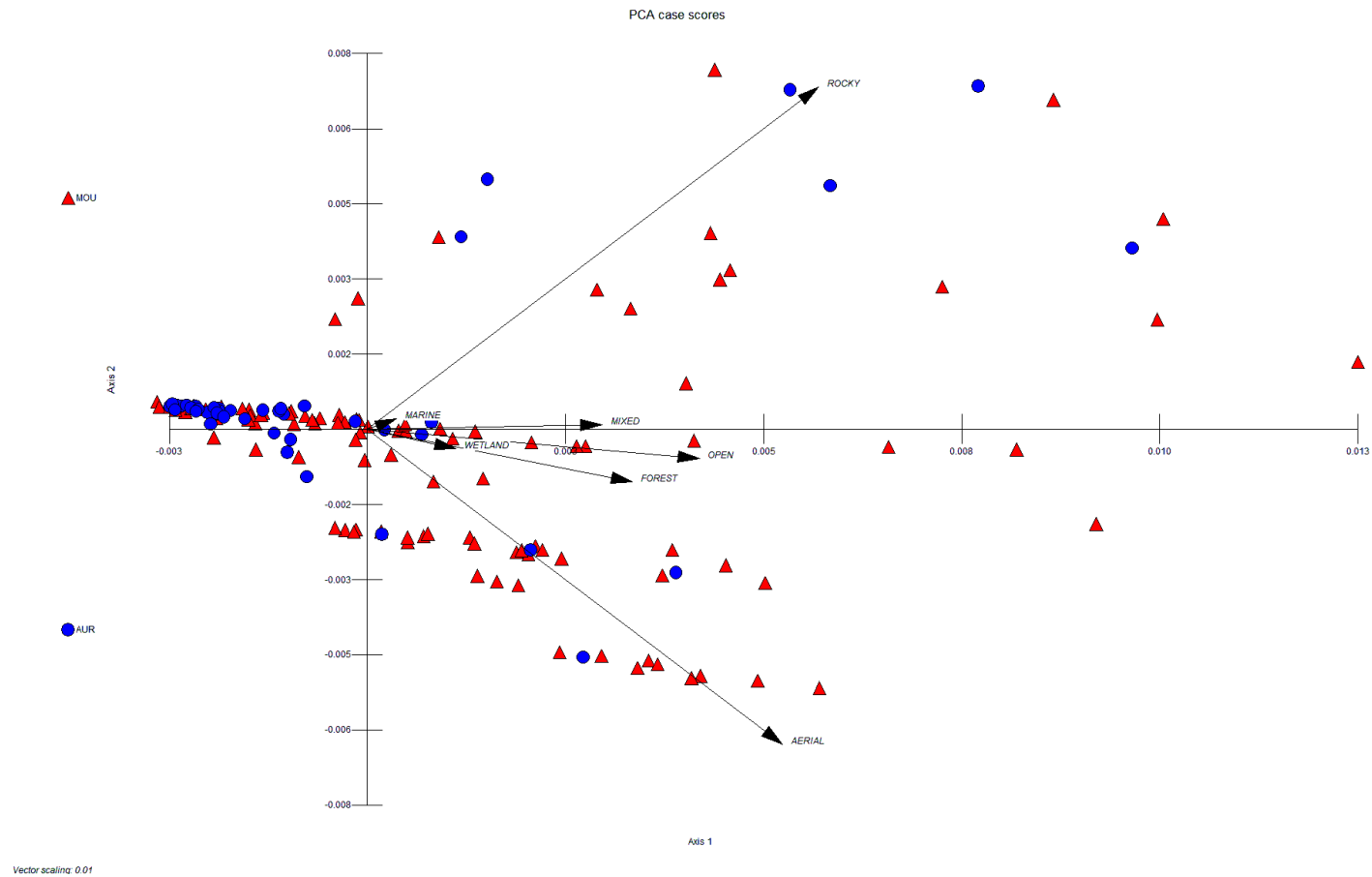


Figure 3.8 Euclidean biplot of Mousterian and Aurignacian sites based on foraging habitat on PCA axes 1 and 2 with foraging habitat as labelled stress vectors. Red triangles = Mousterian; blue circles = Aurignacian

### **3.4.2 Comparing Neanderthals with Gravettians (later modern humans, 34-24kya)**

#### **3.4.2.(a) Comparison of Nesting Habitat**

Adding the Gravettian sites has minimal impact on the PCA results. The first two axes account for 68.5% of the variance: Axis 1 – 67.5% and Axis 2 – 16%. If there is a difference, it is that the Gravettians appear to occupy a wider range of habitats than the Aurignacians, and (but only marginally), so resemble the Mousterians (Figure 3.9).

#### **3.4.2.(b) Comparison of Foraging Habitat**

The first two axes of a PCA including Gravettian sites explain 75.8% of the variance: Axis 1 – 56.1%; Axis 2 – 19.7%. (Figure 3.10). The Gravettian sites appear to follow an axis along the aerial vector (Figure 3.10) but, with two exceptions: Site BRD 16 (Brillenhöhle, Baden-Württemberg, Germany) and BU9 (Section 3.4). The suggested seasonal component in Neanderthal sites, based on aerial foragers (Section 3.3.1(b)), is not as evident in the Aurignacian, which appears to be stronger with the Gravettians who occupy an intermediate position.

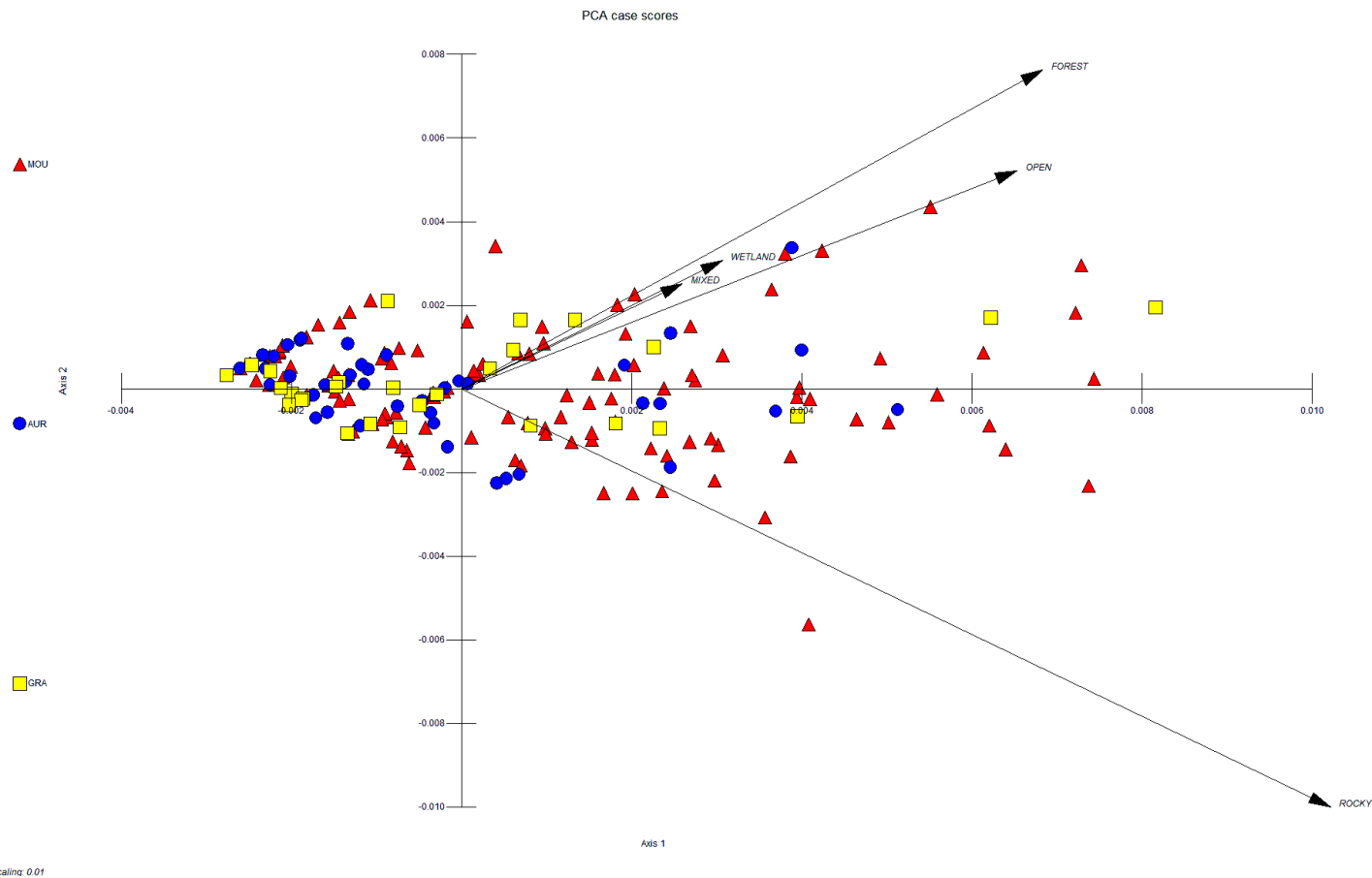


Figure 3.9 Euclidean biplot of Mousterian, Aurignacian and Gravettian sites based on nesting habitat on PCA axes 1 and 2 with nesting habitat as labelled stress vectors. Red triangles = Mousterian; blue circles = Aurignacian; yellow squares = Gravettian

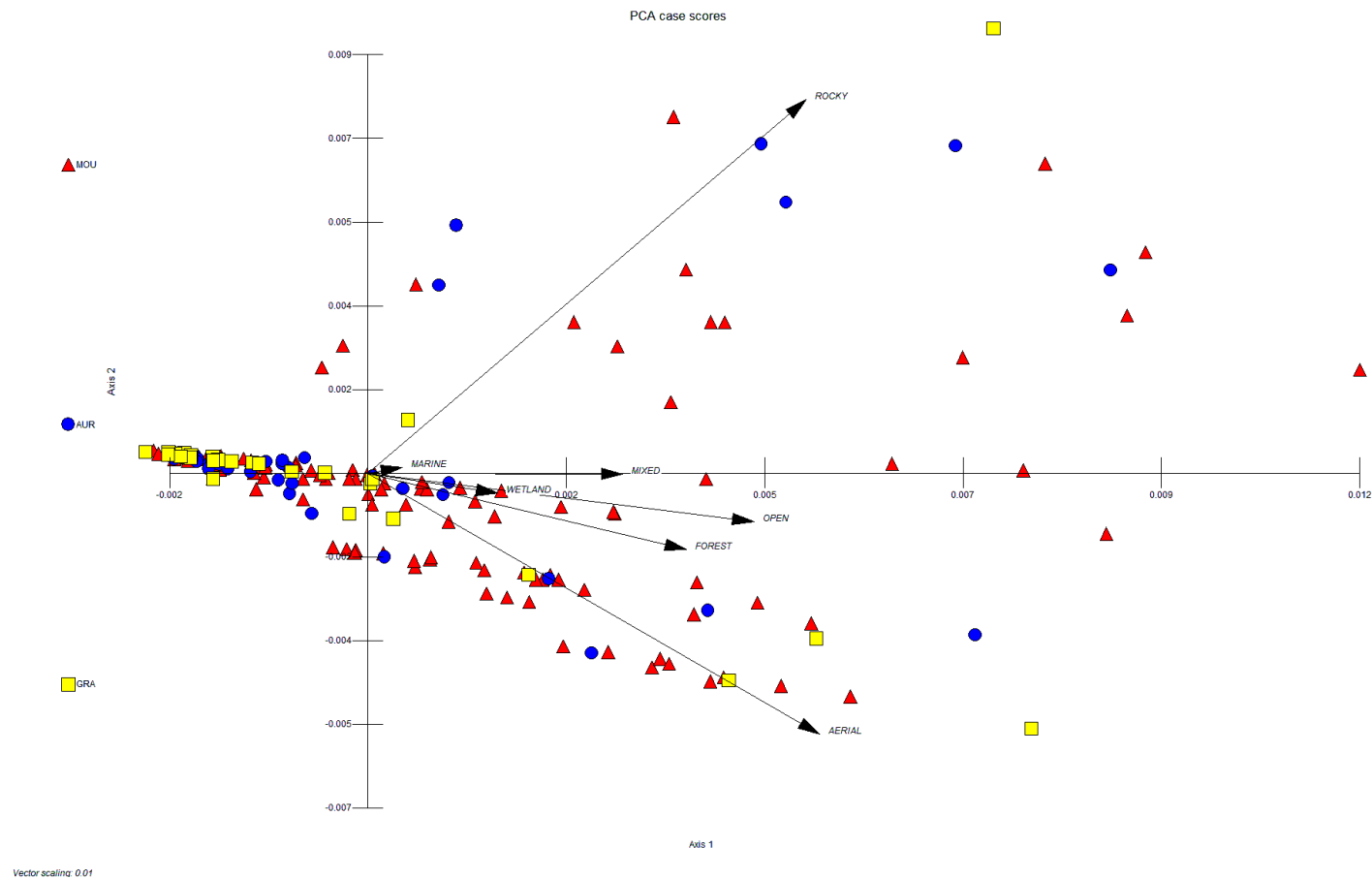


Figure 3.10 Euclidean biplot of Mousterian, Aurignacian and Gravettian sites based on foraging habitat on PCA axes 1 and 2 with foraging habitat as labelled stress vectors. Red triangles = Mousterian; blue circles = Aurignacian; yellow squares = Gravettian

### **3.4.3 Comparing Neanderthals with Magdalenians (LGM modern humans, 20-13 kya)**

#### **3.4.3.(a) Comparison of Nesting Habitat**

PCA reveals a high nesting habitat overlap between Mousterians and Magdalenians (Figure 3.11) if CZ6, IT46 and RO40 outliers were again removed. The first two axes explained 84.1% of the variance: Axis 1 – 65.7% and Axis 2 – 18.4%. There is a partial separation on the second axis, with more Mousterian than Magdalenian sites falling towards rocky habitats.

#### **3.4.3.(b) Comparison of Foraging Habitat**

PCA explains 75% of the variance on the first two axes: Axis 1 – 49.1%; Axis 2 – 25.9% (Figure 3.12). Many of the Mousterian and Magdalenian sites appear to follow a linear trend along the aerial and forest vectors, with Mousterian sites scoring higher than Magdalenian sites. One interpretation of this is that the pattern reflects more open habitats and also a lowered presence of aerial foragers in the Magdalenian. This is consistent with cold climates (associated with the onset of the LGM) which would generate open (steppe/tundra) habitats and a reduction in aerial foragers which are heavily dependent on higher temperatures necessary for insect flight. This interesting trend appears, with fewer sites, along parallel lines higher up axis 1 and is also evident, though less clearly, in Figure 3.11.

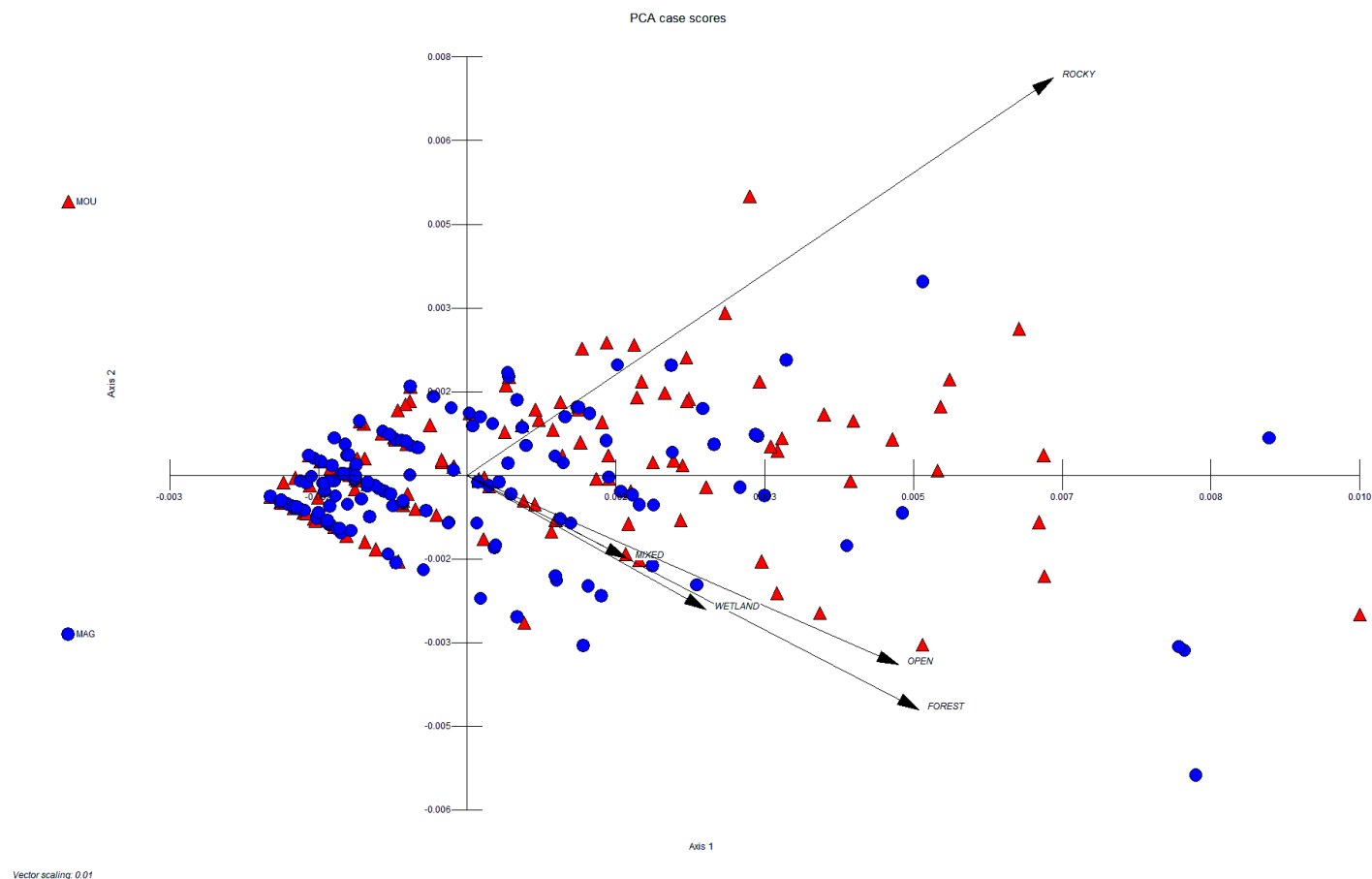


Figure 3.11 Euclidean biplot of Mousterian and Magdalenian sites based on nesting habitat on PCA axes 1 and 2 with nesting habitat as labelled stress vectors. Red triangles = Mousterian; blue circles = Magdalenian



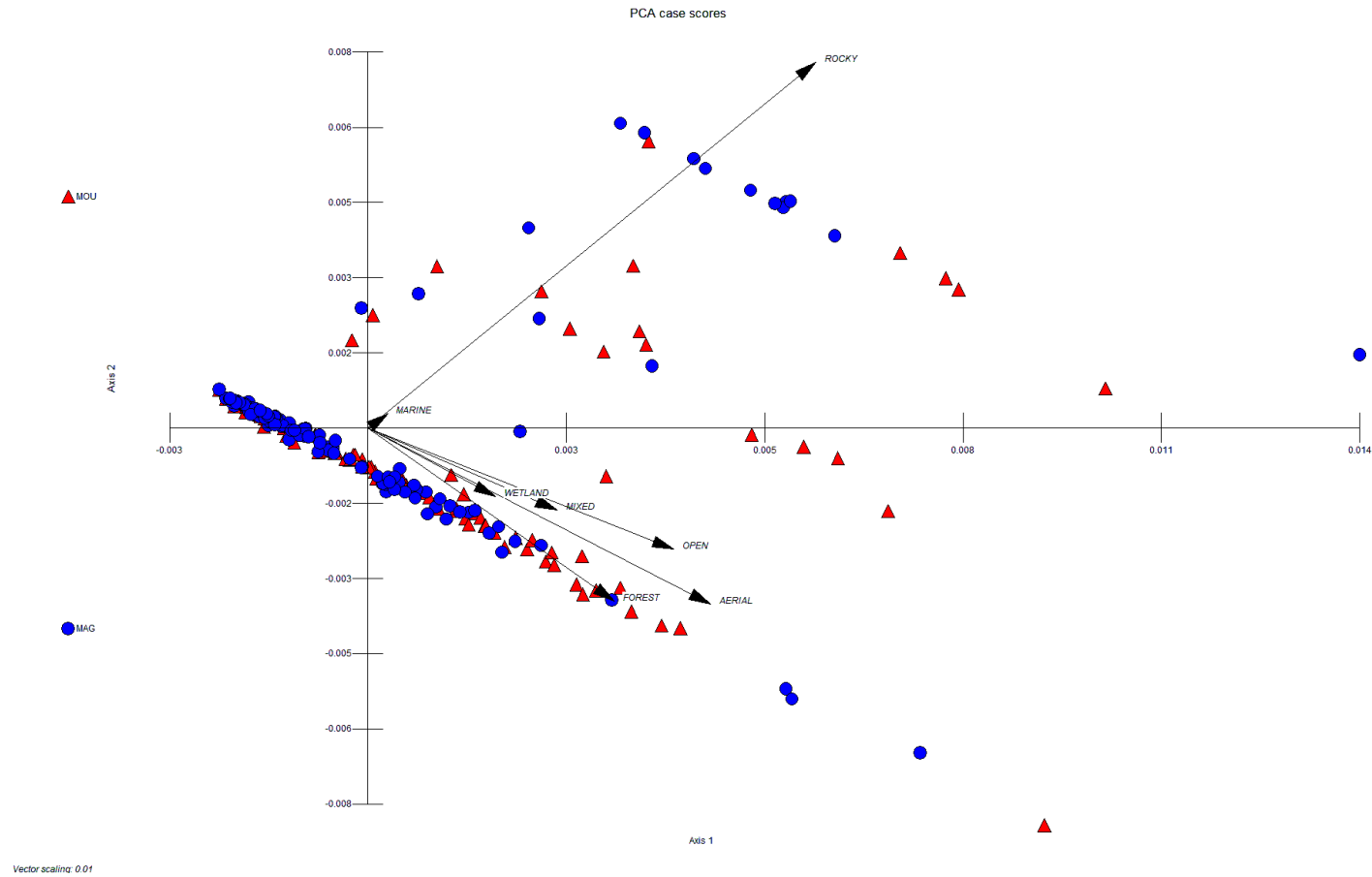


Figure 3.12 Euclidean biplot of Mousterian and Magdalenian sites based on foraging habitat on PCA axes 1 and 2 with foraging habitat as labelled stress vectors. Red triangles = Mousterian; blue circles = Magdalenian. Note that as 'outliers' are removed, the data becomes organized with parallel lines of points suggesting axes 1 and 2 show increasing levels of inter-dependence.

#### **3.4.4 How significant was the rocky habitat to humans?**

I have suggested from the results so far, that the rocky habitat (and in part also supported by the presence of marine and aerial foragers, which breed almost exclusively on these habitats) appears different from other habitats. Here I test how important this habitat was by separating out cave sites from open air occupation sites. Caves tend to act as traps, retaining and preserving bones and artefacts more readily than open air sites which are prone to rapid erosion (Bochenski, *et al.*, 2018). Open air sites accounted for a low proportion of all sites, with the majority (90+%) being caves: nine (5.8%) of 154 Mousterian sites were open air sites; two (3.6%) of 55 Aurignacian sites; three (9.1%) of 33 Gravettian sites; and eight (4.6%) of 176 Magdalenian sites. I carried out PCA analysis of nesting and foraging habitat in these open air sites to test if the rocky habitat presence persisted when cave sites were removed.

PCA of the nesting habitat for the open air sites explained 80.5% of the variance on the first two axes: Axis 1 – 64.4% and Axis 2 – 16.1%. One outlier, Aurignacian site UR17 (Novgorod-Siversk, Ukraine), was removed to give a strong signal related to a mix of forest, open and wetland habitats. Figure 3.13 shows a scatter of sites across a range of habitats and, importantly, the rocky habitat is not well represented. PCA of nesting habitat (also with outlier UR17 excluded) explained 77% of the variance on the first two axes: Axis 1 – 61.4% and Axis 2 – 15.6%. Figure 3.14 also shows a scatter of sites across a range of habitats but, notably, rocky, aerial and marine signals only make a minor contribution. These results indicate that caution is required when interpreting habitat associations and that the influence of rocky habitats may be disproportionately represented as a result of bias from the occupation of caves which are expected to be close to these habitats.

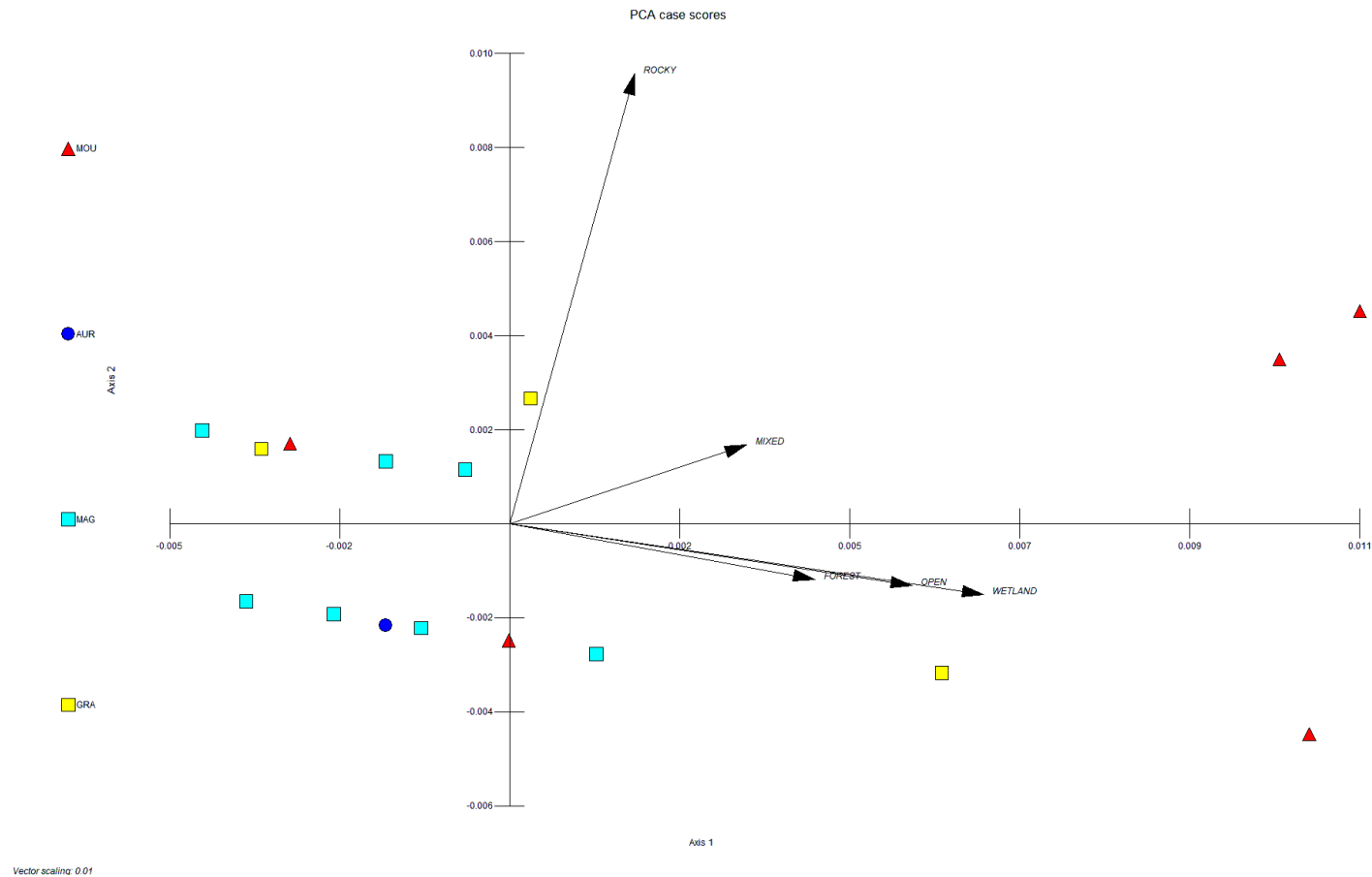


Figure 3.13 Euclidean biplot of open air sites by nesting habitat on PCA axes 1 and 2 with nesting habitat as labelled stress vectors. Red triangles = Mousterian; blue circles = Aurignacian; yellow squares = Gravettian; light blue squares = Magdalenian

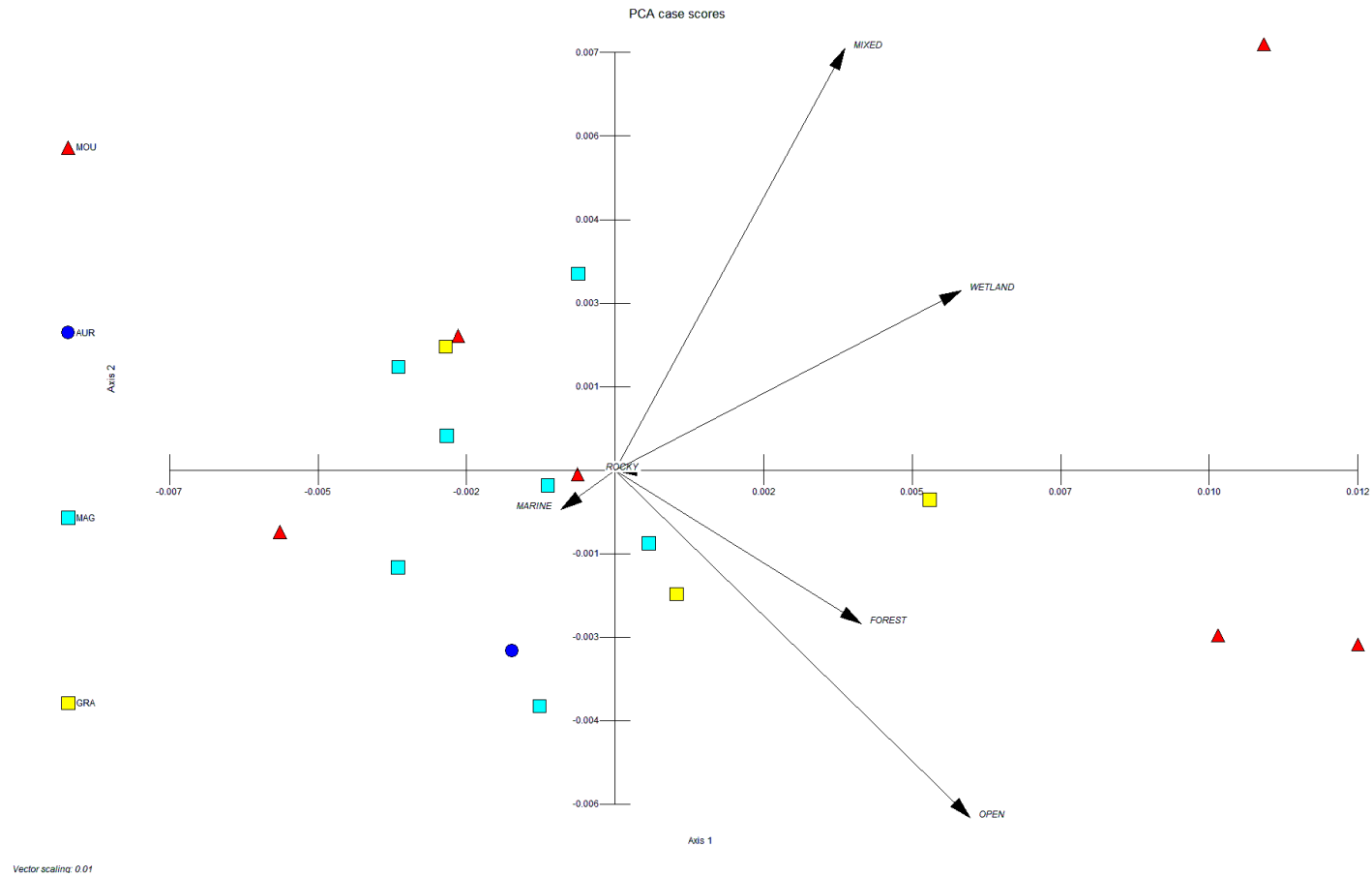


Figure 3.14 Euclidean biplot of open air sites by foraging habitat on PCA axes 1 and 2 with foraging habitat as labelled stress vectors. Red triangles = Mousterian; blue circles = Aurignacian; yellow squares = Gravettian; light blue squares = Magdalenian

#### **3.4.5 Habitat Revisited**

Given the probable bias in favour of rocky (and by association also marine and aerial) habitats, I re-ran the PCAs in Figure 3.7 to Figure 3.12 excluding these habitats. The results (Figure 3.15 to Figure 3.20) show the forest habitat separated along a ‘top left to bottom right’ series of diagonals and so very few sites are associated with that habitat. This applies equally to Neanderthals and modern humans. The trend lines are, instead, towards open habitats, with mixed and wetland habitat components. Sites rarely reach the most open part of the habitat sequence. These results confirm that Neanderthals and modern humans occupied intermediate habitats (between forest and open) or landscapes which combined a mix of various habitats (mosaics).

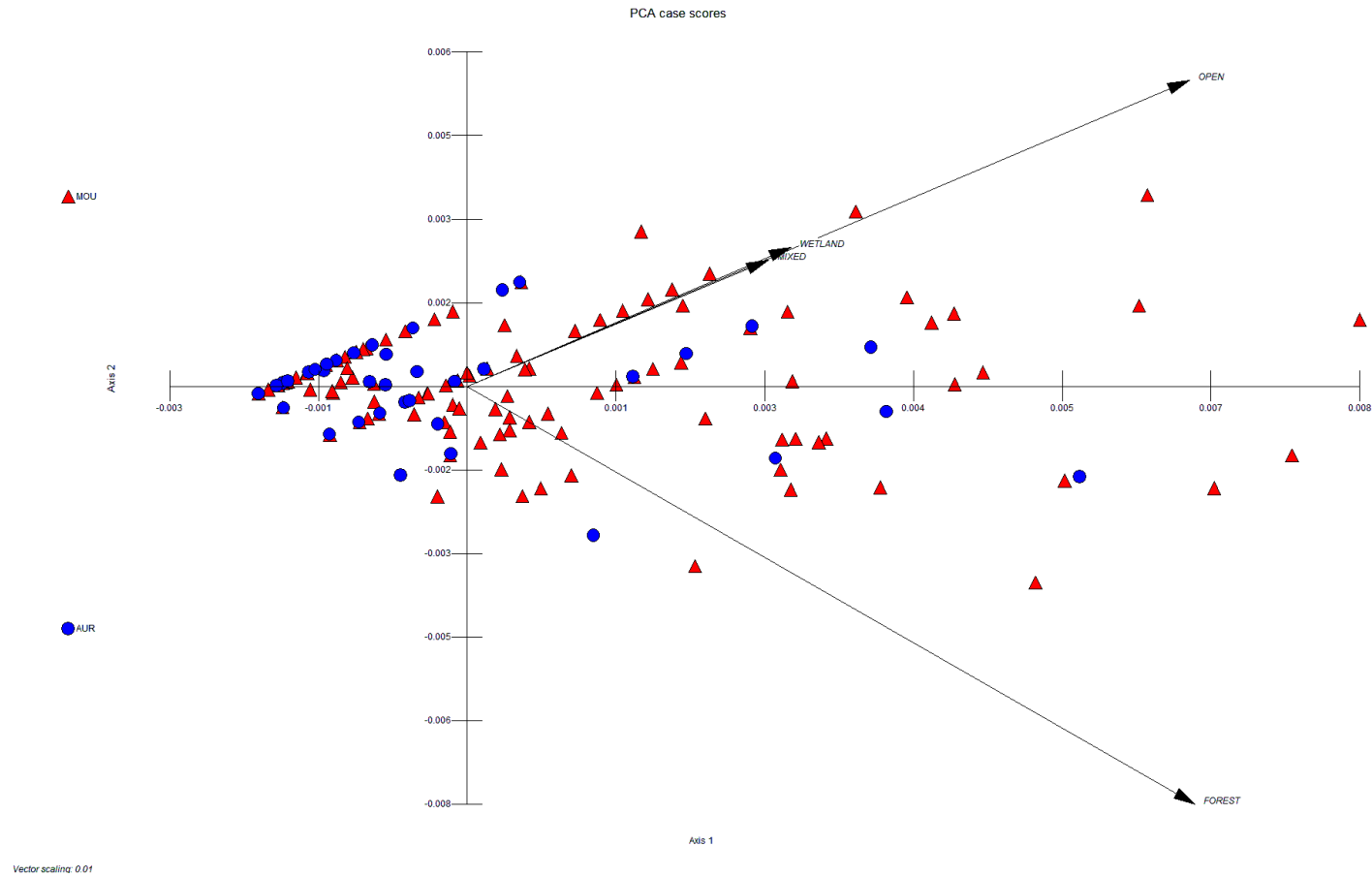


Figure 3.15 Euclidean biplot of Mousterian and Aurignacian sites by nesting habitat on PCA axes 1 and 2 with nesting habitat as labelled stress vectors. Rocky habitat removed. PCA Axis 1 – 70.2%; Axis 2 – 14.8%. Red triangles = Mousterian; blue circles = Aurignacian

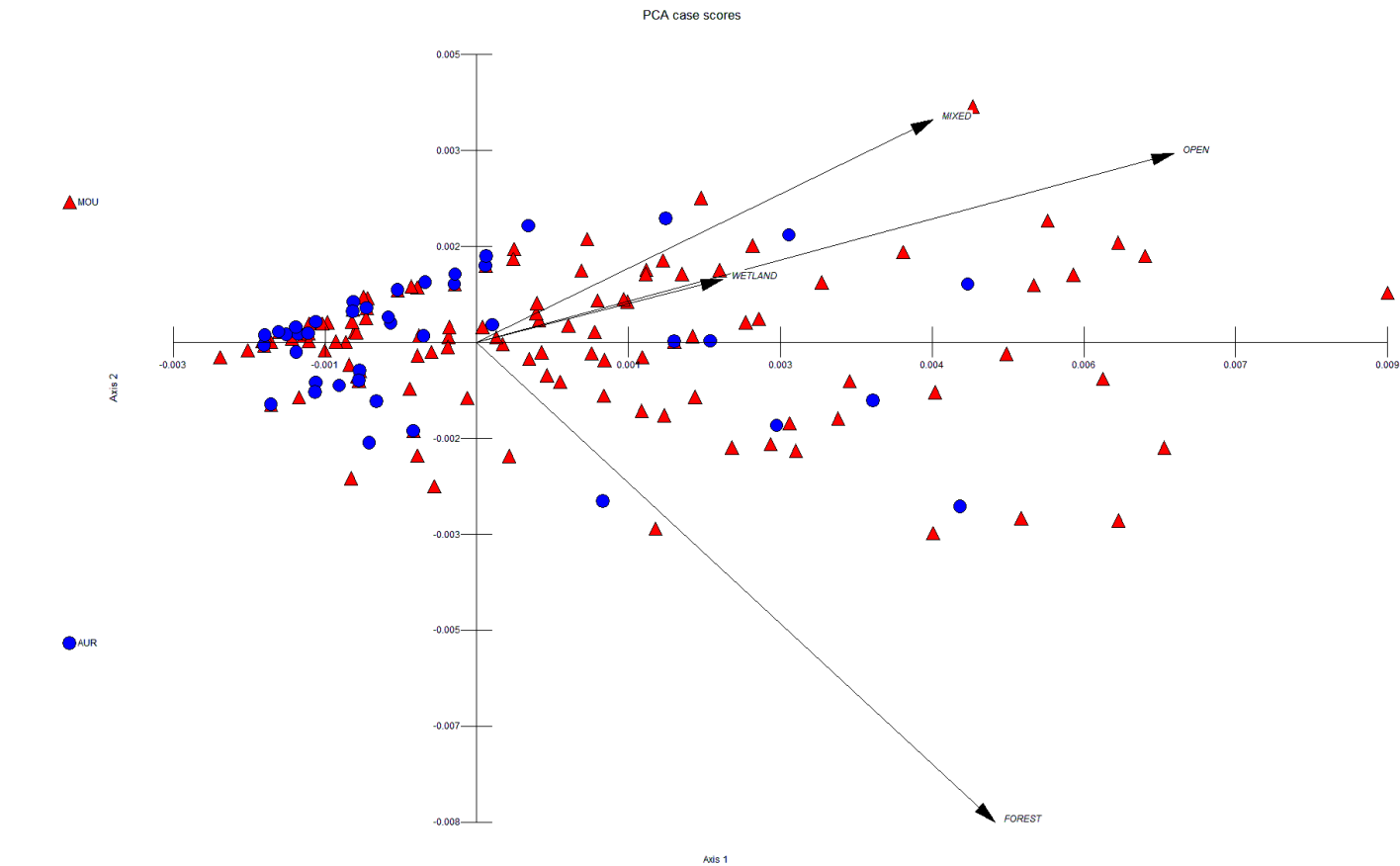


Figure 3.16 Euclidean biplot of Mousterian and Aurignacian sites by foraging habitat on PCA axes 1 and 2 with foraging habitat as labelled stress vectors. Rocky, marine and aerial habitats removed. PCA Axis 1 – 70.7%; Axis 2 – 14.5%. Red triangles = Mousterian; blue circles = Aurignacian

