EXPLOITATION OF ANIMAL RESOURCES BY MESOLITHIC FORAGERS IN THE CENTRAL BALKANS: AN ARCHAEOZOOLOGICAL ANALYSIS OF CRVENA STIJENA, MONTENEGRO.

A Thesis Submitted to the Committee on Graduate Studies in Partial Fulfillment of the Requirements for the Degree of Master of Science in the Faculty of Arts and Science

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Abstract

Exploitation of Animal Resources by Mesolithic Foragers in the Central Balkans: an Archaeozoological Analysis of Crvena Stijena, Montenegro.

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This study examines the foraging strategies of Mesolithic foragers in the Central Balkans, particularly those employed by the occupants of Crvena Stijena, Montenegro. The Prey Choice Model, Patch Choice Model, and Marginal Value Theorem are used to interpret subsistence patterns. The data from the Crvena Stijena assemblages are compared to those from other Mesolithic sites in the region, along with an Upper Paleolithic assemblage at Crvena Stijena, to assess patterns of animal resource use throughout the Late Pleistocene and Early Holocene in the region. Red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and brown hare (*Lepus europaeus*) are the most commonly identified taxa in the assemblages. The analysis suggests that Mesolithic foragers at Crvena Stijena, and at many sites throughout the region, were primarily exploiting high-ranked prey types. There is evidence that Mesolithic foragers engaged in more intensive subsistence strategies than those of Upper Paleolithic foragers.

Keywords: *Human Behavioral Ecology, Foraging Theory, Zooarchaeology, Diet, Mesolithic, Early Holocene, Late Pleistocene, Central Balkans.*

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Dedication

This thesis is dedicated to my grandfather, Allan Bonde.

The last time we spoke, you told me to be a great archaeologist.

Well, I'm getting 'a round tuit'!

Table of Contents

Acknowledgments iii

List of Figures x

List of Tables xi

Chapter 1 Introduction 1

1.1 Research Objectives 2

1.2 Thesis Overview 2

Chapter 2 Archaeological Background 4

2.1 Climatic and Cultural Change During the Late Pleistocene and Early Holocene in Europe 4

2.1.1 The Late Pleistocene: Last Glacial Maximum to the Younger Dryas 4

2.1.2 The Initial-Early the Holocene: Preboreal and Boreal Periods 6

2.1.3 The Early Holocene: Early Atlantic Period 10

2.1.4 The Early-Middle Holocene: Late Atlantic Period 13

2.2 Climatic and Cultural Change During the Late Pleistocene and Early Holocene in the Central Balkans 19

2.2.1 The Late Pleistocene and Upper Paleolithic (ca. 25.0–11.7 ka BP) 20

2.2.2 The Onset of the Holocene and the Early Mesolithic (11.7–8.8 ka BP) 21

2.2.3 The Early to Mid-Holocene and the Late Mesolithic and Neolithic Transition (8.8–8.0/7.6 ka BP) 22

2.3 Comparative Sites 25
2.3.1 The Iron Gates.. 25
2.3.2 The Adriatic (Croatia) 33
2.3.3 Montenegro 37
2.4 Crvena Stijena 42
2.4.1 Crvena Stijena Mesolithic Assemblages 48
Chapter 3 Human Behavioral Ecology and Foraging Theory 53
3.1 Human Behavioral Ecology 53
3.2 Foraging Theory 53
3.3 Prey Ranking... 58
Chapter 4 Methodology 71
4.1 Taphonomy.. 71
4.1.1 Identifying Anthropic Modifications to Bone Surface............................... 71
4.1.2 Identifying Non-Anthropic Modifications to Bone Surface 74
4.1.3 Impacts of Excavation and Collection Methods 76
4.2 Measures of Quantification and Abundance 77
4.2.1 Number of Identified Specimens (NISP) 77
4.2.2 Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) 78

4.2.3 Number of Distinct Elements (NDE) 78

4.2.4 Abundance and Diversity Indices 79

4.3 Age and Sex Determination 80

4.3.1 Age Determination 80

4.3.2 Sex Determination 82

4.4 Differentiating Between Wild and Domestic Fauna 83

4.4.1 Morphological Identification of Domesticated Taxa 83

4.5 Determining Seasonality 84

Chapter 5 Results 86

5.1 Description of the Faunal Sample 86

5.2 Taphonomic Analyses 87

5.2.1 Overall Bone Surface Condition 87

5.2.2 Fragmentation 87

5.2.3 Natural Agents 88

5.2.4 Human Agents.. 90

5.3 Faunal Analyses 91

5.3.1 Taxonomic Composition of the Mesolithic Assemblages........................... 91

5.3.2 Presence of Domesticated Animals and Seasonal Occupation 94

5.3.3 Sample Diversity and Abundance Indices 94

5.4.1 Taxonomic Composition of Layer X 95
5.4.2 Sample Diversity and Abundance Indices 97
Chapter Six Discussion and Concluding remarks.. 99
6.1 Taphonomic Impacts on the Mesolithic assemblages 99
6.1.1 Intensive Carcass Processing 99
6.1.2 Burning 100
6.2 Foraging Strategies 102
6.2.1 Patch Use 102
6.2.2 Diet Breadth 103
6.3 Subsistence at Crvena Stijena and Other Mesolithic Sites in the Central Balkans.. 105
6.4 Concluding Remarks.. 106
References.. 108

List of Figures

Figure 2.1: Physical map of the Central Balkans with important landscapes labeled..19

Figure 2.2: Map of Mesolithic Sites in the Central Balkans……………………23

Figure 2.3: Mesolithic Sites in the Iron Gates region…………………………..26

Figure 2.4: Reconstructed Late Mesolithic settlement at Lepenski Vir Museum.……………………………………………………………………........28

Figure 2.5: Trescovăț, the large cliff on the opposite bank of the Danube from Lepenski Vir………………………………………………………………......29

Figure 2.6: Map of Mesolithic Sites along the Adriatic coast and hinterland….34

Figure 2.7: Map of Mesolithic sites in Montenegro…………………………....37

Figure 2.8: View of Crvena Stijena, entrance to the rockshelter is indicated with an arrow……………………………………………………………………....48

Figure 5.1: Surface state of specimens throughout the assemblages…………...87

Figure 5.2: NISP frequencies in GS 2 and GS 4………………………………..94

Figure 5.3: NISP frequencies in GS 2, GS 4, and X……………………………97

List of Tables

Table 2.1: The stratigraphic sequence at Crvena Stijena……………………….46

Table 2.2: %NISP counts adapted from Dimitrijević 2017………………........50

Table 3.1: Late Pleistocene and Early Holocene taxa documented at Crvena Stijena and other sites in the Central Balkans and estimated prey rank………...60

Table 4.1: Levels of surface preservation and defining criteria………………...75

Table 4.2: Body size classes and examples of corresponding taxa……………..77

Table 4.3: Red deer tooth eruption and wear schedule……………………….....80

Table 4.4: Red deer epiphyseal fusion schedule………………………………..81

Table 5.1: Overview of Mesolithic faunal assemblages from Crvena Stijena….86

Table 5.2: NISP and MNI counts from GS 2…………………………………...92

Table 5.3: NISP and MNI counts from GS 4…………………………………...92

Table 5.4: Adjusted standardized residuals from chi-sq. Test………………......93

Table 5.5: (Upper) Sample Diversity in the Mesolithic layers as measured by Simpson's Reciprocal Index. (Lower) Abundance indices for the terrestrial prey types in the Mesolithic layers……………………………………....……...95

Table 5.6: NISP counts from X…………………………………………….....95

Table 5.7: Adjusted standardized residuals from chi-sq. Test…………………..96

Table 5.8: (Upper) Sample Diversity in the Mesolithic and Upper Paleolithic layers as measured by Simpson's Reciprocal Index. (Lower) Abundance indices for the terrestrial prey types in the Mesolithic and Upper Paleolithic layers…..98

Chapter 1 Introduction

The Pleistocene-Holocene transition largely coincides with the end of the Paleolithic period and the beginning of the Mesolithic period in Europe. As recorded changes in climates and environments occurred throughout much of the continent, foraging communities adjusted their lifeways to adapt to these changes—in some cases significantly altering their settlement and subsistence patterns. The notion that Mesolithic communities adapted to the conditions of the Early Holocene by intensifying their subsistence to include what were previously marginal prey types has long been assumed and has often been the central criterion for the distinction between Paleolithic and Mesolithic subsistence strategies (Gabel 1958; Braidwood 1962; Binford 1968; Bicho 1994; Kitagawa et al. 2018). However, a broad-based subsistence is well-documented at many Paleolithic sites, particularly at sites in Southern Europe (Stiner et al. 1999; Manne and Bicho 2009; Rillardon and Brugal 2014; Blasco and Fernández Peris 2012; Morin et al. 2019; Blasco et al. 2022). Parts of Southern Europe possibly acted as temperate refugia during the Late Pleistocene which supported a rich biodiversity and buffered against the dramatic floral and faunal turnovers observed in more northern regions of Europe (Jochim 1987; Sommer and Nadachowski 2006; Barton et al. 2013); conditions which may have facilitated the development of broader diets at some Paleolithic sites.

This thesis will evaluate the notion that the Mesolithic period coincided with a greater use of marginal animal resources compared to the Upper Paleolithic, indicating an overall intensification of subsistence strategies. Crvena Stijena offers an excellent opportunity to explore such changes in foraging strategies, as its rich archaeological sequence spans from the Middle Paleolithic to the Bronze Age (Baković et al. 2009; Whallon 2017). This thesis will focus particularly on the faunal assemblages from the two Mesolithic strata excavated during the 2006 excavation season. The data from these assemblages will be compared with the faunal assemblage from the most recent Upper Paleolithic layer at the site to changing use of marginal prey types in the diet between the two periods.