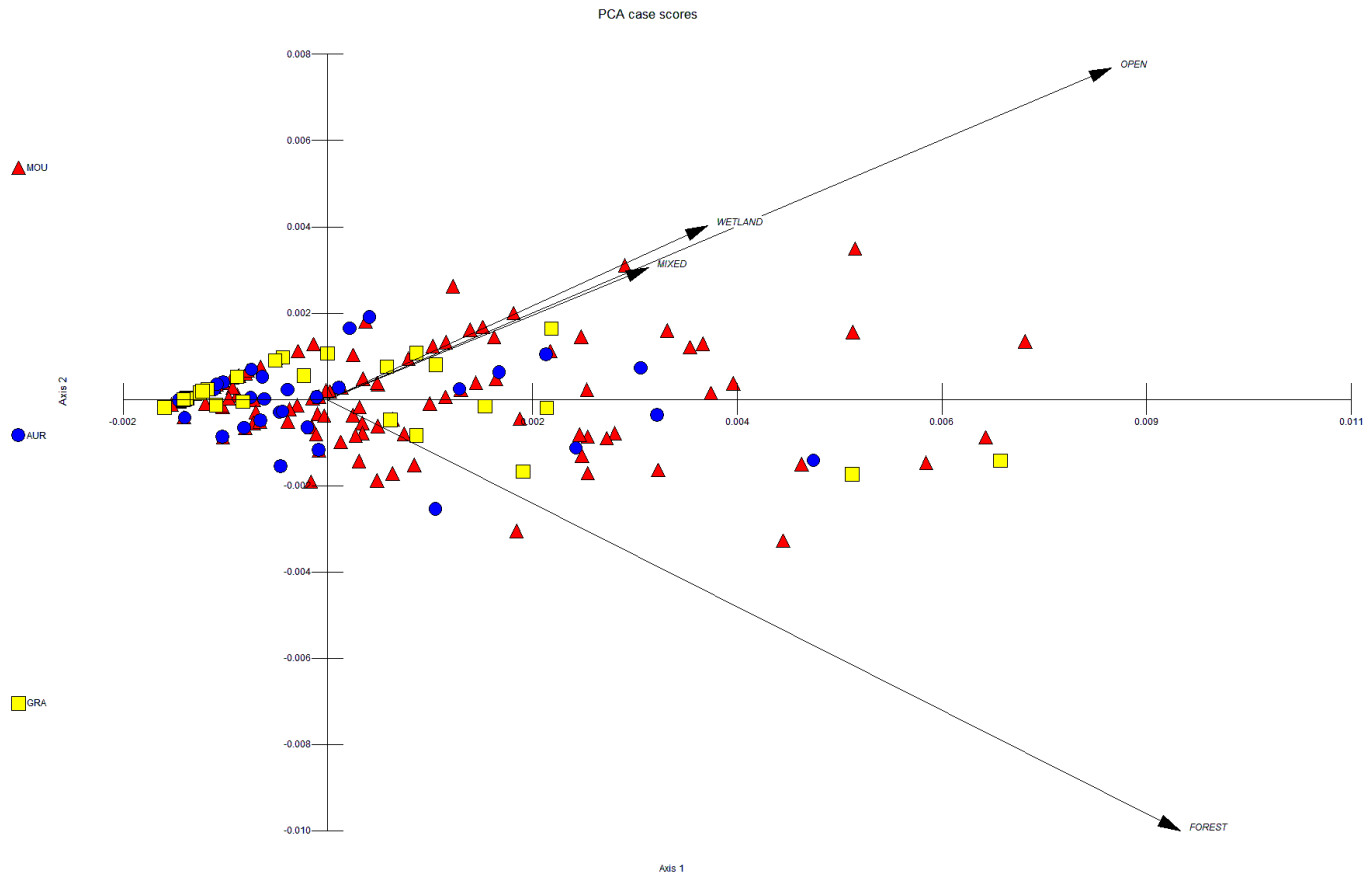


Figure 3.17 Euclidean biplot of Mousterian, Aurignacian and Gravettian sites by nesting habitat on PCA axes 1 and 2 with nesting habitat as labelled stress vectors. Rocky habitat removed. PCA Axis 1 – 71.6%; Axis 2 – 14.2%. Red triangles = Mousterian; blue circles = Aurignacian; yellow squares = Gravettian



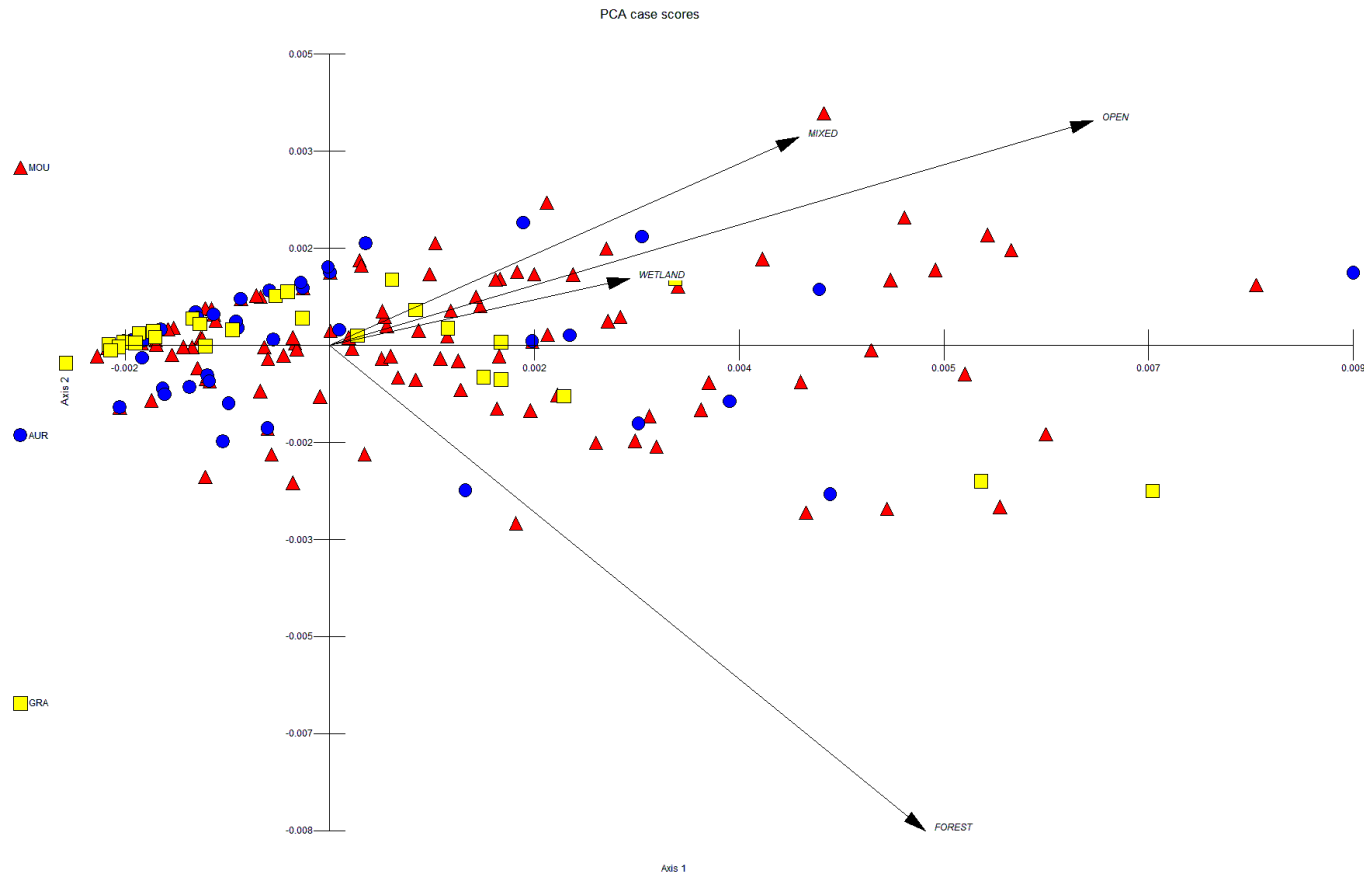


Figure 3.18 Euclidean biplot of Mousterian, Aurignacian and Gravettian sites by foraging habitat on PCA axes 1 and 2 with foraging habitat as labelled stress vectors. Rocky, marine and aerial habitats removed. PCA Axis 1 – 72.8%; Axis 2 – 13.2%. Red triangles = Mousterian; blue circles = Aurignacian; yellow squares = Gravettian

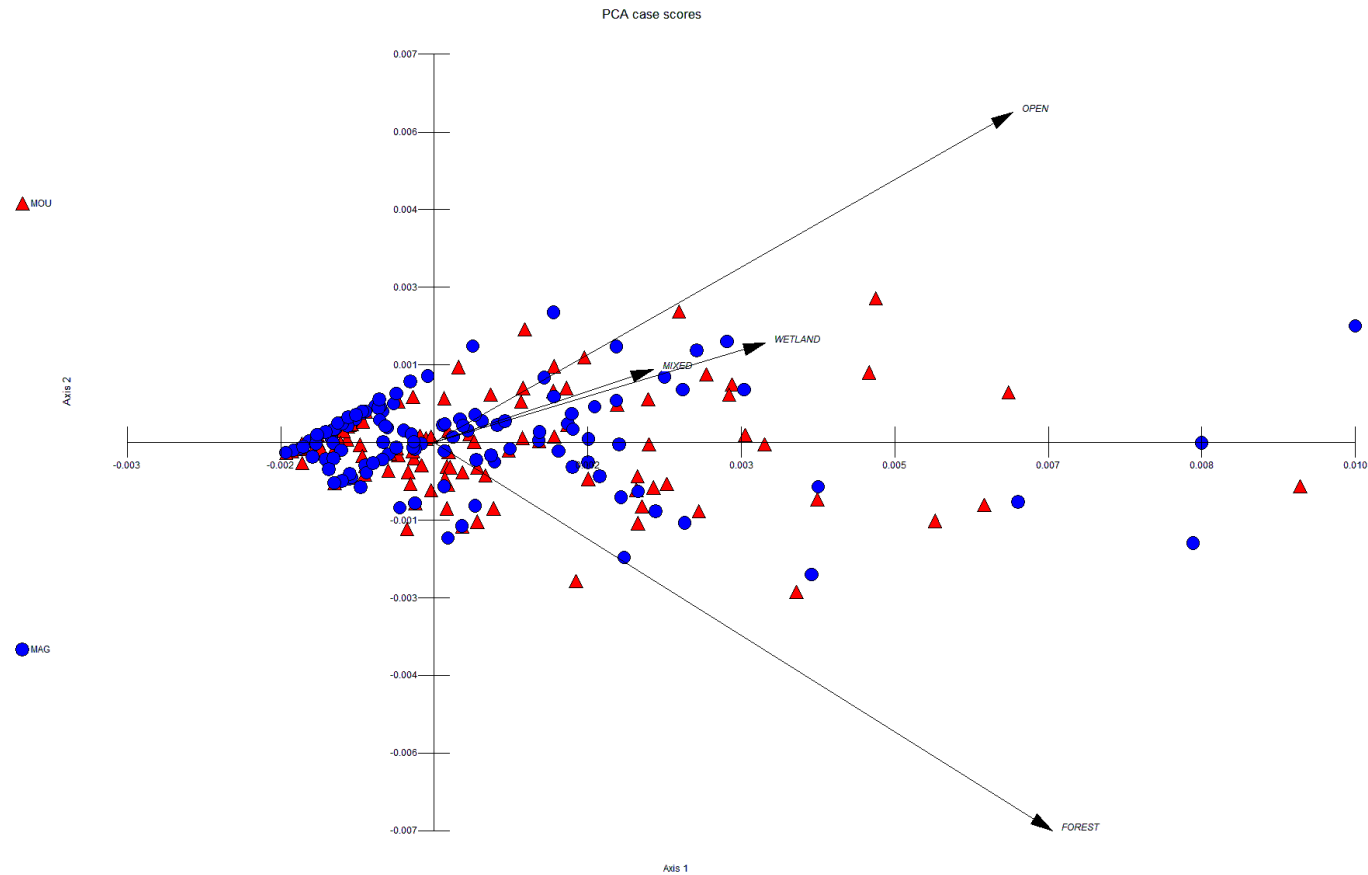


Figure 3.19 Euclidean biplot of Mousterian and Magdalenian sites by nesting habitat on PCA axes 1 and 2 with nesting habitat as labelled stress vectors. Rocky habitat removed. PCA Axis 1 – 74.3%; Axis 2 – 12.9%. Red triangles = Mousterian; blue circles = Magdalenian

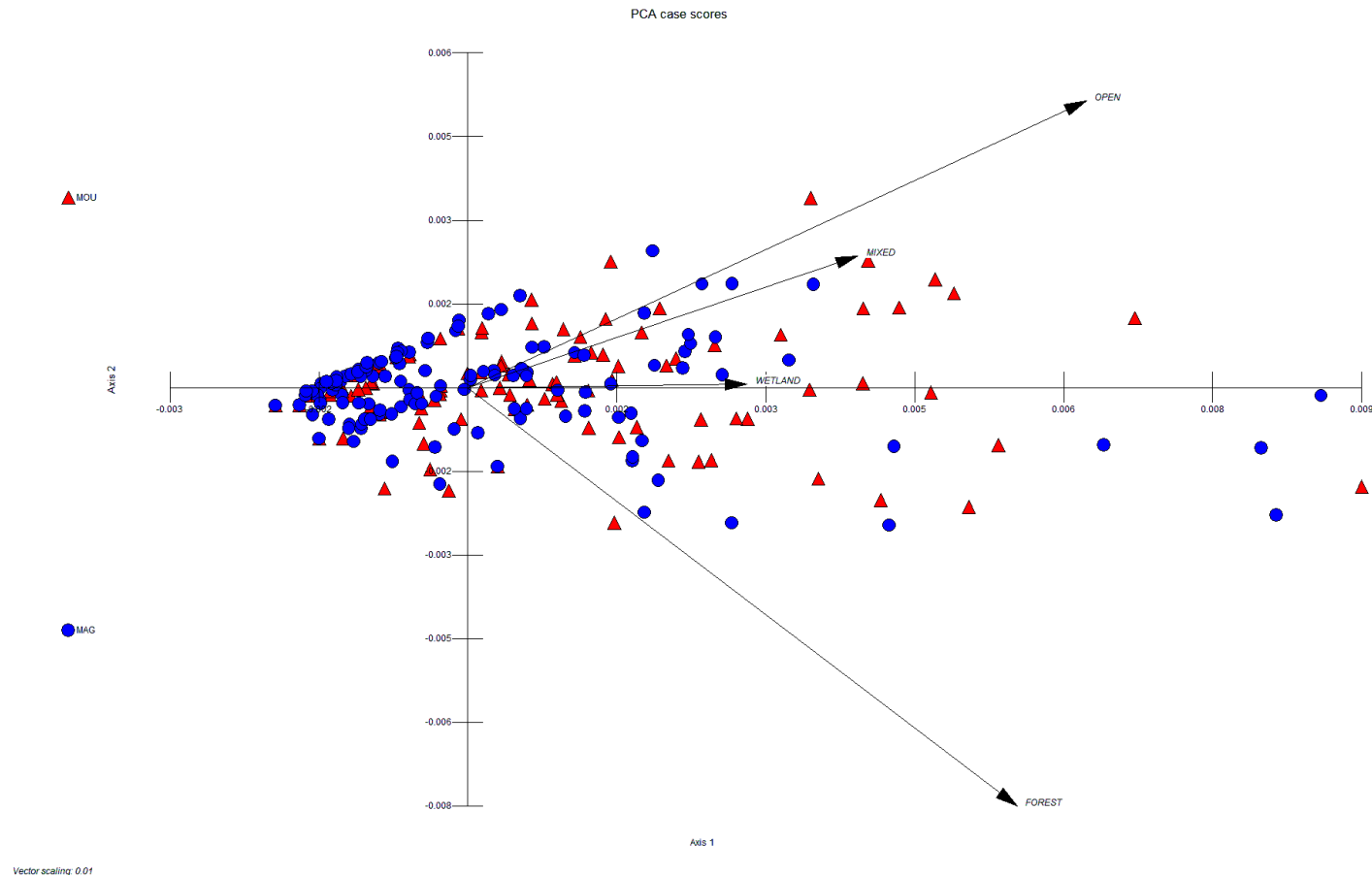


Figure 3.20 Euclidean biplot of Mousterian and Magdalenian sites by foraging habitat on PCA axes 1 and 2 with foraging habitat as labelled stress vectors. Rocky, marine and aerial habitats removed. PCA Axis 1 – 73.8%; Axis 2 – 13.1%. Red triangles = Mousterian; blue circles = Magdalenian.

### **3.5 Was Gibraltar a climate refugium?**

#### **3.5.1 How cold did it get in Gibraltar?**

In this analysis I used the individual archaeological contexts with birds from the Gibraltar sites (at the extreme south of the Neanderthal range, at 36° 07' N 5° 20' W) and included the three Norwegian sites as markers of the extreme cold conditions inhospitable to humans. I have included all Mousterian context and also Solutrean ones (associated with modern humans; Table 2.1). One Solutrean outlier (GOR III) was removed in addition to two Mousterian outliers (GOR IV and GOR 4); these outliers scored strongly on axis 1 along cool and temperate vectors. Interestingly, two of these contexts (GORIV and GORIII) represent the last Neanderthal and the first modern human contexts in Gorham's Cave, at a time known to have been particularly cold in Gibraltar, relative to previous contexts, and which signalled the disappearance of the Neanderthals from the site and the subsequent arrival of modern humans. PCA explained 74%% of the variance on the first two axes: Axis 1 – 47.7% and Axis 2 – 26.6%.

Figure 3.21 shows some overlap between Neanderthal and modern human contexts at Gibraltar but no overlap with the Norwegian sites. There are individual Neanderthal contexts that suggest relatively cool conditions. Nevertheless, these do not approach the extreme conditions of the Norwegian sample which are shown as references of cold glacial conditions. This observation reinforces the view that Gibraltar was a climatic refugium for many species, humans included, and that the extreme conditions of the last glacial cycle never reached these latitudes.

There is an observable trend along the montane vector which suggests that, as climate changed in the different Gibraltar contexts the avian response was one of montane species increasing, presumably with cooling. This montane influence is observable in

Mousterian and Solutrean contexts, indicating that both occupied contexts were marked by the presence of montane species. In all likelihood, these were the coldest conditions affecting Gibraltar, and were far removed from the extreme cold of the Norwegian sites

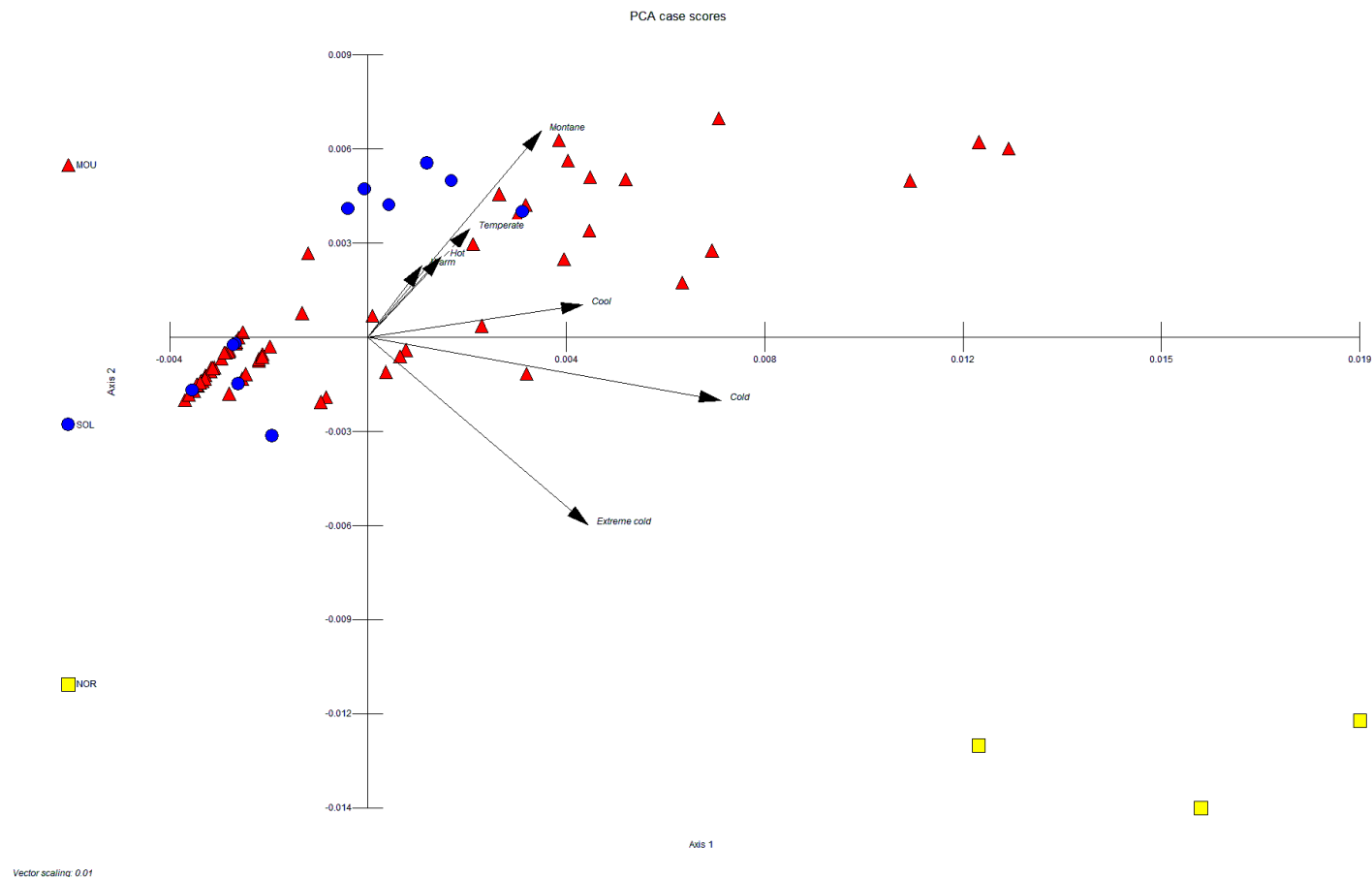


Figure 3.21 Euclidean biplot of Mousterian and Solutrean contexts in Gibraltar and three Norwegian palaeontological sites on PCA axes 1 and 2 with climatic conditions as labelled stress vectors. Red triangles = Mousterian; blue circles = Solutrean; yellow squares = Norwegian sites

### 3.5.2 How does Gibraltar compare with Neanderthal sites to the north?

Gibraltar has been considered a climate refugium and a site of late Neanderthal survival (Finlayson, *et al.*, 2006; Finlayson and Carrion, 2007). How different were conditions in Gibraltar compared to Neanderthal sites further north? Was Gibraltar different, and does the difference support the idea of a glacial climate refugium? To answer these questions, I added two sites from Central Europe with human occupation and with a number of archaeological contexts: Combe Grenal in France and Riparo Fumane in Italy. The former had 30 archaeological contexts, all Mousterian and with birds. The latter had 9 Mousterian and 7 Aurignacian contexts, all with birds. These are among the richest sites in terms of number of contexts and birds associated and they are also sites in which Neanderthal exploitation of birds has been documented (Chapter 5).

PCA of these sites explained 83.6% of the variance in the first two axes: Axis 1 – 50.6% and Axis 2 – 25.2%. Figure 3.22 reveals three trends lines along the temperate-extreme cold gradients along axis 2. The three are separated along axis 1 which separates sites along the montane gradient. The trend line on the left would equate to lowland sites and the one on the right to montane sites with the middle one somewhere in between. The left trend only includes Gibraltar and Combe Grenal contexts. The Gibraltar sites are at sea level and Combe Grenal in the Dordogne (44°48'20" N, 1°13'37" E) at 106 m asl. The nearest mountains with elevations over 2,000 metres are approximately 140 km away from Gibraltar (Betic Range) and 220 km away from Combe Grenal (Pyrenees). In contrast Riparo Fumane (45°35'30" N, 10°54'18" E) is at 356 m asl and only 55 km away from the nearest 2,000 m peaks of the Alps. The middle trend includes Gibraltar and Combe Grenal contexts and the Mousterian contexts from Fumane. The right trend line includes some Gibraltar and Combe

Grenal contexts and all the Fumane Aurignacian contexts, suggesting an overall colder climate in Fumane than at the other two sites and a greater montane influence during the Aurignacian compared to the Mousterian.

These observations, using individual contexts within sites, are consistent with my previous results that compared entire sites in indicating: (a) humans did not occupy climates that we have defined, using birds as indicators, as extreme cold; (b) Neanderthals were no different from modern humans and had some level of tolerance of cooling conditions as shown by some contexts at Gibraltar, Combe Grenal and Riparo Fumane; and (c) conditions appear worse in the Riparo Fumane site (at the base of the Alps) than elsewhere and here the Aurignacian signal suggests greater tolerance of cold conditions by modern humans than Neanderthals at the same site.



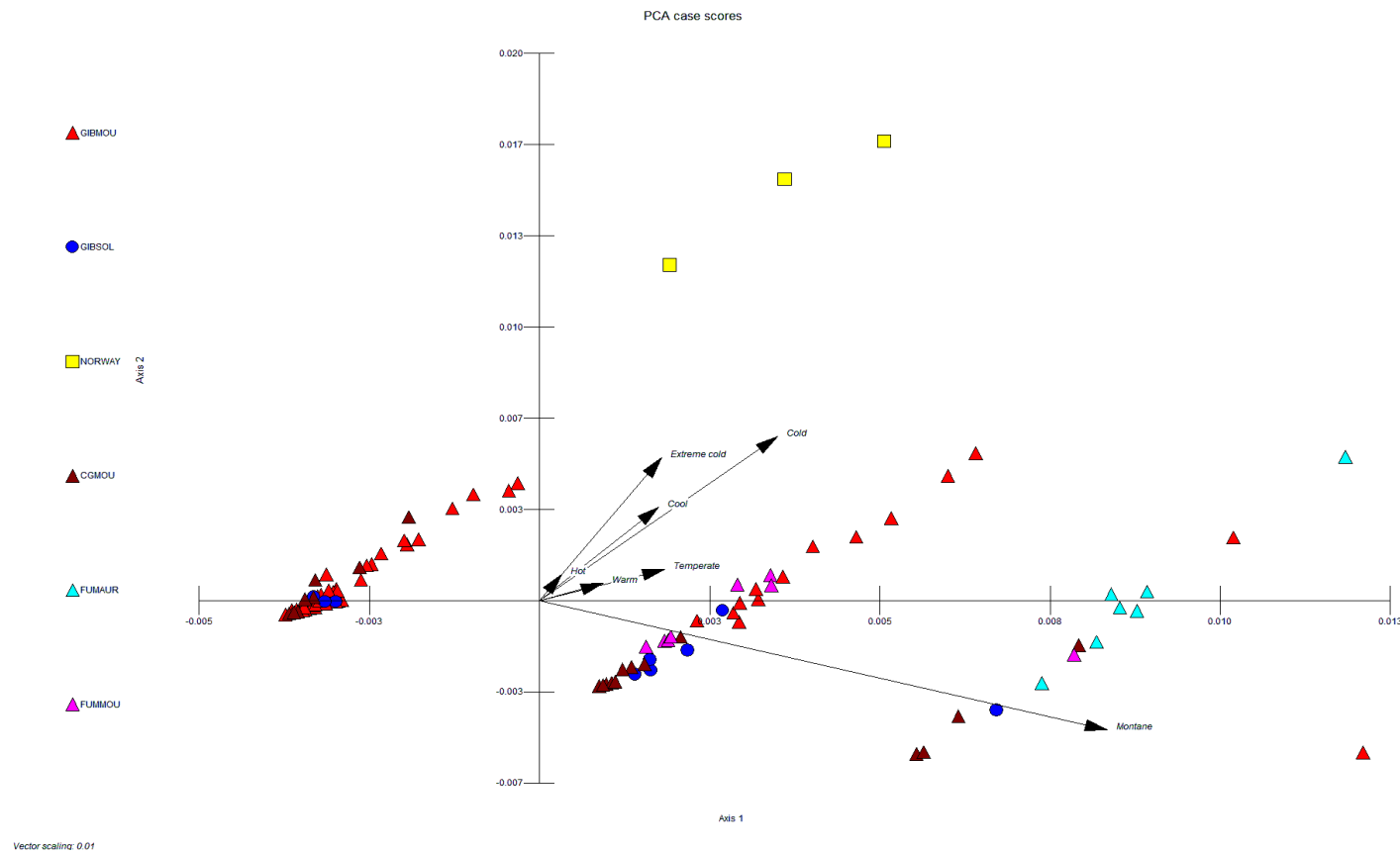


Figure 3.22 Euclidean biplot of human contexts in Gibraltar, Combe Grenal and Riparo Fumane and three Norwegian palaeontological sites on PCA axes 1 and 2 with climatic conditions as labelled stress vectors. Red triangles = Gibraltar Mousterian; blue circles = Gibraltar Solutrean; brown triangles = Combe Grenal Mousterian; light blue triangles = Riparo Fumane Aurignacian; purple triangles = Riparo Fumane Mousterian; yellow squares = Norwegian sites

### **3.6 Summary**

This chapter has examined the relationship between Neanderthals, modern humans, climate and habitat. The results inform on the degree to which these human groups were cold-adapted or were able to occupy open tundra-steppe habitats. Most sites occupied by Neanderthals and modern humans showed a range of climatic conditions, a broad overlap in the climatic conditions and the avoidance of extremes, especially cold.

With the increasingly cold conditions that characterised the time when Gravettians occupied Europe, the response appears to have been a compression of sites within the broad tolerance range of humans and not the occupation sites within of cold climates. If there was a trend towards such expansion into sites with colder climates, it is with the Magdalenians, who inhabited Europe at the LGM. Even so, there was still a significant climatic overlap with Neanderthals and other modern human cultures.

There is little evidence to support the occupation of open tundra-steppe habitats by Neanderthals. In fact, Neanderthals and modern humans appear to have occupied habitat mosaics or combinations of habitats, particularly open, mixed and wetland. Forests and the most open habitats were avoided. Overall, Neanderthals occupied a wider range of habitats than contemporary Aurignacians or the Gravettians that followed.

Neanderthal sites showed a trend towards habitats that included aerial foraging birds. Modern human sites appear not to show such a pronounced trend. Since aerial foragers tend to be summer visitors to Eurasia from the tropics their presence may reflect seasonality and relatively mild summers. The Magdalenian sites, which coinciding

with the LGM, show the weakest signal of aerial foragers which further supports this conclusion.

Finally, evidence supports the view that Gibraltar was a climate refugium with no indication of extreme climatic conditions at this site at any stage of the last glacial cycle (125-10 kyr).



## **4.1 Introduction**

Neanderthals, modern humans and birds would have co-occurred at many sites across space and time. Some of these co-occurrences may have been the result of chance but evidence of repeated presence of (particular) bird species remains in Neanderthal and modern human sites could be interpreted to reflect the climatic or ecological conditions of the sites in which birds and humans were present (Chapter 3). There is another type of association which is of interest in understanding Neanderthal and modern human behaviour: if the association with particular bird species reflected a recurring pattern. This, in turn, could indicate that these associations might be related to aspects of Neanderthal and modern human behaviour, such as hunting of particular bird species. Such patterns of association could then be compared to taphonomic evidence of direct intervention on particular bird species (Chapter 5). Furthermore, if we observe that the species frequently occurring in human sites share common taxonomic or behavioural features, then we might be able to consider how these features might have played out in the human-bird interaction processes.

The approach taken in this chapter looks for patterns of association between birds and Neanderthals in sites in which they coincided. In the first instance, I look for association between Neanderthals and bird species, emphasising those species which occur at highest frequency in Neanderthal sites. However, in a number of cases, a particular species (e.g. rock dove *Columba. livia*) might be frequent in Neanderthal sites, whereas a closely related species (e.g. wood pigeon *C. palumbus*) may be less

so. These differences might reflect behaviour or ecology: in this example rock doves inhabit cliffs, whereas wood pigeons are birds of woodland. Nevertheless, from a human perspective, both species are potentially food resources, so it is useful to combine species into higher taxa. My second approach has therefore been to compare the frequency of occurrence of bird taxa instead of individual species. Third, I have examined the patterns of distribution of birds by behavioural characteristics. I also included additional categories which have the potential to be of relevance to a human hunter such as a Neanderthal. These include edibility (Cott, 1945; 1947 and see Section 4.5.9) and size (body mass).

This chapter therefore describes Neanderthal and modern human associations with birds. My aim is to determine which bird species came into regular contact Neanderthals and modern humans. From this, I look for the behavioural characteristics of the main species associated with Neanderthals and modern humans, and I look for patterns that will inform of how bird species may have been obtained by the hominins.

In order to advance these objectives, this chapter addresses Research Question 2:

Are Neanderthals associated with particular bird species across their range, and if so, what are the features and characteristics of these species? As with Research Question 1, I will compare Neanderthals and modern humans.

## **4.2 Methods**

The first part of this chapter explores the frequency of occurrence of bird species in Neanderthal sites which is calculated as the number of Neanderthal sites in which a bird species is present as a proportion (%) of all the available sites. This permits the identification of the most frequent species of bird at Neanderthal sites. The most

frequent are alpine chough *Pyrrhocorax graculus* (41.9% of sites) and red-billed chough *Pyrrhocorax pyrrhocorax* (30.5%). These are the only two species in the 99<sup>th</sup> percentile and occurring in over 30% of Neanderthal sites (Figure 4.1). Grey partridge *Perdix perdix* (28.3%), common kestrel *Falco tinnunculus* (23.6%) and rock dove *Columba livia* (21.7%) are additional species in the 98<sup>th</sup> percentile. Together, these five species are the only ones occurring in over 20% of sites and are described in detail in Section 4.3.1 – three of these species, the two choughs and the rock dove are among the most frequently found with direct taphonomic evidence of intervention by Neanderthals (see Chapter 5). Black grouse *Tetrao tetrix* (19.2%), mallard *Anas platyrhynchos* (18.4%) and jackdaw *Corvus modedula* (17.9%) are in the 97<sup>th</sup> percentile; rock ptarmigan *Lagopus mutus* (14.2%), magpie *Pica pica* (14.1%) and quail *Coturnix coturnix* (13.6%) are in the 96<sup>th</sup> percentile; golden eagle *Aquila chrysaetos* (12%), carrion crow *Corvus corone* (11.8%) and mistle thrush *Turdus viscivorus* (11.6%) are in the 95<sup>th</sup> percentile. The proportions of species in Neanderthal sites rapidly declines thereafter. The frequencies of all these birds are ranked by order of occurrence in Tables 4.2 to 4.7 , 4.9 and 4.10.

Some bird species may be geographical replacements of each other, for example red-legged partridge (*Alectoris rufa*) is the natural geographical Iberian counterpart of the rock partridge (*A. graeca*) from Italy and the Balkans; in turn the rock partridge is replaced by the chukar (*A. chukar*) to the east. From the perspective of a human (or indeed non-human) predator the taxonomic position of these three partridges would not appear to be important and the reduced frequency of a single species in Neanderthal sites might be actually underrepresenting the association of Neanderthals with *Alectoris* partridges in the example given. For this reason, the second analysis clumps groups of birds into loose taxonomic categories viewed from the perspective of a

human predator. In one case it could be species within a genus (as in the partridges or the thrushes of the genus *Turdus*) while in others the analysis could be taken at the genus level (e.g. *Corvus* crows) and at another scale at the level of the family Corvidae. In the case of the large and diverse genus of falcons (*Falco*) it is one distinct subgroup – the kestrels which separated from other falcons in the Late Miocene (Groombridge *et al.*, 2002; Wink *et al.*, 2004). The gamebirds and ducks provide further examples of scaling up taxonomically in birds that are known to have been of economic importance. With game birds, I examine *Alectoris* and *Perdix* partridges separately, then lump them as partridges and then join them with the grouse (Tetraonidae) into a higher category of game birds (Order Galliformes).

A third approach which I take (after species and taxonomic categories) is to look at bird species by behavioural characteristics (e.g. flocking, scavengers, cliff-nesters, etc.). The aim is to identify if there are categories that stand out as being particularly associated with Neanderthals. In each category I state the proportion of bird species in the category present in Neanderthal sites out of the total number of Palaeartic species available in that category (from Finlayson, 2011). In this case I have additionally run principal component analyses on the behavioural characteristics to tease out further those that are most frequent in Neanderthal sites.

In order to compare and contrast the observed patterns for Neanderthals with the three human cultures that I had most data available for: Aurignacian, Gravettian and Magdalenian, I have compared the birds most frequently associated with each culture also using cluster analysis, using unweighted pair group method with arithmetic mean (UPGMA) and Bray Curtis Distance.



### 4.3 Results

As in the previous chapter, I will subdivide modern humans by cultures. A total of 430 bird species have been recorded in association with either Neanderthals or modern humans during the late Pleistocene of Eurasia (Chapter 2). Figure 4.1 shows the frequency distribution of species found at Neanderthal sites and clearly few species are abundant and a large number appear infrequently with 288 of the 430 species (67%) reported from at least one Neanderthal site.

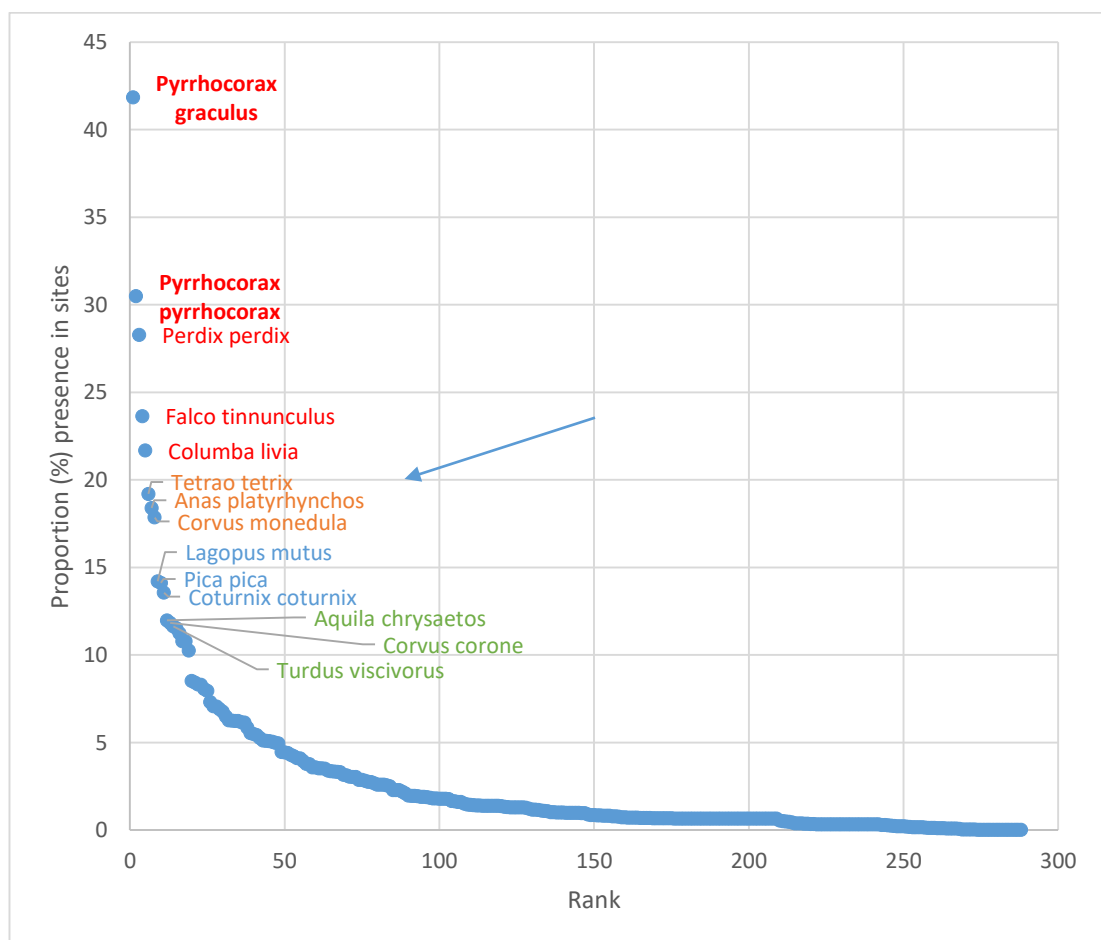


Figure 4.1 Frequency of occurrence of bird species in Neanderthal sites across the Palaearctic ( $n = 288$ ). Species in the 99<sup>th</sup> percentile are shown in red and bold, species in the 98<sup>th</sup> are shown in red. Together, these are the only five species that occur in over 20% of sites (indicated by the arrow) referred to in Section 4.3.1. Species in orange are in the 97<sup>th</sup> percentile, in blue the 96<sup>th</sup> percentile and in green the 95<sup>th</sup> percentile.

#### 4.3.1 Main bird species in Neanderthal sites

Five species stand out by their regular appearance, exceeding 20% of records, in (at least) one of five Neanderthal sites (Figure 4.1). These are high frequencies when we consider the probability of bones being preserved and then being retrieved after tens of thousands of years (Andrews, 1990). These five species are Alpine (or yellow-billed) chough (*Pyrrhocorax graculus*, in 41.9% of all sites), red-billed chough (*Pyrrhocorax pyrrhocorax*, in 30.5%), grey partridge, (*Perdix perdix*, in 28.3%), common kestrel (*Falco tinnunculus*, in 23.6%), and rock dove (*Columba livia*, in 21.7%).

##### 4.3.1.(a) Alpine chough (*P. graculus*)

The most frequent species present in Neanderthal sites is the Alpine chough occurring in 41.9% of all sites. This species is subdivided into three subspecies which occupy the mountains of the mid-latitude belt. This bird had a wider distribution during glacial periods when it appears to have occupied lowland areas across Europe (Yalden & Albarella, 2009). The present distribution of the nominate subspecies includes Morocco (Rif and Atlas mountain ranges), Spain (Cantabrian mountains, Pyrenees and Betic range), Corsica, Alps, north-central Italy (Apennines), east through former Yugoslavia, Albania, Greece, west Bulgaria and south and east Turkey to the Caucasus mountains and northern Iran. The subspecies *digitatus* occurs in south-east Turkey, south to Lebanon and Mount Hermon, east across north Iraq to south-west Iran (Zagros Mountains). The subspecies *forsythi* occupies central Asia from central and northern Afghanistan, north-east through the Pamirs and through Tien Shan and the Altai to the Sayan Mountains and southwards from west-central and northern Pakistan, eastwards

in the Himalayas to Nepal, Bhutan and Arunachal Pradesh, and central and south-west China (Del Hoyo, Elliott & Christie, 2009) .

Within this range the Alpine chough occupies mountain pastures and rocky areas above the tree-line, although it descends into valleys in the winter. The association of this species with humans has been reported in the literature. It is a regular scavenger around human habitation, including ski resorts in Europe, and also camp sites, picnic places and rubbish tips, especially in winter (Del Hoyo, Elliott & Christie, 2009: Goodwin, 1976). It is also tame in the Himalayas where it enters villages and encampments for food (Cramp & Perrins 1994). These authors highlight the remarkably confiding nature of this bird, even following mountain walkers for scraps with cases recorded of catching thrown food items in the air and taking food from the hand. My own experience with this species in Pyrenean ski resorts and in the Cantabrian Mountains confirms these observations (*pers. obs.*; Figure 4.2).



*Figure 4.2 Alpine chough (Pyrrhocorax graculus) feeding on bread crumbs (Photo: Stewart Finlayson).*

Another aspect of the Alpine chough is its highly gregarious nature, often travelling in large flocks between feeding areas. It will gather in large numbers in caves, crevices and chimneys in cliffs and rocky areas, as well as in contemporary buildings. It seems therefore that the Alpine chough's dominant association with Neanderthals has to do with co-occurrence of the two across large areas of the mid-latitude belt, occupation of similar habitats, especially caves, and, the bird's behaviour as a scavenger around human sites. In this regard the scavenging behaviour appears to be much more regular and pronounced than it is with the red-billed chough (Del Hoyo, Elliott & Christie, 2009). The range of published body mass range of this species is 168 to 280g (Cramp & Perrins 1994).

#### 4.3.1.(b) Red-billed chough (*P. pyrrhocorax*)

The second most frequent species present in Neanderthal sites is the red-billed chough occurring in 30.5% of all sites. This species has a similar distribution to the Alpine chough although it tends to occupy lower altitudes. It is subdivided into eight subspecies. The nominate subspecies is found in areas of the British Isles (Ireland, western Scotland, Isle of Man, Wales and Cornwall. The subspecies *P. p. erythroramphos* is found in north-east Portugal, Spain, north-west and South France, south-west Switzerland, central Italy, Sardinia and Sicily. The subspecies *P. p. barbarus* occupies the mountains of Morocco and Algeria and is also found in the Canary Islands. The subspecies *P. p. docilies* occupies the southern Balkans, Greece and Turkey, eastwards, to the Caucasus, the Levant, northern Iraq, Northern Iran, Turkmenistan and Afghanistan. The subspecies *P. p. centralis* is in the north-western Himalayas, north-eastwards through the Altai to Mongolia. It also occurs in south, east through to south-west China and Kashmir. *P. p. himalayanus* occupies the

Himalayas east to Bhutan and north-east India and into central and southern China. The subspecies *P. p. brachypus* occupies north-east and eastern China including Inner Mongolia. Last, *P. p. baileyi* is in the mountain regions of Ethiopia (Del Hoyo, Elliott & Christie, 2009).

The red-billed chough occupies two types of habitat. In western Europe it is associated with coastal cliffs and elsewhere it is a species of high mountain pastures with rocky areas. In some areas, as in the Atlas Mountains it will feed in pastures above the tree line. In the Himalayas it has been reported at 7,950 metres on Mount Everest. There is therefore altitude overlap between the two chough species even though broadly the red-billed chough is lower down. Although less associated with humans than the Alpine chough, this species will feed around grazing stock and does use human habitation for nesting sites and for roosting. It forms large roosts inside caves and chimneys in the winter and it is apparently easy to catch by hand with lights in these situations (Guillermo Blanco, *pers. comm*). It has been known to scavenge for scraps of human food in some areas but not to the extent of the Alpine chough or the jackdaw (*C. monedula*) (Godwin 1976). The published body mass range for this species is from 198 to 390 g (Cramp & Perrins 1994).

#### 4.3.1.(c) Grey partridge (*P. perdix*)

The grey partridge is the third most frequent bird at Neanderthal sites, present at 28.3% of all locations. This is a more geographically widespread species than either of the choughs but it also has a more northerly distribution and is absent from much of Iberia. In central Asia it is replaced by the sister species *P. daurica* with a third – *P. hodgsoniae* – in Tibet, the Himalayas and along its southern flanks. Seven subspecies

of grey partridge are recognised. The subspecies *hispanicus* occurs in northern Spain and north-east Portugal but is largely absent from Mediterranean regions of Iberia where the *Alectoris* partridges predominate. The subspecies *armoricana* ranges from Normandy and central France northwards to the Ardennes and Morvan Mountains. It is replaced in the north-east Netherlands and north-west Germany by *sphagnetorum*. The nominate subspecies occupies a wide belt from the British Isles and Scandinavia to the Alps and the Balkans. The subspecies *lucida* is found from Finland eastwards to the Ural Mountains and south to the Black Sea and northern Caucasus with *canescens* in Turkey, the Caucasus, Transcaucasia and Iran. Finally, *robusta* spreads eastwards of the Urals through Kazakhstan to south-western Siberia and north-western China (del Hoyo, Elliott & Sargatal, 1994). Thus the range of this species would have overlapped broadly with that of the Neanderthals, and almost entirely during cool periods when the northern populations of grey partridge would have disappeared.

Grey partridges occupy temperate zone grasslands and steppe, sometimes with some shrubby cover. In this habitat they spend their entire time on the ground, keeping to the cover of grasses. In this sense, though not sharing the rocky habitats with the choughs, grey partridges would have lived in open areas with little cover, of the sort used by choughs for feeding. Similar to the choughs also, grey partridges are gregarious, living in flocks for 7 to 8 months of the year (Cramp, 1980). The published body mass range for this species is from 310 to 450 g, so heavier than choughs (Cramp, 1980).

#### 4.3.1.(d) Common kestrel (*Falco tinnunculus*)

The common kestrel is the fourth most frequent species in Neanderthal sites, being recorded in 23.6% of these. This is the most geographically widespread of the main species found at Neanderthal sites. Eleven sub-species are recognised. The nominate

subspecies occurs across north Africa, Europe and the Middle East right across to eastern Siberia and the Russian Far East. Most of the other sub-species, except in Africa, are more localised than the nominate: *interstinctus* in Tibet and into northern Indochina and south and central China to Korea and Japan; *objurgatus* in southern India and Sri Lanka; *canariensis* in Madeira and the western Canary Islands; *dacotiae* in the eastern Canary Islands; *neglectus* in the northern Cape Verde Islands; *alexandri* in the south-eastern Cape Verde Islands; *rupicolaeformis* in north-east Africa and Arabia; *archerii* in Somalia, coastal Kenya and Socotra; *rufescens* in western and central Africa eastwards to Ethiopia and southwards to Tanzania and northern Angola; and *rupicolus* from northern Angola south to South Africa (del Hoyo, Elliott & Sargatal, 1994). The Neanderthal range would have therefore been fully within the range of the common kestrel at all times.

The common kestrel is highly adaptable and occupies a wide variety of habitats but these tend to be open, allowing it to hunt from the air or vantage posts. It is at home in rock faces where it nests although it can also do so on trees. It is a species that has adapted to humans, occupying villages, towns and cities. There is no reason to suppose that such behaviour did not apply to the Palaeolithic when Neanderthals and common kestrels would have been regular neighbours around cave and camp sites. In such situations, common kestrels may have benefited from hunting rodents living close to humans, acting as commensals (Larson *et al.*, 2004). Unlike the three most frequently recorded species, the common kestrel is usually solitary but may occur in small flocks during migration or where there is an abundance of food (Ferguson-Lees & Christie, 2001). The published body mass range is from 117 to 260 g (Cramp, 1980).

#### 4.3.1.(e) Rock dove (*Columba livia*)

The fifth and last of the species occurring in over 20% of Neanderthal sites is the rock dove at 21.7%. The natural distribution of the rock dove is complicated to discern given the presence of many populations of feral pigeon that may often appear identical in plumage to the wild type. All the same, it seems clear that this is a species of the rocky habitats of the mid-latitude belt, especially when we add its distribution to those of the closely related hill pigeon *C. rupestris* and the snow pigeon *H. leuconota* of the Himalayas and surrounding areas (del Hoyo, Elliott & Sargatal, 1997). The nominate subspecies is found from the British Isles and western Mediterranean eastwards to the Caucasus and western Siberia. Eleven other subspecies are recognised: *atlantis* in Madeira, the Azores and Cape Verde Islands; *canariensis* in the Canary Islands; *gymnocyclus* in western Africa, from Mauretania to Senegambia; *targia* in the Central Sahara and Sudan; *dakhlæ* in the Dakhla and Kharga oases; *butleri* around the margins of the Red Sea; *schimperi* along the Nile Valley to Khartoum and into Eritrea; *palaestinae* in Palestine, Sinai and Arabia; *gaddi* in the Azerbaijan, Iran, northern Afghanistan and across Transcaspia to Uzbekistan; *neglecta* from Turkestan to the Punjab; and *intermedia* in India and Sri Lanka (del Hoyo, Elliott & Sargatal, 1997). Its geographical range would have therefore been coincident with that of Neanderthals.

The habitat of this species, as the name suggests, is rocky and the feral form has adapted to occupying buildings and other human structures. The natural habitat ranges from coastal cliffs to cliff faces deep in continental areas. It is a sociable species that forms large flocks and is likely to have been commensal with humans, feeding off scraps of food left by people, for much of their shared history (Larson *et al.*, 2004). The published body mass range is from 180 to 360 g for wild birds (Cramp, 1985).



#### 4.3.2 Main species – summary

The five bird species that occur in over 20% of Neanderthal sites have several features in common. They all co-occupy, and would have co-occupied, the entire geographical range of the Neanderthals, with the exception of grey partridge which only reaches southwards into the far north of Iberia. Four species (the two choughs, kestrel and rock dove) would have also co-shared the rocky habitats and its caves, a habitat which would have been plentiful across the mid-latitude belt which was the Neanderthal stronghold (Finlayson, 2004). Three species (Alpine chough, common kestrel and rock dove) show clear associations, commensal in nature, with humans even today. Four species (the choughs, grey partridge and rock dove) are gregarious. All are medium-sized species which fall in the 100 to 450 g body mass range.

#### 4.4 Main taxonomic categories of bird species in Neanderthal sites

Six taxa stand out by their regular appearance. These are corvids (69.5%), gamebirds (64.4%), thrushes (35.9%), ducks (34.4%), pigeons and doves (31.7%) and kestrels (31.6%) (Table 4.1). I examine these below.

*Table 4.1 Number of species and presence of higher taxa in Neanderthal sites. Combinations of groupings are shown to highlight importance of representation within taxa. Only categories exceeding 20% presence in Neanderthal sites are included. N = 154. Falco Kestrels are: common kestrel (F. tinnunculus); lesser kestrel (F. naumanni); red-footed falcon (F. vespertinus).*

<b>Taxonomic category</b>	<b>Number of species</b>	<b>Proportion (%) of sites occupied</b>
<b>All corvids</b>	9	69.5
<b>partridges + tetraonids</b>	12	64.4
<b><i>Pyrrhocorax</i></b>	2	53.5

<b>Taxonomic category</b>	<b>Number of species</b>	<b>Proportion (%) of sites occupied</b>
<i>Alectoris + Perdix + Coturnix</i>	5	47.8
<i>Alectoris + Perdix</i>	4	44.6
<i>Corvus + Pica</i>	5	40.4
<b>All tetraonids</b>	7	35.9
<i>Corvus</i>	4	34.7
<b>all ducks</b>	21	34.4
<i>Turdus</i>	6	35.9
<i>Columba</i>	3	31.7
<i>Falco</i> kestrels	3	31.6
<i>Anas</i>	7	28.1
<i>Tetrao</i>	2	26.1
<i>Alectoris</i>	3	24.3
<i>Lagopus</i>	2	23.7

#### 4.4.1 Corvids – Corvidae

Corvids (Corvidae) is the best represented taxonomic category in Neanderthal sites. Several species of corvids (Table 4.2) fall below the 20% presence level but collectively surpass this mark (Figure 4.3). When they have features in common, they may be grouped into a higher order taxonomic, or ecological, category. The choughs often co-occur with other Corvidae, most notably *Corvus/Coloeus*: jackdaw (*C. monedula*, 17.9%); carrion crow (*C. corone*, 11.8%); raven (*C. corax*, 10.8%); and rook (*C. frugilegus*, 5.5%). These four species are widespread across the Palaearctic and all occupy large areas of the mid-latitude belt, least so in the case of the rook which

is absent from much of Iberia, Italy and Greece (Cramp & Perrins, 1994). The magpie (*Pica pica*) is well represented in Neanderthal sites at 14.1%, which is not surprising as it is also widespread and occupies the entire mid-latitude belt. Most of these species are of open ground with the choughs, jackdaw and raven being particularly associated with rocky habitats. Three woodland corvids are also present: jay (*Garrulus glandarius*, 8.4%), a widespread species that also occupies the mid-latitude belt; spotted nutcracker (*Nucifraga caryocatactes*, 3.4%), a widespread boreal species which is found in the Alps, Balkans and southern Siberia and would have been displaced southwards towards the Neanderthal range during glacials; and Iberian azure-winged magpie (*Cyanopica cooki*, 0.23%), today restricted to the Iberian Peninsula (Finlayson, 2011).



*Figure 4.3 Corvids (Corvidae) is the best represented taxonomic category in Neanderthal sites. This photograph shows a pair of ravens (Corvus corax), a typical corvid species. (Photo: Stewart Finlayson).*

The two choughs put together occupy 53.5% of Neanderthal sites, showing their propensity for association with these humans. The *Corvus* crows are present in 34.71% of sites and, with magpie added, the proportion rises to 40.3%. When all corvids are included, then the proportion of Neanderthal sites with corvids reaches 69.47%, higher than for game birds (Table 4.1).

Table 4.2 Corvid species found in Neanderthal sites ( $n = 154$ )

Common Name	Scientific Name	Proportion (%) present in Neanderthal sites
<b>Alpine Chough</b>	<i>Pyrrhocorax graculus</i>	41.9
<b>Red-billed Chough</b>	<i>Pyrrhocorax pyrrhocorax</i>	30.5
<b>Jackdaw</b>	<i>Coloeus monedula</i>	17.9
<b>Carrion Crow</b>	<i>Corvus corone</i>	11.8
<b>Magpie</b>	<i>Pica pica</i>	14.1
<b>Raven</b>	<i>Corvus corax</i>	10.8
<b>Rook</b>	<i>Corvus frugilegus</i>	5.5
<b>Jay</b>	<i>Garrulus glandarius</i>	8.4
<b>Spotted Nutcracker</b>	<i>Nucifraga caryocatactes</i>	3.4
<b>Iberian Azure-winged Magpie</b>	<i>Cyanopica cooki</i>	0.23

#### 4.4.2 Game birds - Galliformes

In this subsection I look at gamebirds of the order Galliformes, subdivided into the families Tetraonidae (grouse, Figure 4.4) and Phasianidae (partridges, quails, pheasants and allies) (Table 4.3).

The grey partridge is one of the top five species found in Neanderthal sites. A second partridge genus – *Alectoris* – also occurs in these sites but the species fall below the 20% level. These partridges occupy segments of the mid-latitude belt, roughly west to east. Three species have been identified from these sites: red-legged partridge (*A. rufa*, 11.5%); rock partridge (*A. graeca*, 10.2%); and chukar (*A. chukar*, 3.3%). They are geographical counterparts, red-legged in south-west Europe, rock in Italy, the Balkans and southern flanks of the Alps, and chukar from Greece and Turkey eastwards across the mid-latitude belt to China (del Hoyo, Elliott & Sargatal, 1994). The geographic ranges of these three species matches that of Neanderthals. Four other species are found in localised areas of the Palaearctic: *A. melanocephala* in southern Arabia; *A. magna* in north-central China; *A. philbyi* in south-west Arabia and Yemen; and *A. barbara* in north-west Africa, regions largely outside the Neanderthal range. The three *Alectoris* partridges collectively occupy 24.3% of Neanderthal sites (Table 4.1). If we combine the two partridge genera (*Alectoris* and *Perdix*), then the presence of partridges rises to 44.6%; adding the quail (*Coturnix coturnix*), a small migratory species related to partridges found in 13.6% of Neanderthal sites, then the proportion increases to 47.8% (Table 4.1). Thus, partridges were present in almost half of all Neanderthal sites.

The second family of game birds – grouse, Tetraonidae – is also represented in Neanderthal sites by three species of *Tetrao*: black grouse (*T. tetrix*, 19.2%), capercaillie (*T. urogallus*, 5.3%), and the Caucasian black grouse (*T. mlokosiewiczii*,

4.2%), *Lagopus*, with rock ptarmigan (*L. mutus*, 14.2%) and willow grouse (*L. lagopus*, 11.2%). Three other species occur in low frequency: hazel grouse (*Tetrastes bonasia*, 2.6%), Caucasian snowcock (*Tetraogallus caucasicus*, 1.5%) and Altai snowcock (*T. altaicus*, 0.7%).

The three *Tetrao* species occur in 26% of Neanderthal sites. The black grouse and the capercaillie are species that occupy a broad belt of temperate and boreal forest north of the mid latitude belt. There are small populations of these species in the mid latitude belt: black grouse in the Alps and Balkans and also in the Altai Mountains in southern Siberia; Caucasian black grouse in the Caucasus; and capercaillie in the Pyrenees, Alps, Balkans and the Altai Mountains, (del Hoyo, Elliott & Sargatal, 1994). This means that Neanderthals would have co-occurred with these species in the southern parts of their range.



*Figure 4.4 Game birds is the second most frequent taxonomic category in Neanderthal sites. Two main families are represented: Phasianidae and Tetraonidae, represented here by the Black Grouse (Tetrao tetrix). (Photo: Stewart Finlayson).*

The two species of *Lagopus* occur in 23.67% of Neanderthal sites. The willow grouse has a boreal distribution, where it occupies open habitats with some cover, with some populations reaching the Altai Mountains whereas the rock ptarmigan has a similar distribution but occupies tundra. It has relict populations in the Pyrenees, Alps, and in the Altai mountains (del Hoyo, Elliott & Sargatal, 1994). As with *Tetrao*, these grouse would have co-occurred with Neanderthals in the southern parts of their range.

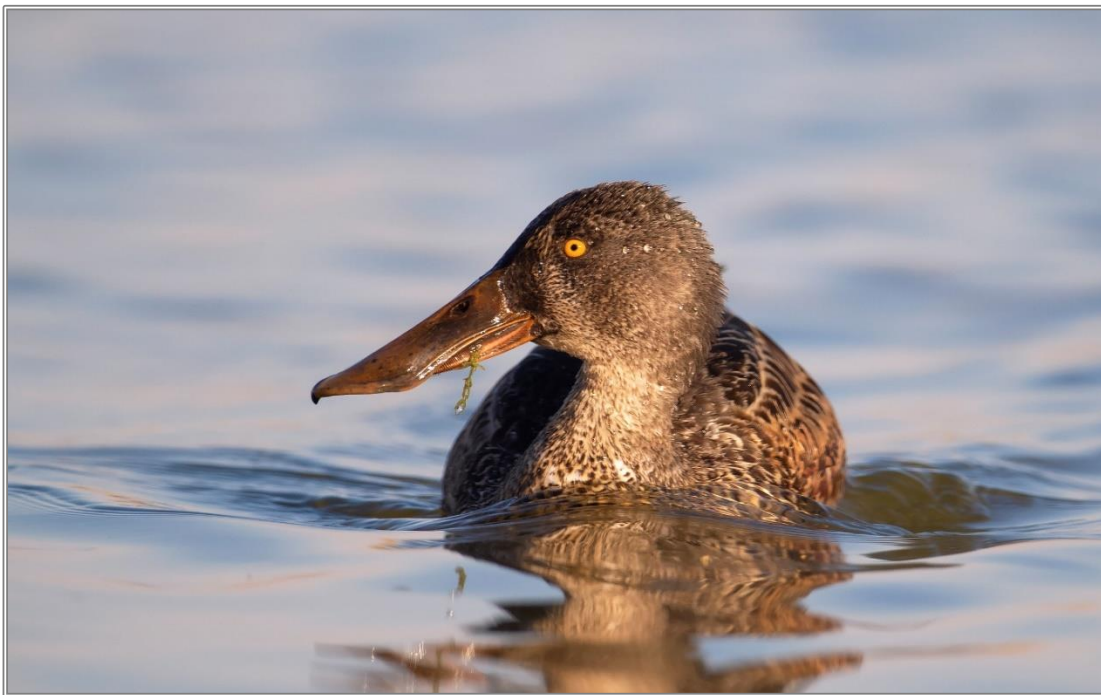
Putting all the tetraonids together, we find that they are present in 35.9% of Neanderthal sites (Table 4.1). If we combine the tetraonids and the partridges, the presence of game birds in Neanderthal sites rises to 64.4%. This means that game birds are present in practically two out of three Neanderthal sites.

*Table 4.3 Game bird species found in Neanderthal sites (n = 154).*

<b>Common Name</b>	<b>Scientific Name</b>	<b>Proportion (%) present in Neanderthal sites</b>
<b>Grey Partridge</b>	<i>Perdix perdix</i>	28.3
<b>Black Grouse</b>	<i>Tetrao tetrix</i>	19.2
<b>Rock Ptarmigan</b>	<i>Lagopus mutus</i>	14.2
<b>Quail</b>	<i>Coturnix coturnix</i>	13.6
<b>Red-legged Partridge</b>	<i>Alectoris rufa</i>	11.5
<b>Willow Grouse</b>	<i>Lagopus lagopus</i>	11.2
<b>Rock Partridge</b>	<i>Alectoris graeca</i>	10.2
<b>Capercaillie</b>	<i>Tetrao urogallus</i>	5.3
<b>Caucasian Black Grouse</b>	<i>Tetrao mlokosiewiczi</i>	4.2
<b>Chukar</b>	<i>Alectoris chukar</i>	3.3
<b>Hazel Grouse</b>	<i>Tetrastes bonasia</i>	2.6
<b>Caucasian Snowcock</b>	<i>Tetraogallus caucasicus</i>	1.5
<b>Altai Snowcock</b>	<i>Tetraogallus altaicus</i>	0.7

#### 4.4.3 Ducks – Anatidae

The third most frequent taxonomic group, after corvids and game birds, is the ducks (Table 4.1, Figure 4.5). In all, 21 species are present in Neanderthal sites (34.36%), with seven belonging to the largest genus, *Anas* (28.11%). The main species, the mallard (*Anas platyrhynchos*) (Table 4.4), is the most cosmopolitan of all ducks and its range encompasses that of Neanderthals. The other species present combinations of widespread temperate or boreal distributions or across the mid-latitude belt. These ducks contrast with the corvids and game birds in being migratory in many instances so, even if their distributions were to the north of Neanderthals, they would have reached Neanderthal territory on migration or in the winter. Of note is the presence of truly arctic species, such as long-tailed duck (*Clangula hyemalis*) or Steller's eider (*Polysticta stelleri*), which presumably reached Neanderthal areas during glacials. These species occur in a very small proportion of sites (Table 4.4). Ducks were present in around a third of all Neanderthal sites.



*Figure 4.5 Ducks (Anatidae) is the third most important taxonomic category in Neanderthal sites. The image shows a female shoveler (Anas clypeata). (Photo: Stewart Finlayson)*



Table 4.4 Duck species found in Neanderthal sites ( $n = 154$ ).

Common Name	Scientific Name	Proportion (%) present in Neanderthal sites
<b>Mallard</b>	<i>Anas platyrhynchos</i>	18.4
<b>Garganey</b>	<i>Anas querquedula</i>	8.1
<b>Wigeon</b>	<i>Anas penelope</i>	6.5
<b>Teal</b>	<i>Anas crecca</i>	5.4
<b>Pintail</b>	<i>Anas acuta</i>	4.1
<b>Ferruginous Duck</b>	<i>Aythya nyroca</i>	3.1
<b>Common Pochard</b>	<i>Aythya farina</i>	2.8
<b>Common Scoter</b>	<i>Melanitta nigra</i>	2.6
<b>Goosander</b>	<i>Mergus merganser</i>	2.6
<b>Shoveler</b>	<i>Anas clypeata</i>	2.5
<b>Gadwall</b>	<i>Anas strepera</i>	2.3
<b>Tufted Duck</b>	<i>Aythya fuligula</i>	1.9
<b>Goldeneye</b>	<i>Bucephala clangula</i>	1.8
<b>Red-breasted Merganser</b>	<i>Mergus serrator</i>	1.4
<b>Long-tailed Duck</b>	<i>Clangula hyemalis</i>	1.4
<b>Smew</b>	<i>Mergus albellus</i>	1.3
<b>Ruddy Shelduck</b>	<i>Tadorna ferruginea</i>	1.3
<b>Common Shelduck</b>	<i>Tadorna tadorna</i>	0.7
<b>Velvet Scoter</b>	<i>Melanitta fusca</i>	0.7
<b>Red-crested Pochard</b>	<i>Netta rufina</i>	0.04
<b>Steller's Eider</b>	<i>Polysticta stelleri</i>	0.02

#### 4.4.4 Thrushes – Turdidae, *Turdus*

The thrushes of the genus *Turdus* distinguish themselves from the rest of their family by their significantly larger size and habits. Six species are found in Neanderthal sites (Table 4.5, Figure 4.6). No single species is present in over 20% of sites but, collectively, thrushes are present in 35.9% (Table 4.1), surpassing the pigeons and doves. Thrushes are birds of wooded vegetation and woodland-open ground ecotones and all, except ring ouzel (*Turdus torquatus*), have adapted to human habitats, particularly gardens and parks. They feed on the ground for invertebrates and in shrubs and trees for fruit (Cramp, 1988).

Mistle thrush (*T. viscivorus*), blackbird (*T. merula*) and song thrush (*T. philomelos*) are widespread across large areas of the Palaearctic including the mid-latitude belt and they are the best represented in Neanderthal sites (Table 4.5). Fieldfare (*T. pilaris*) and redwing (*T. iliacus*) have boreal distributions but are highly migratory reaching south to the shores of the Mediterranean. They would have been seasonally available to Neanderthals, which may explain their relatively low frequency of occurrence (Table 4.5), and possibly all year during glacial periods when the breeding range of these species would have shifted southwards. The ring ouzel (*T. torquatus*) has a disjunct distribution, with populations in the tundra and others in bioclimatically equivalent Alpine zones across the mid-latitude belt (Cramp, 1988). Although potentially the southern part of the range would have coincided with Neanderthals, their low frequency of occurrence in Neanderthal sites (the lowest of all thrushes, Table 4.5) suggests that they may have been separated from Neanderthals by altitude.



Figure 4.6 Thrushes (*Turdus*) is the fourth most important taxonomic category of birds in Neanderthal sites. The image shows the most frequent of these species, the mistle thrush (*Turdus viscivorus*). (Photo: Stewart Finlayson)

Table 4.5 Thrush species found in Neanderthal sites ( $n = 154$ )

Common Name	Scientific Name	Proportion (%) present in Neanderthal sites
<b>Mistle Thrush</b>	<i>Turdus viscivorus</i>	11.63
<b>Blackbird</b>	<i>Turdus merula</i>	10.79
<b>Song Thrush</b>	<i>Turdus philomelos</i>	7.05
<b>Fieldfare</b>	<i>Turdus pilaris</i>	6.24
<b>Redwing</b>	<i>Turdus iliacus</i>	4.94
<b>Ring Ouzel</b>	<i>Turdus torquatus</i>	1.88

#### 4.4.5 Pigeons and doves – Columbidae

The rock dove (*Columba livia*) (Figure 4.7) is one of the top five species to appear in Neanderthal sites (21.68%, subsection 4.1.5; Table 4.6). There are two other species in the genus which are also present in these sites: stock dove (*C. oenas*, 7.1%) and wood pigeon (*C. palumbus*, 6.9%). A fourth species is the migratory turtle dove (*Streptopelia turtur*) which is rare in Neanderthal sites (0.7%).



*Figure 4.7 Pigeons (Columbidae) is the fifth most important taxonomic category in Neanderthal sites. The image shows a rock dove (Columba livia) which is also the fifth most important species. (Photo: Stewart Finlayson)*

Adding the *Columba* doves to rock dove raises the pigeon presence in Neanderthal sites to 31.7% (Table 4.1) while adding the turtle dove does not change this proportion at all. Wood pigeon and stock dove contrast with rock dove by their preference for trees in which to nest and shelter although the latter species may occasionally use rocky habitats where trees are far away from food sources (Cramp, 1985). Both species

forage principally in the forest-open ground ecotone. The difference in habitat with rock dove may account for their lower frequency in Neanderthal sites. The turtle dove has similar arboreal habits and its presence in Neanderthal sites is negligible.

*Table 4.6 Pigeon and dove species found in Neanderthal sites (n = 154)*

Common Name	Scientific Name	Proportion (%) present in Neanderthal sites
Rock Dove	<i>Columba livia</i>	21.7
Stock Dove	<i>Columba oenas</i>	7.1
Wood Pigeon	<i>Columba palumbus</i>	6.9
Turtle Dove	<i>Streptopelia turtur</i>	0.7

#### 4.4.6 *Falco* kestrels

The falcons (genus *Falco*, Figure 4.8) form a diverse group with very different habits. Here I consider the kestrels which form a distinct taxonomic subgroup within the falcons (Finlayson, 2011) given that the common kestrel (*F. tinnunculus*) is one of the top five species in Neanderthal sites. Two other species, lesser kestrel (*F. naumanni*, 4.3%) and red-footed falcon (*F. vespertinus*, 3.3%) are much less frequent (Table 4.7). The lesser kestrel is a colonial cliff nesting species which has adapted to nesting in human constructions, typically abandoned farm buildings. In contrast the red-footed falcon nests in trees, usually taking over stick nests of other species, and does not breed in colonies. Both species are typical of the mid-latitude belt, although red-footed falcon has a more eastern distribution than lesser kestrel, and they exploit steppe and



*Figure 4.8 Small falcons of the kestrel group is the sixth most important taxonomic category in Neanderthal sites. The dominant species is the common kestrel (Falco tinnunculus), which is actually the fourth most common species in these sites. (Photo: Stewart Finlayson).*

grasslands where they primarily hunt large insects. They are highly migratory, wintering in tropical Africa (Cramp, 1980). The much lower presence of these species in Neanderthal sites suggests that, despite a high geographical overlap with Neanderthals, the predilection of lesser kestrels and red-footed falcons for vast expanses of steppe and grassland may have separated them from Neanderthals. Put together the kestrels are present in 31.64% of Neanderthal sites (Table 4.1).

*Table 4.7 Kestrel species found in Neanderthal sites (n = 154)*

Common Name	Scientific Name	Proportion (%) present in Neanderthal sites
Common Kestrel	<i>Falco tinnunculus</i>	23.6
Lesser Kestrel	<i>Falco naumanni</i>	4.3
Red-footed Falcon	<i>Falco vespertinus</i>	3.3

#### **4.4.7 Main taxa - summary**

Several features of the main taxa appearing in Neanderthal sites emerge from this analysis:

- (a) Five (corvids, ducks, thrushes, pigeons and kestrels) of the six main taxa have geographically widespread species and their ranges includes the mid-latitude belt (Finlayson, 2004), which means they would have co-occupied large parts of the Neanderthal range: *C. monedula*, *C. corone*, *C. corax*, *C. frugilegus*, *P. pica*, *G. glandarius*, *A. platyrhynchos*, *A. clypeata*,

*A. strepera*, *T. viscivorus*, *T. merula*, *T. philomelos*, *C. oenas*, *C. palumbus*,  
*S. turtur* (rare) and *F. tinnunculus*;

(b) Four (corvids, game birds, ducks and kestrels) of the six main taxa have species which are typical of the mid-latitude belt and would have also co-occupied large areas of the Neanderthal range: *P. graculus*, *P. pyrrhonorax*, *C. cooki* (localised), *A. rufa*, *A. graeca*, *A. chukar*, *T. mlokosiewicki*, *T. caucasicus* (localised), *T. altaicus* (localised), *T. ferruginea* (rare), *A. nyroca*, *N. rufina* (rare), *F. naumanni* and *F. vespertinus*;

(c) Three (corvids, game birds and ducks) of the six main taxa have species with distribution north of the main Neanderthal range but which would have been displaced southwards into the range during glacial events. Some of these species retain relict modern/ contemporary populations in the mid-latitude belt: *N. caryocatactes*, *P. perdix*, *T. tetrix*, *T. urogallus*, *L. lagopus*, *L. mutus*, *T. tadorna* (rare), *M. fusca* (rare), *M. merganser*, *M. albellus* (rare), *B. clangula* (rare), *C. hyemalis* (rare) and *P. stelleri* (rare);

(d) Two (ducks and thrushes) of the six main taxa have species with distribution north of the main Neanderthal range but which would have entered the Neanderthal range during migration or in the winter months: *A. querquedula*, *M. nigra*, *M. serrator* (rare), *A. ferina*, *A. fuligula* (rare), *A. querquedula*, *A. penelope*, *A. crecca*, *A. acuta*, *T. pilaris* and *T. iliacus*;

(e) Three (corvids, pigeons and kestrels) of the six main taxa have species which are at home in rocky habitats which are used for nesting or roosting. These relatively few but frequently encountered species, includes four of



the top five: *P. graculus*, *P. pyrrhocorax*, *C. monedula*, *C. corax*, *C. livia* and *F. tinnunculus*;

(f) Four (corvids, game birds, thrushes and kestrels) of the six main taxa have species which feed on the ground, usually in open and open/woodland ecotone habitats: *P. graculus*, *P. pyrrhocorax*, *C. monedula*, *C. corone*, *C. corax*, *C. frugilegus*, *P. pica*, *C. cooki*, *P. perdix*, *A. rufa*, *A. graeca*, *A. chukar*, *C. coturnix*, *T. tetrix*, *T. urogallus*, *T. mlokosiewickzi*, *L. mutus*, *L. lagopus*, *T. merula*, *T. viscivorus*, *T. pilaris*, *T. iliacus* and *F. tinnunculus*;

(g) Three (game birds, thrushes and kestrels) of the six main taxa have species of open ground occur in low frequency. Two of these taxa (gamebirds and thrushes) include high mountain species: *T. caucasicus*, *T. altaicus* and *T. torquatus*. The low frequency of the first two may be explained because of their localised geographical spread but the ring ouzel *T. torquatus* is widespread across the mid-latitude belt. The third taxon is of species of open steppe and grassland, typically far away from woodland: *F. naumanni* and *F. vespertinus*. The conclusion from (e) to (g) is that Neanderthals were largely associated with groups of birds of rocky habitats as well as woodland/open ground ecotones, but not from those of high mountain or open steppe/grasslands;

(h) a third of the sites are linked with ducks which implies the presence of water bodies close by;

(i) five corvids (*P. graculus*, *C. monedula*, *C. corone*, *C. corax* and *P. pica*) as well as rock dove *C. livia* and common kestrel *F. tinnuculus* are potential commensals;

- (j) at least four of the six taxa that contribute over 20% of species in Neanderthal sites are potentially edible: game birds (Galliformes); ducks (Anatidae); thrushes (*Turdus*) and pigeons (*Columba*).

In the next section I will look at the ecological properties of the main species associated with Neanderthal sites, paying particular attention to species typical of rocky habitats, open and open/woodland ecotones, water bodies, ground dwellers, commensals, scavengers, lekking birds and those with the potential to have been food sources for the Neanderthals.

#### **4.5 Main behavioural characteristics of birds in Neanderthal sites**

In this section I analyse the distribution of bird species in Neanderthal sites in accordance with their behavioural characteristics (Table 4.8).

##### **4.5.1 Flocking species**

This category has the highest representation in Neanderthal sites with 145 of a possible 198 (73.2%) species occupying 91.1% of all sites (Table 4.8, Figure 4.9). The species represented come from diverse taxonomic backgrounds. They include most of the main taxa recorded in the previous section (corvids, game birds, ducks, pigeons and thrushes). The top 14 best represented species are from these taxa. Other groups represented include starlings (Sturnidae), finches (Fringillidae), swifts (Apodidae), martins (Hirundinidae), sparrows (Passeridae) and buntings (Emberizidae).



*Figure 4.9 Flocking birds are well represented in Neanderthal sites. The image shows a flock of red-billed choughs (Pyrrhocorax pyrrhocorax). (Photo: Stewart Finlayson)*

#### **4.5.2 Commensals and scavengers**

The second category by representation in Neanderthal sites is commensals, a diverse group of species with the potential for taking benefit of Neanderthal camp sites as sources of food (e.g. rodents, food scraps, etc.; Steigerwald, *et al.*, 2015). A total of 53 (out of a possible 81 = 65.4%) species fall in this category are reported from 84.9% of all sites (Table 4.8). The common kestrel is, the pre-eminent representative of this category which includes fifteen diurnal raptors, twelve owls and nine corvids (Table 4.9).

There are only six species of large scavengers in the Palaearctic and all are represented in Neanderthal sites (Table 2.5; Figure 4.10). They are the four vultures – cinereous (*Aegypius monachus*), griffon (*Gyps fulvus*), bearded (*Gypaetus barbatus*) and Egyptian (*Neophron percnopterus*) – along with golden eagle (*Aquila chrysaetos*) and white-tailed eagle (*Haliaeetus albicilla*). Together, these birds occur in 23.3% of Neanderthal sites which is a high proportion when we consider the few species involved. The eagles have widespread distributions and the vultures are all mid-latitude belt species which means that all six species co-occupied large parts of the Neanderthal range. With the exception of the tree-nesting cinereous vulture, the rest are cliff-nesting species.



*Figure 4.10 Although represented by only six species, all large scavengers are found in Neanderthal sites and are present in high frequency. One of the species, represented here, is the griffon vulture (Gyps fulvus). (Photo: Stewart Finlayson)*

There is a group of “lesser” (or partial) scavengers, i.e. species that are attracted to carcasses of smaller animals and which also scavenge on a variety of foods, and which

largely comprise corvids and small- to medium-sized raptors. Twenty-six of 33 such species (78.8%) are present in Neanderthal sites. When added to the six species of large scavengers, they make up a total of 39 species which occupy 58.1% of Neanderthal sites. When these are then added to the commensals, they make up 63 species which are found in 90.1% of Neanderthal sites (Table 4.8).

Table 4.8 Number of species by behavioural characteristics in Neanderthal sites. Only categories exceeding 20% presence in Neanderthal sites ( $n = 154$ ) are included.

Behavioural characteristics	Number of species (S)	Potential number of species showing behavioural characters (P)	Proportion (%) of species (S) out of potential species (P) actually found in Neanderthal sites	Number of sites occupied by species showing behavioural characteristics (S <sub>t</sub> )	Proportion (%) of sites (S <sub>t</sub> ) occupied by species showing behavioural characters (n=154)
ground + cliff/rocky nesters	183	245	74.7	147	95.7
flocking	145	198	73.2	140	91.1
all scavengers + commensals	63	120	52.5	139	90.1
commensals	53	81	65.4	131	84.9
cliff nesters	37	44	84.1	126	82.0
partial scavengers	26	33	78.8	74	48.1
all ground nesters	146	201	72.6	121	78.3
edible	57	81	70.1	120	77.9

<b>Behavioural characteristics</b>	<b>Number of species  (S)</b>	<b>Potential number of species showing behavioural characters  (P)</b>	<b>Proportion (%) of species (S) out of potential species (P) actually found in Neanderthal sites</b>	<b>Number of sites occupied by species showing behavioural characteristics  (S<sub>t</sub>)</b>	<b>Proportion (%) of sites (S<sub>t</sub>) occupied by species showing behavioural characters (n=154)</b>
<b>terrestrial ground nesters</b>	98	137	71.5	107	69.4
<b>ground cryptic</b>	73	95	76.8	106	68.8
<b>arboreal</b>	93	170	54.7	95	61.9
<b>all scavengers</b>	32	39	82.1	89	58.1
<b>large scavengers + lekking</b>	15	16	93.8	68	44.1
<b>wetland ground nesters</b>	44	64	68.8	56	36.3
<b>lekking</b>	9	10	90	44	28.6
<b>large scavengers</b>	6	6	100	36	23.3

Table 4.9 Potential commensal species (n = 53) present in Neanderthal sites. R = diurnal raptor, O = owl, C = corvid.

Common Name	Scientific Name	Proportion (%) of sites occupied (n=154)
<b>Alpine Chough (C)</b>	<i>Pyrrhocorax graculus</i>	41.85
<b>Red-billed Chough (C)</b>	<i>Pyrrhocorax pyrrhocorax</i>	30.49
<b>Common Kestrel (R)</b>	<i>Falco tinnunculus</i>	23.64
<b>Rock Dove</b>	<i>Columba livia</i>	21.68
<b>Jackdaw (C)</b>	<i>Corvus monedula</i>	17.86
<b>Magpie (C)</b>	<i>Pica pica</i>	14.12
<b>Carrion Crow (C)</b>	<i>Corvus corone</i>	11.83
<b>Mistle Thrush</b>	<i>Turdus viscivorus</i>	11.63
<b>Blackbird</b>	<i>Turdus merula</i>	10.79
<b>Raven (C)</b>	<i>Corvus corax</i>	10.78
<b>Eagle Owl (O)</b>	<i>Bubo bubo</i>	8.52
<b>Jay (C)</b>	<i>Garrulus glandarius</i>	8.43
<b>Common Starling</b>	<i>Sturnus vulgaris</i>	8.29
<b>Stock Dove</b>	<i>Columba oenas</i>	7.06
<b>Song Thrush</b>	<i>Turdus philomelos</i>	7.05
<b>Little Owl (O)</b>	<i>Athene noctua</i>	6.77
<b>Fieldfare</b>	<i>Turdus pilaris</i>	6.24



<b>Common Name</b>	<b>Scientific Name</b>	<b>Proportion (%) of sites occupied (n=154)</b>
<b>Tawny Owl (O)</b>	<i>Strix aluco</i>	6.14
<b>Rook (C)</b>	<i>Corvus frugilegus</i>	5.53
<b>Bearded Vulture (R)</b>	<i>Gypaetus barbatus</i>	5.12
<b>Snowy Owl (O)</b>	<i>Bubo scandiacus</i>	5.1
<b>Short-eared Owl (O)</b>	<i>Asio flammeus</i>	5.08
<b>Long-eared Owl (O)</b>	<i>Asio otus</i>	5.04
<b>Redwing</b>	<i>Turdus iliacus</i>	4.94
<b>Griffon Vulture (R)</b>	<i>Gyps fulvus</i>	4.46
<b>Common Buzzard (R)</b>	<i>Buteo buteo</i>	4.4
<b>Lesser Kestrel (R)</b>	<i>Falco naumanni</i>	4.29
<b>House Sparrow</b>	<i>Passer domesticus</i>	4.09
<b>Cinereous Vulture (R)</b>	<i>Aegypius monachus</i>	3.77
<b>Tengmalm's Owl (O)</b>	<i>Aegolius funereus</i>	3.57
<b>White-tailed Eagle (R)</b>	<i>Haliaeetus albicilla</i>	3.03
<b>Scops Owl (O)</b>	<i>Otus scops</i>	2.66
<b>Marsh Harrier (R)</b>	<i>Circus aeruginosus</i>	1.95
<b>Pallid Harrier (R)</b>	<i>Circus macrourus</i>	1.79
<b>Hen Harrier (R)</b>	<i>Circus cyaneus</i>	1.42
<b>Rough-legged Buzzard (R)</b>	<i>Buteo lagopus</i>	1.38

<b>Common Name</b>	<b>Scientific Name</b>	<b>Proportion (%) of sites occupied (n=154)</b>
<b>Herring Gull</b>	<i>Larus argentatus</i>	1.3
<b>Great Grey Shrike</b>	<i>Lanius excubitor</i>	0.99
<b>Black-headed Gull</b>	<i>Larus ridibundus</i>	0.9
<b>Black Kite (R)</b>	<i>Milvus migrans</i>	0.83
<b>Long-Legged Buzzard (R)</b>	<i>Buteo rufinus</i>	0.81
<b>Barn Owl (O)</b>	<i>Tyto alba</i>	0.78
<b>Lesser Black-backed Gull</b>	<i>Larus fuscus</i>	0.69
<b>Egyptian Vulture (R)</b>	<i>Neophron percnopterus</i>	0.67
<b>Great Black-headed Gull</b>	<i>Larus ichthyaetus</i>	0.65
<b>Great Grey Owl (O)</b>	<i>Strix nebulosa</i>	0.65
<b>Pygmy Owl (O)</b>	<i>Glaucidium passerinum</i>	0.33
<b>Tree Sparrow</b>	<i>Passer montanus</i>	0.33
<b>Red Kite (R)</b>	<i>Milvus milvus</i>	0.29
<b>Ural Owl (O)</b>	<i>Strix uralensis</i>	0.26
<b>Iberian Azure-winged Magpie (C)</b>	<i>Cyanopica cyanus</i>	0.23
<b>White Stork</b>	<i>Ciconia ciconia</i>	0.1
<b>Common Gull</b>	<i>Larus canus</i>	0.08

#### 4.5.3 Cliff and rocky habitat nesters

Thirty-seven species of a possible 44 (84.1%) fall into this category. Species typical of cliffs and rocky habitats were present in 82% of Neanderthal sites (Table 4.8). Apart from those species and main taxa already discussed, the remaining species can be allocated to three groups: (a) Raptors - large raptors, owls and falcons; (b) Aerial insect feeders - swifts and swallows; (c) Coastal marine birds (Figure 4.11). Additionally, there are three species that spend most of their time in this habitat - blue rock thrush (*Monticola solitaries*), black wheatear (*Oenanthe leucura*) and wall creeper (*Tichodroma muraria*); and one species, the bald ibis (*Geronticus eremita*), which does not fit into any of the previous categories (Table 4.10). The raptors and aerial insectivores predominate over coastal species, presumably as the latter would be restricted coastal areas within the overall Neanderthal range.