1.1 Research Objectives

This study aims to answer the following questions: **1)** Is there evidence of a broad-spectrum diet at Crvena Stijena during the Mesolithic, in the form of an intensive exploitation of marginal animal resources? **2)** Are there any changes in the range and types of prey exploited between the Early and Late Mesolithic layers? **3)** How do the faunal assemblages at Crvena Stijena compare with those from other Mesolithic sites, particularly in the Central Balkans? And finally, **4)** is there evidence of subsistence intensification throughout the Pleistocene-Holocene transition?

1.2 Thesis Overview

This thesis is divided into six chapters. The chapter provides a general overview of the Mesolithic period throughout Europe and a review of Mesolithic research in the Central Balkans, with an emphasis on Montenegro. Chapter two also introduces Crvena Stijena, the site which is the focus of this thesis.

Chapter three presents the theoretical perspectives that inform interpretations regarding diet breadth at the site, beginning with an overview of Human Behavioral

Ecology and Foraging Theory models. A more detailed discussion of the prey ranking used in this study concludes the chapter. Chapter four presents the methods of analysis used in this study and discusses the criteria used to identify different taphonomic effects in the assemblages. Next, the chapter reviews the zooarchaeological quantification measurements used in the study. The chapter concludes with an examination of the methods for differentiating between wild and domestic specimens, assessing age and mortality profiles, and methods of estimating seasonal occupation at the site.

In chapter five, the results of the study are presented, focusing on the taphonomic history and taxonomic composition of the faunal assemblages. Results from the comparison of taxonomic compositions of the Mesolithic layers and the Upper Paleolithic layer are also presented. Chapter six begins with a discussion of the results from the taphonomic study and continues with a discussion on the inferred foraging decisions made by the occupants at Crvena Stijena. Next, a comparison between the foraging patterns inferred at Crvena Stijena with those inferred from other sites in the region; and a comparison between the Upper Paleolithic and Mesolithic periods at Crvena Stijena. Particular attention is paid to whether there is evidence of intensification of subsistence strategies at the site during transition between the Mesolithic and Paleolithic. Chapter six ends with a summary of the conclusions of the study and offers avenues for future work on the topic.

Chapter 2 Archaeological Background

2.1 Climatic and Cultural Change During the Late Pleistocene and Early Holocene in Europe

2.1.1 The Late Pleistocene: Last Glacial Maximum to the Younger Dryas

To better contextualize the Mesolithic and Early Holocene, it is necessary to briefly discuss the preceding Upper Paleolithic and Terminal Pleistocene. During the Terminal Pleistocene, there were a number of relatively rapid phases of climatic cooling and warming (Rasmussen et al. 2014). Staring with the Last Glacial Maximum (LGM), (26.5–20 ka BP; Clark et al. 2009) climatic and environmental conditions throughout Europe were significantly drier and cooler than those of today (Strandberg et al. 2010; Bartlein at al. 2011). Ice cover in Europe was at its peak, with glaciers covering much of Northern Europe and parts of Central Europe (Strandberg et al. 2010). In the ice-free areas of Central and Southern Europe, steppe grasslands and dry shrubland prevailed, with refugial forests in some areas of Southern and Eastern Europe (Elenga et al. 2001; Ray and Adams 2001; Tarasov et al. 2001; Harrison and Prentice 2003; Davis et al. 2024). Cold-adapted, gregarious grazing ungulates such as reindeer (*Rangifer tarandus*), horse (*Equus* sp.), mammoth (*Mammuthus* sp.), and saiga (*Saiga tatarica*) are well represented in archaeological faunal assemblages during this period (Guthrie 1982; Markova et al. 2010; Ponomarev et al. 2013; Álvarez-Lao and Méndez 2016; Crégut-Bonnoure et al. 2018; Andrés-Herrero et al. 2018; Kitagawa et al. 2018). After the LGM, climates in Europe gradually began to warm, with some oscillations between stadial and interstadial conditions (Dansgaard et al. 1983).

During the warm period after the LGM (Bølling–Allerød Interstadial: 14.6–12.9 ka BP), much of the steppic parkland characteristic of the LGM in Central and Western Europe was gradually replaced with boreal forest (Gerasimenko 2011; Palacios et al. 2023). Along with this environmental change, the herds of steppic fauna that were common in earlier Upper Paleolithic faunal assemblages began to be replaced by woodland species (Rillardon and Brugal 2014). However, immediately preceding the onset of the Holocene, the Younger Dryas (ca. 12.9–11.7 ka BP) was associated with a return to near-glacial conditions (Rasmussen et al. 2014; Cheng et al. 2020; Gerasimenko 2011).

The initial Younger Dryas was characterized by colder and wetter climates, followed by a later period of drier, but warming climates (Lane et al. 2013; Hepp et al. 2019). Across much of Europe, archaeological sites appear to be fewer during the Younger Dryas (YD) compared to the preceding Bølling–Allerød (Bicho et al. 2011; Ordonez and Riede 2022). There is also a decrease in the representation of boreal-type fauna in archaeological assemblages during this period (Blockley and Gamble 2012), probably as a result of the reversal to stadial conditions. There is evidence of broad-spectrum subsistence at some sites, especially in Iberia and parts of Southern France (e.g., Laroulandie 2007; Manne and Bicho 2009; Blasco and Fernández Peris 2012; Manne et al. 2012; Yravedra et al. 2017). In Northwestern and Central Europe, many YD faunal assemblages are characterized by fauna similar to the LGM, with a focus on exploiting reindeer and other steppe-adapted species (Baales 1996; Vermeersch 2011; Weber et al. 2011; Drucker 2012; Andrews 2018; Lengyel et al. 2021), while some sites in Southern Europe show the persistent exploitation of boreal-type fauna similar to the Allerød period (Bicho et al. 2011; Mussi and Peresani 2017).

2.1.2 The Initial-Early the Holocene: Preboreal and Boreal Periods

The warmer climates after the YD mark the beginning of the Holocene. The Preboreal period (11.7–10.5 ka BP) is the earliest period associated with the Holocene in Europe; and corresponds to much of the Early Mesolithic (Walker et al. 2009). Climates in Europe during the Preboreal are characterized as warmer and wetter overall compared to the YD (Bicho et al. 2011; Andrews 2018; Bos et al. 2018; Kopytov et al. 2024). However, climates continued to oscillate during the Preboreal, accompanied by shifting landscapes and vegetation covers, creating unstable environments for much of the period (van Geel et al. 1981; van der Plicht et al. 2004; Bos et al. 2007; Spikins 2008).

The Preboreal environment is generally characterized by an expansion of forests. Throughout much of Europe, birch (*Betula*) and pine (*Pinus*) forests expanded significantly during this period (Borzenkova et al. 2015; Malkiewicz et al. 2016; Bos et al. 2018; Sørensen et al. 2018; López-Sáez et al. 2020). In parts of Southern Europe, temperate deciduous forests were present (Beaulieu et al. 2017; López-Sáez et al. 2020). The Preboreal period also saw a continuation of the sea level rise and isostatic rebound that began after the LGM. These changes in sea level resulted in some dramatic alterations to landscapes throughout the early Holocene (Smith et al. 2011). The flooding of Doggerland, an area between what is now the United Kingdom, the Netherlands, and Germany, began during this period (Hoebe et al. 2024). The Baltic Basin in Northeastern Europe also underwent significant drainage and flooding events during the initial Holocene (Björk 1995, 2008; Schmölcke et al. 2006; Borzenkova et al. 2015). Sea levels also began to rise around the Mediterranean, shifting shorelines and continuing the inundation of the Adriatic basin in the East (Surić et al. 2005; Berné et al. 2007; Storms et al. 2008; Ilijanić et al. 2025).

The Boreal period (ca. 10.5–8.8 ka BP) is characterized by an overall warmer, drier climate than the Preboreal, while showing some significant climatic and environmental oscillations (Seppä and Birks 2001; Randsalu-Wendrup et al. 2012; Aufgebauer et al. 2012; Novenko and Olchev 2015). Temperate deciduous forests continued to expand during the Boreal. Notably, hazel (*Corylus*) expanded across much of Northern and Central Europe, becoming a valuable resource for many Mesolithic communities (Crombé et al. 2023; Hoebe et al. 2024). The inundation of Doggerland reached its peak during the later part of this period as sea levels continued to rise (Cohen et al. 2014; Hoebe et al. 2024), resulting in the withdrawal of Mesolithic populations from the area. Much of the Adriatic basin was inundated as well during this period (Surić et al. 2005; Pilaar-Birch and Vander Linden 2018).

Cultural change during the Initial-Early Holocene

The Preboreal and Boreal periods coincide with the Early Mesolithic across Europe. During the Early Mesolithic, hunter-gatherer populations demonstrated a diverse suite of subsistence and cultural practices, many of which varied geographically and chronologically. Early Mesolithic material culture shows evidence of continued development from Upper Paleolithic technocomplexes, although with a higher diversity of tool types and more standardized production methods (Zvelebil 1986; Fisher 2006; Ricci et al. 2023; Riede et al. 2024). Mesolithic stone tool assemblages are characterized by microliths—created using the microburin technique—and backed bladelets (Fisher 2006; Sørensen et al. 2013; Conneller et al. 2016; Ducrocq et al. 2020). Microlith and blade productions are frequent in both Magdalenian (Western/Central Europe Upper Paleolithic) and Epigravettian (South/Southeastern Europe Upper Paleolithic) assemblages, but blade production generally declined while microliths became more common and standardized during the Mesolithic (Zvelebil 1986; Fisher 2006). Scrapers, burins, retouched blades, axes, and borers are all frequent components of Early Mesolithic stone tool assemblages. Ground stone tools are also present and were likely used to process plant material (Alday et al. 2006; Antonović et al. 2006; Roda Gilabert et al. 2016).