Four of the raptors have widespread distributions that encompass the Neanderthal range: golden eagle (*Aquila chrysaetos*), eagle owl (*Bubo bubo*), white-tailed eagle (*Haliaeetus albicilla*) and peregrine falcon (*F. peregrinus*). Five species are mid-latitude belt and therefore have ranges which coincide with the Neanderthals: bearded vulture (*Gypaetus barbatus*), griffon vulture (*Gyps fulvus*), Bonelli's eagle (*Aquila fasciata*) and Egyptian vulture (*Neophron percnopterus*). Two have boreal/polar distribution but would have entered Neanderthal territory in winter: merlin (*Falco columbarius*); or during glacials: gyr falcon (*F. rusticolus*).

The aerial insectivores are all summer visitors from tropical Africa, except for crag martin (*Ptyonoprogne ruestris*) which winters in southern Europe. This species, Alpine swift (*Tachymarptis melba*) and red-rumped swallow (*Cecropis daurica*) occupy the mid-latitude belt with common swift (*Apus apus*), swallow (*Hirundo rustica*) and house martin (*Delichon urbica*) having broad geographical distributions. All these species would have therefore coincided with Neanderthals over large geographical areas.



*Figure 4.11 Cliff-dwelling birds are highly represented in Neanderthal sites. Some nest in large colonies, like these northern gannets (Morus bassanus). (Photo: Stewart Finlayson)*

Table 4.10 Cliff and rocky habitat nesters present in Neanderthal sites (n=37). R = raptor, A = aerial insect feeder, C = coastal or marine.

Common Name	Scientific Name	Proportion (%) present in Neanderthal sites (n=154)
<b>Alpine Chough</b>	<i>Pyrrhocorax graculus</i>	41.84
<b>Red-billed Chough</b>	<i>Pyrrhocorax pyrrhocorax</i>	30.49
<b>Common Kestrel (R)</b>	<i>Falco tinnunculus</i>	23.64
<b>Rock Dove</b>	<i>Columba livia</i>	21.68
<b>Jackdaw</b>	<i>Corvus monedula</i>	17.86
<b>Golden Eagle (R)</b>	<i>Aquila chrysaetos</i>	11.98
<b>Raven</b>	<i>Corvus corax</i>	10.78
<b>Eagle Owl (R)</b>	<i>Bubo bubo</i>	8.52
<b>Alpine Swift (A)</b>	<i>Tachymarptis melba</i>	7.31
<b>Crag Martin (A)</b>	<i>Ptyonoprogne rupestris</i>	6.23
<b>Swallow (A)</b>	<i>Hirundo rustica</i>	6.15
<b>Bearded Vulture (R)</b>	<i>Gypaetus barbatus</i>	5.12
<b>House Martin (A)</b>	<i>Delichon urbica</i>	4.99
<b>Griffon Vulture (R)</b>	<i>Gyps fulvus</i>	4.46
<b>Lesser Kestrel (R)</b>	<i>Falco naumanni</i>	4.29
<b>White-tailed Eagle (R)</b>	<i>Haliaeetus albicilla</i>	3.03
<b>Peregrine Falcon (R)</b>	<i>Falco peregrinus</i>	2.87
<b>Red-rumped Swallow (A)</b>	<i>Hirundo daurica</i>	1.93
<b>Merlin (R)</b>	<i>Falco columbarius</i>	1.33
<b>Herring Gull (C)</b>	<i>Larus argentatus</i>	1.3

<b>Common Name</b>	<b>Scientific Name</b>	<b>Proportion (%) present in Neanderthal sites (n=154)</b>
<b>Gannet (C)</b>	<i>Morus bassanus</i>	0.96
<b>Blue Rock Thrush</b>	<i>Monticola solitarius</i>	0.86
<b>Shag (C)</b>	<i>Phalacrocorax aristotelis</i>	0.85
<b>Bonelli's Eagle (R)</b>	<i>Aquila fasciata</i>	0.78
<b>Lesser Black-backed Gull (C)</b>	<i>Larus fuscus</i>	0.69
<b>Egyptian Vulture (R)</b>	<i>Neophron percnopterus</i>	0.67
<b>Cormorant (C)</b>	<i>Phalacrocorax carbo</i>	0.67
<b>Great Black-headed Gull (C)</b>	<i>Larus ichthyaetus</i>	0.65
<b>Gyr Falcon (R)</b>	<i>Falco rusticolus</i>	0.65
<b>Wall Creeper</b>	<i>Tichodroma muraria</i>	0.65
<b>Eleonora's Falcon (R)</b>	<i>Falco eleonora</i>	0.49
<b>Guillemot (C)</b>	<i>Uria aalge</i>	0.38
<b>Black Wheatear</b>	<i>Oenanthe leucura</i>	0.34
<b>Fulmar (C)</b>	<i>Fulmarus glacialis</i>	0.29
<b>Kittiwake (C)</b>	<i>Rissa tridactyla</i>	0.13
<b>Common Gull (C)</b>	<i>Larus canus</i>	0.08
<b>Bald Ibis</b>	<i>Geronticus eremita</i>	0.02

#### **4.5.4 Ground-dwelling species**

Ground-nesting birds, wetland ground nesters, ground cryptic and lekking species come under a generic grouping of species that essentially live on the ground. Within this, ground-nesting birds constitute another well-represented category with 98 species

of a possible 137 (71.5%) occupying 69.4% of Neanderthal sites (Table 4.8). These birds come from diverse families but game birds with the top seven species in this group (*P. perdix*, *T. tetrix*, *L. mutus*, *C. coturnix*, *A. rufa*, *L. lagopus* and *A. graeca*) stand out. The proportion of cryptic ground birds (typically showing marked streaking on the dorsal side of the plumage) is also very high with 73 of a possible 95 species (76.8%) occupying 68.8% of Neanderthal sites (Table 4.8). These results further indicate that ground-dwelling birds are well represented in Neanderthal sites and the high proportion of cryptic species highlights that many are birds which have the habit of “freezing” or sitting tight on the nest when predators are detected (Figure 4.12).



*Figure 4.12 Many species of cryptic ground birds are found in Neanderthal sites. Species, such as the red-necked nightjar (Caprimulgus ruficollis), will freeze on the ground and rely on camouflage. The plumage in these birds is usually heavily streaked or barred. (Photo: Stewart Finlayson)*

A second group of ground-nesters consists of birds that nest in floating platforms and on the margins of water bodies, always very low down. Of 64 species of wetland ground nesters, 44 (68.8%) are present in Neanderthal sites, occupying 36.3% of the sites (Table 4.8). They are largely ducks, geese and wading birds. When added to the terrestrial ground nesting species, they total 146 species which jointly occupy 78.3% of Neanderthal sites.

As with the large scavengers, lekking birds (i.e. those species that select particular places of ground where they perform elaborate nuptial displays, Figure 4.13) are few in the Palaearctic. Leks are always on the ground so this is a version of the ground dwelling category. There are nine species present in Neanderthal sites, out of a possible ten species, and they occupy 28.6% of sites. These are the three *Tetrao* grouse, two cranes (common crane, *Grus grus* and demoiselle crane, *Anthropoides virgo*), two bustards (great bustard, *Otis tarda* and little bustard, *Tetrax tetrax*), the great snipe (*Gallinago media*) and the ruff (*Philomachus pugnax*). Lekking birds share a feature in common with the large scavengers – they come to ground for prolonged periods in a fixed spot. When they do so they enter a state of frenzy when activity is focused on either a carcass or rival males and potential mates. It is therefore useful to combine the two categories to see how many Neanderthal sites have either lekking birds or large scavengers. The proportion of sites occupied is 44.1% which is very high for a set of 15 species (Table 4.8).





*Figure 4.13 The few lekking birds are well represented in Neanderthal sites. They perform elaborate nuptial displays in traditional sites. The image is of a displaying male great bustard (Otis tarda). (Photo: Stewart Finlayson).*

These results support previous observation that the majority of birds occupying Neanderthal sites are cliff and ground nesting species. Together they are found in almost all Neanderthal sites (183 spp., 95.7% of sites; Table 4.8).

#### **4.5.5 Arboreal species**

Ninety-three arboreal species out of a potential 170 (54.7%) arboreal species occupy 61.9% of Neanderthal sites (Table 4.8). They include species native to shrublands as well as woodland and forest. They come from a variety of groups but none are from

the main species and very few from the main taxa. The proportion indicates the presence of a large number of Neanderthal sites close to trees but not necessarily dense forest. The proportion is nevertheless much lower than for cliff- and ground-species as is the actual number of bird species represented.

#### **4.5.6 Edible species**

Fifty-seven bird species out of 81 potentially edible by humans were present in 77.9% of Neanderthal sites. Most bird species are potential food so this proportion should be regarded as a minimum estimate which is based on species that have typically been human food sources (Cocker, 2013; Shrubbs, 2013). Edible species are dominated by four of the six main taxa which I have previously considered (Section 4.4): game birds, ducks, thrushes and pigeons and doves. It also includes, in significantly lower frequencies, geese (*Anser* 6 spp.; *Branta* 2 spp.), swans (*Cygnus* 2 spp.), snipes and woodcock (*Gallinago* 3 spp.; *Scolopax* 1 sp.), corncrake *Crex crex* and great bustard *Otis tarda*.

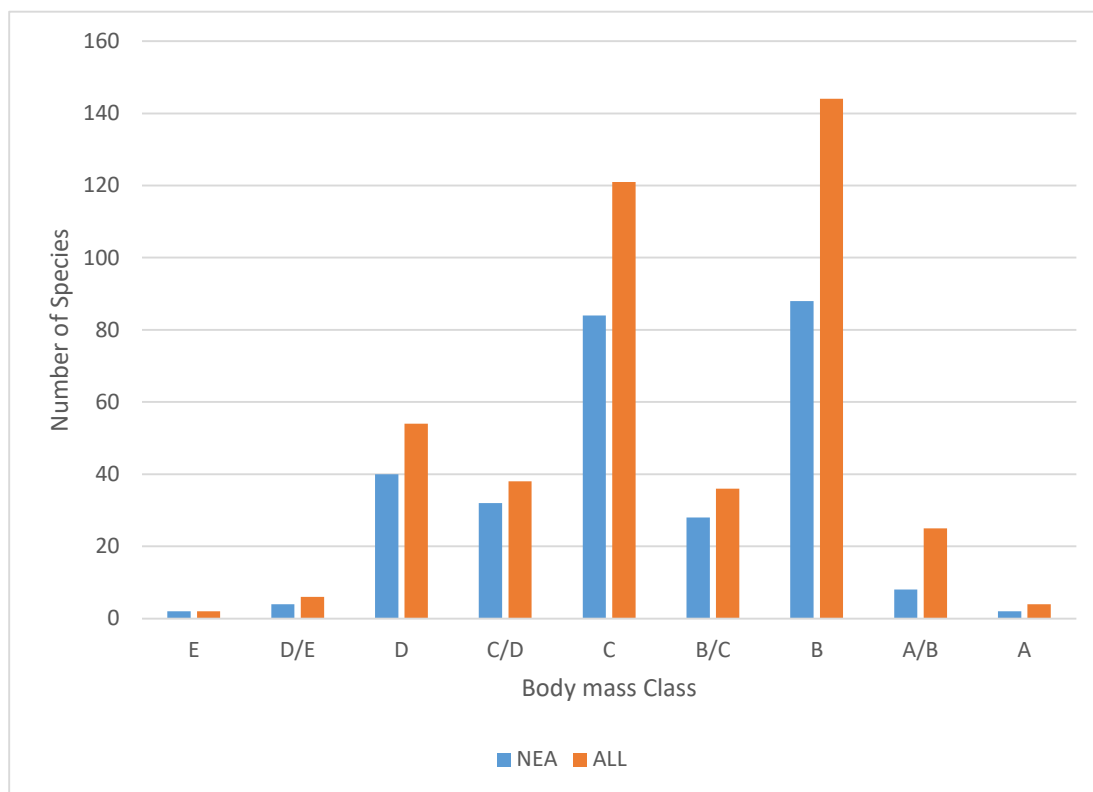
#### **4.5.7 Body mass classes**

Each of 430 bird species in the database was allocated to a body mass class, using data contained in the nine volumes of the *Handbook of the Birds of Europe, the Middle East and North Africa* (Table 4.11). Body mass classes of birds in Neanderthal sites are compared with the overall pattern in Figure 4.14. There is an under-representation of small birds (body mass classes A and A/B). The most highly represented categories were in the range of over 101 g including those over 10,000 g. There is a clear peak around the weight class C (101-1,000 g), including C/D and B/C, in Neanderthal sites.

Compared with the pattern for all species, weights in this range are higher than expected (one-way Chi Square = 30.7, df = 4, N = 288,  $p < 0.001$ ). For analysis, highest and lowest categories in Figure 4.14 were lumped into D + (D, D/E, E) and B- (B, A/B, A).

*Table 4.11 Body mass classes of Palaearctic birds and of those found in Neanderthal sites. Masses are rounded off to the nearest gram (g). Intermediate classes are for species whose weights include two categories. Thus A/B would be species whose weights would include a range  $\leq 10$  g and also in the 11 g to 100 g category, etc.*

<b>Body mass Class</b>	<b>Body mass Range (g)</b>	<b>Species in Neanderthal sites</b>	<b>All species</b>	<b>Proportion of (%) species in Neanderthal sites</b>
<b>A</b>	$\leq 10$	2	4	50
<b>A/B</b>		8	25	32
<b>B</b>	11-100	88	144	61.1
<b>B/C</b>		28	36	77.8
<b>C</b>	101-1000	84	121	69.4
<b>C/D</b>		32	38	84.2
<b>D</b>	1001-10,000	40	54	74.1
<b>D/E</b>		4	6	66.7
<b>E</b>	$\geq 10,001$	2	2	100



*Figure 4.14 Distribution of weight classes of birds found in Neanderthal sites with the overall pattern for all species.*

#### **4.5.8 Principal components analysis of species by behavioural characteristics.**

To determine the relative importance of the different bird species by behavioural category, I ran a PCA. I subdivided the 430 bird species into those present in Neanderthal sites, those present in negligible proportions (< 1% of sites) and those absent (Table 4.12). I then calculated the proportion of species present in each category by the number of available species in each category. So, for example, there were 31 species of cliff and rocky habitat nesters in the “Present” category out of a possible 44 giving a figure of 70.5% (see Table 4.12).

*Table 4.12 Proportion (%) of all species available in each category by presence, negligible presence or absence in Neanderthal sites*

<b>Behavioural characteristics</b>	<b>Present</b>	<b>Negligible Presence</b>	<b>Absent</b>
<b>flocking (n=198)</b>	54	17.2	28.3
<b>commensal (n=81)</b>	62.9	9.9	27.2
<b>large scavenger (n=6)</b>	100	0	0
<b>partial scavenger (n=33)</b>	60.6	12.1	24.2
<b>cliff nester (n=44)</b>	70.5	13.6	15.9
<b>ground nester (n=137)</b>	54.7	16.8	28.5
<b>wetland ground nester (n=64)</b>	54.7	14.1	31.3
<b>ground cryptic (n=95)</b>	76.8	13.7	32.6
<b>lekking (n=10)</b>	80	10	10
<b>arboreal (n=170)</b>	43.5	16.5	39.4

The PCA results (Figure 4.15) explains 92.7% of net variance (axis 1) and 5.9% (axis 2), equivalent to 98.7% of total variance. The first axis loads strongly positively with species presence in Neanderthal sites and negatively with absence and, to a lesser degree, negligible presence. The second axis loads strongly positively with absence and less so with presence of any kind.

The strongest relationship with presence of species in Neanderthal sites is linked with scavengers and lekking birds. Some caution is needed in interpreting this result given

that few species are present in these behavioural characteristics but, at the same time, they are almost all present in Neanderthal sites. There is a second group also positively linked with Neanderthal sites and these are cliff nesters and ground birds with cryptic plumage. Commensals and partial scavengers come next, though loading negatively with this axis, while ground nesters, wetland ground nesters, flocking birds and, especially, arboreal birds score negatively.

Repeating the PCA, after removing scavengers and lekking birds (Figure 4.16) reinforces the previous results and confirms that cliff nesters, ground cryptic species, commensals and partial scavengers are positively correlated with Neanderthal sites. Arboreal species again are highly negatively correlated and ground nesters and wetland ground nesters to a lesser degree.

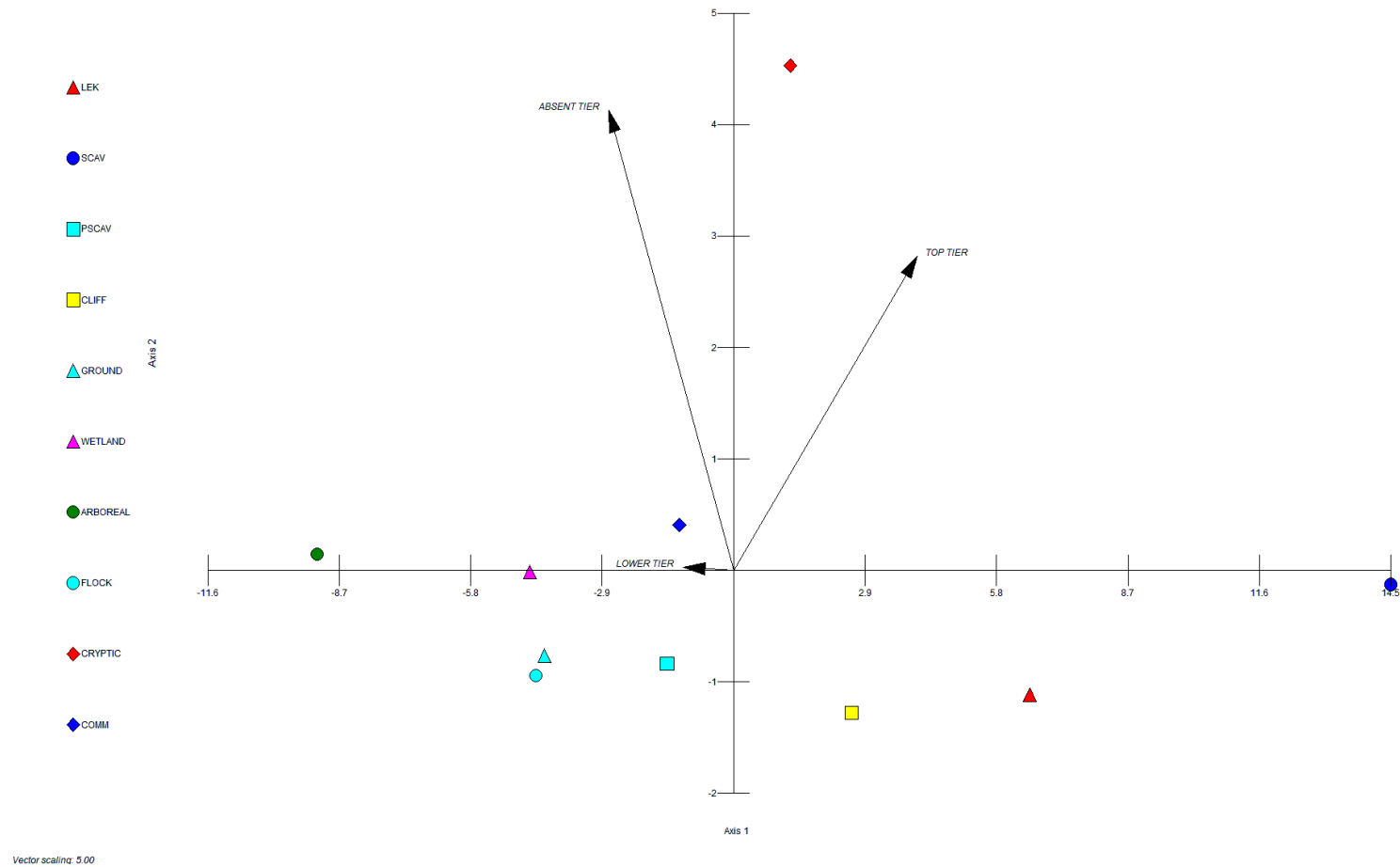


Figure 4.15 Results of PCA by behavioural characteristics. Euclidean bi-plot with arrows showing vector strength. Data from Table 4.12: Top Tier = present; Lower Tier = negligible presence; Absent Tier = absent.

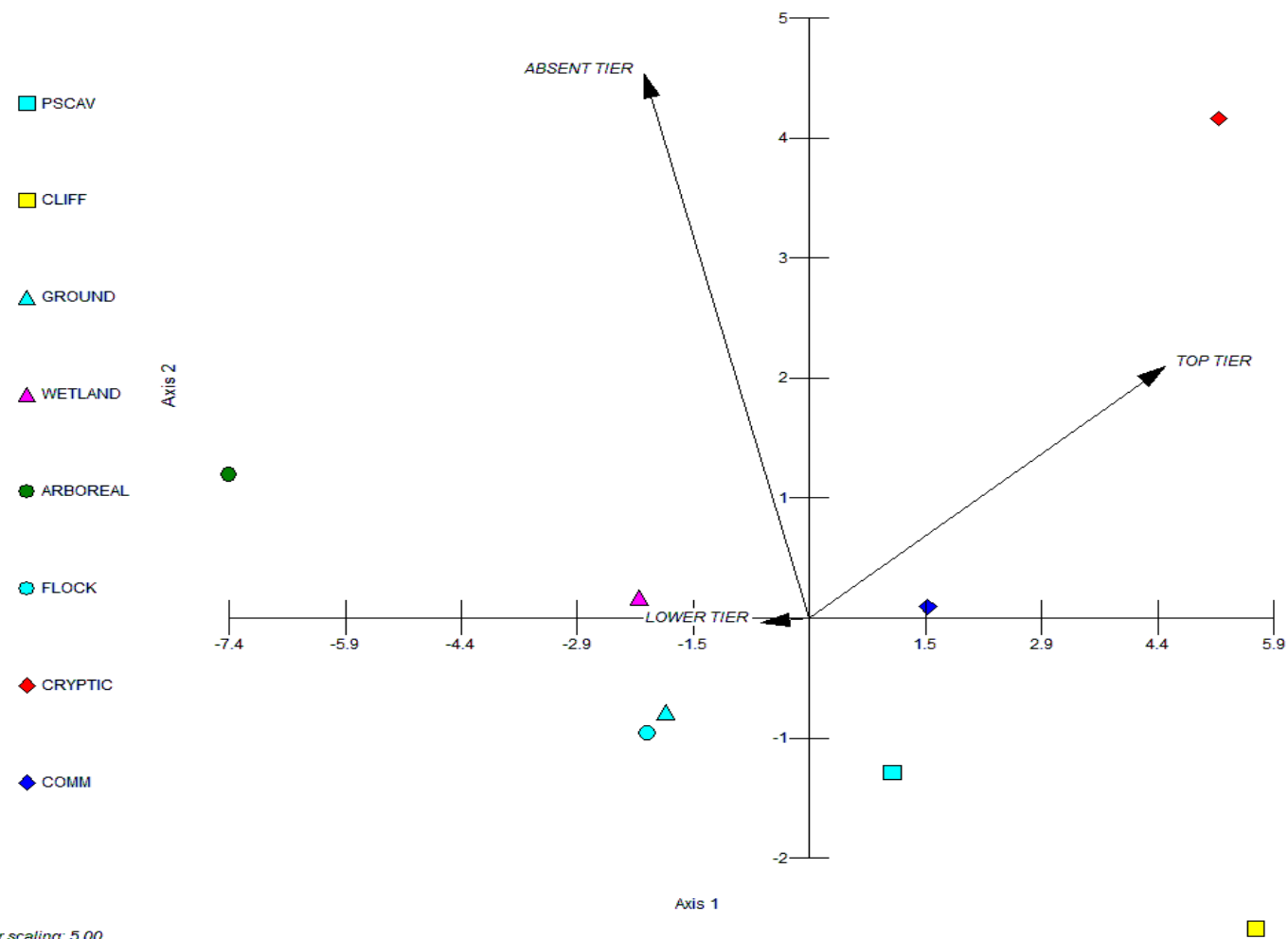


Figure 4.16 Results of PCA by behavioural characteristics. Scavengers and lekking birds removed. Euclidean bi-plot with arrows showing vector strength. Data from Table 4.12



#### **4.5.9 Behavioural characteristics – summary**

Bird species associated with Neanderthal sites were those species that nested or occupied cliffs, rocky, and ground habitats. Species nesting on the surface in aquatic vegetation are included. There is a high representation of cursorial species which have cryptic, generally brown/olive and heavily streaked, plumage and which behave by remaining motionless and relying on camouflage when detected.

Flocking birds are well represented in Neanderthal sites. It is possible that such species may have been targeted by Neanderthals because of this habit of aggregation. Another important group of species are ground dwellers that scavenge large carcasses or which perform elaborate nuptial displays in leks. They would be particularly vulnerable to being ambushed.

Potentially edible species (particularly game birds, ducks, thrushes and pigeons; Cott, 1945; 1948; see also discussion in Chapter 6) are present in many Neanderthal sites. Many of these species fall in intermediate weight classes, of 101 to 1,000 g, which appears to be the norm in Neanderthal sites. Small birds appear to have been avoided.

Thus, the overall pattern would appear to be of Neanderthals associating with birds of cliffs and open country/woodland ecotones. Many were ground dwelling birds. In contrast arboreal species were less well represented. The predominance of cryptic ground species suggests that there may have been a way of obtaining these species by stealth. Ambush hunting, a well-established Neanderthal strategy for mammals, may have been practised on birds that would concentrate for predictable periods on carcasses, to perform nuptial displays or birds flocking at vulnerable times (e.g. roosts). Many of the species present were potentially edible and of substantial size, with small birds avoided. In the next chapter I will review the evidence of direct

intervention of Neanderthals on birds to determine if the conclusions arrived at here are supported.

#### **4.6 Comparison with modern humans**

In this section I attempt to establish if there are any differences in the bird species associated with Neanderthals with those associated with modern humans. In order to narrow down the question I have chosen the three modern human cultures used in this thesis for comparison. (1) Aurignacian was the first modern human culture after the Neanderthal extinction and with which there may have been some temporal and geographic overlap; (2) Gravettian culture followed the Aurignacian and (3) Magdalenian which is associated with the last glacial maximum when conditions were harshest in Europe (Chapter 2, section 2.2.2; Table 2.1 and Figure 4.17). There are further advantages to choosing these three cultures. First, all were widespread across large areas of Europe and occupied similar territory to Neanderthals. Other modern human cultures were more localised than these. Second, they offer relatively large sample sizes (Aurignacian = 55, Gravettian = 33, Magdalenian = 176) sample sites compared with other cultures/ sites.

The first striking observation is that very few species are consistently associated with Neanderthal and modern human sites. Looking at those species which occupy over 20% of sites (Mousterian, Aurignacian, Gravettian or Magdalenian) only 12 (2.8%) of a potential pool of 430 species (Table 4.13) are represented. This indicates that bird species associations were very similar to each other across human taxa and that differences were only a matter of degree. Cluster Analysis, using unweighted pair group method with arithmetic mean (UPGMA) and Bray Curtis Distance, shows the Aurignacian and Gravettian sites to be much closer to each other and to the Mousterian ones than either is to the Magdalenian (Figure 4.18). This means that similarities and

differences in bird presence in human sites appear not to be determined by the human taxon involved, but I would suggest would have more to do with ecology. In other words, bird species association with human taxa has more to do with climatic and ecological conditions; associations with bird species are often very similar when comparing Neanderthals to modern humans.

The species most frequent in Mousterian sites (Section 4.3) are Alpine chough (*Pyrrhocorax graculus*), red-billed chough (*P. pyrrhocorax*), grey partridge (*Perdix perdix*), common kestrel (*Falco tinnunculus*) and rock dove (*Columba livia*) (Table 4.13). These are species typical of rocky habitats of the mid-latitude belt with the exception of grey partridge which is an open ground species with widespread distribution. Rock dove and jackdaw are also well represented in Aurignacian sites suggesting similar associations between Mousterian and Aurignacian sites.

If the differences between Neanderthals and Aurignacians/Gravettians appears minor, it is with the Magdalenian that we observe the greatest contrast. The species which appear to be most frequent in Magdalenian sites are willow grouse (*Lagopus lagopus*), rock ptarmigan (*L. mutus*), snowy owl (*Bubo scandiacus*), black grouse (*Tetrao tetrix*) and raven (*Corvus corax*) (Table 4.13, Figure 4.19). The first three species are those of open tundra or tundra transition into dwarf birch habitats. The fourth, black grouse, is a predominantly boreal species while raven has a broad distribution. Not surprisingly, no mid-latitude belt species is represented in this group, which are birds of northern areas and of predominantly open habitats.

The differences in bird species are evident from Figure 4.19 which clearly separates the tundra species mostly associated with the Magdalenian (snowy owl *B.scandiacus* and the two grouse *Lagopus*) and the open country black grouse *T. tetrix* and raven

*C.corax*. Two rock dwelling species of temperate areas mainly linked to the Mousterian (rock dove *C. livia* and jackdaw *C. monedula*) cluster together with red-billed chough (*P. pyrrhocorax*) close to them. The Alpine chough (*P. graculus*) stands out as unique and the remaining species form a cluster of species that share widespread geographical distributions in common.



*Figure 4.17 Although the same group of species dominates all human sites, some predominate in certain cultures over others. This is the case of tundra birds (e.g. snowy owl (*Bubo scandiacus*) represented here) which are best represented in Magdalenian sites coinciding with the last glacial maximum. (Photo: Stewart Finlayson)*

In conclusion, similarities outweigh differences in the bird species associated with Neanderthals and modern humans. It is remarkable that there are only 12 species occurring in over 20% of sites in the Mousterian, Aurignacian, Gravettian and Magdalenian and that these are always present in sites associated with the four cultures. Differences in frequency between cultures are clearly ascribable to climatic and ecological context.

*Table 4.13 Number of sites bird species present in over 20% of sites occurred. The numbers shown in the table are the actual number of sites where the species was present. Pale grey shows species predominant in Mousterian sites, middle grey are species predominant in Mousterian and Aurignacian sites, and dark grey are species predominant in Magdalenian sites*

Species	Mousterian n=154	Aurignacian n=55	Gravettian n=33	Magdalenian n=176
<b>Alpine Chough</b> - <i>Pyrrhocorax graculus</i>	64	30	16	62
<b>Red-billed Chough</b> - <i>Pyrrhocorax pyrrhocorax</i>	47	13	5	23
<b>Grey Partridge</b> - <i>Perdix perdix</i>	44	17	8	42
<b>Common Kestrel</b> - <i>Falco tinnunculus</i>	36	14	9	31
<b>Rock Dove</b> - <i>Columba livia</i>	33	14	2	12
<b>Willow Grouse</b> - <i>Lagopus lagopus</i>	17	17	10	78

Species		Mousterian n=154	Aurignacian n=55	Gravettian n=33	Magdalenian n=176
<b>Jackdaw</b> <i>Coloeus monedula</i>	-	28	15	9	11
<b>Mallard</b> <i>Anas platyrhynchos</i>	-	28	15	4	39
<b>Raven</b> <i>Corvus corax</i>	-	17	13	7	42
<b>Rock Ptarmigan</b> <i>Lagopus mutus</i>	-	22	13	6	62
<b>Black Grouse</b> <i>Tetrao tetrix</i>	-	30	12	8	45
<b>Snowy Owl</b> <i>Bubo scandiacus</i>	-	8	4	5	38

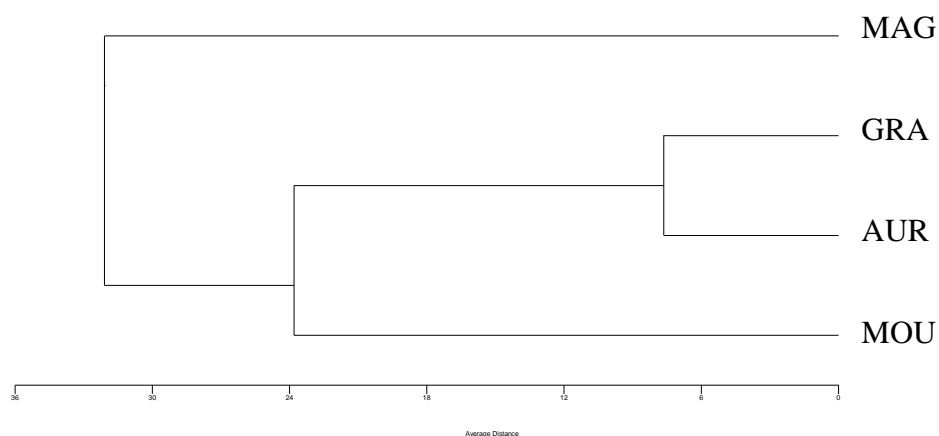
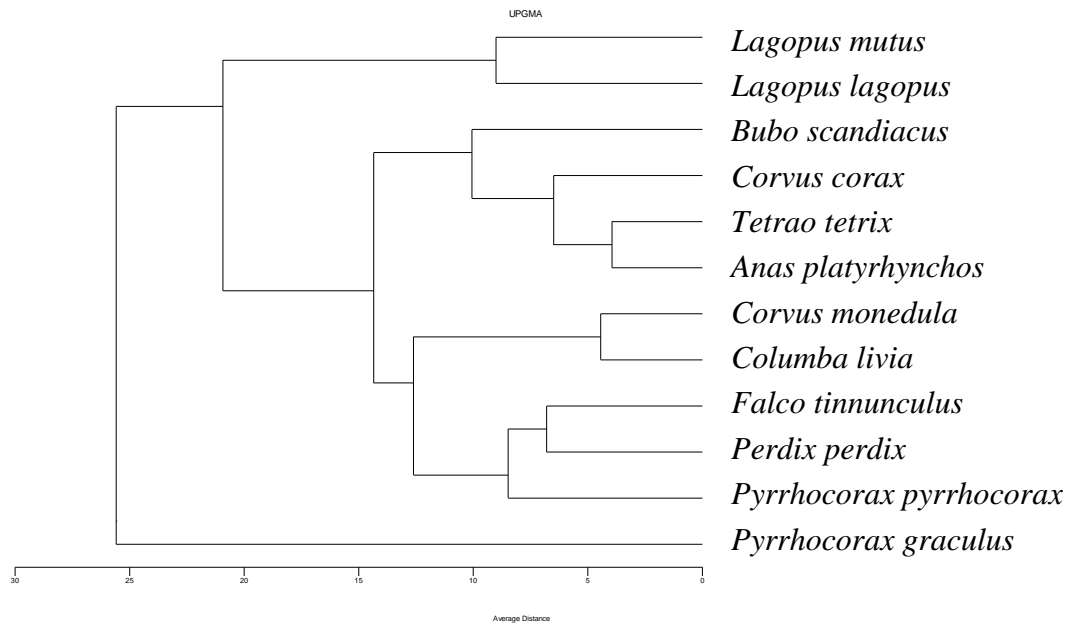


Figure 4.18 Dendrogram based on cluster analysis of Mousterian, Aurignacian, Gravettian and Magdalenian sites based on main bird species (>20%) presence. Data from Table 4.13, Cluster Method UPGMA, Bray Curtis Distance



*Figure 4.19 Dendrogram based on cluster analysis of main bird species (>20%) associated with Mousterian, Aurignacian, Gravettian and Magdalenian sites. Data from Table 4.13, using observed data only. Cluster Method UPGMA, Bray Curtis Distance*

#### **4.7 Summary**

A feature of the birds most regularly associated with Neanderthal sites (at species and higher taxonomic levels) is that they co-occupied large parts of the Neanderthal geographical range. This implies frequent and regular contact with these birds. Very few bird species actually co-occurred regularly with Neanderthals in comparison to the overall number of species co-sharing parts of the geographical range. Only five species: alpine chough, red-billed chough, grey partridge, common kestrel and rock dove occurred in over 20% of sites. This is a noteworthy result given that 430 species were entered into the main database (Appendix 1). Corvids, game birds, ducks, thrushes, pigeons and kestrels were the regular higher taxa (orders/families/genera) at Neanderthal sites and it is noteworthy that some species within these groups are ‘traditional’ human food sources which I have defined under the ‘edible’ category.

This observation is supported by the mass distribution of the most frequent birds: small (< 100 g) bird species were underrepresented at Neanderthal sites, with the majority falling in the >101 g to 1,000 g category, while larger (and naturally rarer) species were also present.

The behavioural characteristics of many of the birds associated with Neanderthals are also linked with the use of similar habitats, particularly rocky, open and open/woodland ecotones as well as fresh water bodies. Dense woodland species are under-represented. These results corroborate those of Chapter 3. Neanderthal sites are most frequently associated with birds showing scavenging (including commensals), lekking, ground-dwelling cryptic and flocking behaviours.

Even though there are differences between Neanderthals and modern humans in terms of bird species, these are likely to reflect circumstances (e.g. tundra species with the Magdalenian culture during the Last Glacial Maximum) and not differences associated with hominin taxon.

Overall, the number of birds associated regularly (in over 20% of sites) with Neanderthals and modern humans is surprisingly small: only 12 of 430 species (3.5%), indicating similar patterns of association between Neanderthals and modern humans in relation to birds most commonly found in their occupation sites.



## **5.1 Introduction**

The data presented so far only provide indirect evidence of Neanderthal behaviour in relation to birds. In order to satisfy criteria that confirm direct action of Neanderthals on birds we need tangible evidence of such action. This is within the realm of taphonomy which seeks such evidence on bone, for example in the form of marks left by stone tools, tooth imprints, or of burning. The evidence for birds has been much harder to find than for large mammals, where stone tools would have been used frequently in the process of butchering carcasses. In the case of birds, especially small ones, processing may have been done mostly directly with hands, leaving little, or no, tell-tale evidence of action. For this reason in particular, evidence of Neanderthal action on birds has been largely lacking and has been, taken to mean that Neanderthals did not catch and consume birds. However, in recent years a growing body of data, using increasingly refined techniques, has been building up showing the contrary (e.g. Blasco and Fernandez Peris, 2009; Peresani *et al.*, 2011; Finlayson *et al.*, 2012; Morin and Laroulandie, 2012; Blasco *et al.*, 2014).

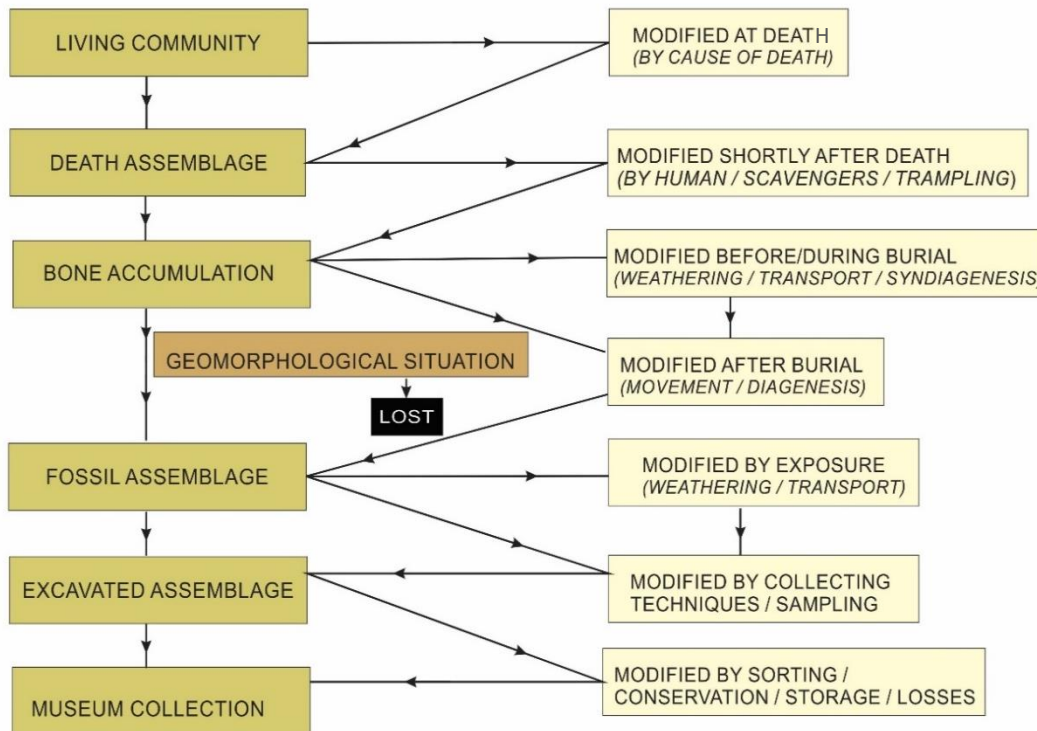
The objective of this chapter is the exploration of the taphonomic evidence for the exploitation of birds by Neanderthals. In order to advance this objective, this chapter addresses Research Question 3:

If there are links with particular bird species, how many of these have taphonomic evidence linking them to Neanderthals? As with previous Research Questions, I will compare Neanderthals and modern humans.

Then I use this information to predict what other species could be found in the future with similar taphonomic evidence, and identify sites which, because of the type of bird species found, should be targeted for future taphonomic work.

Taphonomy, the science of investigating the accumulation and preservation of fossil faunas is summarised in Figure 5.1 (after Andrews, 1990). It starts with a living community of animals and how a death assemblage is created post-mortem, with a focus on any modification. Peri-mortem modifications (e.g. by scavengers or by trampling) may also have affected animal remains leading to bone accumulations. Subsequent, clearly post-mortem, processes would be modifications before, during or after burial and modifications by exposure. Finally, the material leading to museum collections may have been modified during collection, sampling or sorting. One consideration is loss of the entire bone accumulation as a result of local geomorphological factors. Open air sites may, for example, be more exposed to loss of bones than sheltered caves. A high frequency of cave sites could be seen to indicate that humans were occupying caves in preference to open air sites, even though the latter are likely to have been used more frequently (Straus, 1990b). It seems likely, however, that caves are simply much more effective in protecting deposits from the elements (Bochenski, *et al.*, 2017).

The modifications resulting from cause of death can be varied. The simplest case would be death from natural causes which would leave no bone modification and the skeleton would remain intact and unmodified where it died (Andrews, 1990). However, a major cause of mortality is predation. In the case of birds, their predators could be mammals, reptiles, diurnal birds of prey and owls. This study focuses on one genus of mammalian predator, *Homo*.



*Figure 5.1 Stages in the formation and modification of bone assemblages (after Andrews, 1990).*

Superimposed on these primary modifications would be secondary ones which could happen soon after death but are unrelated to the cause of death. Taphonomists are interested in separating these secondary causes, including bone-damage as result of decay, scavenging and trampling, from fractures caused by (primary) predation.

In Chapters 3 and 4 I have focused on presence or absence of species in sites. I have done this because of the difficulties in estimating abundance of species from bones and also because of large differences in the way species representation is reported in different studies (Klein & Cruz-Urbe, 1984). One way of estimating species abundance has been to calculate the number of identified specimens (NISP). There

are several problems related to calculating species abundance from fossil material. First, a major problem with the use of NISP is that the skeletons of some species have more parts than those of others (Marshall and Pilgram, 1993). Second, species reaching a site intact as opposed to dismembered before transport will over-represent their importance. Third, we need to assume that the bone fragmentation has affected all species equally. For these reasons I prefer to avoid NISP. Another measure of abundance is minimum number of individuals (MNI) (Marshall and Pilgram, 1993). This is simply the number of individuals necessary to account for all the identified bones. It follows that MNI must always be less than NISP. The problem is, in my experience, that when a bone assemblage is translated from NISP to MNI the sample size is typically very small and makes statistical analysis of the data difficult.

It is often the case that many bones found in archaeological sites represent the leftovers of meals (Stiner, 1994). Skeletons are widely scattered as a result of butchering, while individual bones would have been subjected to rough treatment, for example being put into a fire and broken open to extract marrow. Other bones may have been shaped into tools. In the case of large mammals, the small phalanges, carpals, tarsals and teeth generally escape the worst treatment (Davis, 1987). The problem is that birds, being generally smaller than large mammals, probably escaped such intense treatment. Thus the apparent absence of such evidence in bird bones (Stiner *et al.*, 1999; 2000) associated with Neanderthal sites has been taken to mean that Neanderthals did not catch birds.

In those cases, where cut marks had been found on bird bones, they were interpreted as evidence of occasional bird consumption (de Lumley, 2005). This was the situation until 2009 when evidence of bird consumption at Bolomor Cave in Valencia (Spain), was published (Blasco and Fernández Peris, 2009). These authors examined 202 bird

remains (NISP) which all belonged to ducks of the genus *Aythya*. These remains represented an MNI of 8. The level in which they were found was dated to  $152 \pm 23$  kya. These authors found cut marks made by Neanderthal stone tools in 8.9% of the bones; evidence of burning (52.5% of the bones), and, evidence of Neanderthal tooth marks in the form of pits, scores and crenulated edges. The degree of burning was graded: 0 – unburned; 1 – bone surface presented small dots and scattered brown; 2 – brown staining was more or less homogeneous across the bone surface; 3 – bone charred, colour black; 4 – grey stain, occasional veins with bluish tones; 5 – calcined, completely white. The largest proportion of bones scored grades 2 ( $n = 41$ ) and 3 ( $n = 50$ ) of burning. In addition, 4.7% of the burnt bones showed a double colouration resulting from uneven burning in fires, usually more burnt where the part of the bone had little flesh or other attached tissue compared with areas where a large muscle mass attached to the bone. The authors concluded that this indicated roasting.

Later, our study of rock doves (*Columba livia*) at Gorham's Cave in Gibraltar (Blasco *et al.*, 2014) added to the earlier results. Here, a total of 1,724 (NISP) pigeon bones were examined from twenty discrete archaeological levels (19 Neanderthal, one modern human) covering the period from 67 to 28 kya. Cut marks, produced by Neanderthal stone tools on pigeon bones, were found in 28, mainly wing and lower limb, bones. We argued that although this number might seem low, it reflected the likelihood that, once skinned, the birds were processed with hands and mouth and without the need of tools. This argument was reinforced by the presence of human tooth imprints on 15 bones, as well as signs of overextension of joints and other related procedures. There was also evidence of burning in 158 of a sample of 1,364 (11.6%) bones. Twenty-nine (18.3%) showed the double coloration that signified roasting. In contrast to this evidence, carnivore activity was considered negligible. The most

important conclusion from this paper was that Neanderthal intervention on pigeon bones was recorded on eleven (57.9%) of the levels. Previous evidence of bird exploitation could have been argued to have been sporadic, but this new evidence showed that Neanderthals had been exploiting pigeons for over 40 kyr. Bird exploitation by Neanderthals was not rare, in this site at least.

## **5.2 Methods**

A database consisting of species identified with taphonomic evidence of intervention by Neanderthals was compiled from the literature (Appendix 2). This database comprised species in rows versus sites as columns (Chapter 2, Section 2.4). There were few equivalent cases for modern humans in the Aurignacian and Gravettian, but there was sufficient published material to allow for an equivalent database for the Magdalenian (Appendix 3; Chapter 2, Section 2.4).

A total of fifty-two confirmed bird species, and an additional nineteen identified to generic level, provide evidence of Neanderthal intervention, using evidence as described above, from nineteen different sites across Europe (Appendix 2). The data were compiled from an extensive search of the relevant literature in peer-reviewed journals. Most of this material was familiar to me as this is a new field and I am in contact with most of the researchers looking at bird taphonomy in Neanderthal sites. In this regard, it should be noted that only three sites were published prior to 2010 and the remainder after that (including ten - 52.63% - in the last five years), showing the very recent upsurge of publications on this subject. These sites were compiled into Appendix 2 and form the dataset for analysis in this chapter.

All bird species present in Neanderthal sites were separated into quartiles by frequency of occurrence (Appendix 4 shows all species in the top quartile). The bird species were divided into four quartiles according to their frequency of occurrence in Neanderthal sites, using the data from Appendix 1, and the total number of species with taphonomic evidence is shown by quartile. The data were analysed principally using Regression and Chi Square analysis (Sokal and Rohlf, 1981; Hawkins, 2009), with SPSS (IBM, 2017).

### 5.3 Results

In this section I compare the species exploited by Neanderthals, from direct taphonomic evidence, with those found in Neanderthal sites (Chapter 4, Appendix 1). These results are summarised in Table 5.1, which is a synthesis of the data in Appendix 2.

#### 5.3.1 Species

Table 5.2 records the number of published taphonomic cases per species (from Appendix 2) by quartile. Bird species occurring most frequently at Neanderthal sites are more likely to show evidence of intervention (TE), than those that are less frequent (Table 5.1; two-way Chi-Square  $X^2 = 55.365$ ,  $df = 3$ ,  $N = 288$ ,  $3 p < 0.001$ ). Figure 5.2 represents the results using the data in Table 5.2 (Fisher's Exact Test Statistic = -2.807  $N = 54$   $p = 0.004$ ). Those in the top quartile of frequency of occurrence dominate and include all cases where more than one case has been reported for a species (Table 5.2 and Figure 5.2). The five species (alpine chough (*Pyrrhocorax graculus*), red-billed chough (*P. pyrrhocorax*), grey partridge (*Perdix perdix*), common kestrel (*Falco*

*tinnunculus*) and rock dove (*C. livia*)) that occurred in over 20% of Neanderthal sites (Appendix 4) show evidence of processing by Neanderthals. Alpine chough and rock dove are evidenced in four published cases, and red-billed chough in three. These results show an association of the most frequent species in Neanderthal sites, and the degree in which they show taphonomic evidence of intervention. This suggests that the presence of these birds in Neanderthal sites was related, in part at least, to exploitation.

In addition, seventeen in the top twenty species occurring in Neanderthal sites (Appendix 4) show direct evidence of intervention by Neanderthals. Only rock ptarmigan (*Lagopus mutus*), mistle thrush (*Turdus viscivorus*) and eagle owl (*Bubo bubo*) are missing although we should note that *L. lagopus/ mutus* and *Turdus* spp. (*sensu lato*), have been recorded with taphonomic evidence of Neanderthal intervention (Appendix 2), and so could refer to these species *sensu stricto*. Eight of these twenty species have been reported in studies of Neanderthal intervention in more than one case. The proportion of species known to have been processed by Neanderthals drops in those which occurred in lower frequencies in Neanderthal sites and these have been reported only in single instances (Figure 5.2). Importantly, the main species showing evidence of processing by Neanderthals are all corvids, game birds and thrushes along with common kestrel, rock dove, mallard and golden eagle (Appendix 4), i.e. a disparate, but clearly-defined, group of bird species.



*Table 5.1 Taphonomic evidence of Neanderthal intervention on bird species. Data of taphonomic evidence from Appendix 2. Ranking of species into quartiles uses data from Appendix 1. Expected values, calculated from the 4 x 2 contingency table, are shown in italics in brackets.*

<b>Quartile – Bird species present in Neanderthal sites based on frequency of occurrence (Q)</b>	<b>Total number of species with taphonomic evidence (TE)</b>	<b>Total number of species with no taphonomic evidence (NTE)</b>	<b>Total number of species in quartile (SPP)</b>	<b>Proportion (%) of species with taphonomic evidence in quartile (TE/SPP) x 100</b>
<b>Top</b>	33 (12.6)	37 (57.4)	70	48
<b>Second</b>	10 (12.8)	61 (58.2)	71	14.1
<b>Third</b>	6 (13.2)	67 (59.8)	73	8.2
<b>Fourth</b>	3 (13.4)	71 (60.6)	74	4.1
<b>All quartiles</b>	52	234	288	18.8

*Table 5.2 Taphonomic evidence of Neanderthal intervention on bird species, by number of cases reported (from Appendix 2). Fisher Exact Test of data is in Table 5.3.*

<b>Quartile – Bird species present in Neanderthal sites based on frequency of occurrence (Q)</b>	<b>Species with one case of taphonomic evidence reported (A)</b>	<b>Species with two cases of taphonomic evidence reported (B)</b>	<b>Species with three cases of taphonomic evidence reported (C)</b>	<b>Species with four or more cases of taphonomic evidence reported (D)</b>
<b>Top</b>	22	6	2	3
<b>Second</b>	10	0	0	0
<b>Third</b>	6	0	0	0
<b>Fourth</b>	3	0	0	0
<b>All quartiles</b>	41	6	2	3

Table 5.3 Contingency Table for Fisher's Exact Test (two-sided). Data from Table 5.2.

Quartile (Q)	A Observed	A Expected	B + C + D Observed	B + C + D Expected	Total Observed
Top	22	26	11	7	33
Other quartiles combined	19	15	0	4	19
All quartiles	41	41	11	11	52

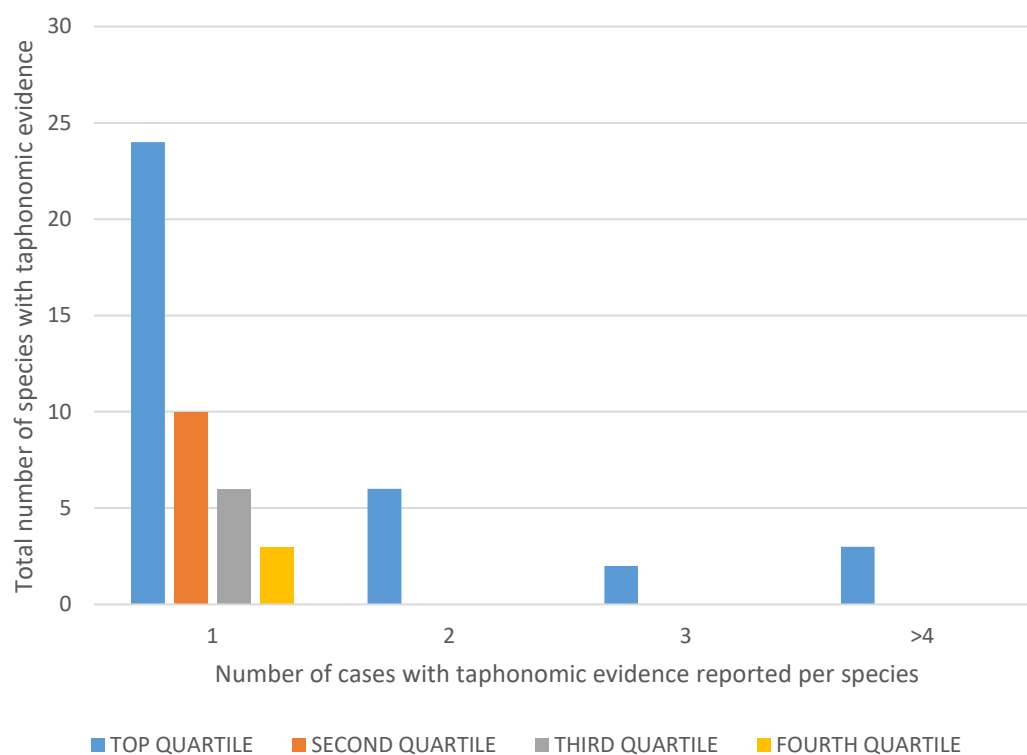


Figure 5.2 Total number of species with taphonomic evidence of Neanderthal intervention in relation to the number of cases with taphonomic evidence reported. Data from Table 5.2.

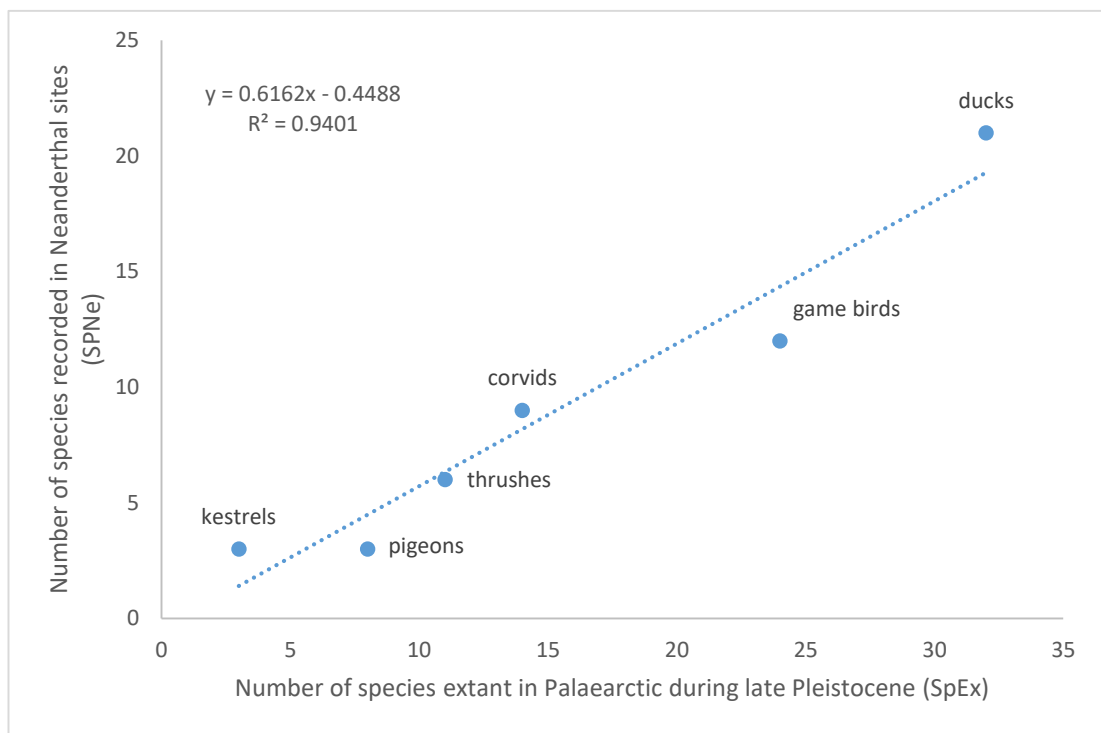
### 5.3.2 Taxonomic Categories

Table 5.4 summarises the evidence of Neanderthal intervention on bird bones classified by the main taxa described in Chapter 2, and Chapter 4. Figure 5.3 shows the relationship between taxa represented in Neanderthal sites and the availability of species in these categories in the Palaearctic. This relationship is statistically significant: regression:  $y = 0.6162x - 0.4488$ ;  $F_{1,4} = 62.8$ ,  $P = 0.001$ ;  $R^2 = 0.9401$ . There is no relationship when species, by taxonomic category, known to have been processed by Neanderthals are compared to those found in Neanderthal sites (Figure 5.4): regression:  $y = 0.0897x + 3.1923$ ;  $F_{1,4} = 0.25$ ,  $P = 0.643$ ;  $R^2 = 0.06$ , NS. The residual plots show that there is currently more than expected evidence of Neanderthal intervention on corvids and game birds and an underrepresentation of ducks and thrushes (Figure 5.5). These results suggest that Neanderthal intervention on bird taxa is independent of frequency in Neanderthal sites, i.e. corvids > game birds > other taxonomic categories.

*Table 5.4 Number of species recorded with taphonomic evidence compared with number of species recorded in Neanderthals sites and total number of species extant in the Palaearctic during the late Pleistocene by taxonomic category*

<b>Taxonomic Category (from Section 4.3)</b>	<b>Number of species recorded with taphonomic evidence (SPTE) (from Appendix 2)</b>	<b>Number of species recorded in Neanderthal sites (SPNe) (from Appendix 1)</b>	<b>Number of species extant in Palaearctic (SpEx) during the late Pleistocene (Finlayson 2011)</b>	<b>Residuals (RES) of regression analysis of SPTE against SPNe in Figure 5.5</b>
<b>corvids</b>	6	9	14	2
<b>ducks</b>	3	21	32	-2.1
<b>game birds</b>	8	12	24	3.7
<b>kestrels</b>	3	3	3	-0.5

<b>Taxonomic Category (from Section 4.3)</b>	<b>Number of species recorded with taphonomic evidence (SPTE) (from Appendix 2)</b>	<b>Number of species recorded in Neanderthal sites (SPNe) (from Appendix 1)</b>	<b>Number of species extant in Palaearctic (SpEx) during the late Pleistocene (Finlayson 2011)</b>	<b>Residuals (RES) of regression analysis of SPTE against SPNe in Figure 5.5</b>
<b>pigeons</b>	3	3	8	-0.5
<b>thrushes</b>	1	6	11	-2.7
<b>Totals</b>	24	54	92	



*Figure 5.3 The relationship between number of species recorded in Neanderthal sites (SPNe) and number of species extant (SpEx) in the Palaearctic during the late Pleistocene by taxonomic category. Data from Table 5.4.*

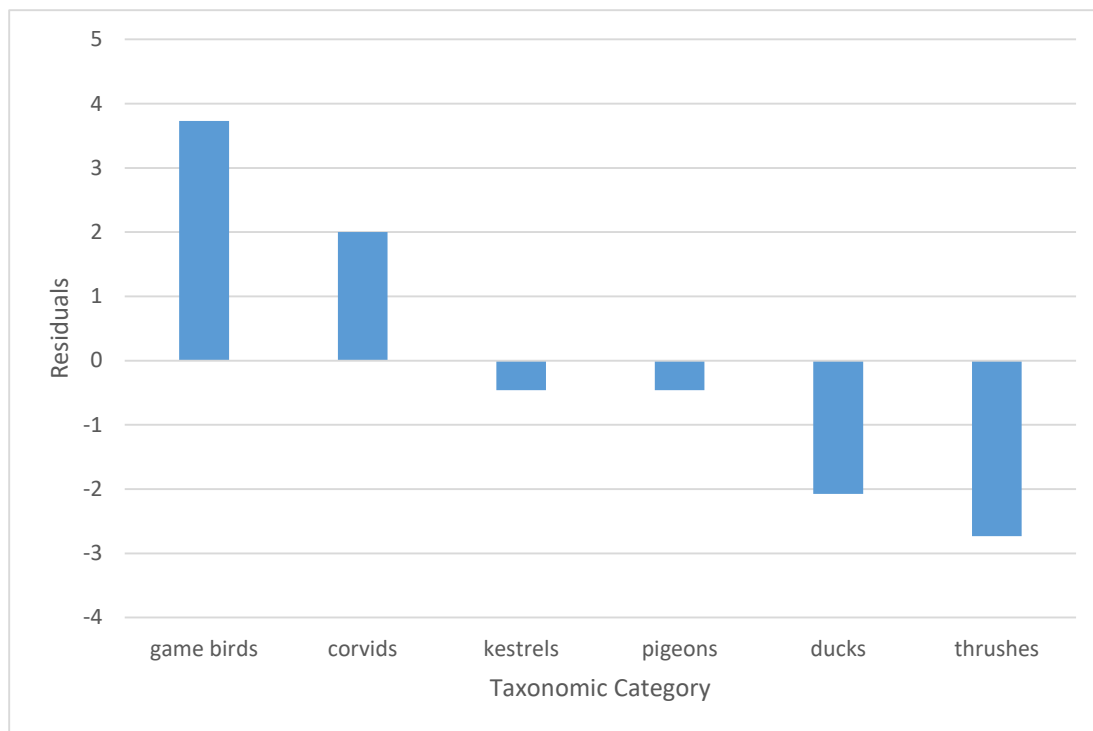


Figure 5.4 Residual plots from Figure 5.5.

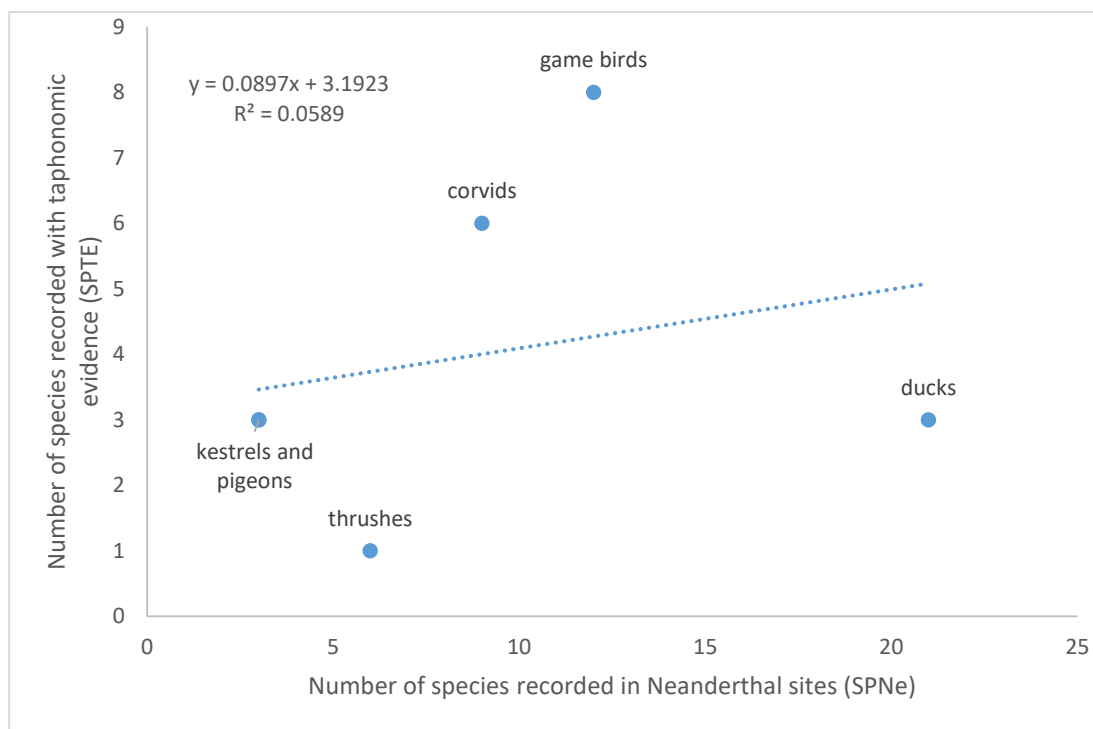


Figure 5.5 The relationship between species recorded with taphonomic evidence (SPTE) and species in those categories recorded in Neanderthal sites (SPNe). Data from Table 5.4

### 5.3.3 Behavioural Characteristics

Table 5.5 summarises the evidence of Neanderthal intervention on bird bones classified by the behavioural characteristics described in Chapter 2, Table 2.5 and Chapter 4. Figure 5.6 shows a statistically significant relationship between ecological categories represented in Neanderthal sites and the availability of species in these categories in the Palaearctic: regression:  $y = 0.6498 x + 3.9443$ ;  $F_{1,8} = 182.3$ ,  $P = 0.000$ ;  $R^2 = 0.958$ . There is also a statistically significant relationship when species, by behavioural characteristics, known to have been processed by Neanderthals are compared to those found in Neanderthal sites (Figure 5.7): Regression:  $y = 0.1498 x + 5.4536$ ;  $F_{1,8} = 8.239$ ,  $P = 0.021$ ;  $R^2 = 0.5074$ . The residual plots show that there is currently evidence of Neanderthal intervention on cliff-nesting birds, commensals and, less so, flocking birds and an underrepresentation of arboreal birds and, less so, lekking birds (Figure 5.8). These results suggest that Neanderthal intervention on bird species at the level on behavioural characteristics is also independent of how often these categories are represented in Neanderthal sites. Cliff-nesting birds appear to be consistently best represented, followed by scavengers and commensals.

*Table 5.5 Number of species with different behavioural characteristics recorded with taphonomic evidence compared with number of species recorded in Neanderthal sites and total number of species extant in the Palaearctic during the late Pleistocene*

<b>Behavioural Characteristics</b>	<b>Number of species recorded with taphonomic evidence (SPTE) (from Appendix 2)</b>	<b>Number of species recorded in Neanderthal sites (SPNe) (from Appendix 1)</b>	<b>Number of species extant in Palaearctic during the late Pleistocene (SpEx) (Finlayson 2011)</b>	<b>Residuals (RES) of regression analysis of SPTE against SPNe in Figure 5.8</b>
<b>flocking</b>	32	145	198	4.8
<b>commensal</b>	23	53	81	9.6
<b>large scavenger</b>	5	6	6	-1.4
<b>partial scavenger</b>	10	26	33	0.7
<b>cliff nester</b>	21	37	44	10
<b>ground nester</b>	17	98	137	-3.1
<b>wetland ground</b>	10	44	64	-2
<b>ground cryptic</b>	14	73	95	-2.4
<b>lekking</b>	1	9	10	-5.8
<b>arboreal</b>	9	93	170	-10.4
<b>Totals</b>	142	584	838	

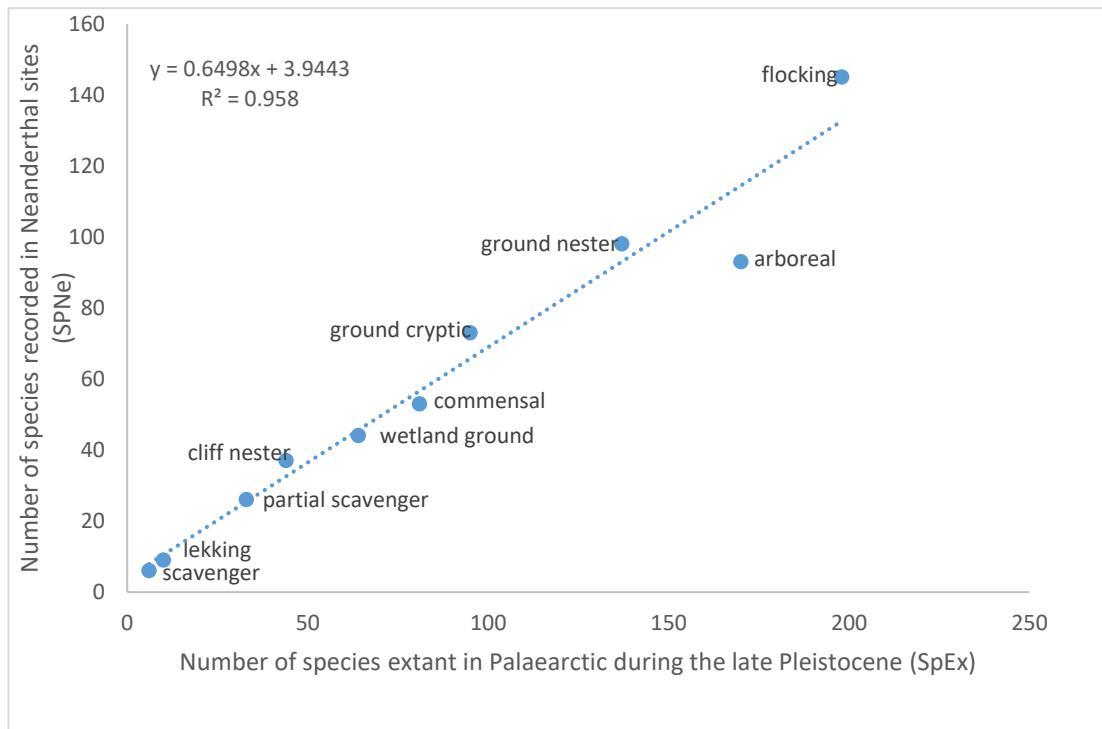


Figure 5.7 Number of species with different behavioural characteristic recorded in Neanderthal sites compared to number of species extant in Palaeartic during the late Pleistocene. Species classified by ecological category. Data from Table 5.5.

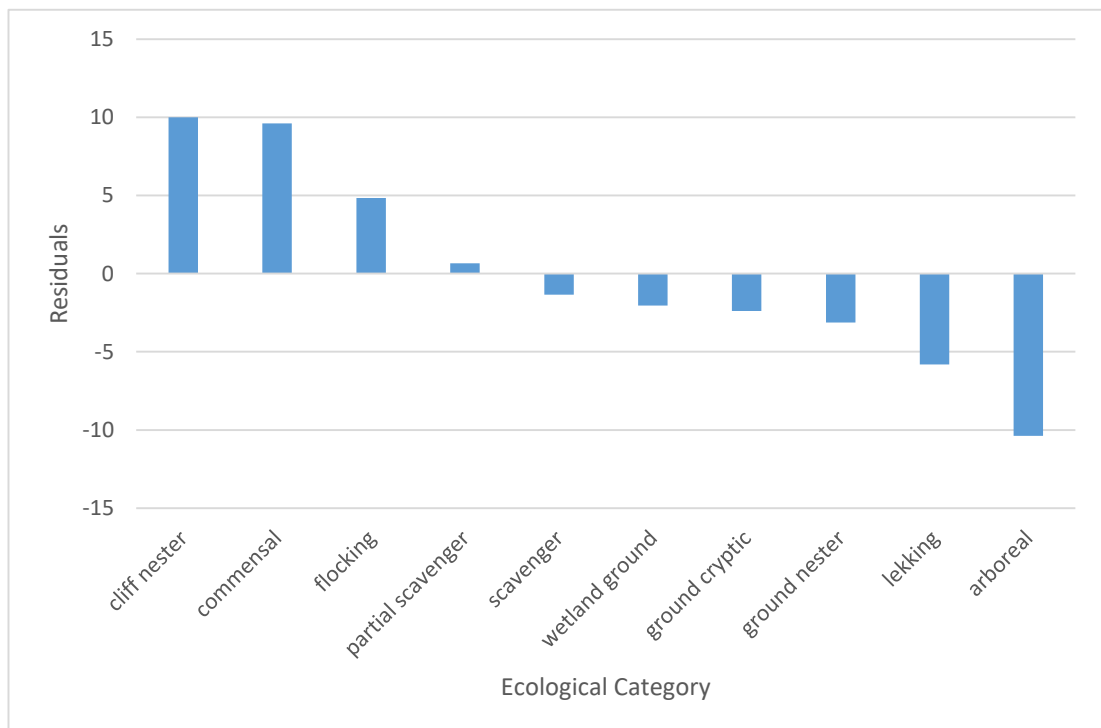
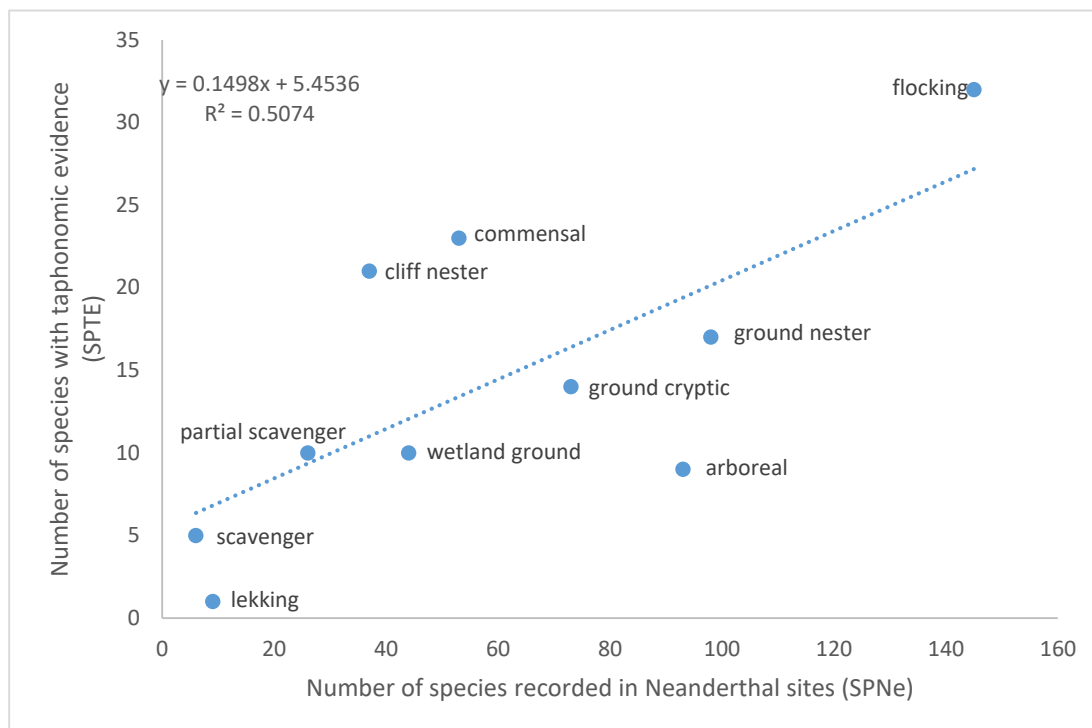


Figure 5.6 Residual plots from Figure 5.8





*Figure 5.8 Number of species with taphonomic evidence compared to number of species recorded in Neanderthal sites. Species classified by ecological category. Data from Table 5.5.*

### 5.3.4 Body mass classes

A statistical analysis of the body mass classes (Table 4.11) for bird species known to have been intervened by Neanderthals (Appendix 2) indicates an under-representation of small species (< 100 g)(Table 5.6). In contrast, it is the medium sized species (101 g to 1,000 g) which appear best represented. These results appear to confirm the conclusions drawn in Chapter 4 regarding the association of Neanderthals with species of particular body mass.

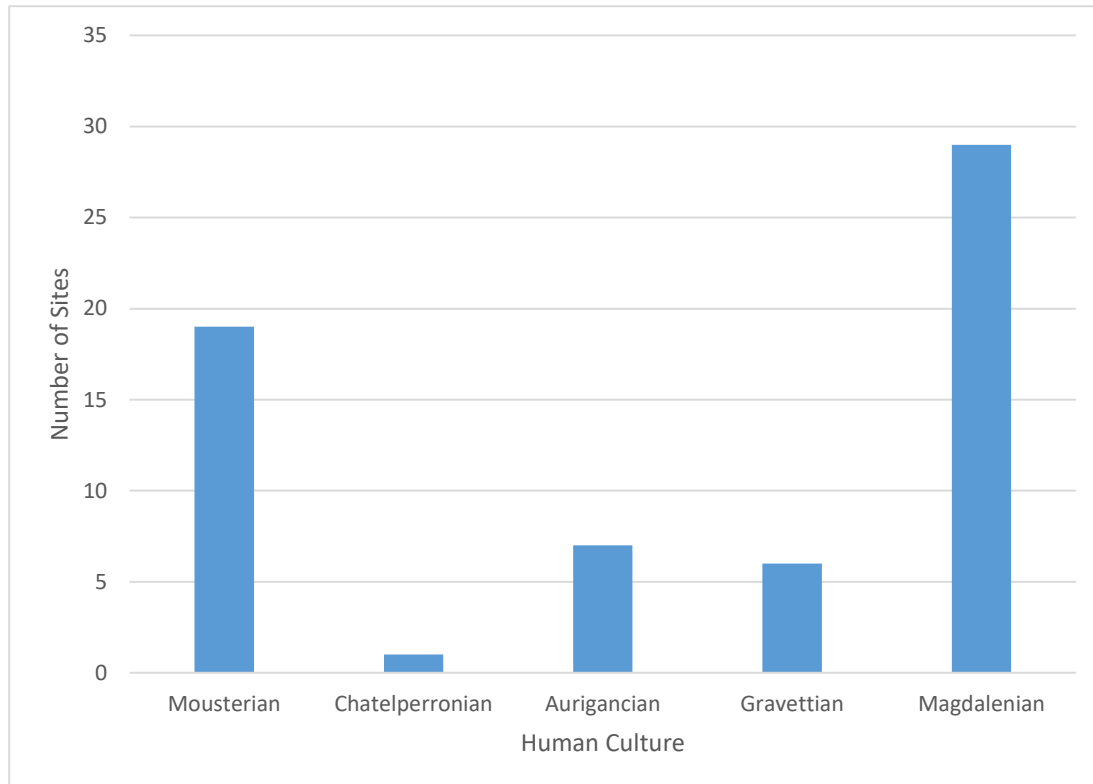
*Table 5.6 Number of species with taphonomic intervention in Neanderthal sites by body mass classes. Classes are merged from categories in Table 4.1. Expected classes, calculated from total number of species in each class are shown in italics in brackets. One-way Chi-Square = 18.5, df = 2, N = 52, p<0.0001.*

Body mass class	Number of species with taphonomic intervention	Number of species in class
< 100 g (Categories to A to B)	6 (21)	173
101 -1,000 g (Category B/C to C/D)	36 (23)	195
> 1,001 g (Categories D to E)	10 (8)	62
Totals	52	430

## 5.4 Taphonomic evidence for modern humans

As previously explained in Section 5.1, arguments suggesting significant differences between modern humans and Neanderthals in relation to bird exploitation have dominated the literature until recently (Stiner 1991; Stiner *et al.*, 2000; Klein, 1999,

2001). Yet these claims are unsupported by published evidence. Figure 5.9 shows the number of sites with reported cases of bird exploitation based on direct taphonomic evidence. It reveals that the modern human cultures that were contemporary with, or immediately succeeded, the Neanderthals have provided little evidence of bird exploitation. It is with the Magdalenian culture, post-dating the last Neanderthals by at least 12 kyr, that we see strong evidence of bird exploitation. Indeed, the Mousterian only falls short of the Magdalenian as the culture with strongest evidence of bird exploitation. This level of evidence is only recent as all papers post-date 2009 and reflect an interest on the part of researchers in this new field. A similar comparison pre-2009 would have revealed no evidence of Neanderthal exploitation of birds, presumably why it was thought to have been practised only by modern humans, when what was really meant was by Magdalenians, a long time after the disappearance of the Neanderthals. What is clear is that there is growing evidence of Neanderthal exploitation of birds, mirroring that of Magdalenians but we must remain open to new evidence that might reveal similar evidence for other cultures. Indeed, the high level of evidence for the Magdalenian may reflect significant work carried out on the Magdalenian of France by French researchers. Given the paucity of data on modern human bird exploitation, other than from the Magdalenian, I will limit my statistical comparison to the Mousterian with the Magdalenian but I will provide an overview of the evidence from other cultures, contemporary or temporarily close to the Neanderthals, for completeness. These are the Aurignacian and Gravettian, which I have discussed throughout this thesis. In addition, I have added the Chatelperronian in Figure 5.9. This is regarded as a transitional industry, representing a novel technology adopted by Neanderthals (Mellars, 1996), and is included for completeness. It succeeds the Mousterian in France and north-western Spain.



*Figure 5.9 Number of sites with direct taphonomic evidence of bird exploitation by humans. Cultural categories, human attributions and chronology are at Table 2.1. The Chatelperronian, not included in Table 2.1, is regarded as a transitional industry made by Neanderthals. Data for Neanderthals (Mousterian) from Appendix 2, data for modern humans (Magdalenian) from Appendix 3, and limited data for Chatelperronian, Aurignacian and Gravettian are referred to in Sections 5.4.1 and 5.4.2.*

### **5.4.1 Aurignacian**

Evidence comes from three French sites (Laroulandie, 2004) and a Greek site (Tomek & Bochenski, 2002): a “flute” made from the ulna of a large raptor from Isturitz (Pyrénées-Atlantiques); eleven tubes made from bird long bones and decorated with incisions from Gatzarria (Pyrénées-Atlantiques); and a similar example from La Tuto de Camalhot (Ariege). From Klisoura Cave in Greece, there is evidence of burnt bones from rock partridge (*Alectoris graeca*), great bustard (*Otis tarda*), jackdaw (*Corvus*

*monedula*) and an owl. Additionally, Hardy *et al.* (2008) found feather fragments on stone tools at Hohle Fels in Germany. At Geißenklosterle in Germany, occasional anthropogenic modifications suggest that a proportion of the avifauna is the result of human activities related to subsistence and the procurement of bones for flutes and feathers. At Geißenklosterle and in Vogelherd in Germany bird bone flutes were made from swan radii and at Hohle Fels a well-preserved bone flute was carved out of the radius of a griffon vulture (*Gyps fulvus*) (Conard *et al.*, 2013).

#### **5.4.2 Gravettian**

Laroulandie (2004) provides evidence from five French sites: fifteen pieces, including a “flute” made from the ulnas of large raptors, specifically bearded vulture (*Gypaetus barbatus*) and griffon/cinereous vulture (*Gyps/Aegypius*), from Isturitz; a bearded vulture ulna from Pair-non-Pair (Gironde); a long bone from a large bird from Abri Lespiaux (Gironde); a cut tube made from the femur of a large bird from Tarté (Haute-Garonne); and the ulna of a swan (*Cygnus*) from Le Flageolet (Dordogne). There is also evidence of bird exploitation at the Czech site of Pavlov I (Bochenski *et al.*, 2009). Here, more than 1,000 bird bones of 19 taxa were recovered and included many tetraonids and ravens (*Corvus corax*). Direct taphonomic evidence of human intervention was limited, however: a partly burned distal carpometacarpus of a grouse (*Lagopus* spp.); a distal humerus of a black grouse (*Tetrao tetrix*) with a cut mark; a humerus of a whooper swan (*Cygnus cygnus*) with cut marks on the anterior side of its proximal end; a raven ulna shaft with polished ends; a complete right ulna of Bewick’s Swan (*Cygnus bewickii*) with five distinct cuts forming a design on the ventral side of the proximal end; and a long fragment of the left ulna of a griffon vulture (*Gyps fulvus*) with cuts at the proximal end.

### 5.4.3 Magdalenian

A total of thirty-six confirmed bird species and an additional nine identified to genus level, provide evidence of Magdalenian intervention from twenty-eight different sites across Europe (Appendix 3). This means that to date more species have been identified with anthropic modifications in Neanderthal ( $n = 52$ ) than Magdalenian sites ( $n = 36$ ) even though the latter have been regarded as providing the benchmark of human exploitation of birds. The number of sites described with such evidence is, nevertheless higher in Magdalenian ( $n = 28$ ) than in Neanderthal ( $n = 19$ ) sites. These differences may simply be a reflection of effort on the part of researchers. The comparison may also be flawed because the Magdalenian period was significantly shorter than the Mousterian of the Neanderthals (Table 2.1). Nevertheless, the Magdalenian is, today, the best available culture for comparison with the Neanderthals in terms of bird exploitation.

If we compare the species exploited by Magdalenians, from direct taphonomic evidence, with those found in Magdalenian sites (Chapter 4), the results show that the main species found in Magdalenian sites show evidence of direct intervention (Figure 5.10; Table 5.7 to Table 5.9; and Appendix 5).