Bone tools, including points, scrapers, awls, and needles are also frequently found in Early Mesolithic assemblages (Cristiani 2009; Vitezović 2011; Dekker et al. 2021). Bone fishhooks and harpoon points begin to appear more regularly during the Early Mesolithic (Mansrud 2017 and references therein; Clark 1975; Cristiani and Borić 2016), although sporadic evidence for such technology is documented in the Upper Paleolithic (Gramsch et al. 2013). At sites with exceptional organic preservation, a variety of wooden and other organic material artifacts have been uncovered (Mordant et al. 2013; Crombé and Robinson 2014; Taylor et al. 2018; Kabaciński et al. 2023).

Early Mesolithic subsistence centered on exploiting woodland ungulates, with red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), and roe deer (*Capreolus capreolus*) being the most common species represented in faunal assemblages (Bridault and Fontana 2003). Compared with faunal assemblages from the Upper Paleolithic, Mesolithic assemblages generally show that a more diverse suite of animal resources were incorporated into the diet and that subsistence strategies were regionally diverse (Bicho et al. 2000; Lidén et al. 2004; Milner 2006; Bonsall 2008; Kitagawa et al. 2013; Oxilia et al. 2021). Small, fast mammals like rabbits were important in the Early Mesolithic diet, particularly in Southern Europe; although these were already important resources at several sites in the region during the Upper Paleolithic (Rufà and Vaquero 2018; Stiner et al. 2000). Land snails were frequently incorporated into the diet of Early Mesolithic foragers in Southern Europe (Franco 2007; Ritzer et al. 2009; Fernández-López de Pablo et al. 2011; Girod 2011).

Carnivores, particularly marten (*Martes* sp.), beaver (*Castor fiber*), otter (*Lutra lutra*), lynx (*Lynx lynx*) and other fur-bearing species, represent significant proportions of Early Mesolithic faunal assemblages (Charles 1997; Crezzini et al. 2014; Zhilin 2014; Overton 2016). Throughout Europe, fishing and exploitation of other aquatic resources were important during this period (Kitagawa et al. 2013; Boethius et al. 2014; Zhilin 2014). The exploitation of fish and other marine resources has been documented during the Paleolithic (Le Gall 1992, 1993; Richards et al. 2001; Adán et al. 2009; Colonese et al.2011; Álvarez-Fernández 2015). During the Early Mesolithic, there is much evidence to support the increased importance of freshwater fishing (Mordant et al. 2013; Robson and Ritchie 2019; Bridault et al. 2022). Due to the significant rise in sea levels during the Early Holocene, it is difficult to fully assess the importance of marine resources as many coastal sites from the Early Mesolithic are now underwater. The available evidence suggests that marine fish and mollusks were important resources and frequently exploited when accessible (Bicho et al. 2010; Robson and Ritchie 2019). Plants also became increasingly important dietary resources during the period (Clarke 1976; Bishop 2021; Ptáková et al. 2021; Bishop et al. 2023). For example, as hazel (*Corylus*) forests expanded during the Boreal period, Mesolithic foragers increasingly incorporated hazelnuts into their diet (Holst 2010; Bishop et al. 2014; Crombé et al. 2023).

2.1.3 The Early Holocene: Early Atlantic Period

After the Boreal period, the Atlantic period (8.8-5.3 ka BP) and the Holocene Thermal Optimum (ca. 8.0-5.7 ka BP) characterize much of the rest of the Early Holocene. During the Early Atlantic, temperatures rose across the continent (Seppä and Birks 2001; Novenko et al. 2009). Lower lake levels at the beginning of the period suggest that precipitation may have initially decreased in some areas but increased during the later part of the period (Kalis et al. 2003). Forest cover reached its maximum around the start of the Holocene Thermal Optimum (HTO; ca. 8.0-5.7 ka BP) (Hofman-Kamińska et al. 2019). Dense deciduous woodlands expanded further during this period, covering much of Southern, Central, and Eastern Europe in mixed oak (*Quercus*), linden (*Tillia)*, elm (*Ulmus*), and alder (*Alnus*) forests (Rossignol-Strick 1999; Borzenkova et al. 2015; Novenko 2020). In areas around the eastern Mediterranean Sea, a quasi-savannah environment developed (Rossignol-Strick 1999). The pine and birch forests that were common during the Preboreal and Boreal periods retreated to higher latitudes in Northern and Central Europe (Kalis et al. 2003). In some parts of Eastern Europe where a drier climate prevailed, open grasslands became widespread (Hejcman et al. 2013; Pokorný et al. 2015).

Cultural change during the Early Holocene

The Late Mesolithic (ca. 9.0~6.0 ka BP) largely correlates with the beginning of the Atlantic period and the Holocene Thermal Optimum. During the Late Mesolithic, much of the regional variability in lithic industries disappear, and across many regions of Europe the Castelnovian became the dominant lithic industry (Kozłowski 2009). The Castelnovian is characterized by notched blade production and geometric microliths called "trapezes" (Dini et al. 2008; Binder et al. 2012; Marchand 2014; Mazzucco et al. 2016; Soto et al. 2023). These small, trapezoidal microliths were presumably used as arrow points and are believed to have enhanced damage to animal tissues, resulting in increased efficiency while hunting in dense forests (Larsson 1978). Ground stone tools—likely used to process plant foods—become core components of some Late Mesolithic tool assemblages (Antonović et al. 2006; Holst et al. 2024; Zupanchich et al. 2025). At sites in Northern Europe, polished stone axes and chisels appear in Late Mesolithic assemblages (Ahlbeck and Gill 2010). Well-preserved material culture related to fishing (i.e., traps and weirs) have been preserved at several Late Mesolithic sites (Andersen 1995; Pickard and Bonsall 2007). A variety of bone tools and other organic technologies ere manufactured and used in ways similar to the Early Mesolithic aside from changes in lithic technology, Late Mesolithic material culture seems largely continuous with that of the Early period (Marquebielle 2014; Marchand and Perrin 2017).

Subsistence patterns in the Late Mesolithic differed little from the Early period, although there is some evidence increased variation in subsistence patterns at the regional scale (Bailey and Spikins 2008; Real et al. 2024). During this period, subsistence centered around woodland ungulates, with red deer, wild boar, and roe deer being the most frequently represented species. Small game and fur-bearing carnivores are also frequently found in these assemblages. Plant foods remained important during the period, with hazelnuts being core components of the diet at some sites, along with roots and tubers (Kubiak-Martens 1999; Cristiani et al. 2018; Jacomet and Vandorpe 2022; Bishop et al. 2023). During the Late Mesolithic, it appears that aquatic resources—especially fish—became a more prominent component of the human diet (Enghoff 1994; Pickard and Bonsall 2007; Rainsford et al. 2014; Cristiani et al. 2018). The Late Mesolithic has sometimes been associated with the exploitation of seasonal fish spawning runs, which could have allowed some human groups to reduce their residential mobility (Radovanović 1996; Dimitrijević et al. 2016; Boethius et al. 2020). An increasingly sedentary lifestyle may have facilitated the incorporation of some domestic ungulates and cultigens into the diet at the end of the period as interactions with expanding populations of farmers increased in frequency (Krause-Kyora et al. 2013; Cristiani et al. 2016; Filipović et al. 2018).

2.1.4 The Early-Middle Holocene: Late Atlantic Period

While much of the early Atlantic period was characterized by warm climate similar or even slightly warmer than those of today (Seppä and Birks 2001; Novenko et al. 2009; Sundqvist et al. 2010; Renssen et al. 2012; Hofman-Kamińska et al. 2019), this episode was punctuated by a brief, but intense, cooling event at 8.2 ka BP which lasted around 160 years (Thomas et al. 2007). The 8.2 ka event brought about significantly drier, cooler climates throughout Europe, with temperatures dropping as much as -.6 to -1.2°C annually (Alley et al. 1997; Leuenberger et al. 1999; Seppä and Birks 2001; Allen et al. 2007; Prasad et al. 2009; Aufgebauer et al. 2012; Morill et al. 2013). In southern Europe, lake levels lowered and there was a pause in sea level rise due to increased aridity (Reed et al. 2001; Aufgebauer et al. 2012; Pilaar-Birch and Vander Linden 2018). Throughout Europe, temperate forest cover decreased, particularly *Quercus* and *Corylus*, while *Pinus* and *Betula* forests rapidly expanded (Tinner and Lotter 2001; Ghilardi and O'Connell 2013).

After the 8.2 ka event, climates rapidly warmed, increasing by an estimated 3°C over 300 years, which facilitated a rapid expansion of temperate forests (Novenko and Olchev 2009; Aufgebauer et al. 2012). This climate event has been associated with several significant cultural phenomena, including lower population densities (Wicks and Mithen 2014) and abandonment of sites or regions (Bonsall et al. 2002; Gonzalez-Samperiz et al. 2009), while other regions saw stable or increased population densities (Griffiths and Robinson 2018; García-Escárzaga et al. 2022). The 8.2 ka event possibly coincided with the initial spread of agriculture and the process of Neolithization throughout Europe (Weninger et al. 2006, 2009; Özdoğan 2011), although the presence of some Neolithic settlements in Southeastern Europe that date before this event complicates this interpretation.