Eight (willow grouse (*L. lagopus*), alpine chough (*P. graculus*), rock ptarmigan (*L. mutus*), black grouse (*Tetrao tetrix*), raven (*Corvus corax*), mallard (*Anas platyrhynchos*), snowy owl (*Bubo scandiacus*) and golden eagle (*A. chrysaetos*)) of the top ten species that occurred in Magdalenian sites (Appendix 5) show evidence of processing by Magdalenians. In the case of the *Lagopus* grouse it is up to thirteen cases, although caution is required as twelve of these are recorded at the genus level.

The raven is also well represented with eleven cases with alpine chough ( $n = 6$ ) and black grouse and mallard ( $n = 4$ ). The exceptions are grey partridge and kestrel, with only one example each of direct processing. Overall, the evidence clearly indicates that the presence of these birds in Magdalenian sites is related, in part at least, to human exploitation. Of the species occurring in lower frequencies in Magdalenian sites, three raptors are noteworthy because of repeated evidence of anthropic action, in spite of their relative scarcity in Magdalenian sites: griffon vulture (five taphonomic cases and only occurring in 5% of sites;  $n = 5$ , 5%); bearded vulture ( $n = 3$ , 8%); and white-tailed eagle ( $n = 2$ , 8.6%).

*Table 5.7 Taphonomic evidence of Magdalenian intervention on bird species. Data of taphonomic evidence from Appendix 3. Ranking of species into quartiles uses data from Appendix 1. Expected values, calculated from the 4 x 2 contingency table, are shown in italics in brackets. Two-way Chi-Square = 34.361,  $df = 3$ ,  $N = 232$ ,  $p < 0.0001$ .*

<b>Quartile - Proportion (%) of species present in Magdalenian sites (Q)</b>	<b>Total number of species with taphonomic evidence (TE)</b>	<b>Total number of species with no taphonomic evidence (NTE)</b>	<b>Total number of species in quartile (SPP)</b>	<b>Proportion (%) of species with taphonomic evidence in quartile</b>
<b>Top</b>	20 (7.4)	32 (44.6)	52	38.5
<b>Second</b>	5 (7.4)	47 (44.6)	52	9.6
<b>Third</b>	5 (5.8)	36 (35.2)	41	12.2
<b>Fourth</b>	3 (12.4)	84 (74.6)	87	3.5
<b>All quartiles</b>	33	199	232	14.2

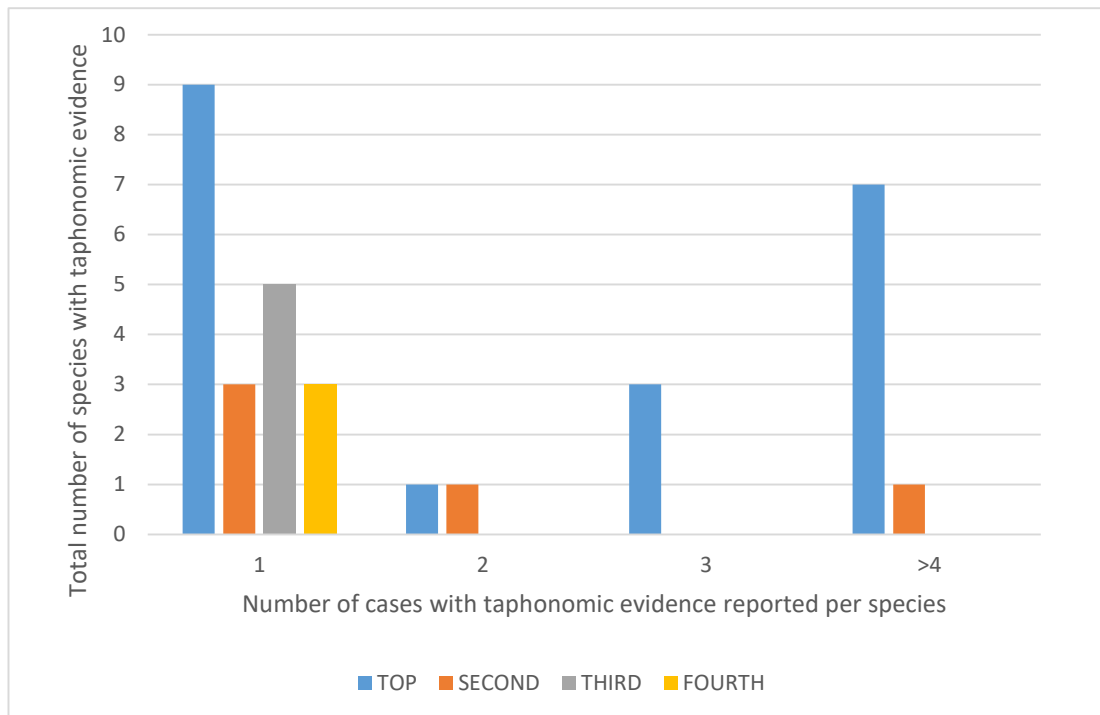
*Table 5.8 Taphonomic evidence of Magdalenian intervention on bird species by number of cases reported (from Appendix 3).*

<b>Quartile - Proportion (%) of species present in Magdalenian sites (Q)</b>	<b>Species with one case of taphonomic evidence reported (A)</b>	<b>Species with two cases of taphonomic evidence reported (B)</b>	<b>Species with three cases of taphonomic evidence reported (C)</b>	<b>Species with four or more cases of taphonomic evidence reported (D)</b>
<b>Top</b>	9	1	3	7
<b>Second</b>	3	1	0	1
<b>Third</b>	5	0	0	0
<b>Fourth</b>	3	0	0	0
<b>All quartiles</b>	20	2	3	8

*Table 5.9 Contingency Table for Fisher's Exact Test (two-sided). Fisher's Exact Test Statistic = -2.241 N = 33 p = 0.032. Data from Table 5.8.*

<b>Quartile (Q)</b>	<b>A Observed</b>	<b>A Expected</b>	<b>B + C + D Observed</b>	<b>B + C + D Expected</b>	<b>Total Observed</b>
<b>Top</b>	9	12.1	11	7.9	20
<b>Other quartiles combined</b>	11	7.9	2	5.1	13
<b>All quartiles</b>	20	20	13	13	33





*Figure 5.10 Total number of species with taphonomic evidence of Magdalenian intervention in relation to the number of cases with taphonomic evidence reported. Data from Table 5.8.*

## 5.5 The use of birds by Neanderthals and modern humans compared

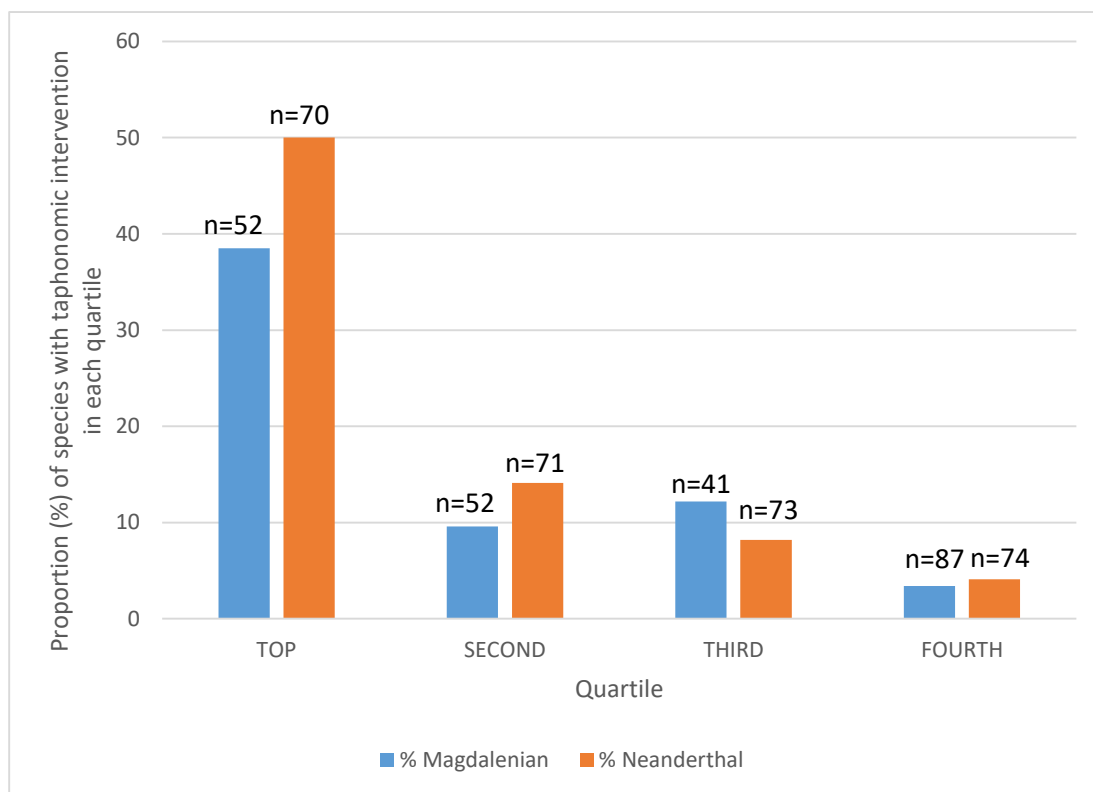
In this section I will limit the comparison with Neanderthals to the modern human culture which provides a comparable sample, i.e. the Magdalenians. Several features emerge from a comparison of the presence of birds and of the taphonomic evidence of bird exploitation by Neanderthals and Magdalenians. The first is the great similarity in the choice of target species, with a clear predominance of species that are well-represented in sites (Figure 5.11). This could be the result of the clear targeting of the most frequent species, suggesting hunting of the most commonly encountered species. In other words, species were hunted as they were encountered.

On the other hand, it could mean that the main agents accumulating bird remains in most sites are people selecting particular species. Thus, the abundance of bird species in human sites would reflect hunting intensity on those species. If the latter is the case, then we have grounds for using species lists from human occupation sites as good indicators of species being targeted. The importance of game birds, wildfowl and other potential food species, and also of species which are sources of large feathers and talons for use in decoration, in both Neanderthal and Magdalenian sites would seem to support this latter view.

The main difference lies in the actual species targeted (Figure 5.12). ‘Targeted’ means species for which taphonomic evidence of intervention has been found. This could be cut marks on bone, evidence of roasting, and so on. In most cases (e.g. evidence of roasting or cut marks in leg bones where concentrations of muscle tissue occurs), this evidence points in the direction of food consumption. In other cases, such as the predominance of marks on wing bones of raptors (Finlayson, *et al.*, 2012), or the regular marks on a raven bone (Majkić, *et al.*, 2006), imply processing which is unrelated to consumption. I have not distinguished between these activities and in my opinion the data available would be insufficient to make valid comparisons. I am simply limiting myself to evidence of Neanderthal activity on birds. It must be borne in mind that this is a new field in which evidence of Neanderthal intervention on birds has only been reported in the last few years. In my comparison with modern humans, I have limited myself to comparing the Neanderthal evidence with that of the Magdalenian modern humans for which most evidence is currently available. The Magdalenians are therefore the baseline for the Neanderthals.

Game birds are targeted by both Neanderthals and Magdalenians but the actual species for which we have direct taphonomic evidence are different. In the case of Neanderthals, the main game birds are red-legged partridge (*Alectoris rufa*), grey partridge (*P. perdix*) and quail (*Coturnix coturnix*), while the Magdalenians appear focused on rock ptarmigan (*L. mutus*), willow (*L. lagopus*) and black grouse (*T. tetrix*), with grey partridge (*P. perdix*) occasionally. Of the species with anthropic intervention, those of rocky habitats – choughs (*Pyrrhocorax* sp.), rock dove (*Columba livia*), and golden eagle (*Aquila chrysaetos*) – predominate in Neanderthals sites. The dominant species in Magdalenian sites, on the other hand, particularly snowy owl (*Bubo scandianus*), willow grouse (*Lagopus lagopus*) and rock ptarmigan (*Lagopus mutus*), are birds of the tundra. The raven (*Corvus corax*) also features in Magdalenian sites, and is a species that is at home in many environments and climates including tundra. These differences reflect clear ecological differences, with Neanderthals in mild climates, in rocky habitats and environments with some arboreal cover, and Magdalenians in open tundra.

In terms of species that provide large feathers and talons, Neanderthals appear to principally target golden eagles (*A. chrysaetos*), followed by a host of other, but less frequent, large raptors, while Magdalenians show a very clear preference for snowy owl (*B. scandiacus*) and raven (*C. corax*), both species they would have readily encountered in the open tundra. Neanderthals also show a preference for species of rocky habitats, presumably those they encountered close to caves: the choughs (*Pyrrhocorax* spp.), jackdaw (*Corvus monedula*), kestrel (*F. tinnunculus*) and rock dove (*C. livia*).



*Figure 5.11 Proportion (%) of species with taphonomic evidence by quartile, in relation to proportion (%) in Magdalenian and Neanderthal sites. Data from Table 5.1 and Table 5.7*

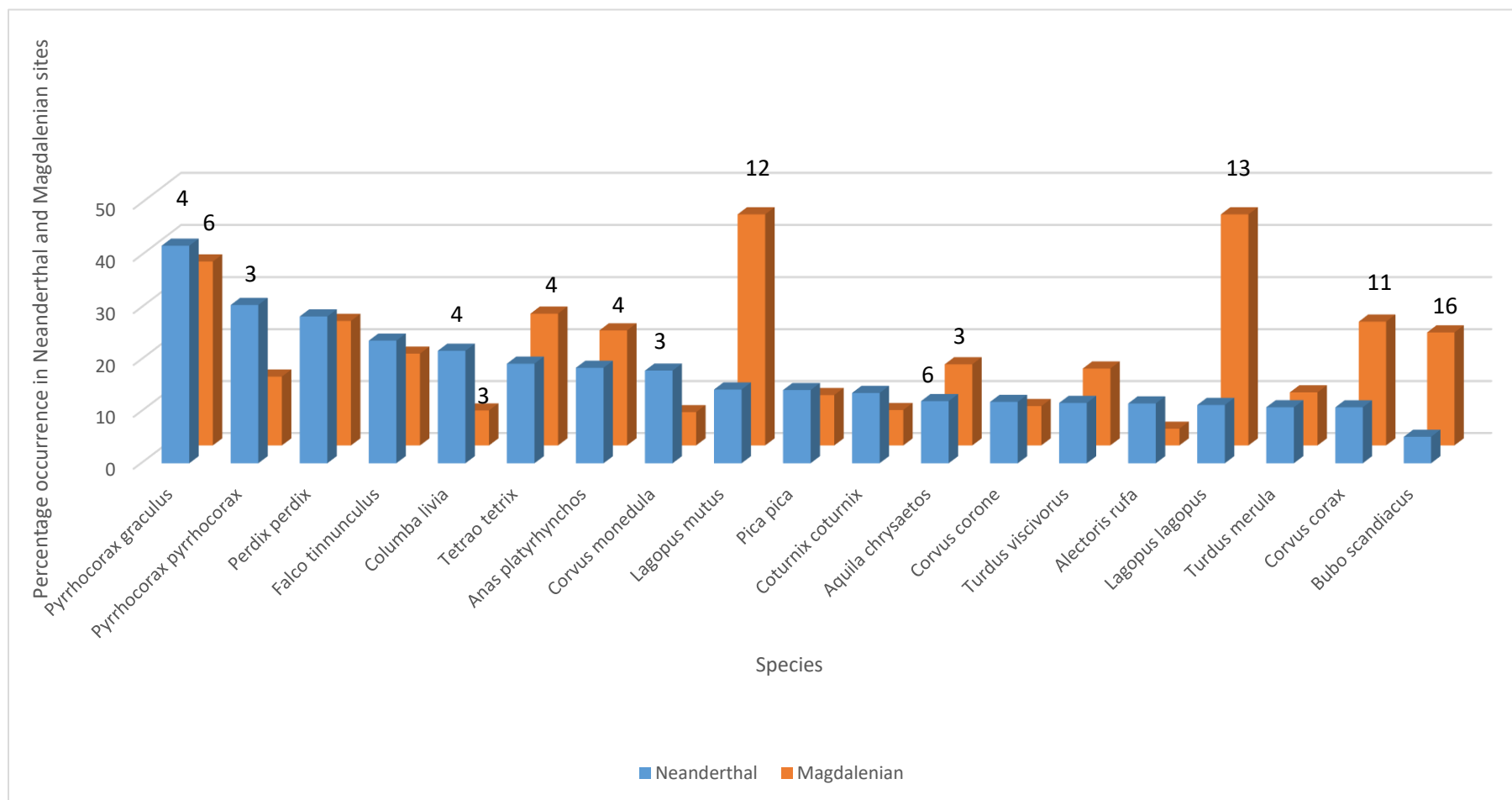


Figure 5.12 Percentage occurrence in Neanderthal and Magdalenian sites. Numbers over columns indicate number of cases of known anthropic intervention. Only three or more cases are shown. Data from Table 5.1 and Table 5.6.

## 5.6 Implications for future taphonomic studies

In this section I aim to answer the follow-up question to research question 3, using the data presented in this chapter in particular. That is, to predict species and sites which would appear to show potential for future taphonomic work.

### 5.6.1 Species

The taphonomic evidence currently available points to corvids, gamebirds and pigeons as categories of birds that appear to be particularly sought after by Neanderthals, and so would be good targets for further study. Of all the species which have been included in the main database of species found in Neanderthal sites (Appendix 1), the species that show no taphonomic evidence of Neanderthal intervention are those species that are infrequent in Neanderthal sites. This may be because they are localised in distribution or geographically marginal. Examples are Iberian azure-winged magpie (*Cyanopica cooki*) or chukar (*Alectoris chukar*). It is noteworthy that all the regularly occurring species from these groups have been found with taphonomic evidence of Neanderthal intervention. The only exceptions appear to be two corvids: the Eurasian jay (*G. glandarius*) and the rook (*Corvus frugilegus*); and one gamebird: capercaillie (*Tetrao urogallus*) (Appendix 4). Jay and capercaillie are birds of woodland and rook is a tree-nesting species so their absence may be connected to habitat as cliff-nesting birds were found to predominate in Neanderthal sites.

Birds with two behavioural characteristics, in particular appeared to show the strongest evidence of Neanderthal intervention: cliff-nesters and scavengers/commensals. Species which fall under these categories would appear to be good candidates for examination. Of those currently not well-represented by evidence of Neanderthal

activity, it is the seabirds which would appear to be strong candidates for further study, within the cliff-nesting category. The reason for this is that these species will naturally appear underrepresented because they would only be found on coastal sites, which would represent a small subset of all sites. Furthermore, there are indications that Neanderthals did target seabirds where these were available (Appendix 2): soft-plumage petrel (*Pterodroma* spp.), Cory's shearwater (*Calonectris diomedea*), shag (*Phalacrocorax aristotelis*), razorbill (*Alca torda*) and puffin (*Fratercula arctica*). Additional species of seabird that would appear to be good candidates for further study include the gulls (Laridae), northern gannet (*Morus bassanus*), great cormorant (*P. carbo*), shearwaters (*Puffinus* spp.), guillemot (*Uria aalge*), fulmar (*Fulmarus glacialis*), little auk (*Alle alle*) and great auk (*Pinguinus impennis*). The gulls would appear to be particularly good candidates as they are additionally scavengers and commensals.

The main scavengers (three vultures plus golden eagle and white-tailed eagle) have all been shown to have been targeted by Neanderthals except for the miratory Egyptian vulture (*Neophron percnopterus*) which Finlayson *et al.* (2016) have used in support of the argument that Neanderthals caught scavenging birds primarily in the winter months. This is a time when the Egyptian vulture is wintering in tropical Africa, outside the range of the Neanderthals.

In order to prioritise species which might be good candidates for further taphonomic study, I ranked species according to the known cases of intervention by Neanderthals (Table 5.10). I chose the top five taxonomic categories (leaving kestrel out – it is a group consisting of a single frequent species and two very scarce ones in Neanderthals sites; see Section 4.4.6) and the top five ecological categories. Table 5.10 is indicative and aimed at informing researchers as to likely species or groups of species to be

targeted. The focus on taxonomic and ecological categories is intended to allow researchers in different geographical areas to compare like with like. For example, a researcher working in an Iberian site may have red-legged partridge *Alectoris rufa*, and another in Greece, rock partridge *A. graeca*. For all intents and purposes, it is the *Alectoris* category, and not the species, that is relevant to both. It is possible that in adopting this approach, some species not in the main taxonomic or ecological categories, may have been left out of the ranking, although these will be very few, but at the current level of the study of bird taphonomy (where there are still very few examples published) it seems best to concentrate on the major groups over large geographic areas.

Each of the taxonomic and ecological categories were given a score from 5 (maximum) to 1 (minimum) in accordance with their observed importance. For example, pigeons are in the top taxonomic category and always score a 5 irrespective of species; thrushes are in the lowest category and always score a 1; and so on. To avoid circularity, this table of 288 species was reduced to 141 species by removing all species currently known to have evidence of Neanderthal intervention. This list was further reduced by removing small birds (weight categories < 100 g) which are known to have been underrepresented in Neanderthal sites and further by removing very geographically localised species (unlikely to have been met by Neanderthals with any regularity). Thus, the list was narrowed down to 105 potential species (Table 5.11). This list is dominated by several groups of birds: ducks, geese and swans (Anseriformes) 29 species; waders (Charadriiformes) 23 species; raptors (Accipitriformes) and gulls (Laridae) with seven species each. This prioritisation is testable by examining bird collections from Neanderthal sites and it is suggested as an avenue for further research.



Table 5.10 Ranking of species with potential for taphonomic evidence of Neanderthal activity using currently known evidence of such activity. Taxonomic category ranking from Table 5.4 and behavioural characteristics ranking from Table 5.5. Note: kestrel has been removed from ranking as it is a single species; large and partial scavengers have been amalgamated. Scores for taxonomic and behavioural groups pertain to the top five groups in each case. The scores allocated by taxonomic and behavioural characteristics are indicative, and intended as a guide as to which species are likely to be most promising with regards to future study. Species with total scores  $\geq 10$  are highlighted in grey; species with total scores  $\geq 5$  are highlighted in light grey.

SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Corvus monedula</i>		4					4	3	2		13
<i>Columba livia</i>	5						4	3			12
<i>Pyrrhocorax graculus</i>		4					4	3			11
<i>Corvus corax</i>		4					4		2		10
<i>Pica pica</i>		4					4		2		10
<i>Larus argentatus</i>							4	3	2	1	10
<i>Larus fuscus</i>							4	3	2	1	10
<i>Cyanopica cyanus</i>		4					4		2		10
<i>Columba oenas</i>	5						4				9
<i>Columba palumbus</i>	5						4				9
<i>Aquila chrysaetos</i>						5		3			8

SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Gypaetus barbatus</i>						5		3			8
<i>Gyps fulvus</i>						5		3			8
<i>Haliaeetus albicilla</i>						5		3			8
<i>Neophron percnopterus</i>						5		3			8
<i>Pyrhcorax pyrrhcorax</i>		4						3			7
<i>Falco tinnunculus</i>							4	3			7
<i>Larus ridibundus</i>							4		2	1	7
<i>Larus canus</i>							4		2	1	7
<i>Corvus corone</i>		4							2		6
<i>Corvus frugilegus</i>		4							2		6
<i>Milvus migrans</i>							4		2		6
<i>Larus ichthyaetus</i>								3	2	1	6
<i>Milvus milvus</i>							4		2		6
<i>Aegypius monachus</i>						5					5
<i>Buteo lagopus</i>								3	2		5
<i>Streptopelia turtur</i>	5										5
<i>Garrulus glandarius</i>		4									4
<i>Strix aluco</i>							4				4

SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Passer domesticus</i>							4				4
<i>Nucifraga caryocatactes</i>		4									4
<i>Tyto alba</i>							4				4
<i>Pandion haliaetus</i>								3		1	4
<i>Puffinus hohleae</i>								3		1	4
<i>Pterodroma sp.</i>								3		1	4
<i>Uria aalge</i>								3		1	4
<i>Alca torda</i>								3		1	4
<i>Passer montanus</i>							4				4
<i>Fulmarus glacialis</i>								3		1	4
<i>Alle alle</i>								3		1	4
<i>Rissa tridactyla</i>								3		1	4
<i>Puffinus mauretanicus</i>								3		1	4
<i>Puffinus puffinus</i>								3		1	4
<i>Hydrobates pelagicus</i>								3		1	4
<i>Puffinus assimilis</i>								3		1	4
<i>Perdix perdix</i>			3								3
<i>Tetrao tetrix</i>			3								3

SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Anas platyrhynchos</i>				2						1	3
<i>Lagopus mutus</i>			3								3
<i>Coturnix coturnix</i>			3								3
<i>Alectoris rufa</i>			3								3
<i>Lagopus lagopus</i>			3								3
<i>Alectoris graeca</i>			3								3
<i>Bubo bubo</i>								3			3
<i>Anas querduedula</i>				2						1	3
<i>Tachymarptis melba</i>								3			3
<i>Athene noctua</i>								3			3
<i>Anas penelope</i>				2						1	3
<i>Ptyonoprogne rupestris</i>								3			3
<i>Hirundo rustica</i>								3			3
<i>Apus apus</i>								3			3
<i>Anas crecca</i>				2						1	3
<i>Tetrao urogallus</i>			3								3
<i>Delichon urbica</i>								3			3
<i>Falco naumanni</i>								3			3

SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Tetrao mlokosiewiczii</i>			3								3
<i>Anas acuta</i>				2						1	3
<i>Montifringilla nivalis</i>								3			3
<i>Alectoris chukar</i>			3								3
<i>Aythya nyroca</i>				2						1	3
<i>Falco peregrinus</i>								3			3
<i>Aythya ferina</i>				2						1	3
<i>Tetrastes bonasia</i>			3								3
<i>Melanitta nigra</i>				2						1	3
<i>Mergus merganser</i>				2						1	3
<i>Anas clypeata</i>				2						1	3
<i>Anas strepera</i>				2						1	3
<i>Tetrax tetrax</i>			3								3
<i>Hirundo daurica</i>								3			3
<i>Aythia fuligula</i>				2						1	3
<i>Bucephala clangula</i>				2						1	3
<i>Tetraogallus caucasicus</i>			3								3
<i>Mergus serrator</i>				2						1	3

SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Clangula hyemalis</i>				2						1	3
<i>Mergus albellus</i>				2						1	3
<i>Tadorna ferruginea</i>				2						1	3
<i>Fratercula arctica</i>								3			3
<i>Calonectris diomedea</i>								3			3
<i>Morus bassanus</i>								3			3
<i>Monticola solitarius</i>								3			3
<i>Phalacrocorax aristotelis</i>								3			3
<i>Buteo rufinus</i>								3			3
<i>Aquila fasciata</i>								3			3
<i>Apus affinis</i>								3			3
<i>Apus pacificus</i>								3			3
<i>Falco rusticolus</i>								3			3
<i>Hirundapus caudacutus</i>								3			3
<i>Perdix daurica</i>			3								3
<i>Tetraogallus altaicus</i>			3								3
<i>Tichodroma muraria</i>								3			3
<i>Melanitta fusca</i>				2						1	3

SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Falco eleonora</i>								3			3
<i>Otis tarda</i>			3								3
<i>Netta rufina</i>				2						1	3
<i>Catharacta skua</i>									2	1	3
<i>Polysticta stelleri</i>				2						1	3
<i>Stercorarius parasiticus</i>									2	1	3
<i>Buteo buteo</i>									2		2
<i>Aquila clanga</i>									2		2
<i>Aquila nipalensis</i>									2		2
<i>Buteo hemilasius</i>									2		2
<i>Aquila pomarina</i>									2		2
<i>Ciconia ciconia</i>									2		2
<i>Turdus viscivorus</i>					1						1
<i>Turdus merula</i>					1						1
<i>Turdus philomelos</i>					1						1
<i>Turdus pilaris</i>					1						1
<i>Turdus iliacus</i>					1						1
<i>Gallinula chloropus</i>										1	1

SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Rallus aquaticus</i>										1	1
<i>Cygnus cygnus</i>										1	1
<i>Vanellus vanellus</i>										1	1
<i>Branta bernicla</i>										1	1
<i>Anser anser</i>										1	1
<i>Anser albifrons</i>										1	1
<i>Anser fabalis</i>										1	1
<i>Limosa limosa</i>										1	1
<i>Calidris minuta</i>										1	1
<i>Turdus torquatus</i>					1						1
<i>Tringa totanus</i>										1	1
<i>Ardea cinerea</i>										1	1
<i>Porzana porzana</i>										1	1
<i>Gallinago gallinago</i>										1	1
<i>Calidris ferruginea</i>										1	1
<i>Calidris canutus</i>										1	1
<i>Anser brachyrhynchus</i>										1	1
<i>Numenius phaeopus</i>										1	1



SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Aquila heliaca</i>									1		1
<i>Grus grus</i>										1	1
<i>Gallinago media</i>										1	1
<i>Anthus spinoletta</i>										1	1
<i>Cygnus columbianus</i>										1	1
<i>Podiceps nigricollis</i>										1	1
<i>Tringa nebuaria</i>										1	1
<i>Podiceps auritus</i>										1	1
<i>Alcedo atthis</i>										1	1
<i>Recurvirostra avosetta</i>										1	1
<i>Chlidonias niger</i>										1	1
<i>Pluvialis squatarola</i>										1	1
<i>Actitis hypoleucos</i>										1	1
<i>Calidris alpina</i>										1	1
<i>Phalacrocorax carbo</i>										1	1
<i>Anser indicus</i>										1	1
<i>Branta leucopsis</i>										1	1
<i>Gallinago solitaria</i>										1	1

SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Philomachus pugnax</i>										1	1
<i>Pluvialis apricaria</i>										1	1
<i>Podiceps grisegena</i>										1	1
<i>Sterna hirundo</i>										1	1
<i>Tachybptus ruficollis</i>										1	1
<i>Tadorna tadorna</i>										1	1
<i>Tringa erythropus</i>										1	1
<i>Tringa glareola</i>										1	1
<i>Gavia stellata</i>										1	1
<i>Anser erythropus</i>										1	1
<i>Ceryle rudis</i>										1	1
<i>Halcyon smyrnensis</i>										1	1
<i>Ixobrychus minutus</i>										1	1
<i>Larus minutus</i>										1	1
<i>Pelecanus onocrotalus</i>										1	1
<i>Tringa ochropus</i>										1	1
<i>Fulica atra</i>										1	1
<i>Phalaropus fulicaria</i>										1	1

SCORE	Taxonomic category					Behavioural characteristics					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	large scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Haematopus ostralegus</i>										1	1
<i>Gavia arctica</i>										1	1
<i>Ardea purpurea</i>										1	1
<i>Calidris maritima</i>										1	1
<i>Geronticus eremita</i>										1	1
<i>Glareola pratincola</i>										1	1
<i>Himantopus himantopus</i>										1	1
<i>Plegadis falcinellus</i>										1	1

Table 5.11 Shortlist of bird species with potential for taphonomic study of Neanderthal intervention. Data from Table 5.10 and shortlisting explained in text.

SCORE	Taxonomic category					Ecological category					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Larus argentatus</i>							4	3	2	1	10
<i>Larus fuscus</i>							4	3	2	1	10
<i>Columba oenas</i>	5						4				9
<i>Neophron percnopterus</i>						5		3			8
<i>Larus ridibundus</i>							4		2	1	7
<i>Larus canus</i>							4		2	1	7
<i>Corvus frugilegus</i>		4							2		6
<i>Larus ichthyaetus</i>								3	2	1	6
<i>Buteo lagopus</i>								3	2		5
<i>Garrulus glandarius</i>		4									4
<i>Strix aluco</i>							4				4
<i>Nucifraga caryocatactes</i>		4									4
<i>Tyto alba</i>							4				4
<i>Pandion haliaetus</i>								3		1	4
<i>Uria aalge</i>								3		1	4

SCORE	Taxonomic category					Ecological category					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Fulmarus glacialis</i>								3		1	4
<i>Rissa tridactyla</i>								3		1	4
<i>Lagopus mutus</i>			3								3
<i>Bubo bubo</i>								3			3
<i>Anas querduedula</i>				2						1	3
<i>Anas penelope</i>				2						1	3
<i>Anas crecca</i>				2						1	3
<i>Tetrao urogallus</i>			3								3
<i>Anas acuta</i>				2						1	3
<i>Alectoris chukar</i>			3								3
<i>Aythya nyroca</i>				2						1	3
<i>Aythya farina</i>				2						1	3
<i>Tetrastes bonasia</i>			3								3
<i>Melanitta nigra</i>				2						1	3
<i>Mergus merganser</i>				2						1	3
<i>Anas clypeata</i>				2						1	3
<i>Anas strepera</i>				2						1	3
<i>Tetrax tetrax</i>			3								3

SCORE	Taxonomic category					Ecological category					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Aythia fuligula</i>				2						1	3
<i>Bucephala clangula</i>				2						1	3
<i>Mergus serrator</i>				2						1	3
<i>Mergus albellus</i>				2						1	3
<i>Tadorna ferruginea</i>				2						1	3
<i>Morus bassanus</i>								3			3
<i>Aquila fasciata</i>								3			3
<i>Falco rusticolus</i>								3			3
<i>Melanitta fusca</i>				2						1	3
<i>Otis tarda</i>			3								3
<i>Netta rufina</i>				2						1	3
<i>Catharacta skua</i>									2	1	3
<i>Polysticta stelleri</i>				2						1	3
<i>Stercorarius parasiticus</i>									2	1	3
<i>Aquila clanga</i>									2		2
<i>Aquila nipalensis</i>									2		2
<i>Aquila pomarina</i>									2		2
<i>Ciconia ciconia</i>									2		2

SCORE	Taxonomic category					Ecological category					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Gallinula chloropus</i>										1	1
<i>Rallus aquaticus</i>										1	1
<i>Branta bernicla</i>										1	1
<i>Anser anser</i>										1	1
<i>Anser albifrons</i>										1	1
<i>Anser fabalis</i>										1	1
<i>Limosa limosa</i>										1	1
<i>Tringa tetanus</i>										1	1
<i>Ardea cinerea</i>										1	1
<i>Porzana porzana</i>										1	1
<i>Gallinago gallinago</i>										1	1
<i>Calidris ferruginea</i>										1	1
<i>Calidris canutus</i>										1	1
<i>Anser brachyrhynchus</i>										1	1
<i>Numenius phaeopus</i>										1	1
<i>Aquila heliacal</i>									1		1
<i>Grus grus</i>										1	1
<i>Gallinago media</i>										1	1

SCORE	Taxonomic category					Ecological category					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Cygnus columbianus</i>										1	1
<i>Podiceps nigricollis</i>										1	1
<i>Tringa nebuaria</i>										1	1
<i>Podiceps auritus</i>										1	1
<i>Recurvirostra avosetta</i>										1	1
<i>Chlidonias niger</i>										1	1
<i>Pluvialis squatarola</i>										1	1
<i>Actitis hypoleucos</i>										1	1
<i>Calidris alpine</i>										1	1
<i>Phalacrocorax carbo</i>										1	1
<i>Anser indicus</i>										1	1
<i>Branta leucopsis</i>										1	1
<i>Gallinago solitaria</i>										1	1
<i>Philomachus pugnax</i>										1	1
<i>Pluvialis apricaria</i>										1	1
<i>Podiceps grisegena</i>										1	1
<i>Sterna hirundo</i>										1	1
<i>Tachybptus ruficollis</i>										1	1



SCORE	Taxonomic category					Ecological category					TOTAL
	pigeons	corvids	game birds	ducks	thrushes	scavenger	commensal	cliff nester	partial scavenger	wetland ground	
	5	4	3	2	1	5	4	3	2	1	
<i>Tadorna tadorna</i>										1	1
<i>Tringa erythropus</i>										1	1
<i>Tringa glareola</i>										1	1
<i>Gavia stellate</i>										1	1
<i>Anser erythropus</i>										1	1
<i>Ixobrychus minutus</i>										1	1
<i>Larus minutus</i>										1	1
<i>Pelecanus onocrotalus</i>										1	1
<i>Tringa ochropus</i>										1	1
<i>Fulica atra</i>										1	1
<i>Phalaropus fulicaria</i>										1	1
<i>Haematopus ostralegus</i>										1	1
<i>Gavia arctica</i>										1	1
<i>Ardea purpurea</i>										1	1
<i>Calidris maritima</i>										1	1
<i>Glareola pratincola</i>										1	1
<i>Himantopus himantopus</i>										1	1
<i>Plegadis falcinellus</i>										1	1

### 5.6.2 Sites

Another productive line of research would appear to be to examine entire bird collections from Neanderthal sites, which would require identifying sites that are most likely to have evidence of Neanderthal intervention on birds and then examine the entire range of bird species. In doing so, the criteria identified so far for species should be borne in mind. In Table 5.12 I have attempted to rank known sites with Neanderthals and birds; I have limited the list to sites that have bird species that have to date been demonstrated to have been intervened by Neanderthals somewhere throughout their range. I have used the number of reported cases of Neanderthal intervention (Appendix 2) to produce a site ranking. This has been simply done by listing the species in each site with the corresponding score. For example, a site with alpine chough (4 cases), red-billed chough (3 cases) and rock dove (4 cases) would score 11. I have then ranked the sites by making the site with the highest score 100% and calculating the others as proportions of the top site.

The table makes two suggestions for further study:

- (a) sites already known to have bird species with taphonomic evidence of intervention should be re-examined. Bird species known to have taphonomic evidence from other sites, but not the site being examined, should be looked at in detail;
- (b) sites without current evidence of taphonomic intervention should be examined. Ideally, they should be examined in the order listed in Table 5.12.

These are therefore also testable.

*Table 5.12 Ranking of Neanderthal sites with birds known to have been intervened, based on taphonomic evidence, by Neanderthals. The number of species in each site is taken from Appendix 1 and are therefore independent of the taphonomic data (Appendix 2). In other words, the ranking is a probability of discovering evidence based on the species most likely to have such evidence even if actual evidence has not been documented for that particular site. As the sources of the data are independent, circularity is avoided. This is clear when the sites with actual published taphonomic evidence (in bold) are seen not to fall in order at the top of the table. They are, instead, interspersed and some fall low down the ranking.*

NAME	SCORE	PROPORTION (%) OF TOP SITES SCORE
<b>Gorham's Cave, Gibraltar</b>	<b>70.4</b>	<b>100.0</b>
Grotta del Principe, Liguria, Italy	48.4	68.8
<b>Baume de Gigny, Jura, France</b>	<b>39.0</b>	<b>55.4</b>
Devil's Tower Rock Shelter, Gibraltar	37.6	53.4
Soulabe, Ariège, France	36.2	51.4
Grotta Breuil, Latina, Italy	36.2	51.4
Tournal, Aude, France	34.5	48.9
Vanguard Cave, Gibraltar	33.7	47.9
Ust'-Kanskaya Peshchera, Gorno-Altai, Russia	33.3	47.3
Hortus, Hérault, France	33.3	47.3
Salpetre a Pompignan, Hérault, France	33.2	47.2
Kebara, Galilee, Israel	33.1	47.1
Sibiryachikha Cave, Altai, Russia	32.4	46.1
<b>Arbreda, Gerona, Spain</b>	<b>31.5</b>	<b>44.7</b>
Torre Nave, Calabria, Italy	30.5	43.3

NAME	SCORE	PROPORTION (%) OF TOP SITES SCORE
<b>Combe Grenal, Dordogne, France</b>	<b>30.5</b>	<b>43.3</b>
<b>Riparo di Fumane, Verona, Italy</b>	<b>30.2</b>	<b>42.9</b>
Cueva de Valdegoba, Burgos, Spain	29.9	42.4
<b>Pie Lombard, Alpes-Maritimes, France</b>	<b>28.8</b>	<b>40.9</b>
Grotta dei Giganti, Puglia, Italy	28.2	40.0
Grottoni, Abruzzo, Italy	27.1	38.4
Ibex Cave, Gibraltar	25.6	36.3
Ripa, Bihor, Romania	25.2	35.8
<b>Pech de l'Aze I, Dordogne, France</b>	<b>24.8</b>	<b>35.2</b>
Tsutskhvat, Grusinien, Imeretia, Georgia	24.2	34.4
Tana del Colombo, Liguria, Italy	23.6	33.5
Adzhi-Koba, Krim, Ukraine	23.4	33.2
<b>Cova Negra, Valencia, Spain</b>	<b>23.3</b>	<b>33.1</b>
Vindija, Croatia	23.3	33.0
Kudaro I, South Ossetia, Georgia	22.6	32.1
Gruta da Figueira Brava, Setubal, Portugal	22.5	32.0
Abri Olha, Pyrenees-Atlantiques, France	21.8	31.0
Avenc del Gegant, Barcelona, Spain	20.6	29.3
Balazuc, Ardeche, France	20.3	28.8
Cueva de Zafarraya, Malaga, Spain	20.0	28.4
Hyaena Cave, Gibraltar	19.8	28.2
Pin Hole Cave, Derbyshire, United Kingdom	19.0	27.0

NAME	SCORE	PROPORTION (%) OF TOP SITES SCORE
Bacho Kiro, Bulgaria	18.0	25.5
Schafstallhöhle, Baden-Wurttemberg, Germany	17.5	24.9
Pech de l'Aze II	17.3	24.6
Matuzka, Krasnodar, Russia	17.3	24.5
Prolom 2, Krim, Ukraine	17.2	24.5
Pestera Bordu Mare, Hunedoara, Romania	17.1	24.3
Pestera Curata, Hunedoara, Romania	16.9	24.0
Kiik-Koba, Krim, Ukraine	16.7	23.6
Subalyuk, Bukk, Hungary	16.4	23.4
Castelcivita, Salerno, Italy	16.4	23.3
Buhlen Upper Rock Shelter, Hessen, Germany	15.4	21.9
Grotta del Caviglione, Liguria, Italy	14.8	21.0
Carnello, Sora, Lazio, Italy	14.0	19.9
<b>Les Fieux, France</b>	<b>14.0</b>	<b>19.9</b>
Mezmaiskaya, Krasnodar, Russia	13.7	19.4
Baume-Vallee, Haute-Loire, France	13.6	19.3
Teshik-Tash, Uzbekistan	13.3	18.9
Cueva del Toll, Barcelona, Spain	13.3	18.9
Dzhurchula, Imeretia, Georgia	13.3	18.8
Marie-Jeanne, Namur, Belgium	13.2	18.7
Balauziere, Gard, France	13.1	18.7
La Crouzade, Aude, France	12.7	18.0

NAME	SCORE	PROPORTION (%) OF TOP SITES SCORE
Kudaro 3, South Ossetia, Georgia	12.4	17.6
Grotte du Moustier, Dordogne, France	12.0	17.0
Adaouste, Bouches-de-Rhone, France	12.0	17.0
Kogelstein, Baden-Wurttemberg, Germany	11.8	16.8
Shaitan-Koba, Krim, Ukraine	11.6	16.4
Ksar Akil, Lebanon	11.3	16.0
Amalda, Guipuzcoa, Spain	11.2	15.8
Grotta Dvuglaska, Yenisey, Russia	11.0	15.7
Riparo Zampieri, Venezia, Italy	11.0	15.6
Gudenushohle, Niederosterreich, Austria	10.8	15.3
Grotta Romanelli, Puglia, Italy	10.7	15.2
Valle radice, Sora, Frosinone, Italy	10.3	14.6
<b>Zaskalnaya, Krim, Ukraine</b>	<b>10.0</b>	<b>14.2</b>
El Salt, Alicante, Spain	9.7	13.7
Grotta del Fossellone, Lazio, Italy	9.7	13.7
Ramandils, Aude, France	9.3	13.2
Gudskiy Naves I, Krasnodar, Russia	9.2	13.0
Sesselfelsgrutte, Bayern, Germany	9.1	13.0
Chokurcha, Krim, Ukraine	9.0	12.8
Grotte des Fees a Chatelperron, Allier, France	8.8	12.5
Petit Puymoyen, Charente, France	8.7	12.3
Abri Romani, Barcelona, Spain	8.1	11.4

NAME	SCORE	PROPORTION (%) OF TOP SITES SCORE
Abri de Roquecourbiere, Ariege, France	8.0	11.4
Grotte du Hyene, France	8.0	11.4
Saint-Cesaire, France	8.0	11.4
<b>Mandrin Cave, France</b>	<b>8.0</b>	<b>11.4</b>
<b>Rio Secco, Italy</b>	<b>8.0</b>	<b>11.4</b>
Grotta di Veja A, Verona, Italy	7.7	10.9
Jarama VI, Guadalajara, Spain	7.3	10.4
Amud Cave, Galilee, Israel	7.2	10.2
Kitsos, Attika, Greece	7.1	10.1
Grotta S. Agostino, Lazio, Italy	7.0	9.9
Akhshatyr, Krasnodar, Russia	7.0	9.9
Lezetxiki, Guipuzcoa, Spain	7.0	9.9
Mugharet-el-Zuttiyeh, Galilee, Israel	7.0	9.9
Kudaro 2, South Ossetia, Georgia	6.8	9.6
Abri Bourgeois-Delaunay, Charente, France	6.7	9.5
Barakaeskaya Peshchera, Krasnodar, Russia	6.7	9.5
Grotta della Cava di Sezze Romano, Lazio, Italy	6.3	9.0
Vergisson 2, Saone-et-Loire, France	6.3	9.0
Cauna de Belvis, Aude, France	6.3	9.0
Breitenfurter Hohle, Bayern, Germany	6.0	8.5
Liesbergmuhle, Hohle, Baselland, Switzerland	6.0	8.5
Gubs Shelter No1, Krasnodar, Russia	6.0	8.5

NAME	SCORE	PROPORTION (%) OF TOP SITES SCORE
Grotta all'Onda, Toscana, Italy	5.8	8.3
Grotte Simard, Charente, France	5.2	7.4
Riparo Mezzena, Verona, Italy	5.1	7.3
Grotta Titti, Puglia, Italy	5.0	7.1
Pestera Binder, Cluj, Romania	5.0	7.1
Me'arat Shovakh, Galilee, Israel	5.0	7.1
Torre in Piedra, Lazio, Italy	4.7	6.6
Tournal, Aude, France	4.7	6.6
Sefunim Cave, Mt Carmel, Israel	4.7	6.6
<b>Grotte du Lazaret, Alpes-Maritimes, France</b>	<b>4.7</b>	<b>6.6</b>
Malisina Stijena, Montenegro	4.5	6.4
El Castillo, Santander, Spain	4.2	6.0
Wildkirchli, St Gallen, Switzerland	4.0	5.7
Aven Bouet, Herault, France	4.0	5.7
Tsona, South Ossetia, Georgia	4.0	5.7
Kepshinskaya Peshchera, Krasnodar	4.0	5.7
Cueva del Conde, Oviedo, Spain	4.0	5.7
Maly Vorontovskaya Peshchera, Krasnodar, Russia	3.8	5.3
Buca del Tasso, Toscana, Italy	3.4	4.9
Nietoperzowa, Krakow, Poland	3.2	4.5
Cotte de Saint Brelade, Jersey, United Kingdom	3.2	4.5
Shagat-Khokh-Leget, South ossetia, Georgia	3.0	4.3



NAME	SCORE	PROPORTION (%) OF TOP SITES SCORE
Gruta de Caldeirao, Portugal	3.0	4.3
Cova Forada, Alicante, Spain	3.0	4.3
Kosh-Koba, Krim, Ukraine	3.0	4.3
<b>Bolomor, Valencia, Spain</b>	<b>2.8</b>	<b>4.0</b>
Buchberg bei Munster, Bayern, Germany	2.4	3.4
Roc de Marsal I, Dordogne, France	2.3	3.3
Abri Suard, Charente, France	2.3	3.2
La Quina, Charente, France	2.2	3.1
Sirgenstein, Baden-Wurttemberg, Germany	2.0	2.8
Irpfelhohle, Baden-Wurttemberg, Germany	1.4	2.0
<b>Krapina, Croatia</b>	<b>1.3</b>	<b>1.8</b>
Erd, Buda Hills, Hungary	1.2	1.7
Betalov Spodmol, Slovenia	1.2	1.7
Rebibbia-Casal de' Pazzi, Lazio, Italy	1.1	1.6
Liesbergmuhle, Hohle, Baselland, Switzerland	1.0	1.4
Barma Grande, Liguria, Italy	1.0	1.4
Sambughetto Valstrona, Novara, Italy	1.0	1.4
Koziarnia, Krakow, Poland	1.0	1.4
Cova dels Ermitons, Sales de Llierca, Girona, Spain	1.0	1.4
<b>Geisenklosterle, Germany</b>	<b>1.0</b>	<b>1.4</b>
<b>Cova Forada, Spain</b>	<b>1.0</b>	<b>1.4</b>
<b>Salzgitter/Lebenstedt, Germany</b>	<b>0.7</b>	<b>1.0</b>

NAME	SCORE	PROPORTION (%) OF TOP SITES SCORE
Contrada Ianni di San Calogero, Calabria, Italy	0.5	0.7
Saccopastore, Lazio, Italy	0.4	0.5
Navalishinskaya Peshchera, Krasnodar, Russia	0.4	0.5
<b>Le Noisetier, France</b>	<b>0.2</b>	<b>0.3</b>
Baume de Gonvillars, Haute-Saone, France	0.1	0.2

## 5.7 Summary

This chapter establishes a clear pattern between the main bird species found in Neanderthal sites and those showing evidence of Neanderthal action. These include 33 of 70 species in the top quartile of frequency of occurrence at Neanderthal sites and 17 of the top 20 species occurring at these sites. The main taxa exploited by Neanderthals were corvids, game birds and pigeons, with cliff nesting species, scavengers and commensals among the ecological categories.

Taphonomic evidence of bird exploitation by modern humans contemporary, or immediately following, the Neanderthals is relatively scarce, on present evidence; only the Magdalenians appear to have exploited birds on a similar scale to the Neanderthals. Neanderthals and Magdalenians were similar in that they exploited the most frequent bird species at their sites but they differed in the degree of exploitation of different bird species. Even so, the main species exploited by both was limited to only nineteen Palearctic species. The behavioural differences of bird species exploited by Neanderthals and Magdalenians, reflected the selective exploitation of rocky habitats by Neanderthals and of tundra by Magdalenians. The under-representation of small

birds (< 100 g) and over-representation of medium sized birds ( 101 to 1,000 g) supports the view that birds were being selected as food resources. Apart from using birds as food sources, Neanderthals and Magdalenians utilised feathers and talons. This utilisation focused on golden eagle and other large raptors in Neanderthals. In the case of the Magdalenians, they exploited the large raptor of the tundra - the snowy owl – which they presumably encountered on a regular basis.

Finally, in this chapter I make predictions, based on current evidence, regarding species and sites to be looked at in future research in terms of potential for finding evidence of Neanderthal intervention on birds.



## **6.1 Introduction**

The aims of this chapter are (a) to discuss the results presented in this thesis in the context of our understanding of Neanderthal ecology and behaviour, and (b) to establish to what degree this knowledge serves to support, modify or even reject models of Neanderthal extinction. I will construct the discussion around the three main research questions outlined in Chapter 1 and summarised below:

- (1) Did Neanderthals associate with particular climates and habitats?
- (2) Were Neanderthals associated with particular bird species across their geographical range? If so, what features characterised these species?
- (3) Which bird species have provided taphonomic evidence of Neanderthal intervention?

In all questions a comparison with modern humans is made.

There is a degree of overlap in the answers to these questions so, to avoid duplication and repetition, I will structure the discussion under the following headings:

- (a) Neanderthals and Climate (Research Question 1) - Were Neanderthals cold-adapted? If so, the implication is that their extinction, at a time of climatic cooling within their geographical range, would have been caused by factors other than climate, particularly the arrival of modern humans. This will be covered in Section 6.2.
- (b) Neanderthals and Habitat (Research Question 1) - Did Neanderthals occupy extreme glacial habitats (e.g. tundra) within their geographical range? If so, the

implication is also that their extinction, at a time of expansion of these habitats within their geographical range, would have been caused by factors other than habitat loss, and particularly by the arrival of modern humans. This will be covered in Section 6.3.

(c) Neanderthals, consumable bird products and methods of obtaining these (Research Questions 2 and 3) - Were Neanderthals incapable of systematically exploiting birds? Is this in contrast with the abilities of modern humans? If so, the implication is that the Neanderthals' inability reflects a significant difference in ecology and behaviour that could have given modern humans a competitive edge over them. Were Neanderthals incapable of thinking symbolically? If so, the implication is that the Neanderthals' inability reflects a significant difference in cognition that should also have given modern humans a competitive edge over them. This competitive edge, part of a wider "modern behaviour package", would have been significant in the spread of modern humans at the expense of the Neanderthals, leading to their eventual extinction. This will be covered in Section 6.4.

I will end with a conclusions section (Section 6.5).

## **6.2 Neanderthals and Climate (Research Question 1)**

### **6.2.1 Cold-adaptation and ecogeographical rules**

In Chapter 1 (Section 1.2.1) I introduced the debate on the question of cold-adaptation in Neanderthals. The idea that Neanderthals were cold-adapted originated with palaeoanthropologists who studied Neanderthal skeletons and compared them with those of modern humans (Brose & Wolpoff, 1971; Trinkaus, 1981; Ruff *et al.*, 1993; Ruff, 1994; Holliday, 1997 a & b). Some of these authors went as far as describing

the Neanderthal body form as arctic (Ruff *et al.*, 1993), even hyperarctic (Holliday, 1997a), basing their arguments on the observation that Neanderthal body form (Figure 6.1) corresponded to, or even exceeded, that found in modern cold-adapted peoples. The development of the cold-adaptation hypothesis was based largely on examination of the Neanderthal post-cranial skeleton and focused on the relative shortness of the limbs as well as the large body mass and broad trunk. What these palaeoanthropologists attempted to do was to apply ecogeographical rules to fossils.

Two such rules were of particular relevance: (a) Bergmann's Rule (Bergmann, 1847) which states that, in warm-blooded animals, body size in geographically variable species averages larger in cooler parts of the range of a species; and (b) Allen's Rule (Allen, 1877) which states that, in warm-blooded animals, protruding body parts (e.g. bills, tails and ears) are shorter in cooler than in warmer climates. Allen's is an extension of Bergmann's Rule, both dealing with the surface-to-volume relation (Mayr, 1963); the net effect is a reduction in the surface area of the animal exposed to the environment in cold climates, with the consequent reduction of heat loss.

Two features of these rules are of particular importance to this discussion. The first is that the rules only have statistical validity and are not unalterable "laws" and that the degree of validity varies between groups of animals and between regions (Mayr, 1963). The second is that the validity of the rules is restricted to intraspecific variation (Mayr, 1956). These points were highlighted by Finlayson (2004), who questioned the validity of the application of ecogeographical rules to fossils spanning large tracts of time as well as to fossils that palaeoanthropologists considered to belong to different species (as Neanderthals *Homo neanderthalensis* and modern humans *H. sapiens* were).



*Figure 6.1 Forensic reconstructions of Gibraltar 1 and 2 Neanderthals (Nana and Flint) by Kennis & Kennis, showing details of Neanderthal anatomy (courtesy Gibraltar National Museum).*



### 6.2.2 Physiological considerations

The cold adaptation hypothesis was not limited to the post-cranium, with suggestions that the large and protruding nose of the Neanderthal (Figure 6.2) was an adaptation to extreme cold and arid conditions (Stringer & Gamble, 1993). For these authors, the large nose warmed air entering the lungs but provided no empirical evidence in support of the idea. In contrast, Franciscus & Trinkaus (1988) argued that the function of a large nose was to facilitate heat loss, which they considered important in Neanderthals who were thought to have had a very active life style.



*Figure 6.2 Detail of Gibraltar 1 (Nana) forensic reconstruction by Kennis & Kennis showing the large nose typical of Neanderthals (courtesy Gibraltar National Museum).*

Taking a physiological, as opposed to morphological, approach to this question Aiello & Wheeler (2004) concluded that Neanderthals would only have had a modest advantage over modern humans in their lower critical and minimum sustainable

temperatures. Allowing for the insulating effect of increased muscle mass and for a dietary-related elevated Basal Metabolic Rate (BMR) did not change their results. When Aiello & Wheeler looked at sites which were known to have been occupied by Neanderthals, for which wind chill temperatures had been modelled, they found that inferred Neanderthal temperature tolerances were insufficient for survival. They concluded that Neanderthals could not have survived in these sites without additional cultural insulation.

It is clear from the above that the idea that Neanderthals were cold-adapted was fundamentally flawed on theoretical grounds and had very little empirical or experimental support. In spite of these problems, the idea that Neanderthals were cold-adapted has been accepted and has persisted in the literature until today (e.g. Stringer & Gamble, 1993; Klein, 1999; Churchill, 2014).

### **6.2.3 Birds and cold-adaptation**

The results obtained using birds as climate indicators, and presented in Chapter 3 do not support the idea that Neanderthals were cold-adapted. In particular, they do not support the definition of Neanderthals as arctic or hyperarctic in character.

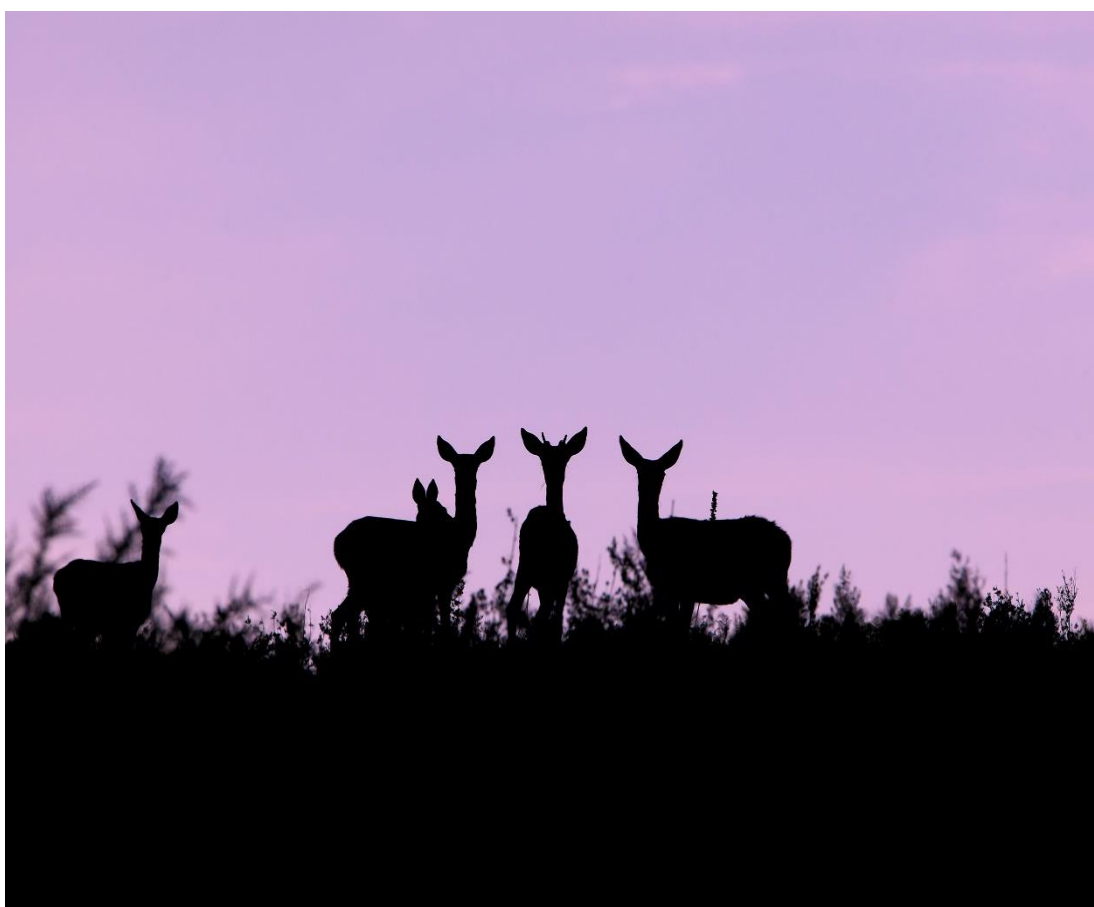
Most sites of Neanderthal occupation were clustered around the warm-temperate-cool part of the climatic gradient, which showed a degree of diversity of the climatic conditions that were tolerable but an avoidance of extremes, particularly cold extremes. The Doñana National Park (Figure 6.3) in southwest Spain typifies these conditions. The variability in the climatic range occupied by Neanderthals reflects the highly variable and oscillating climate of Eurasia during the Late Pleistocene (Burroughs, 2005), particularly during Marine Isotope Stage (MIS) 3 (57-29 kya)

when Neanderthals were still occupying Eurasia but were by then in decline (Finlayson, 2004; van Andel & Davies, 2004).

I have previously argued that not all archaeological sites with Neanderthals (or indeed any humans) need have been of the same ecological quality (Finlayson *et al.*, 2016). There were significant differences between Neanderthal sites that were separated by fewer than 150 kilometres. Some sites were visited sporadically and seasonally while others appeared to be of permanent or semi-permanent occupation. Using a metapopulation approach (Hanski & Gilpin, 1997), we should be aware of the possibility that some archaeological sites could represent sink populations. This could mean that Neanderthal sites at the cold end of the spectrum might represent populations on the edge in terms of survival. At this stage, this must remain speculation but it is an area of research that could prove productive in the future. For now, our main conclusion is that Neanderthals did not occupy extremely cold climates at any stage.

The second main conclusion regarding climate is the large overlap in climatic conditions occupied by Neanderthals and early modern humans. The climatic cooling associated with the Gravettians (34-24 kya) appears to have been met by a compression into sites within the tolerance boundaries of all humans. Even when the Magdalenians, who occupied Europe at the height of the Last Glacial Maximum (LGM) some twelve thousand years after the last Neanderthals, are considered we still find a high degree of overlap in climatic tolerance. These results suggest that similarities outweigh differences when comparing climatic tolerances of Neanderthals and modern humans with an avoidance of extreme cold by all humans, in spite of cultural insulation properties which may have existed (e.g. clothing and control of fire). Neanderthals and modern humans predominantly co-occupy the warm-temperate climatic

conditions of Eurasia, and there appears to be very little difference between them, with the possible exception of a tendency towards occupation of boreal climatic conditions by Magdalenian modern humans at the LGM. Part of the reason for the absence of humans from such extreme cold habitats may have had to do with other aspects of ecology (e.g. procurement of food resources) and not just the inability to survive the cold.



*Figure 6.3 Red deer (Cervus elaphus) in Doñana National Park, SW Spain. Red deer and Neanderthals were typical mammals occupying sites in warm or temperate climatic conditions. The Doñana National Park typifies these conditions today. (Photo: Stewart Finlayson).*

#### **6.2.4 Cold-adaptation and the Neanderthal extinction**

If Neanderthals were cold-adapted, then the implication is that their extinction, at a time of climatic cooling within their geographical range (van Andel & Davies, 2004), would have been caused by factors other than climate, particularly the arrival of modern humans. Linked to the view that Neanderthals were cold-adapted is the perception that the morphology of modern humans emerging out of Africa was one which revealed adaptation to tropical climates (e.g. Stringer & McKie, 1996). So engrained was this idea, that it led some leading palaeoanthropologists to suggest that the entry into Europe and the Mediterranean of the tropical-adapted modern humans at a time of increasing cooling was “of specific interest because it appears to occur against the grain of climatic change” (Lahr & Foley, 1998).

The underlying reasoning behind these views may be summarised as follows: (a) Neanderthals were cold-adapted and had survived previous cold periods in Eurasia; (b) they went extinct during the onset of the Last Glacial Maximum and their disappearance coincided with the arrival of modern humans in Eurasia (Mellars’ “Impossible Coincidence”, 2005); (c) modern humans were cognitively superior to Neanderthals and the modern behavioural package that they brought with them out of Africa allowed them to survive the cold conditions of Eurasia “against the grain of climatic change” and to outcompete the Neanderthals; and (d) as a result the Neanderthals were replaced by the superior modern humans.

As we have seen, the results presented in this thesis do not support the argument that Neanderthals were cold-adapted. Instead, it is clear that there was a large overlap in the climatic conditions of sites occupied by Neanderthals and modern humans. The likelihood that Neanderthals and modern humans had cultural buffers that permitted survival in Europe at a time of cooling has been suggested. Neanderthals and modern

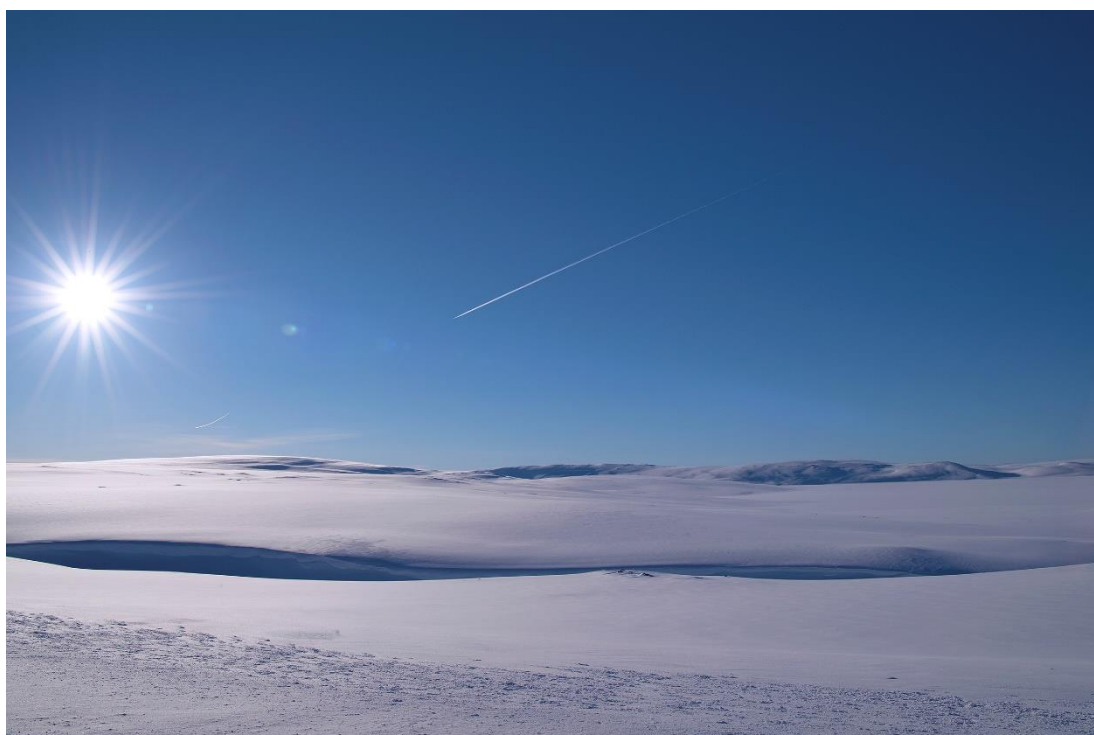
humans at this stage were both able to control fire (Figure 6.4; the earliest evidence dates to 790 kya; Goren-Inbar *et al.*, 2004). Needles were an original cultural innovation that emerged in Asia around 45 kya (d’Errico *et al.*, 2018), and possibly a modern human invention, but removal of pelts, the use tools used to manufacture clothes and hide-processing were practices that predated needles (Gilligan, 2017) and would have been used by Neanderthals as well as modern humans.



*Figure 6.4 Neanderthals were able to control fire. This painting shows Neanderthals around a hearth within Gorham’s Cave, Gibraltar. Painting by Mauricio Anton (courtesy Gibraltar National Museum).*

If there was a time in the Late Pleistocene when humans were able to enter the cold world of the tundra, it was long after the extinction of the Neanderthals. The results presented in this thesis suggest that it was the Magdalenians, who survived the LGM, who came closest to the model of cold-adaptation, although it would probably have been cultural buffers that permitted survival in hostile climatic conditions. It was the

Magdalenians, with their “tropical” body form, who regularly exploited such animals as reindeer (*Rangifer tarandus*) (Grayson *et al.*, 2001) and, as we have seen in this thesis snowy owls, willow grouse and rock ptarmigan, all species of the arctic tundra today (Figure 6.5).



*Figure 6.5 The exploitation of tundra habitats and animals appears to have become a regular feature of the Magdalenian culture. Photograph of tundra in winter, Varanger Peninsula, Norway. (Photo: Stewart Finlayson).*

The Neanderthal cold-adaptation perspective created a paradox – why did they become extinct when it was cold? Understanding the Neanderthals as humans of temperate climates instead, changes the argument completely and sees their extinction, whether caused by climate fully, partially or not at all, as running parallel to the climatic trends. The extinction was not happening against the climatic grain. In this context, Gibraltar at the south-western extreme of the Neanderthal range (Figure 1.1) is considered to have been one of the places of late Neanderthal survival (Finlayson *et al.*, 2006). The



data that I have presented in this thesis have supported this view by showing that the climatic conditions at Gibraltar (thermo- to meso-Mediterranean; sub-humid to arid; Rivas-Martínez (1987); see also Finlayson, 2006) fell within the optimal climatic range of the Neanderthals at all times and was never exposed to cold extremes, supporting the view that this site fell within a glacial climatic refugium (see also Jennings *et al.*, 2011).

### **6.3 Neanderthals and Habitat (Research Question 1)**

#### **6.3.1 Research to date**

The habitats and landscapes occupied by members of the genus *Homo*, and indeed of earlier African hominins, on different continents have received considerable attention (de Menocal and Bloemendal, 1995; Reed, 1997, 2008; Carrión *et al.*, 2003; Segalen *et al.*, 2007; Joordens *et al.*, 2009; Reynolds *et al.*, 2011). Most studies have relied on plant and mammal data and habitat descriptions have been largely qualitative (Finlayson *et al.*, 2011). For example, fauna-based reconstructions have relied on interpreting fossil localities using methods of taxonomic uniformitarianism, functional or ecological morphology, species diversity indices, faunal resemblance indices and ecological structure analysis (Reed, 1997).

Birds have rarely featured, until recently, in habitat analyses of hominin sites (Finlayson *et al.*, 2011). The first detailed attempt to quantify a hominin habitat using birds as indicators was that of Finlayson (2006) working with Neanderthals at Gibraltar. She built on preliminary quantitative work carried out by Finlayson & Giles (2000) who had concluded that “the southernmost European Neanderthals had been dwellers of open, probably highly seasonal, savannah-type and wetland environments which would be expected to be those with the highest resource yield, combining a large



mammal fauna in structurally accessible conditions with a range of alternative potential resources (fruit, seeds, smaller animals and lithic raw materials).”

Finlayson (2006) focused her attention on a subset of bird species found in Neanderthal occupation levels at Gorham’s Cave in Gibraltar, supported by data from other Gibraltar caves. The subset was composed of terrestrial birds, particularly but not exclusively from the order Passeriformes. One advantage that birds had over large mammals in this type of study was that practically all species found in Neanderthal sites still exist today, not necessarily in Gibraltar but certainly elsewhere in the Iberian Peninsula or broader Palaearctic. Birds are also much more visible than reptiles, amphibians or small mammals and are therefore ideal subjects for obtaining field data. Finlayson (2006) quantified habitat structure across the Iberian Peninsula (Bell, McCoy & Mushinsky, 1991) of living representatives of bird species that had been found as subfossils (partially fossilised bones) in Neanderthal archaeological contexts in the Gibraltar caves.

Combining the data for all the living species, that had also been found in a particular archaeological level, allowed Finlayson (2006) to quantify the Neanderthal habitat and its structure. She concluded that the reconstructed Neanderthal habitats outside Gorham’s Cave were of a ‘savannah’-type with scattered shrubs and trees (Figure 6.6). It was a type of landscape that had been associated with humans since the very origin of the genus *Homo* (Foley, 1997). Finlayson (2006) went on to highlight the importance of coastal landscapes, combining the savannah habitats she had described with wetlands and the coast; in Gorham’s Cave cliffs added further to the mosaic. It was the ecotones between these habitats which were the richest and most productive.

These results, which supported and expanded Finlayson & Giles' (2000) conclusions on the Neanderthal habitat of southern Iberia, were corroborated and reinforced by Finlayson *et al.* (2011) looking at the genus *Homo* as a whole. They concluded that there was a striking association between *Homo* and habitat mosaics. A mix of open savannah-type woodland, wetlands and rocky habitats emerged as the predominant combination occupied by *Homo* across a wide geographical area. These results therefore imply that these habitat mosaics and ecotones were the “default” habitat of the genus *Homo*; the Neanderthals, in Iberia at least, appeared to fit well into this scheme.



*Figure 6.6 Reconstruction of coastal shelf off Gibraltar during a low sea level stand outside Gorham's Cave showing a 'savannah'-type with scattered shrubs and trees. Painting by Mauricio Anton (courtesy Gibraltar National Museum).*

### 6.3.2 Birds and the Neanderthal habitat

Here I aim to expand on these results to see to what the degree the conclusions on Neanderthal habitat, based largely on datasets from the Iberian Peninsula, have wider geographical applicability. Thus, the dataset used examined sites from across the Neanderthal range. I also expanded the types of birds used as indicators, from the terrestrial species used by Finlayson (2006), to all Palaearctic species. In addition, I sought to confirm that the broader conclusions on the *Homo* habitat niche applied specifically to Neanderthals.

The results of the habitat analyses confirm the conclusions reached from analysis of Iberian sites and also from sites occupied by other members of the genus *Homo*. Neanderthals occupied a wide range of habitats but rarely, if ever, single habitats. Instead, the signals provided by birds found in sites of Neanderthal occupation show a repeated occupation of habitat mosaics or combinations of habitats particularly open, mixed and wetland habitats (Figure 6.7), such as grassland, shrubland, park-like savannah, and lakes. In contrast, the two extremes of the habitat range – open, treeless, habitats and dense forest – were avoided. There was also a distinct preference for rocky habitats but caution is required when interpreting this particular result as most Neanderthal sites studied were caves and rock shelters. When only open air sites were examined, the strength of the rocky habitat signal was significantly diminished. The inverse may be the case when considering the coastal/pelagic habitat as only eleven of the 154 Neanderthal sites examined were on the coast, including five on Gibraltar. We would expect proportionately fewer sites on the coast for the simple reason that coasts take up much less surface area than continental land masses, and also many would have been lost due to sea level rise.



*Figure 6.7 Neanderthal occupation shows a repeated occupation of habitat mosaics or combinations of habitats particularly open, mixed and wetland habitats. Painting by Mauricio Anton which draws on the role played by raptors in Neanderthal life (courtesy Gibraltar National Museum).*

### **6.3.3 Implications for the Neanderthal extinction**

One aspect of the information that birds are unable to provide regards the mobility of Neanderthals and modern humans. The scale of operation of Neanderthals and modern humans may have been an important factor distinguishing them (Finlayson, 2004; 2014) and would not, necessarily, be reflected in habitat occupation patterns. The morphological evidence available seems quite clear in this respect. Modern humans are characterised by having a generally gracile morphology, i.e. having thin-walled long bones with relatively small articular surfaces (Stringer *et al.*, 1984). They have long limbs relative to trunk height and body mass, a narrow pelvis and a low estimated

body mass relative to stature (Holliday 1997 a & b; Ruff *et al.*, 1997; Holliday, 2000; Pearson, 2000). Their anatomy, which includes a well-developed Achilles tendon, indicates endurance running and long-distance walking (Bramble & Liebermann, 2004; Steudel-Numbers & Tilkens, 2004; Steudel-Numbers, 2006; Steudel-Numbers *et al.*, 2007). In contrast the muscular Neanderthals (Stringer & Gamble, 1993) appear to have been best suited for power-based locomotion, including short-distance power sprinting (Stewart *et al.*, 2018) (Figure 6.8). In this context, the decline of the Neanderthals in Eurasia (between 60 and 32 kyr) coincides with the expansion of open habitats and large-scale loss of woodland (van Andel & Davies, 2004). In a Pleistocene world in which wooded environments were being replaced by open mammoth-steppe (Guthrie, 1990) and tundra habitats, the ability to efficiently roam across long distances of open habitats would have been an advantage. The available evidence, largely based on data on the transport of raw materials for tools, suggests that Neanderthals operated at smaller spatial scales than modern humans (Feblot-Augustins, 1993). This evidence also points to Neanderthals increasing the distances they covered in places where they were close to these open habitats, as in Eastern Europe, but there is little evidence of them exploiting the mammoth-steppe or the tundra.

It is modern humans who first occupied the Russian Plain (Soffer, 1985). The large-scale exploitation of such habitats characterised the modern humans who followed after the Neanderthal extinction. The bird habitat data presented in this thesis suggests that the Gravettians (who, at the heart of the mammoth-steppe, in Central and Eastern Europe may have been separated from the Neanderthals by as much as seven thousand years) had a narrower habitat focus than Neanderthals. The Magdalenians, whose



presence coincided with the LGM, were certainly exploiting the mammoth-steppe and tundra habitats as I have shown.



*Figure 6.8 The muscular Neanderthals appear to have been best suited for power-based locomotion, including short-distance power sprinting. Painting by Mauricio Anton (courtesy Gibraltar National Museum).*

Part of the difficulty in showing a clearer habitat distinction between Neanderthals and the Gravettians may have had to do with lifestyle and preservation of evidence in caves. I showed that most of the archaeological sites with bird remains were cave sites. The Gravettians exploited the open plains of Central and Eastern Europe where they constructed tents and other shelters, often made from mammoth bones (Soffer & Praslov, 1993; Roebroeks *et al.*, 1999; Otte, 2013). Although some of the sites in the database used in this thesis were open air Gravettian sites, it is possible that there was an element of underrepresentation of the open habitats as most Gravettian sites with

birds were in caves. In contrast, the Magdalenians inhabited Western Europe (Soffer & Gamble, 1990), where caves are more abundant than in the plains of Central and Eastern Europe, so they probably inhabited caves within the mammoth-steppe and tundra habitats. In their case the habitat (and indeed climate) signal would have been stronger than with the Gravettians, as was indeed the case.

In conclusion, I have found considerable overlap in habitat between Neanderthals and modern humans. Within this overlap it appears that Magdalenians, and possibly also Gravettians, occupied more open habitats than Neanderthals. In the case of the Gravettians, the habitat range appeared narrower than that of the Neanderthals which may indicate specialisation towards the more open end of the habitat spectrum. With the Magdalenians it seems to have been more a case of a clear incorporation of open habitats at a time of severe cold and dry climate. Did a gracile morphology and the consequent ability for endurance running give modern humans the edge over Neanderthals at a time when climate favoured the expansion of open habitats over wooded ones? The evidence provided by birds in this thesis is suggestive but not conclusive.

## **6.4 Neanderthals, consumable bird products and methods of obtaining these (Research Questions 2 and 3)**

### **6.4.1 Birds in the Diet**

In chapter 4, I presented evidence of associations between birds and Neanderthals. In chapter 5, I supported these data with direct taphonomic evidence of Neanderthal intervention on the bones of birds. The taphonomic evidence is nevertheless limited

to showing physical marks, staining and related evidence indicating the application of stone tools and fire on these bones. In some cases, the evidence goes as far as to show the imprints left by Neanderthal teeth on bird bones (Blasco *et al.*, 2014).

It is implied from these data that Neanderthals were consuming birds, at least those with taphonomic evidence. Others, without such evidence, may also have been consumed without leaving physical traces of intervention. This would not be surprising, particularly among smaller birds that could be processed without tools. An actual example from today would be the few marks left on chicken bones after being consumed. Although knives and forks are typically used in western culture, they leave relatively little impact on chicken bones and the consumption of drumsticks and wings is often done only using the hands. To interpret the absence of tell-tale marks on chicken bones as indicative of non-consumption would be erroneous (Ruth Blasco, *pers. comm.*). Additionally, at most we might only find evidence of roasting if the chicken had been cooked, and then only depending on the nature of the heating; this of course assumes cooking prior to consumption which need not have always been the case. In this regard, it is important to note that a review of the available evidence by Wrangham (2009), indicated the deep origins of cooking by humans, traced as far back as *Homo erectus*, and therefore present in the common ancestor of Neanderthals and modern humans.

Taphonomic evidence has also been used to argue that some Neanderthal processing activities were geared towards feather extraction and the removal of talons, or just claws, from raptors and corvids (Peresani *et al.*, 2011; Finlayson *et al.*, 2012; Romandini *et al.*, 2014; Radovic *et al.*, 2015). I will discuss the interpretation of feathers and talons in ornamentation in Section 6.4.3. In this section, I will discuss those aspects pertaining to the consumption of birds as food.



There is surprisingly little information in the literature regarding the palatability and edibility of birds of different species. There are useful summaries in Shrubbs (2013) and Cocker (2013). One early and very detailed exception is the work carried out by Hugh Cott in the 1940s (Cott, 1945; 1947). Cott found that there was an inverse correlation between bird visibility and palatability. In other words, cryptic birds with plumage designed for hiding away from predators, tended to be more palatable than brightly coloured birds. Cott developed a method of ranking bird species by how vulnerable they were to attack. He found that of the non-vulnerable birds, all, whether edible or not, were highly conspicuous. Among the vulnerable species, he got a close inverse correlation between colouration and edibility. He states “It is well known that the birds which are most prized for the table are those which are, in fact, specialists in cryptic camouflage” (Cott, 1947) (Figure 6.9). He then went on to produce a long list of species under different categories of conspicuousness, vulnerability, and, edibility.



*Figure 6.9 Studies have shown that birds which are most prized for the table are those which are specialists in cryptic camouflage. Photograph shows a Stone Curlew (Burhinus oedicnemus). (Photo: Stewart Finlayson).*

In Chapter 4 I showed that fifty-seven bird species potentially edible by humans were present in Neanderthal sites. This figure represented 77.9% of the sites. In Chapter 5 I showed that there was a clear dominance of birds with evidence of taphonomic intervention in the top quartile of species based on frequency of occurrence in Neanderthal sites. Seventeen of the top twenty species in this group showed taphonomic evidence of intervention (Appendix 4). Only three of these top twenty species showed no taphonomic evidence of Neanderthal intervention, but I argued that this may have been a sampling bias as very similar species had been shown to have been processed by Neanderthals. Of these twenty species, at least thirteen (65%) fall under the category of edible based on the accounts referred to above. Additionally, thirteen species had cryptic plumage which, according to Cott's predictions, should be edible. Combining the edible and the cryptic species we find that fifteen of the twenty most frequent bird species in Neanderthal sites (75%) fall into one of these two categories. This suggests that catching birds for food may have been a major part of Neanderthal behaviour.

These conclusions are supported by direct evidence of Neanderthal intervention. In Appendix 2, I list all the bird taxa known to date to have provided evidence of Neanderthal activity. Of the 71 taxa (species and genera) listed, 64.8% fall into the edible category.

#### **6.4.2 Eggs in the Diet**

Following his work on edibility of birds, Cott conducted a series of experiments on bird egg palatability using hedgehogs, rats and humans as tasters (Cott 1951; 1953; 1954). As with birds, Cott developed a ranking of eggs based on palatability. His

rankings showed a close correspondence of preference in humans, rats and the hedgehog. Among his conclusions Cott found that acceptability in eggs was largely independent of broad taxonomic position. There was also no close correlation between palatability and the food of the parents, nor between the quality of a bird's flesh and the palatability of the egg. Cott listed, for example, species with palatable eggs but distasteful flesh. An example was the herring gull (*Larus argentatus*), which was considered distasteful but whose eggs ranked first in the palatability ranking, even surpassing those of chickens (Figure 6.10).



*Figure 6.10 Birds eggs may have been a food resource of Neanderthals but have left no trace in the archaeological record. Photograph shows a hatching chick of herring gull (*Larus argentatus*). The eggs of this species are considered highly palatable even though the adult birds are not. (Photo: Stewart Finlayson).*

Cott came to the conclusion that distastefulness of an egg, was a protective adaptation in otherwise vulnerable species and edibility was inversely proportional to egg size. Colonial nesters predominated among species with palatable eggs and the opposite

applied to solitary birds. He found the highest edibility in the eggs of cliff nesters followed by birds which nested on floating vegetation or on the ground. The opposite was the case for tree- and bush-nesting birds. A high grade of palatability was a general attribute of cryptic eggs and the reverse was also true. Overall, there was therefore a clear link between palatability and vulnerability. It is worth noting that eggs are not only important sources of nutrient. It has been suggested that for Palaeolithic paintings, eggs and blood would have been useful binding agents and eggs can also be used to assist in emulsifying fats and deliver them to hides evenly as part of the final stages of the tanning process (Hurcombe, 2014).

Revisiting Appendix 4, I found that at least seven of the twenty species (35%) were known to produce palatable eggs. Fourteen (19.7%) of the seventy-one taxa with known Neanderthal intervention (Appendix 2) were producers of edible eggs. Examining the eleven coastal Neanderthal sites (Figure 6.11) referred to in Section 6.3.2, all species ( $n = 29$ ) found in these sites are known to lay edible eggs. Eighteen of these (62.1%) are cliff- or rocky-habitat nesting seabirds, seven (24.1%) are ground-nesting waders and skuas, and the remaining four (13.8%) are water-nesting wildfowl. This means that the bird remains found in coastal Neanderthal sites were all, without exception, of the three main categories of palatable egg-producing birds. Furthermore, eighteen of the twenty-nine (62.1%) are colonial nesting birds, the predominant category of palatable egg-layers according to Cott (1951; 1953; 1954).





*Figure 6.11 Neanderthals exploited coastal habitats which were particularly rich ecotones. Painting by Mauricio Anton (courtesy Gibraltar National Museum).*

If finding tell-tale marks and signs of Neanderthal exploitation of birds using taphonomic techniques on bones is difficult, then the chances of obtaining direct evidence of egg-collecting for consumption – a component of the huge array of perishable materials that have been described as the “missing majority” (Hurcombe, 2014) – must remain, for now, remote. Nevertheless, we should not discard the possibility that egg-collecting may well have been practised by Neanderthals during the breeding season of birds, particularly colonial cliff-, ground- and water-nesters, which in Eurasia would have been the spring (January to July depending on latitude).