Cultural change during the Early-Middle Holocene

The Mesolithic ends with the emergence of agricultural societies, an event which varies temporally across the continent during the Mid-Holocene. These initial farming communities have often been identified in the archaeological record by the appearance of a distinct 'Neolithic package' of material culture typically including pottery, polished stone tools, and domesticated species of flora and fauna (Childe 1925; Thomas 2008; Özdoğan 2014; Jovanović et al. 2021; Roy et al. 2023). However, the full suite of these artifacts may or may not be found in all Late Mesolithic or Neolithic contexts. The Mesolithic-Neolithic transition is also presumed to have been marked by an abrupt change in subsistence patterns at some sites. At many Late Mesolithic sites, a diet consisting of a variety of wild terrestrial and aquatic resources is abruptly replaced by a narrow diet overwhelmingly dominated by domestic species (Lubell et al. 1994; Bonsall et al. 1997; Schulting et al. 2004; Richards and Schulting 2006; Bickle 2018).

While a variety of models have been argued to explain the Mesolithic-Neolithic transitions, including models arguing for indigenous development (Zvelebil 1996) or mixed indigenous-exogenous development (Gkiasta et al. 2003), The most widely supported model argues for the exogenous development of agriculture and subsequent replacement of Mesolithic populations with incoming agricultural populations with origins in Southwestern Asia (Ammerman and Cavalli-Sforza 1973, 1984; Krauß et al. 2018). This model is largely supported by changes in material culture seen in the archaeological record and genetic data which show that most Neolithic populations in Europe have genetic origins in Central Anatolia (Bramanti et al. 2009; Haak et al. 2010; Hofmanová et al. 2016, Kılınç et al. 2016; Krauß et al. 2018; Yu et al. 2022).

While it is clear that the Neolithic transition is associated with significant demographic and material transitions caused by the expansion of farming populations originating in Southwestern Asia, the transition cannot be fully explained by a simple replacement model. Several studies show evidence of genetic integration between the local hunter-gatherer groups and the new incomers (i.e., Fernandez et al. 2010; Carvalho et al. 2015; Lipson et al. 2017; González-Fortes et al. 2019; Thomas 2022; Carvalho et al. 2023). For example, Lipson et al. (2017) found significant genetic admixture between some indigenous Mesolithic hunter-gatherers and early farmers in what are today Spain, Germany, and Hungary. Several studies also emphasize the contributions of hunter-gatherer DNA to Neolithic populations in areas of Southern Europe (Mathieson et al. 2018; Villalba-Mouco et al. 2019; Rivollat et al. 2020; Carvalho et al. 2023). The exact proportion of Mesolithic DNA in early farmers varies greatly depending on the period, region, site, and even among individuals (Skoglund et al. 2014; Lipson et al. 2017; Mathieson et al. 2018; Jones et al. 2017; Carvalho et al. 2023). The contributions of indigenous Mesolithic DNA to Neolithic populations are generally highest in the early farmers of the Central Balkans and around the Mediterranean, and lower in populations from more central regions of Europe (Mathieson et al. 2018; Rivollat et al. 2020).

The earliest Neolithic radiocarbon dates in Europe come from sites in Greece, which have been dated to as early as 8.4–7.9 ka BP (Davison et al. 2006). After Greece, agricultural communities appear in the Balkans around 7.9–7.0 ka BP, in Central Europe by 7.5–6.8 ka BP, Western Europe by 7.5–7.3 ka BP, in parts of Eastern and Northern Europe by 7.8–6.2 ka BP, and around the Mediterranean coastline by 7.4 ka BP (Davison et al. 2006; Tresset and Vigne 2011). The British Isles and Scandinavia were colonized by early agriculturalists by 6.0–5.6 ka BP (Tresset and Vigne 2011; Sørensen and Karg 2012). Although the transition to agricultural societies is complex and variable throughout the continent, it seems that agriculture spread across Europe in a Southeast-Northwest direction from its source in Southwestern Asia (Ammerman and Cavalli-Sforza 1973, 1984; Davison et al. 2006; Krauß et al. 2018). There are two proposed routes of diffusion by these early agriculturalists. The first posits that they spread westward and dispersed along the Mediterranean margins (Zilhão 1993, 2001; Cortés Sánchez et al. 2012). This route was likely taken by some of the early agriculturalists that settled in Southwestern Europe (Bicho et al. 2017). Another diffusion corridor was the Danube River; with farming populations moving from Southeastern Europe into Central Europe and further dispersing (Clark 1965; Ammerman and Cavalli-Sforza 1973; Davison et al. 2006; Bocquet-Appel et al. 2009).

In some regions of Europe, the transition appears to have taken place rapidly with the appearance of Neolithic material culture and the genetic replacement of local populations (Hofmanová et al. 2016; Bickle 2018; Yu et al. 2022). In other regions of Europe, the Neolithic transition was prolonged, with some genetic introgression and aspects of Neolithic culture being incorporated into local lifeways in a piecemeal fashion while maintaining local lifeways and population characteristics from the Mesolithic (Mateiciucová 2008; Malmström et al. 2009; Bollongino et al. 2013; Jones et al. 2017). For example, in some areas of Central and Northern Europe, there is evidence that local hunter-gatherers maintained their lifeways while living alongside agricultural groups during the Neolithic (Malmström et al. 2009; Bollongino et al. 2013; Jones et al. 2017). Thus, the material and demographic conditions of the Mesolithic-Neolithic transition are complex and highly variable throughout the continent, varying at all scales from individuals to whole cultural groups.

Continental Trends

The variability of regional environments and subsistence strategies make it difficult to define any unifying patterns for the whole of Mesolithic Europe. Across much of the continent, environments and climate shifted from the colder, drier environments of the terminal Pleistocene to the warmer, wetter environments of the Early to Mid-Holocene. Broadly, it appears that the Mesolithic represents a period of human innovation and adaptation to the forested environments of the Early Holocene. Significant changes in lithic and bone technology took place, perhaps as adaptations for more successful and efficient foraging in post-glacial environments. In terms of foraging strategies, throughout much of Europe, there were changes in the high-ranked types of prey from the Late Pleistocene to the Early Holocene that correlate with the environmental changes during the period. These changes manifest in a focus on exploiting primarily large steppic herd animals (i.e., horse, reindeer) to the exploitation of less gregarious woodland species (i.e., red deer, wild boar) accompanied by an increased exploitation of plants, particularly hazelnuts, and other animal resources; especially aquatic animals like fish and shellfish. These changes are not equally apparent in all regions of Europe. For example, Pleistocene populations in southern Europe had already adopted a more diverse, woodland or marine diet which was maintained throughout the Early Holocene.

The end of the period is defined by the transition away from variable manifestations of hunter-fisher-gatherer lifeways to a more uniform mode of subsistence that relied heavily on agriculture. These early agricultural populations were largely descended from Anatolian farmers settling in Southeastern Europe around 8.4 ka BP. From there, they gradually dispersed following the Mediterranean coastline and the Danube River. By 5.6 ka BP, prehistoric communities across Europe had settled into agricultural societies.

2.2 Climatic and Cultural Change During the Late Pleistocene and Early Holocene in the Central Balkans

This Central Balkans includes parts of present-day Hungary, Romania, Bulgaria, Serbia, Montenegro, Bosnia and Herzegovina, and Croatia. The landscapes of this area are primarily hilly and montane, with the Danube River valley running through the center, the Pannonian Basin to the North and the Carpathian Mountains, Lower Danube Basin, and the Black Sea to the East. The Dinaric alps and the Adriatic Sea define the Western region, and the Balkan Mountains the Southeast. The Central Balkans can be divided into several geographic regions, including the Eastern Adriatic coast and

Figure 2.1: Physical map of the Central Balkans with important landscapes labeled.

hinterland and the Iron Gates of the Southern Danube. These two areas are the most well-documented subregions of the Balkan Mesolithic (Radovanović 1996; Miracle et al. 2000; Bonsall 2008; Branscombe et al. 2021).

2.2.1 The Late Pleistocene and Upper Paleolithic (ca. 25.0–11.7 ka BP)

The Balkan peninsula has been, and continues to be, incredibly biodiverse (Griffiths et al. 2004) with faunal, botanical, and sedimentary records suggesting that the region served as a refugium for temperate species and humans during the LGM (Tzedakis 2002; Miracle et al. 2010; Boev and Miloševic 2020). During the succeeding Bølling–Allerød, these species further expanded throughout the region (Aufgebauer et al. 2012). During the YD, climate in the region was cool, but with regular precipitation in some areas and decreased precipitation in others, resulting in some subtle vegetation change favoring steppic flora and halting the expansion of the temperate flora and fauna seen during the Bølling–Allerød (Lawson et al. 2004; Aufgebauer et al. 2012; Veličković et al. 2015; Magyari et al. 2019; Hughes et al. 2024). During the LGM, sea levels in the Adriatic were approximately 130 m lower than in the present day (Lambeck et al. 2002). Due to the rapid warming of the climate following the LGM, sea levels in the Adriatic rose significantly, beginning the inundation of what was previously a large basin to the North, although a brief pause in sea level-rise took place during the YD (Shackleton et al. 1984; Miracle 1995; Surić et al. 2005; Pilaar-Birch and Vander Linden 2018).

The Late Glacial Epigravettian (or Tardigravettian) technocomplex characterizes the Upper Paleolithic technocomplexes in the region during the Late Pleistocene. This technocomplex is marked by the use of high-quality flint to manufacture a variety of scrapers, blades and bladelets (Kozłowski 1999; Mihailović 2008). Upper Paleolithic subsistence in the Central Balkans focused primarily on medium and large terrestrial ungulates including ibex, red deer, bison, and giant deer, among others (Miracle et al.

2010; Morin and Soulier 2017; Dimitrijević et al. 2018; Stiner et al. 2022). Small game, fur-bearing species, carnivores, fish, and birds are also present in faunal assemblages during the Upper Paleolithic, but in relatively small proportions (Miracle et al. 2010; Dimitrijević et al. 2018; Stiner et al. 2022).

2.2.2 The Onset of the Holocene and the Early Mesolithic (11.7–8.8 ka BP)

During the Preboreal and Boreal periods, the warming climate brought about an increase in mixed oak and elm deciduous forest cover throughout the region beginning around 11.5 ka BP (Willis 1994; Aufgebauer et al. 2012; Tonkov et al. 2018; Magyari et al. 2019; Borić et al. 2021). At high elevations, pine and birch forests remained (Tonkov et al. 2018). After the YD, the Adriatic Sea continued to rise, inundating the northern third of the basin and partially submerging several small mountains, forming the Dalmatian Islands (Shackleton et al. 1984; Miracle 1995; Surić et al. 2005; Forenbaher 2009; Pilaar-Birch and Vander Linden 2018).

During the Early Mesolithic, regional lithic traditions are characterized by Epigravettian and Sauveterrian technocomplexes. The Mesolithic Epigravettian has been regarded as a continuation of the lithic traditions from the LGM, but with a more limited repertoire of artifacts and intensive use of low-quality raw materials (Mihailović 2008). Rarely reported in the Central Balkans, the Sauveterrian was limited to the Northwestern areas of the Balkans, whereas the Epigravettian is widespread throughout the region. Ground stone tools are found at Early Mesolithic sites in the Iron Gates (Antonović et al. 2006; Zupanchich et al. 2025) but do not become a core component of the toolkit until the Late Mesolithic. Bone points, scrapers, awls, needles, fishhooks, and harpoon points are found in Early Mesolithic assemblages (Cristiani 2009; Vitezović 2011; Cristiani and Borić 2016). The dense forests of the region possibly played a role in the 'decline' of local lithic traditions, and the lower connectivity of social groups during the early Mesolithic (Mihailović 2007, 2008, 2009). Red deer, wild boar, roe deer, hare (*Lepus europaeus*) and ibex (*Ibex ibex*) are among the most frequently represented terrestrial species (Radovanović 1996; Dimitrijević 2008; Boric et al. 2014; Cristiani and Borić 2016; Filipović et al. 2018; Borić et al. 2019). At sites located in riparian and marine environments, fish bones comprise substantial portions of faunal assemblages (Radovanović 1996; Rainsford et al. 2014; Živaljević et al. 2020; Branscombe et al. 2021).

2.2.3 The Early to Mid-Holocene and the Late Mesolithic and Neolithic Transition (8.8–8.0/7.6 ka BP)

During the Atlantic period, precipitation increased, and temperatures reached their peak in the region between 9.3 and 8.3 ka BP (Aufgebauer et al. 2012). The 8.2 ka cooling event brought about a brief reversal of the overall warm, wet conditions of the period, after which the environment quickly recovered (Aufgebauer et al. 2012). This event may have briefly halted sea level rise in the Adriatic, which then continued throughout the period until the present shoreline was formed around 6.0 ka BP (Lambeck et al. 2004; Pilaar-Birch and Vander Linden 2018).

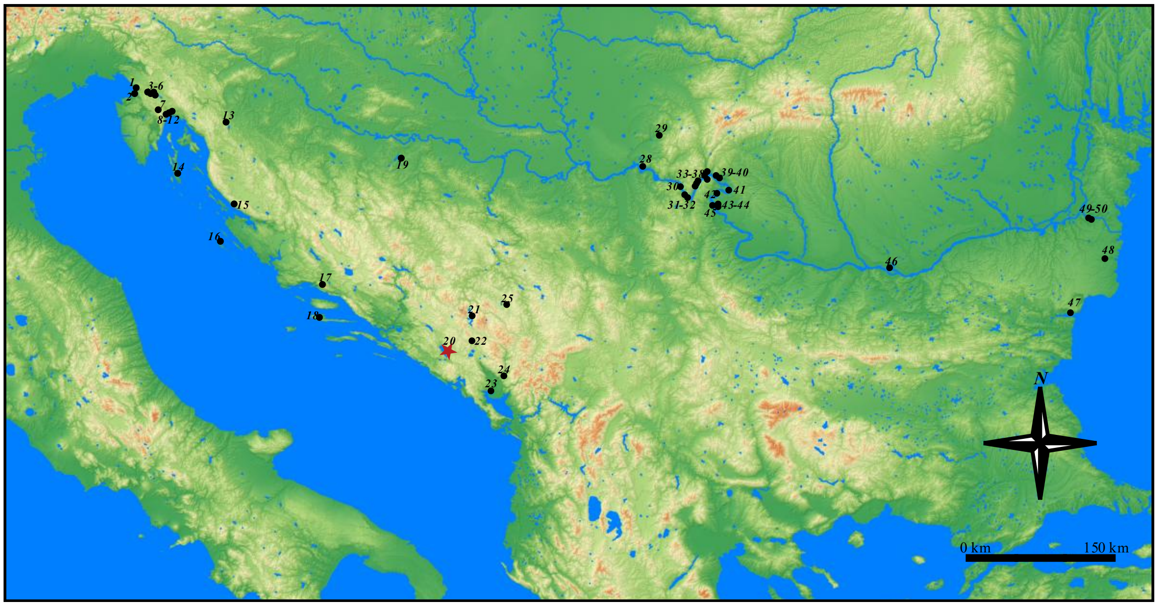


Figure 2.2: Map of Mesolithic Sites in the Central Balkans. Locations– 1: Biarzo; 2: Benussi; 3: Edera; 4: Ciclami; 5: Mala Triglavca; 6: Viktorjev Spodmol; 7: Pupićina peć; 8: Vela peć; 9: Ovčja; 10: Abri Sebrn; 11: Klanjčeva; 12: Nugljanski peć; 13: Zala; 14: Vela Spila (Lošinj); 15: Vaganačka; 16: Vlakno; 17: Zemunica; 18: Vela Spila (Korčula); 19: Ratuša; 20: Crvena Stijena; 21: Odmut; 22: Vrbička, 23: Seocka; 24: Vruća; 25: Medena Stijena; 26: Grabovac; 27: Bukovac; 28: Alibeg; 29: Hoţu; 30: Padina; 31: Lepenski Vir; 32: Vlasac; 33: Cuina Turcului; 34: Climente II; 35: Veterani; 36: Răzvrata; 37: Icoana; 38: Hajdučka Vodenica; 39: Ostrovul Banului; 40: Schela Cladovei; 41: Ostrovul Corbului; 42: Velesnica; 43: km 873; 44: km 875; 45: Kula; 46: Poiana; 47: Pobitite Kamuni; 48: Albeşti; 49: Medgidia; 50: Cuza Vodă. Adapted from Borić et al. (2019) and Bonsall et al. (2025).

The lithic industries of the Late Mesolithic in the Eastern Adriatic region are characterized by a replacement of the local Epigravettian with the Castelnovian technocomplex. The Castelnovian is characterized by a production of standardized blades and bladelets, some of which were further worked using the microburin technique into typical Late Mesolithic trapeze and notched blade implements (Kačar 2021). In the Iron Gates region, there is much technological continuity between the Early and Late Mesolithic lithic industries (Bonsall et al. 2025). During the Late Mesolithic, ground stone tools become essential parts of the toolkit at some sites, particularly in the Iron Gates region (Antonović et al. 2006; Zupanchich et al. 2025). The increased importance of ground stone tools in these assemblages has been interpreted as reflecting an increased importance of plants in the Late Mesolithic diet (Zupanchich et al. 2025).

As discussed above the Central Balkans likely played a significant role in the Mesolithic-Neolithic transition throughout Europe, as the region was likely used as a corridor by early agriculturalists in their expansion into Europe from Southwestern Asia (Ammerman and Cavalli-Sforza 1973; Davison et al. 2006; Mihailović 2007; Bocquet-Appel et al. 2009; Branscombe et al. 2021). As a result of this strategic position, much of the Mesolithic research in the Central Balkans has focused on assessing the potential roles that the Late Mesolithic groups played in the Neolithization of the region (e.g., Kozłowski and Kozłowski 1984; Bonsall 1997; Forenbaher and Miracle 2006; Cristiani et al. 2014; Dimitrijević et al. 2016; Kačar 2021). The Neolithization process in the region has been explained by a variety of models, with earlier research arguing for a local, indigenous development of Neolithic lifeways from 'Protoneolithic' cultures present in the region during the Mesolithic (i.e., Srejović 1979, 1988; Bogdanović 1998; for an overview of the history of research regarding the Neolithization of the region, see Vitezović 2023).

Current research regarding the Mesolithic-Neolithic transition in the Central Balkans suggests that like other regions of Europe, populations of farmers originating in Southwestern Asia are credited with bringing the Neolithic package to the region (Porčić et al. 2016; Mathieson et al. 2018). However, there is some evidence of cultural continuity between the Mesolithic and Neolithic cultures in the region. Aspects of local Mesolithic technocomplexes were still present during the Neolithic occupations at sites in the Iron gates (Antonović et al. 2019). In the Adriatic region, Castelnovian implements continue to be produced throughout the Mesolithic-Neolithic transition (Kačar 2021). The continuity of these technologies through the transition has been argued as evidencing acculturation or active participation by the local Mesolithic populations in Neolithic lifeways (i.e., Mihailović 2007; Kačar 2021). Several important sites, considered representative of regional subsistence patterns, have been selected to give the background to understand economic and social change throughout the Central Balkans during the Mesolithic.