### 6.4.3 Feathers and Talons

One intriguing aspect of the relationship between Neanderthals and birds which has emerged in recent years is the exploitation of raptors and corvids for their feathers and talons (Peresani *et al.*, 2011; Finlayson *et al.*, 2012; Morin & Laroulandie, 2012; Romandini *et al.*, 2014; Radovicic *et al.*, 2015). As this new evidence has accumulated, with an increasing number of publications in recent years, it has become clear that the practice of catching these large birds for their feathers and talons was geographically and temporally widespread. In other words, Neanderthals utilised raptor feathers and talons over a large part of their geographical range, from Gibraltar in the west (Finlayson *et al.*, 2012) to Crimea in the east (Majkić *et al.*, 2017), and over a long period of time, spanning around 100 kyr, with the earliest evidence dated to 130 kya (Radovicic *et al.*, 2015). This was, therefore, not an isolated practice. The results presented in this thesis have emphasized the importance of corvids in terms of representation in Neanderthal sites. They have also confirmed a wide range of raptor species present in Neanderthal sites. Their frequency in these sites is lower than for other taxonomic groups but this, in my view, is a reflection of the general principle that large predators are, by their very nature, rare in ecosystems (Colinvaux, 1980). In any case, many raptors fall within the cliff-nesting and scavenging behavioural categories that I have shown to have been among the most important in Neanderthal sites.

A study of species targeted by Neanderthals by Finlayson *et al.* (2012) has suggested that birds with dark flight and tail feathers were preferred. This study showed that body mass was not a factor influencing the choice of species. Neanderthals also showed a degree of selectivity at the level of raptor species with the golden eagle (*A. chrysaetos*) overshadowing all other species (Finlayson *et al.*, 2019) (Figure 6.12).

This dominance would appear to be the result of active targeting of this species as it is a difficult and dangerous bird to handle (e.g. Mails, 1972), contrasting with vultures whose talons are much weaker (O'Neal Campbell, 2015). At the same time, golden eagles are highly territorial and scarcer across the landscape when compared to the more social raptors, such as the vultures and the sea eagles (Fergusson-Lees and Christie, 2001).



*Figure 6.12 Analyses of the species targeted by Neanderthals has suggested that raptor and corvid feather and talon use was a regular feature of their behaviour. Photograph shows golden eagle (Aquila chrysaetos) (Photo: Stewart Finlayson)*

In the case of the talons of a white-tailed eagle (*H. albicilla*) from Croatia, it appears that they formed part of a necklace ((Radovic *et al.*, 2015). Four talons bore multiple, edge-smoothed cut marks; eight showed polishing facets and/or abrasion. Three of the largest talons had small notches at roughly the same place along the plantar surface, interrupting the proximal margin of the talon blade. These features suggested that they were part of a jewellery assemblage, the manipulations having been a consequence of

the mounting of the talons in a necklace or bracelet. An associated phalanx articulated with one of the talons and had numerous cut marks, some of which are smoothed. A raven bone (*C.corax*) from a Neanderthal site in Crimea, dated to between 43 and 38 kya, bore a set of evenly spaced notches, demonstrating the ability and intention of producing a visual conformity comparable to the one that characterized modern human productions (Majkić *et al.*, 2017). The authors claimed that it reflected modern cognition.

The inference from these results is that these raptors and corvids were taken to use their body parts for symbolic purposes, implying higher cognitive abilities in the Neanderthals and not just in modern humans. In the case of the golden eagle, but in other species also, its Palaearctic and Nearctic distribution, means that the practice of catching them must have originated in regions where Neanderthals lived, and outside Africa, where modern humans originated. I have argued that the age of some of the published results of exploitation by Neanderthals, long before the arrival of modern humans in Eurasia, clearly precludes any arguments of acculturation in Neanderthals by observing and learning the practice from modern humans (Finlayson *et al.*, 2019). This is particularly important given a long-standing discussion about the extent to which examples of modern behaviour in Neanderthals are attributed to copying (acculturation) newly-arrived modern humans (d’Errico *et al.*, 1998; Mellars, 1999; Zilhao & d’Errico, 1999). It is now possible to consider that raptor and corvid feather and talon use may reflect transmission of a symbolic-cultural behaviour from Neanderthals to modern humans, who would have picked it up by observing Neanderthals when they came into contact with them in Eurasia. This may appear speculative, but what is certain is that these practices could only have started in modern humans either by observing Neanderthals, or they were independently developed as



the modern humans entered Neanderthal territory. In neither case, did the Neanderthals learn it by observing modern humans as they were catching the large birds thousands of years before any modern human entered their territory. On current evidence, it was the Neanderthals who first practised raptor and corvid hunting for feathers and talons.

#### **6.4.4 Foraging and Hunting Behaviour**

Taphonomy can reveal evidence of the processing of animals by humans and, from this evidence, we infer the purpose of the human activity. In most cases the evidence can, as discussed in the previous section, be related to the processing (e.g. butchery) of an animal for consumption,. In a few cases, it has been possible to interpret other activities from taphonomic evidence. A recent example is the presumed exploitation of lion pelts by humans in the Magdalenian period (~14,800 cal BC) in the Cantabrian Mountains in Spain (Cueto *et al.*, 2016). In the case of birds, it is evidence of exploitation of raptors for feathers and talons (Peresani *et al.*, 2011; Finlayson *et al.*, 2012; Romandini *et al.*, 2014; Radovic *et al.*, 2015) that is a unique example. Our discussion and conclusions therefore will be inevitably speculative. However, as with food and other consumable products, we can draw from other sources of information that can assist us in our understanding. The ethnographic literature can be particularly helpful in this regard.

The golden eagle is one of the best documented cases in the ethnographic literature (Figure 6.13). In Japan golden eagles are closely linked to people living in the mountains where they are regarded as a symbol of power and superior ability and may have been the inspiration for the Tengu, a mythical monster (Watson, 2010). In North

America, it is a bird that was revered throughout the continent as the lord of the air and symbol of the sun and the wind. It was blessed with superb skills which could be obtained by capturing the bird following a precisely specified ritual (Mails, 1972). The eagle was captured in a sacred ritual: through the eagle pit method, which was done so as not to damage the birds' abilities to continue to serve as a special messenger and power transmitter from the deity above. A warrior would dig a pit in the ground which was covered with straw and other grasses by an assistant once he went inside. Above this, bait was placed and, often, a stuffed wolf appearing to be eating the bait. The eagle would come in for the bait and the warrior would jump out of the pit and catch the eagle by the talons, wrestling with it and attempting to kill it with his bare hands (Mails, 1972; Wilson, 1928).



*Figure 6.13 The golden eagle (Aquila chrysaetos) is one of the best documented birds in the ethnographic literature. (Photo: Stewart Finlayson).*

The choice of location for preparing an eagle pit revealed an intimate knowledge of the behaviour of the birds. A pit was never placed on the top of a hill but instead on the top of a flat bluff. The eagle would approach the site from the west and circle above the top of the hill, or occasionally, halfway down. Hidatsa warriors knew that above the flat prairie and above small hills, an eagle always flew down the river without resting. Coming to a height it would pause and circle above it. An eagle coming from the west and passing over the bait would spy it at once but would not pause. Instead it would fly onto the hill and turn. An eagle always turned like this and stooped to the bait against the wind. Thus, the Hidatsa only hunted eagles on days when the wind was from the west, in the knowledge that the eagles would turn and strike the bait flying into the wind (Wilson, 1928).

Published data on Neanderthal exploitation of golden eagles, as we have seen, indicates that feathers and talons were prime targets of attention. For the North American indigenous people at least, feathers and talons of the golden eagle had a special significance. Since the golden eagle was the solar or sun bird and favoured emissary of god, its feathers became the most preferred item for recording warrior coups. Eagle claw necklaces were also made and sometimes an entire eagle's foot would hang from the centre of a beaded string. Sioux doctors' medicine pouch included the entire foot of an eagle (Mails, 1972).

The use of raptor talons may be related to symbols of supremacy as they are extremely powerful weapons used in prey restraint and immobilisation (Fowler *et al.*, 2009). In the family Accipitridae, which includes the eagles, the hind talon (DI) and the distal front talon (DII) are hypertrophied, significantly larger than in other raptor families. This is an adaptation for capturing large prey that cannot be gripped with all the talons. Prey is prevented from escaping by standing on it, placing the raptor's weight on the

victim and using the talons to maintain the grip. Here the hypertrophied DI and DII talons are vital as the raptor tumbles about while keeping latched onto the prey. As the prey is often consumed alive, the grip of the hypertrophied talons is essential in keeping hold of it (Fowler *et al.*, 2009). In golden eagles, this powerful grip enables Kazakhs to use them to hunt down foxes and even wolves (Mohan, 2015). Among the sea-eagles (which include the white-tailed eagle whose talons have also been reported with cut marks made by Neanderthals as described previously; Figure 6.14), the claws are sub-equally sized, very large, and highly curved. These are adaptations for catching fish (Fowler *et al.*, 2009).



*Figure 6.14 White-tailed eagle (Haliaeetus albicilla) talons have been reported with cut marks made by Neanderthals. (Photo: Stewart Finlayson).*

Although golden eagles are generally solitary and highly territorial birds there are places where several birds can be together when bait is put out for them. In Finland in

the winter, I have observed up to seven eagles attracted to and constantly fighting for bait (Figure 6.15). There may therefore have been occasions when Neanderthals could have had access to a number of eagles at a time, in the autumn and winter, when the birds scavenge, a practice that I have previously associated with the Neanderthals (Finlayson & Finlayson, 2016). Accounts of Blackfoot catching up to forty eagles in a single day may seem far-fetched but there may be circumstances when catching so many birds would have been possible. In the northern plains, five eagles were considered an even trade for a good horse but further south two eagles would purchase a horse (Mails, 1972). This suggests that the northern plains and adjacent regions of North America may have been particularly special for golden eagles.



*Figure 6.15 Golden eagles (Aquila chrysaetos) fighting over food. Photograph taken in Finland in the winter. (Photo: Stewart Finlayson).*

The Blackfoot occupied large areas of present-day Montana, Idaho, British Columbia, Saskatchewan and Alberta. It is precisely in this region that recent work has revealed a large migration of golden eagles, particularly in the autumn as birds move south from northern North America (Dickson, 2018). At Mount Lorette, Alberta, golden eagle migration numbers have averaged over 3000 each autumn in the period 1992-2017 (Rocky Mountain Eagle Research Foundation, 2019). The migration takes place between late September and mid-November, with strongest passage during October when over 400 birds have been sighted in a single day. This is precisely the time of year that golden eagles were hunted using eagle pits (Mails, 1972). Such concentrations are unusual today and reflect the movement of eagles away from cold regions in the winter. It is possible that similar movements took place in different parts of the Neanderthal range in Eurasia during the Pleistocene, as ice sheets took a grip in the north. If so, Neanderthals may have been exposed to larger concentrations of golden eagles than are present in Holocene Eurasia with its interglacial climate.

Although these ethnographical observations cannot be used to support the methods that Neanderthals used, they do show us the range of possible tactics that could have been employed. They show both that a knowledge of the ecology and behaviour of birds was a key element, and that the technology needed and the materials required would have left little trace on the archaeology. How Neanderthals caught birds, including the largest ones, may be an impossible question to answer: it is certainly an unknown today and may well fall into the realm of the unknowable (Ungar, 2007). Nevertheless, the ethnographical literature can guide us by showing the possible. Other sources of evidence may also be of help.

When discussing Neanderthal hunting strategies, close-range hunting appears as a recurring theme. In a recent paper, Gaudzinski-Windheuser *et al.* (2018) found

perforations on two fallow deer (*Dama dama*) skeletons that had been deposited in 120 kyr lake bed deposits in Germany. Detailed studies of the perforations, including micro-computed tomography imaging and ballistic experiments, demonstrated that they resulted from close-range use of thrusting spears. This recent evidence would appear to support the long-standing view that Neanderthals were close-quarter hunters (Churchill, 1998).

This view was developed from the study of Neanderthal morphology. I summarise this evidence briefly. In Neanderthals, the scapular glenoid fossa is narrow relative to its height, a feature that indicates that forceful throwing was not an important component in the daily hunting life of Neanderthals (Churchill & Trinkaus, 1990; Churchill & Rhodes, 2009). Compared to modern humans, Neanderthals differ in aspects of elbow morphology. Ulnae have more anteriorly directed trochlear notches which is interpreted to mean adaptation to habitual loading regimes in which peak loads were incurred with the elbow in partial flexion, as when forcefully using a thrusting spear (Schmitt *et al.* (2003). Neanderthal ulnae also have proximodistally longer olecranon processes, which would have permitted greater leverage of the triceps. This, in turn, would have improved the forceful extension of the forearm at the elbow but reduced their ability in long-distance throwing (Churchill & Rhodes, 2006; Churchill, 2014). The elongated superior pubic ramus of Neanderthals has been ascribed a role in generating and resisting forces in the torso during close-range hunting with thrusting spears (Black, 1999). Neanderthal upper limbs were adapted to withstand high-magnitude forces, humeri could sustain high-magnitude bending forces, and they had high levels of bilateral strength asymmetry mainly favouring the right limb (Churchill, 2014). To this evidence we can add that the evidence from upper

limb muscularity supports the idea of close contact predatory behaviour and may, instead, reflect a disadvantage in overhand throwing (Churchill, 2014).

Further support for the close-quarter hunting view had been the long-held view that Neanderthal bones often revealed evidence of healed trauma, with particular frequency of injuries to the head and neck, which resembled the injuries of modern day rodeo riders (Berger & Trinkaus, 1995). This interpretation was subsequently questioned, as early modern humans in Europe who were equipped with projectile technology, revealed similar patterns of bone trauma (Trinkaus, 2012). Recently, Milks *et al.* (2019) used trained javelin athletes to determine performance using replicas of 300 kyr-old spears from Schöningen (Germany). These authors concluded that distance hunting was within the likely repertoire of Neanderthals and the resulting flexibility mirrored that of modern humans.

This last point most likely reflects the reality of Neanderthal hunting tactics: rather than pigeon-hole them into a single category of hunting, a more realistic scenario would be one in which a diversity of tactics was exploited, depending on circumstances. These tactics would have included scavenging where opportunities arose. Scavenging or hunting is another long-standing debate in the study of human origins (Binford 1985, 1989; Chase 1988, 1989; Stiner 1991, 1993, 1994; Marean, 1998; Speth & Tchernov, 1998) when the reality is likely to have been that Neanderthals (and other hominins) were opportunistic omnivores who varied their foraging strategies according to a variety of ecological, behavioural and physiological conditions.

The issue of hunting birds, for a long time considered outside the scope of Neanderthal behavioural abilities (Klein, 2001; Klein *et al.*, 2004), has to be seen as an extension



of the arguments put forward above. It is now clear that Neanderthals exploited birds but we would be falling in the same trap if we were to try and ascertain a single way in which these birds were taken. If the ethnographic literature – which reveals the myriad techniques which humans have used to catch birds (e.g. Crowe, 2000; Cocker, 2013; Shrubb, 2013) – is anything to go by, then we would best be advised to stay clear of such an attempt, particularly when relying solely on zooarchaeological data. Uniformitarian application of such ethnographic data to the past also has to be approached with caution and should, at best, only be used to understand the possible when looking at historical contexts. In addition, the use of perishable materials, such as netting (Hurcombe, 2014), in bird catching is common across many hunting societies. It makes it very likely that such techniques were used in prehistory but we are limited by poor preservation. Our inability to find such evidence should not be used to discard such practices in the same way that we cannot confirm that they were indeed in use.

One final point concerns taxonomic attribution. With 10,738 extant species of birds (Gill & Donsker, 2019) in the world, ranging from ostriches to hummingbirds, we find that many zooarchaeological studies (e.g. Stiner *et al.*, 1999; 2000; Stiner & Munro, 2002; Steele & Klein, 2009) produce lists of large mammal species for particular sites but then relegate other taxa to very broad categories (e.g. birds, small mammals, reptiles, amphibians, molluscs, herps, shellfish, small game, fast and slow prey). Conclusions should not be drawn without an understanding of the individual species. This level of detail is possible, as I have shown in this thesis.

Using this approach, of looking at individual bird species within sites and seeking patterns of ecology or behaviour that could help us understand possible ways in which they may have been taken, I concluded that Neanderthals exploited particular species

of raptors and corvids which had the common characteristic of being scavengers (Finlayson & Finlayson, 2016). In this thesis I have expanded this categorisation to include commensals, species that would have benefited from living around camp sites and taking human refuse (e.g. pigeons) or animals feeding off that refuse (owls and kestrels; e.g. Steigerwald, *et al.*, 2015). The relationship between Neanderthals and scavenging birds may have involved waiting for the birds to land and start feeding on the carcasses and then attacking them by surprise. In this regard it is noteworthy that a recent paper (Stewart *et al.*, 2018) has suggested that Neanderthals were adapted to power-based locomotion, including the ability for short-distance power sprinting. The conclusions were supported by the identification of alleles associated with power locomotion versus endurance running in Neanderthals. Finlayson & Finlayson (2016) also concluded that the practice of catching scavenging birds may have been played out during the winter months in particular. This conclusion was arrived at because some of the principal species taken by Neanderthals (golden eagle *A. chrysaetos* and white-tailed eagle *H. albicilla*) almost exclusively visited carcasses in winter (Figure 6.16; Fergusson-Lees and Christie, 2001); and reinforced by the low presence of certain scavengers (Egyptian vulture *Neophron percnopterus* and black kite *Milvus migrans*) that were summer visitors to Europe from tropical Africa. These results take us some way into understanding how a hunting pattern may have been played out and it is the result of a detailed understanding of individual bird species and their behaviour.



*Figure 6.16 Golden eagles (Aquila chrysaetos) and white-tailed eagles (Haliaeetus albicilla) only visit carcasses in autumn and winter. Photograph shows golden eagle on a red fox (Vulpes vulpes) carcass taken in Sweden in the winter. (Photo: Stewart Finlayson).*

In Chapter 4, I showed that the most frequent bird species in Neanderthal sites were flocking birds, commensals and scavengers, cliff and rocky habitat nesters, and ground-dwelling birds (including birds that made their nests on floating platforms and others that performed elaborate displays in leks). Taphonomic evidence (Chapter 5) indicated the exploitation of species in all these categories by Neanderthals, and in particular, commensals, scavengers and cliff-nesters. These behavioural features of birds share common aspects which may permit an understanding of how they may have been captured. Flocking birds may have attracted Neanderthals by their sheer numbers and may have been particularly vulnerable at roosts. This would imply Neanderthals hunting these birds at dusk or even in the dark. The practice of catching birds at roosts appears to have been a widespread practice in historical times (Cocker,

2013), but I have found no reference to the practice among Palaeolithic modern humans.

Commensals and scavengers share a common feature, of being attracted to resources located in a fixed point (carcasses, or offal and scraps at a camp site) and often in large numbers. They would have been particularly prone to ambush and being taken by surprise by rushing. I have seen many instances of vultures lying flat on the ground satiated after gorging on a carcass. Such animals become temporarily flightless and vulnerable to a rapidly sprinting predator, like a Neanderthal. I have also observed two cases where wild vultures have been fed regularly by humans and have become habituated to human presence, associating it with food (Figure 6.17).



*Figure 6.17 Wild vultures being fed by hand. Photo taken in Huesca, Spain. (Photo: Stewart Finlayson).*



In these cases, vultures approach their human feeders within touching distance. In spite of this relative ease of capture, the under-representation of vultures in the samples, both in terms of frequency at sites and those showing intervention, is probably related to: (a) the relative scarcity of raptors (including vultures), a feature that is common for all predators (e.g. Colinvaux, 1980); (b) the generally southerly geographical distribution of vultures (O'Neal Campbell, 2015) which would have limited Neanderthal vulture contact to these parts of the range; and (c) the specific practice of Neanderthals catching these birds for their feathers and not for consumption.

Cliff-nesting birds feature prominently in Neanderthal sites (Figure 6.18), many of these are colonial and produce highly palatable eggs. It is possible to consider that Neanderthal activities around cliffs may have been related, in part at least, to egg-collecting.



*Figure 6.18 Cliff-nesting seabirds feature prominently in Neanderthal sites. Photograph shows guillemots (Uria aalge) in Farne Islands, Northumberland, United Kingdom. (Photo: Stewart Finlayson).*

I have visited seabird breeding colonies on cliffs (e.g. northern gannets *Morus bassanus* on the Bass Rock, Scotland) where the birds are so determined to defend their nests that they can be picked up with bare hands. Cliff-nesting seabird colonies would have been a resource restricted to the coast. Although absent from inland areas of the Neanderthal geographical range, the sheer numbers and density of birds in seabird colonies would have made this a very attractive and rewarding seasonal resource for Neanderthals with access to the coast. Currently, there is no published evidence of Neanderthal seafaring, so I am unable to determine whether or not they had access to island colonies. Inland, they could potentially have had access to large colonies of breeding raptors, for example, griffon vulture *Gyps fulvus* or lesser kestrel *Falco naumanni*; corvids (e.g. choughs *Pyrrhocorax* sp. and jackdaws *Corvus monedula*); or even storks (*Ciconia* sp.). These may form colonies at high density, reaching hundreds, or even thousands of pairs (*pers. obs.*). Observations today may be distorted as a result of impoverishment and colonies of these birds may have been much larger at the time of the Neanderthals. For example, Irby (1895) recorded that lesser kestrels nested on the north face of the Rock “in vast numbers”; by 1980, the colony had been reduced to 15 pairs (Cortes *et al*, 1980) and there are none today (*pers. obs.*). The features of cliff-nesting bird colonies are therefore that they are discrete in the landscape, but where they occur, are likely to provide a resource at high density. Birds that nest on the ground and in floating vegetation, often with cryptic coloration, are known to produce palatable eggs and are themselves highly palatable. Neanderthals may have been attracted to these birds when nesting and at their most vulnerable. This would have been an easy practice for a predator tuned in to picking up cryptic birds and eggs. Finally, lekking birds include highly palatable species (such as bustards, Otididae, and grouse, Tetraonidae) which frequently appear in

Neanderthal sites. Some of these birds become totally oblivious of danger when displaying and, like scavengers, would have been prone to being rushed. In the case of the capercaillie (*Tetrao urogallus*) (Figure 6.19) I have personally witnessed displays when a male has taken a person to be a rival and has attacked him. The bird could have been easily despatched. In addition to giving us clues as to how Neanderthal foraging and hunting behaviour may have played out, these observations also inform us on the degree of difficulty of catching particular species of birds at particular times of the year. The approach taken in this part of the thesis offers possibilities for the development of future research on Neanderthal foraging and hunting behaviour.



*Figure 6.19 Capercaillie (Tetrao urogallus) performing display in its lek. Photograph taken in Sweden. (Photo: Stewart Finlayson).*

## **6.5 Conclusions**

My first research question asked did Neanderthals associate with particular climates and habitats and were there differences with modern humans? The evidence presented in this thesis suggests that the climatic and habitat conditions of Neanderthals and modern humans may best be described as temperate with a mix of habitats, but avoiding exclusively open (treeless) or closed (dense forest) biomes. There is a broad overlap in the climatic conditions and habitats at sites occupied by Neanderthals and modern humans, particularly contemporary ones.

I have found no evidence of Neanderthal occupation of Palaeartic sites in the Late Pleistocene that could be classed as having an arctic climate or arctic habitats, such as tundra. The Gravettians, occupying the plains of Central and Eastern Europe during the build-up to the LGM, appear to diverge to some degree towards cold and open conditions. It is only with the Magdalenians, at the LGM, however that we observe a human trend towards occupying tundra-steppe habitats in cold climatic conditions. The entry into such environments included the exploitation of arctic species such as reindeer, snowy owl, willow grouse and rock ptarmigan.

The view that Neanderthals were cold-adapted is therefore unsupported by the results presented in this thesis. These results have a bearing on our understanding of the course of the Neanderthal extinction by showing that this protracted process occurred at a time when climate would have stressed them directly and also by fragmenting their usual habitats. This does not demonstrate a direct cause-effect of climate and habitat on the Neanderthal extinction but it does show that these factors should, at least, be considered as components in the extinction equation.



My second research question asked if Neanderthals associated with particular bird species across their geographical range, what features characterised these species and were there differences with modern humans? In comparison to the overall number of bird species available within the Neanderthal geographical range, very few actually regularly co-occupied sites with the Neanderthals. Only five bird species occurred in over 20% of Neanderthal sites. At taxonomic levels higher than species, clusters of species that were frequently found in Neanderthal sites were corvids, game birds, ducks, thrushes, pigeons and kestrels; many of these birds co-occupied large parts of the Neanderthal geographical range and a number of species within these groups are 'traditional' human food sources with small species (<100 g) being avoided. Neanderthal sites were most frequently associated with birds showing scavenging (including commensals), lekking, ground-dwelling cryptic and flocking behaviours.

Overall, the number of birds associated regularly (in over 20% of sites) with Neanderthals and modern humans was surprisingly small: only 12 of 430 species (3.5%), indicating similar patterns of association between Neanderthals and modern humans in relation to birds most commonly found in their occupation sites. Where differences between Neanderthals and modern humans in terms of bird species were found, these are considered likely to reflect circumstances (e.g. tundra species with the Magdalenian culture during the Last Glacial Maximum) and not differences associated with hominin taxon.

My third research question asked which bird species have provided taphonomic evidence of Neanderthal intervention? There was a clear pattern that established that the main bird species with evidence of Neanderthal action were those that occurred most frequently in Neanderthal sites with sixteen of the eighteen most frequent bird species in Neanderthal sites revealing clear taphonomic evidence of intervention. The

main taxa exploited by Neanderthals were corvids, game birds and pigeons with cliff-nesting species, along with scavengers and commensals, as the main ecological categories exploited by Neanderthals.

Taphonomic evidence of bird exploitation by modern humans contemporary, or immediately following, the Neanderthals was, in contrast, relatively rare and, on present evidence, only the Magdalenians appear to have exploited birds at a similar scale to the Neanderthals. Neanderthals and Magdalenians were similar in the exploitation of the most frequent bird species at their sites but they differed in the degree of exploitation of different bird species; these ecological differences reflected the exploitation of rocky habitats by Neanderthals and tundra by Magdalenians.

The results that have given us answers to questions 2 and 3 have shown that the exploitation of birds was a widespread phenomenon, in space and time, which was common to Neanderthals and modern humans. As such the results call into question theories related to a Broad Spectrum Revolution which marked a diversification of diet by modern humans. My results, instead, show that all humans (at least from the Neanderthals onwards) had broad spectrum diets which regularly included birds. The Neanderthals were therefore capable of catching so-called “fast moving small prey” without apparent difficulty. Furthermore, the clear selectivity of species with particular features and which were of economic value as well as the evidence of seasonal targeting of certain species, shows that Neanderthals were perfectly capable of planning foraging and hunting activities; such activities have also been previously regarded as part of the exclusive modern human package. To all this we must add the growing evidence of the use of feathers and talons for apparently symbolic purposes.

Overall, my conclusion is that Neanderthals were part of a larger human (*Homo sapiens*) taxon, possibly a polytypic species (Mayr, 1963). Their ecological and behavioural boundaries were delimited by the borders of this polytypic species so we would expect considerable overlap between the different component members. That is what we observe in respect of Neanderthal and modern human climatic tolerance, habitat occupation and the exploitation of birds. The bulk of research into Neanderthals seems to have focused on differences with modern humans; instead I have focused on similarities and these, at least in respect of climate, habitat and bird exploitation, far outweigh the differences. The differences between Neanderthals and modern humans in these cases are not of a greater order of magnitude than differences between distinct modern human cultures and the differences between modern human cultures are, sometimes at least, greater than between Neanderthals and modern humans. There is a clear need for a paradigm shift (Kuhn, 1970) in the study of human origins and the place of the Neanderthals in the human story.



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## Appendices





## Appendix 1

Available electronically – please contact [stewart.finlayson@gibmuseum.gi](mailto:stewart.finlayson@gibmuseum.gi) for pdf copy.



**Appendix 2.** Bird species and sites which have provided direct evidence of Neanderthal intervention on birds. Site codes and sources of data: **BM** Baume de Gigny, France (Laroulandie, 2004); **PA** Peche de l’Aze I, France (Laroulandie, 2004); **LZ** Lazaret, France (de Lumley, 2005); **BO** Bolomor, Spain (Blasco & Peris, 2009; 2012); **RF** Riparo Fumane, Italy (Peresani et al., 2011); **CG** Combe Grenal, France (Morin & Laroulandie, 2012); **GC** Gorham’s Cave Complex, Gibraltar (Finlayson et al., 2012; Blasco et al., 2014, 2015; and unpublished); **NO** Le Noisetier, France (Morin & Laroulandie, 2012); **FI** Les Fieux, France (Morin & Laroulandie 2012; Laroulandie et al., 2015); **SZ** Salzgitter/Lebenstedt, Germany (Morin & Laroulandie, 2012); **GE** Geisenklosterle, Germany (Conard, 2013); **MA** Mandrin Cave, France (Romandini et al., 2014); **SE** Rio Secco, Italy (Romandini et al., 2014); **KP** Krapina, Croatia (Radovic et al., 2015); **CN** Cova Negra, Spain (Martinez et al., 2016); **PL** Pie Lombard, France (Romero et al., 2017); **ZK** Zaskalnaya, Russia (Majkic et al., 2017); **AR** Arbreda, Spain (Lloveras et al., 2018); **CF** Cova Forada, Spain (Rodriguez-Hidalgo et al., 2018).

SPECIES	SITE																		
	BM	PA	LZ	BO	RF	CG	GC	NO	FI	SZ	GE	MA	SE	KP	CN	PL	ZK	AR	CF
<i>Pterodroma spp.</i>							+												
<i>Calonectris diomedea</i>							+												
<i>Phalacrocorax aristotelis</i>							+												
<i>Cygnus cygnus</i>	+																		
<i>C.olor</i>				+															
<i>Cygnus spp.</i>										+									

SPECIES	SITE																		
	BM	PA	LZ	BO	RF	CG	GC	NO	FI	SZ	GE	MA	SE	KP	CN	PL	ZK	AR	CF
<i>Anas platyrhynchos/strepera</i>							+												
<i>Anas spp.</i>				+						+									
<i>Aythya spp.</i>				+			+												
<i>Clangula hyemalis</i>							+												
<i>Aquila chrysaetos</i>		+				+	+		+			+	+						
<i>A. adalberti</i>																			+
<i>Gypaetus barbatus</i>					+														
<i>Aegypius monachus</i>					+				+										
<i>Gyps fulvus</i>							+												
<i>Haliaeetus albicilla</i>									+					+					
<i>Accipiter nisus</i>							+												
<i>A. gentilis</i>							+												
<i>Milvus migrans</i>							+												
<i>M. milvus</i>							+												
<i>Buteo buteo</i>							+												
<i>Falco peregrinus</i>							+												

SPECIES	SITE																		
	BM	PA	LZ	BO	RF	CG	GC	NO	FI	SZ	GE	MA	SE	KP	CN	PL	ZK	AR	CF
<i>F. subbuteo</i>							+												
<i>F. tinnunculus</i>							+												
<i>F. naumanni</i>							+								+				
<i>F. vespertinus</i>					+														
<i>Falco spp.</i>							+	+										+	
<i>Tetrao tetrix</i>					+														
<i>Lagopus lagopus</i>					+														
<i>L. lagopus/mutus</i>											+								
<i>Perdix perdix</i>																		+	
<i>Alectoris graeca</i>																+			
<i>A. rufa</i>							+								+				
<i>Alectoris spp.</i>																		+	
<i>Coturnix coturnix</i>							+											+	
<i>Crex crex</i>					+														
<i>Scolopax rusticola</i>							+												
<i>Numenius phaeopus</i>							+												
<i>Vanellus vanellus</i>							+												

SPECIES	SITE																		
	BM	PA	LZ	BO	RF	CG	GC	NO	FI	SZ	GE	MA	SE	KP	CN	PL	ZK	AR	CF
<i>Pluvialis</i> spp.							+												
<i>Charadrius</i> spp.							+												
<i>Calidris alba/alpine</i>							+												
<i>Stercorarius parasiticus</i>							+												
<i>Alca torda</i>							+												
<i>Fratercula arctica</i>							+												
<i>Columba livia</i>			+				+								+	+			
<i>C. palumbus</i>					+														
<i>Columba</i> spp.				+														+	
<i>Streptoptelia turtur</i>							+												
<i>Athene noctua</i>							+												
<i>Otus scops</i>							+												
<i>Apus apus/pallidus</i>							+												
<i>Coracias garrulus</i>															+				
<i>Galerida cristata</i>							+												
<i>Ptyonoprogne rupestris</i>							+								+				
<i>Anthus</i> spp.							+												

SPECIES	SITE																		
	BM	PA	LZ	BO	RF	CG	GC	NO	FI	SZ	GE	MA	SE	KP	CN	PL	ZK	AR	CF
<i>Motacilla flava</i>							+												
<i>Monticola solitarius</i>							+												
<i>Erithacus/Luscinia spp.</i>							+												
<i>Turdus merula</i>															+				
<i>Turdus spp.</i>							+												
<i>Pyrrhocorax pyrrhocorax</i>							+								+	+			
<i>P. graculus</i>					+		+								+	+			
<i>Pyrrhocorax spp.</i>																		+	
<i>Corvus corax</i>									+								+		
<i>C. corone</i>							+												
<i>C. monedula</i>							+								+			+	
<i>C. corone/frugilegus</i>							+												
<i>Pica pica</i>							+												
<i>Sturnus spp.</i>							+												
<i>Chloris chloris</i>							+												





SPECIES	SITE																											
	GZ	EG	VA	MD	BR	PC	RO	EB	LC	FO	LT	TO	LM	MA	FA	GC	BO	CS	GA	JA	DU	MP	IS	FO	EY	AN	GO	CA
<i>Morus bassanus</i>																												*
<i>Cygnus olor</i>							*																					
<i>Cygnus spp.</i>																											*	*
<i>Anser spp.</i>																												*
<i>Branta leucopsis</i>																												*
<i>Branta spp.</i>																												*
<i>Tadorna spp.</i>																												*
<i>Anas platyrhynchos</i>					*																							*
<i>A. clypeata</i>																												*
<i>A. crecca</i>																												*
<i>Anas spp.</i>																												*
<i>Aythya fuligula</i>																												*

SPECIES	SITE																											
	GZ	EG	VA	MD	BR	PC	RO	EB	LC	FO	LT	TO	LM	MA	FA	GC	BO	CS	GA	JA	DU	MP	IS	FO	EY	AN	GO	CA
<i>Aythya</i> spp.																												*
<i>Somateria mollissima</i>																												*
<i>Polysticta stelleri</i>																												*
<i>Clangula hyemalis</i>																												*
<i>Melanitta nigra</i>																												*
<i>M. fusca</i>																												*
<i>Mergus serrator</i>																												*
<i>Aquila chrysaetos</i>							*																					
<i>A. fasciata</i>																												*
<i>Haliaeetus albicilla</i>																												*
<i>Gypaetus barbatus</i>																												*
<i>Falco tinnunculus</i>																												*

SPECIES	SITE																											
	GZ	EG	VA	MD	BR	PC	RO	EB	LC	FO	LT	TO	LM	MA	FA	GC	BO	CS	GA	JA	DU	MP	IS	FO	EY	AN	GO	CA
<i>Lagopus lagopus</i>																												*
<i>Lagopus spp.</i>	*	*	*	*				*	*	*	*	*														*		*
<i>Tetrao tetrix</i>						*																						*
<i>T. urogallus</i>	*																											
<i>Perdix perdix</i>																												*
<i>Grus grus</i>													*												*			
<i>Tringa erythropus</i>																												*
<i>Larus spp.</i>																												*
<i>Uria spp.</i>																												*
<i>Alca torda</i>																												*
<i>Pinguinus impennis</i>																												*
<i>Fratercula arctica</i>																												*

SPECIES	SITE																											
	GZ	EG	VA	MD	BR	PC	RO	EB	LC	FO	LT	TO	LM	MA	FA	GC	BO	CS	GA	JA	DU	MP	IS	FO	EY	AN	GO	CA
<i>Bubo scandiacus</i>					*	*							*	*	*	*	*	*	*	*	*	*	*	*				*
<i>Columba livia</i>																												*
<i>Pyrhacorax graculus</i>	*		*	*		*	*																					*
<i>P. pyrrhacorax</i>																												*
<i>Corvus corax</i>		*	*		*	*	*																			*	*	*
<i>Pica pica</i>																												*

*Appendix 4. The top quartile species in Neanderthal sites compared to taphonomic evidence of exploitation by Neanderthals.*

Species	Percentage occurrence in Neanderthal sites	Number of published cases of Neanderthal intervention
<i>Pyrrhocorax graculus</i>	41.9	4
<i>Pyrrhocorax pyrrhocorax</i>	30.5	3
<i>Perdix perdix</i>	28.3	1
<i>Falco tinnunculus</i>	23.6	1
<i>Columba livia</i>	21.7	4
<i>Tetrao tetrix</i>	19.2	1
<i>Anas platyrhynchos</i>	18.4	0
<i>Corvus monedula</i>	17.9	3
<i>Lagopus mutus</i>	14.2	0
<i>Pica pica</i>	14.1	1
<i>Coturnix coturnix</i>	13.6	2
<i>Aquila chrysaetos</i>	12.0	6
<i>Corvus corone</i>	11.8	1
<i>Turdus viscivorus</i>	11.6	0
<i>Alectoris rufa</i>	11.5	2
<i>Lagopus lagopus</i>	11.2	1
<i>Turdus merula</i>	10.8	1
<i>Corvus corax</i>	10.8	2
<i>Alectoris graeca</i>	10.3	1
<i>Bubo bubo</i>	8.5	0
<i>Garrulus glandarius</i>	8.4	0
<i>Alauda arvensis</i>	8.3	0
<i>Sturnus vulgaris</i>	8.3	0
<i>Anas querquedula</i>	8.1	0
<i>Coccothraustes coccothraustes</i>	8.0	0
<i>Tachymarptis melba</i>	7.3	0
<i>Columba oenas</i>	7.1	0
<i>Turdus philomelos</i>	7.1	0

Species	Percentage occurrence in Neanderthal sites	Number of published cases of Neanderthal intervention
<i>Columba palumbus</i>	6.9	1
<i>Athene noctua</i>	6.8	1
<i>Anas penelope</i>	6.5	0
<i>Scolopax rusticola</i>	6.3	1
<i>Turdus pilaris</i>	6.2	0
<i>Ptyonoprogne rupestris</i>	6.2	2
<i>Falco subbuteo</i>	6.2	1
<i>Hirundo rustica</i>	6.2	0
<i>Strix aluco</i>	6.1	0
<i>Crex crex</i>	5.8	1
<i>Corvus frugilegus</i>	5.5	0
<i>Apus apus</i>	5.5	1
<i>Anas crecca</i>	5.4	0
<i>Tetrao urogallus</i>	5.3	0
<i>Gypaetus barbatus</i>	5.1	1
<i>Bubo scandiacus</i>	5.1	0
<i>Asio flammeus</i>	5.1	0
<i>Asio otus</i>	5.0	0
<i>Delichon urbica</i>	5.0	0
<i>Turdus iliacus</i>	4.9	0
<i>Gyps fulvus</i>	4.5	1
<i>Accipiter nisus</i>	4.4	1
<i>Buteo buteo</i>	4.4	1
<i>Falco naumanni</i>	4.3	2
<i>Tetrao mlokosiewickzii</i>	4.2	0
<i>Anas acuta</i>	4.1	0
<i>Passer domesticus</i>	4.1	0
<i>Oenanthe oenanthe</i>	3.9	0
<i>Aegypius monachus</i>	3.8	2
<i>Emberiza calandra</i>	3.8	0

<b>Species</b>	<b>Percentage occurrence in Neanderthal sites</b>	<b>Number of published cases of Neanderthal intervention</b>
<i>Montifringilla nivalis</i>	3.6	0
<i>Aegolius funereus</i>	3.6	0
<i>Petronia petronia</i>	3.5	0
<i>Gallinula chloropus</i>	3.5	0
<i>Rallus aquaticus</i>	3.5	0
<i>Galerida cristata</i>	3.4	0
<i>Nucifraga caryocatactes</i>	3.4	0
<i>Cygnus cygnus</i>	3.3	1
<i>Falco vespertinus</i>	3.3	1
<i>Alectoris chukar</i>	3.3	0
<i>Vanellus vanellus</i>	3.2	1
<i>Lullula arborea</i>	3.1	0

**Appendix 5.** The top quartile species in modern human (Magdalenian) sites compared to taphonomic cases of exploitation by Magdalenians.

Species	% occurrence in Magdalenian sites	Number of published cases of Magdalenian intervention
<i>Lagopus lagopus</i>	44.4	13
<i>Pyrrhocorax graculus</i>	35.4	6
<i>Lagopus mutus</i>	35.0	12 <sup>1</sup>
<i>Tetrao tetrix</i>	25.4	4
<i>Perdix perdix</i>	24.0	1
<i>Corvus corax</i>	23.9	11
<i>Anas platyrhynchos</i>	22.2	4
<i>Bubo scandiacus</i>	21.8	16
<i>Falco tinnunculus</i>	17.7	1
<i>Aquila chrysaetos</i>	15.6	3
<i>Turdus viscivorus</i>	14.8	0
<i>Pyrrhocorax pyrrhocorax</i>	13.3	1
<i>Turdus pilaris</i>	10.5	0
<i>Turdus merula</i>	10.2	0
<i>Tetrao urogallus</i>	10.1	1
<i>Bubo bubo</i>	9.9	0
<i>Pica pica</i>	9.7	1
<i>Garrulus glandarius</i>	8.6	0
<i>Asio flammeus</i>	8.1	0
<i>Anas crecca</i>	7.6	1
<i>Corvus corone</i>	7.6	0
<i>Turdus philomelos</i>	7.5	0
<i>Coturnix coturnix</i>	6.8	0
<i>Columba livia</i>	6.7	3
<i>Turdus iliacus</i>	6.9	0
<i>Sturnus vulgaris</i>	6.7	0
<i>Corvus monedula</i>	6.4	1
<i>Montifringilla nivalis</i>	5.1	0



Species	% occurrence in Magdalenian sites	Number of published cases of Magdalenian intervention
<i>Hirundo rustica</i>	5.1	0
<i>Asio otus</i>	4.9	0
<i>Columba palumbus</i>	4.8	0
<i>Columba oenas</i>	4.5	0
<i>Crex crex</i>	4.5	0
<i>Cygnus cygnus</i>	4.4	0
<i>Alauda arvensis</i>	4.3	0
<i>Turdus torquatus</i>	4.3	0
<i>Cinclus cinclus</i>	4.2	0
<i>Oenanthe oenanthe</i>	4.1	0
<i>Strix aluco</i>	3.9	0
<i>Vanellus vanellus</i>	3.9	0
<i>Falco peregrinus</i>	3.8	0
<i>Ptyonoprogne rupestris</i>	3.8	0
<i>Scolopax rusticola</i>	3.8	0
<i>Haliaeetus albicilla</i>	3.8	2
<i>Porzana porzana</i>	3.6	0
<i>Gypaetus barbatus</i>	3.5	3
<i>Falco subbuteo</i>	3.3	0
<i>Aegypius monachus</i>	3.3	1
<i>Alectoris rufa</i>	3.2	0
<i>Gallinago gallinago</i>	3.2	0
<i>Anas querquedula</i>	3.2	0
<i>Anser anser</i>	3.2	1
<i>Fringilla coelebs</i>	3.0	0
<i>Rallus aquaticus</i>	3.0	0