2.3 Comparative Sites

2.3.1 The Iron Gates

The Iron Gates Gorges of the Danube River is the best documented subregion of the Balkan Mesolithic. Cutting through the Carpathian Mountains at the border of Eastern Serbia and Western Romania, coinciding with the widest section of the Danube, the gorges separate the lowlands of the Central Balkans: The Pannonian and the Lower Danube Basins. The Iron Gates region contains many archaeological sites from the Early Holocene (Fig. 2.3) (Živaljević et al. 2021; Radovanović 1996; Borić 2016). In the 1960s

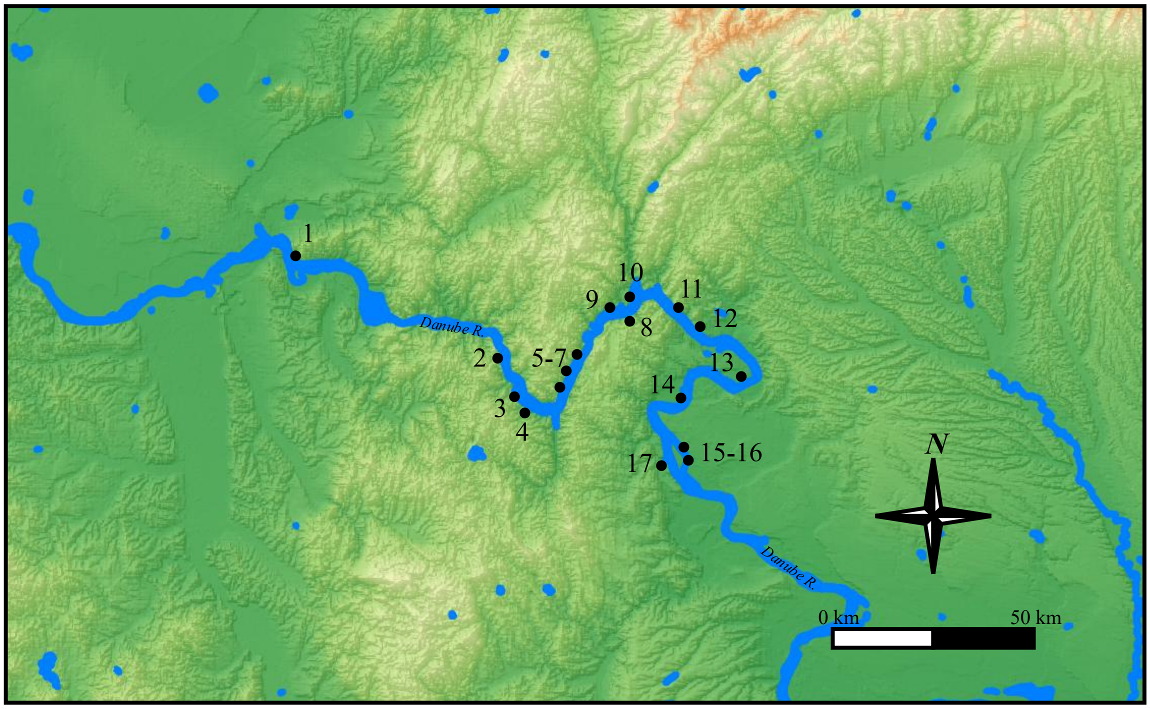


Figure 2.3: Map of Mesolithic Sites in the Iron Gates. Locations– 1: Alibeg; 2: Padina; 3: Lepenski Vir; 4: Vlasac; 6: Cuina Turcului; 7: Veterani; 8: Hajdučka Vodenica; 9: Răzvrata; 10: Icoana; 11: Ostrovul Banului; 12: Schela Cladovei; 13: Ostrovul Corbului; 14: Velesnica; 15: km 873; 15: km 875; 17: Kula. Adapted from Bonsall et al. (2025).

and 1970s, intensive archaeological survey of the region uncovered many open-air Mesolithic sites of a previously unknown technocomplex. This technocomplex has been referred to as the 'Lepenski Vir culture,' owing its title to the eponymous site. Early Mesolithic occupations in the regions are dated to ca. 11.5–9.4 ka BP (Borić 2011). The Late Mesolithic dates to ca. 9.4–8.3/8.2 ka BP, with the transitional period between the Mesolithic and Neolithic occurring between ca. 8.3/8.2–8.0/7.9 ka BP (Borić 2011). Early Mesolithic occupations are generally sparse throughout the region, with the most intensive and well-documented occupations occurring during the Late and Final Mesolithic.

In this region, subsistence during the Mesolithic, particularly during the Late period, appears to have been centered around terrestrial herbivores as suggested by the abundance of red deer, wild boar, aurochs (*Bos primigenius*), and roe deer in archaeological assemblages (Radovanović 1996; Dimitrijević 2008; Filipović et al. 2018). Dogs (*Canis lupus familiaris*) are also frequently represented in the Mesolithic faunal assemblages. Many of these remains show evidence of butchery, indicating that dogs were part of the Mesolithic diet in the region. Studies of the morphological traits of these canid remains suggests that dogs were locally domesticated in the Iron Gates region during the Mesolithic (Bökönyi 1975; Dimitrijević and Vuković 2012). Fish bones are also frequently recovered at sites in the region. At some sites, large anadromous sturgeons such as Beluga sturgeon (*Huso huso)* and Russian Sturgeon (*Acipenser gueldenstaedtii*) are well represented in faunal assemblages, suggesting exploitation of seasonal fish spawning runs (Borić 2001, 2002; Bartosiewicz et al. 2008; Dinu 2010; Filipović et al. 2018; Živaljević et al. 2021). Živaljević et al. (2021) estimates that many of the Beluga sturgeon reached lengths of over 2m—with some individuals larger than 4m. Research also suggests that some of these settlements were occupied year-round, perhaps indicating that semi-sedentary or sedentary lifeways were present in the region prior to the Neolithic (Dimitrijević et al. 2016). The intensive exploitation of aquatic resources may have allowed for the prolonged habitations of some Iron Gates sites (Radovanović 1996; Dinu 2010; Živaljević 2015; Dimitrijević et al. 2016). In the following pages, a couple of key sites from the region are discussed.

Lepenski Vir

Excavations at Lepenski Vir began in 1965 under the direction of Yugoslavian archaeologist Dragoslav Srejović (Srejović 1966). The site was recognized for its Mesolithic and Mesolithic-Neolithic occupations, as evidenced by the distinct trapezoidal dwellings, figural sculptures, and distinct burial traditions (Srejović 1966a; Radovanović 1996; Borić et al. 2011). Lepenski Vir was occupied throughout the Mesolithic (11.4–7.9 ka BP). The occupation at the site was most intensive during the Late Mesolithic (8.3–7.9 ka BP), a phase during which many of the distinctive features of the Lepenski Vir culture were established (Borić and Dimitrijević 2006).

Figure 2.4: Reconstructed settlement at Lepenski Vir Museum. Author's Photo.

The chipped stone tools from Lepenski Vir include end scrapers, irregular scrapers, burins, retouched blades, perforators, backed blades, and microliths; all a continuation from local Epipaleolithic traditions (Kozłowski and Kozłowski 1984; Radovanović 1996). The Lepenski Vir culture has also been interpreted as a predecessor to the Neolithic "Starčevo culture" (Srejović 1966a; Kozłowski and Kozłowski 1984; Kozłowski 1987), with some scholars noting that the ground stone tools from the site appear identical to those associated with the later Starčevo-Vinča technocomplex (Antonović 2006).

During the excavations at Lepenski Vir, faunal remains were hand-collected by the excavators, and many were later discarded after their initial analysis, creating a relatively small assemblage for study (Borić and Dimitrijević 2006; Dimitrijević 2008). This collection protocol likely biases the sample against smaller taxa. Despite these limitations, studies of the fauna from Lepenski Vir have produced insights regarding local subsistence strategies (see Radovanović 1996; Bonsall 1997, Dimitrijević 2008; Dinu 2010; Filipović et al. 2018). The Mesolithic inhabitants of Lepenski Vir primarily exploited terrestrial ungulates and freshwater fish species. Red deer was the most common taxon, the remains of which represent between 62.8–73.0% of the faunal assemblages from the site (Radovanović 1996:53). Aurochs and wild boar are also relatively frequently, comprising between 7.7–4.6% and 5.5–3.9% of the faunal assemblages (Radovanović 1996:53). Dog bones are likewise common in the assemblage, some of which show evidence of butchery, suggesting that dogs were used as a food source (Dimitrijević

Figure 2.5: Trescovăț, the large cliff on the opposite bank of the Danube from Lepenski Vir. Author's photo.

2008). Many of the ungulate remains bear cut marks, percussion notches, and show evidence of burning (Dimitrijević 2008). Some of these bones also bear evidence of canid gnawing, likely related to feeding or scavenging of domesticated dogs at the site (Dimitrijević 2008).

The fish sample at Lepenski Vir is dominated by indeterminate carp (*Cyprinidae*) remains (35.4–1.9%), followed by Wels catfish (*Silurus glanis*) (9.4–1.2%). Along with a variety of other freshwater species and anadromous sturgeon (Radovanović 1996:53; Borić and Dimitrijević 2006). Due to the biases imposed by the collection methods, it is difficult to accurately assess the role that fish played in the Lepenski Vir diet from faunal assemblages alone. Nitrogen ($\delta^{15}N$) isotope values from the burials at Lepenski Vir show that during the Early Mesolithic dietary proteins were largely derived from aquatic resources, a trend which continued through the Late Mesolithic (Bonsall et al. 1997, 2004). The analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes suggest that during the Mesolithic-Neolithic transition there was a significant shift in subsistence from an earlier diet consisting mostly of aquatic resources to one in which terrestrial resources were the primary focus (Bonsall et al. 1997, 2004; Filipović et al. 2018). This shift has been interpreted as demonstrating an introduction of cultivated and domesticated food sources in the region (Bonsall et al. 1997; Filipović et al. 2018).

Vlasac

Vlasac is situated just a few kilometers downstream from Lepenski Vir on the Danube. The site was partially excavated in the early 1970's, with more recent excavations resuming at the site in 2006 (Borić et al. 2008). Occupation at Vlasac began during the Early Mesolithic (ca. 11.5 ka BP), with the most intensive occupation occurring ca. 9.4–8.2 ka BP during the Late Mesolithic (Borić et al. 2008; Borić et al. 2009; Borić 2011; Cristiani et al. 2014). The site contains many features reminiscent of Lepenski Vir including trapezoidal dwellings with red limestone floors and is largely contemporaneous with the settlement upstream (Borić et al. 2008). Notably, at Vlasac the trapezoidal dwellings are present in earlier phases than at Lepenski Vir (Borić et al. 2008). The site was continuously used throughout the Mesolithic-Neolithic transition (ca. 8.2–7.9 ka BP) and into the Neolithic (Cristiani et al. 2014).

The chipped stone industry at the site is focused on flake production like the industry at Lepenski Vir. Lithic assemblages include blades, irregular scrapers, perforators, and various microliths (Kozłowski and Kozłowski 1982; Borić et al. 2014). The technocomplex at Vlasac appears to be largely a continuation of the local Epigravettian tradition, despite the presence of two trapezes in the Late Mesolithic assemblage (Borić et al. 2014). During the early excavations, a sizeable assemblage (n = 131) of ground stone implements were recovered, with an additional 70 specimens recovered during the 2006–2009 excavations (Srejović and Letica 1978; Borić et al. 2014). These tools were used for a variety of tasks, including the processing of plant materials for consumption (Zupancich et al. 2025). The excavations at Vlasac also recovered a wide variety of osseous tools including, awls, points, gorges, and chisels (Cristiani and Borić 2021).

During the early excavations, fine sieving was not used. Despite this, an assemblage of ca. 30,000 bones was recovered (Bonsall et al. 1997). Red deer comprises

69.1% of the terrestrial fauna, followed by wild boar (12.2%), and roe deer (5.2%) (Radovanović 1996:53). The faunal assemblages also include a small portion of avifaunal remains, most notably of white-tailed eagle (*Haliaeetus albicilla*) (Bökönyi 1978; Radovanović 1996; Bonsall et al. 1997; Borić et al. 2014). In the assemblages from the 2006-2009 excavations, dogs represent 46.0% of identified mammalian specimens, followed by red deer (28.1%), wild boar (10.9%) and roe deer (6.8%) (Boric et al. 2014). The faunal remains from the more recent excavations are of largely similar composition to those from the 1970's, with the most significant difference being the greater representation of dog remains in the more recent material (Borić et al. 2014). As is the case with other sites in the region, cutmarks and burning are documented on the dog remains (Borić et al. 2014), indicating that this species was likely part of the human diet. Dogs likely also played an active role in the modification of the faunal assemblages at Vlasac, as some of the faunal specimens from the recent excavations also bear traces of gnawing by canids (Borić et al. 2014).

Sixty percent of the identified specimens in the faunal assemblages excavated in the 1970's are fish (Bökönyi 1978; Bonsall et al.1997). Of the 1970's ichthyofaunal assemblage, indeterminate cyprinid remains dominate the assemblage (30.0%), followed by Wels catfish (13.1%), and carp (8.9%), with pike (.1%) being poorly represented (Radovanović 1996). In the faunal assemblages from the more recent excavations, 89.9% of the fauna are represented by fish remains (Borić et al. 2014). The vast majority of the ichthyofauna is represented by indeterminate cyprinids (98.6%) (Borić et al. 2014). remains were also uncovered in small quantities (1.3%) (Borić et al. 2014). High $\delta^{15}N$

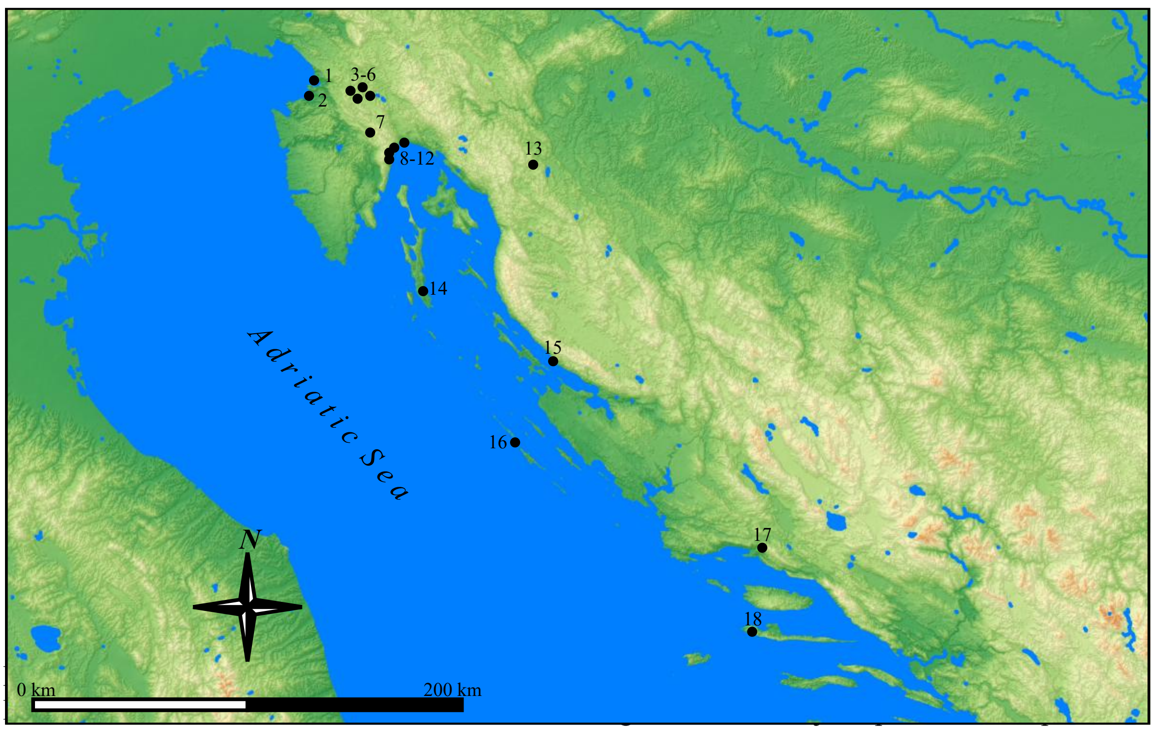
values recorded in human and dog burials at Vlasac suggest that aquatic resources were a staple in the diet throughout the Mesolithic (Bonsall et al. 1997; Borić et al. 2014). The faunal assemblages point to a seasonal abandonment of the site during the summer and winter months (Radovanović 1996). However, Dimitrijević et al. (2016) suggest that the site may have been occupied year-round.

2.3.2 The Adriatic (Croatia)

The Adriatic region is characterized primarily by the karstic Dalmatian coast and Dinaric Alps. The region, particularly along the coastlines, underwent significant changes during the Pleistocene–Holocene transition. Sea levels rose drastically in the Northern Adriatic, inundating the Adriatic Basin and doubling the surface area of the sea between 18,000 and 8000 BP (Shackleton et al. 1984; Surić et al. 2005; Pikelj and Juračić 2013; Pilaar Birch and Vander Linden 2018). In contrast to the open-air sites of the Iron Gates region, Mesolithic sites in this region are often found in caves or rock shelters, typical geological features of the Dinaric Karst. There are many known Mesolithic sites in Croatia (Fig. 2.4) (see Komšo 2006). However, accessing published data from these sites has proven difficult, as reports remain unpublished or are poorly diffused. Most studies in the region focus on the lithic assemblages or environmental conditions of the period (i.e., Vukosavljević et al. 2011; Vukosavljević et al. 2014; Vukosavljević and Perhoč 2017; Kaczanowska and Kozowski 2018; Pilaar Birch and Vander Linden 2018; Dean et al. 2020). Despite the limited subsistence data, some general trends are apparent. At sites near the coast and its immediate hinterlands, marine and terrestrial molluscs formed an important part of the diet (Komšo 2006; Rainsford et al. 2014; Branscombe et al. 2021).

Marine fish were also an important dietary resource at coastal sites (Rainsford et al. 2014; Branscombe et al. 2021). Along with marine resources, various species of terrestrial ungulates and small game were exploited (Branscombe et al. 2021; Lightfoot et al. 2011).

Subsistence on inland sites remains relatively unknown, due to a lack of data (Komšo 2006).



peć; 8: Vela peć; 9: Ovčja; 10: Abri Sebrn; 11: Klanjčeva; 12: Nugljanski peć; 13: Zala; 14: Vela Spila (Lošinj); 15: Vaganačka; 16: Vlakno; 17: Zemunica; Vela Spila (Korčula). Adapted from Bonsall et al. (2025).

Vela Spila, Korčula

Vela Spila is a large cave site located about 3km from the small town of Vela Luka on the island of Korčula, Croatia. The site was discovered in the mid-1900's, and the first excavations took place from 1974–1995, with more recent excavations from 2010–2018 (Branscombe et al. 2021). The site's stratigraphy contains deposits spanning from the Upper Paleolithic to the Bronze Age (Branscombe et al. 2021). An Early Mesolithic layer at the site was radiocarbon-dated to 9.3–9.0 ka BP (Rainsford et al. 2014). Radiocarbon dates from the final Mesolithic layer range from 8.3–8.0 ka BP (Rainsford et al. 2014). Despite the significant changes in sea levels during the Early Holocene, the environment surrounding the site during the Mesolithic occupations was likely similar to that of today, with the shoreline only about 1–2 km from the cave (Rainsford et al. 2014; Dean et al. 2020). The site was occupied seasonally during this period, likely for short durations to catch and process fish (Rainsford et al. 2014).

Information regarding the terrestrial faunal assemblages at Vela Spila is limited. The most abundant terrestrial vertebrate remains are from roe deer, with smaller game, such as fox, also documented (Cristiani et al. 2014). Evidence from the Mesolithic faunal assemblages suggests that the site was occupied in all seasons, with primary reliance on small game species during the spring and summer, roe deer from the spring to autumn, and red deer during the winter and autumn (Branscombe et al. 2021). A decrease in the estimated body sizes and relative abundances of some mammalian taxa correspond with an increase in marine taxa, which has been interpreted to reflect a decrease in high-ranked prey and subsequent diet expansion throughout the Mesolithic occupations (Dean et al. 2020).

More information is available regarding the marine fauna at the site. The ichthyofaunal assemblages are primarily comprised of fish and molluscs, with some indeterminate dolphin remains (Cristiani et al. 2014). Most of the fish specimens from the site date to the earlier Mesolithic phases (Rainsford et al. 2014). Fish remains represent around 90% of the vertebrate NISP in Mesolithic layers A and B (the earliest layers), with values dropping to around 50–60% in later layers C and D (Rainsford et al. 2014). Chub mackerel (*Scomber japonicus*) is the most abundant fish species in layers A and B, representing approximately 75% of the fish sample in A and 60% of the fish sample in layer B (Rainsford et al. 2014). There is a significant decline of mackerel in the later Mesolithic layers with chub mackerel representing 36% of fish remains in layer C, and 17.0%, in the final Mesolithic layer (D) (Rainsford et al. 2014:314). This decline is associated with an increase in eel species (*Conger conger*, *Muraena helena*), sea breams (Sparidae), mullets (Mugilidae), and wrasses (Labridae) (Rainsford et al. 2014:314-315). In the Neolithic assemblage, fish represent less than one tenth of the faunal remains (Rainsford et al. 2014). Fishing has been interpreted as a central part of the subsistence during the Mesolithic but became a less frequently practice, more opportunistic activity during the Neolithic (Rainsford et al. 2014).

The faunal assemblages from Vela Spila also include high relative frequencies of marine and terrestrial molluscs (Branscombe et al. 2021), some of which were used as personal ornaments (Cristiani et al. 2014). The primary molluscan species at the site are limpets (*Patella caerulea* and *P. rustica*) and top-shells, mostly *Phorcus turbinatus* (Branscombe et al. 2021). During the Mesolithic, molluscan resources were primarily collected in the summer and autumn (Branscombe et al. 2021). Like fish, molluscs are better represented in the Mesolithic assemblages than in those from the Neolithic (Branscombe 2017). The decline in the importance of molluscs and a shift to winter seasonal exploitation of these resources after the Neolithic transition have been interpreted as the result of increased reliance on agricultural resources (Branscombe et al. 2021; Forenbaher and Miracle 2006).

2.3.3 Montenegro

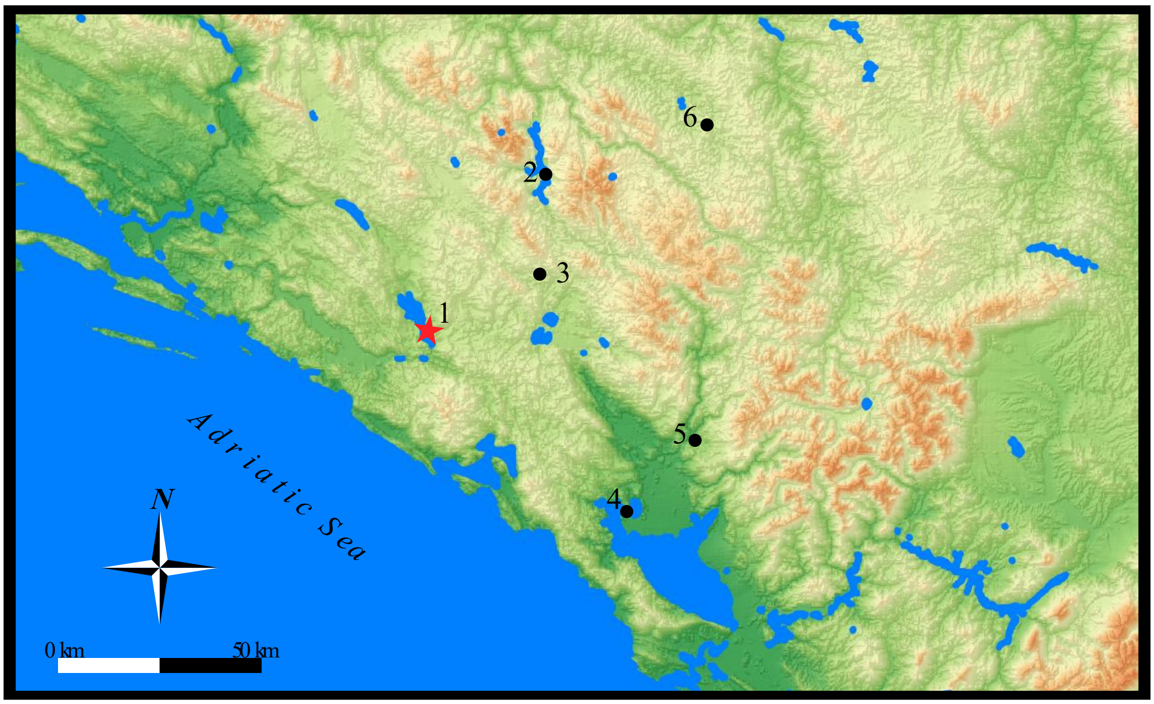


Figure 2.7: Map of Mesolithic sites in Montenegro. Locations– 1: Crvena Stijena; 2: Odmut; 3: Vrbička; 4: Seocka; 5: Vruća; 6: Medena Stijena. Adapted from Borić et al. (2019).

Montenegro shares many of the same environmental and geological features as Croatia and can be considered as an extension of the Adriatic region. Unlike Croatia, many of the known Mesolithic sites in Montenegro are located inland, well into the Dinaric Alps. Much of the country's physical geography is characterized by rugged, karstic systems (Bonacci 2014; Djurović and Djurović 2016; Radusinović and Pajović 2024; Barović et al. 2018). There are currently six sites with known Mesolithic occupations in Montenegro: Crvena Stijena, Medena Stijena, Odmut, Seocka, Vrbička cave, and Vruća cave (Fig. 2.5).

Like Croatia, most research on the Mesolithic in the country has focused on lithic and bone tool industries (e.g., Mihailović 1996, 1999; Cristiani and Borić 2016). Some of the chipped stone assemblages recovered from Mesolithic sites in Montenegro are associated with Epigravettian technocomplexes; while others, particularly later assemblages, appear more aligned with the Castelnovian tradition (Mihailović 1999). The Mesolithic faunal assemblages suggests that subsistence in Montenegro was primarily focused on terrestrial resources, including cervids, wild boar, chamois (*Rupicapra rupicapra*), and ibex (*Capra ibex*). At Seocka cave, there is evidence that fish were a significant dietary resource (Živaljević et al. 2020). Research in the region suggests that there was continuity between the Mesolithic and Early Neolithic (Borić et al. 2019; Borić et al. 2021).

Medena Stijena

Medena Stijena is a rock shelter site in the Ćeotina river canyon near the town of Pljevlja in Northern Montenegro. The site was originally excavated in the 1980s–90s (Srejović 1996). The stratigraphy at the site contains deposits from the Upper Paleolithic to the Bronze Age, including a Mesolithic layer (Mihailović 1996, 2009; Tomasso et al. 2020). There are no radiocarbon dates available for this site. The Mesolithic lithic assemblage consists predominantly of endscrapers and flake implements, although with a lesser laminar flake component compared to other sites in the region (Mihailović 1996, 2009). Along with these, trapeze and geometric implements were also recovered (Mihailović 1996, 2009). Many of the lithic artifacts from Medena Stijena are manufactured from low-quality raw materials (Mihailović 2009). The faunal remains from the Mesolithic layer could not be distinguished from those deriving from later occupations. However, it is likely that a number of land snail shell originate in this layer (Mihailović 2009; Dimitrijević 1996).

Odmut

Situated in the Plužine municipality of Northwestern Montenegro, the cave sits above the confluence of the Vrbnica and Piva rivers (Borić et al. 2021). The cave was occupied from the Mesolithic to the Bronze age (Cristiani and Borić 2016). Mijanović et al. 2024). The Mesolithic deposits contain layers from the Early (10.1–8.7 ka BP) and Late (8.7–7.2 ka BP) periods (Mijanović et al. 2024). The tool types recovered at Odmut show Tardigravettian and Castelnovian affinities and include endscrapers, irregular scrapers, retouched blades, perforators, trapezes and microretouched bladelets, which present some technological continuity with the Neolithic (Kozłowski et al. 1994; Cristiani and Borić 2016). A number of perforated osseous harpoon points were also discovered in the cave (Cristiani and Borić 2016). Cristiani and Borić (2016) interpret these tools as being used as detachable-head harpoons, perhaps as a means to exploit aquatic resources. The kind of drilling technology used to create the perforations in the harpoon points was not present in the Adriatic before the late-9th millennium BP, around the time that the earliest agricultural communities are documented (Cristiani and Borić 2016). Cristiani and Borić (2016) hypothesize that the spread of this perforated harpoon technology is linked with the spread of agriculture, as indigenous hunter-gatherer communities adapted this technology from nearby Neolithic communities.

The Mesolithic faunal assemblages from Odmut consist primarily of ungulate species. During the early Mesolithic, ibex is the most represented ungulate (58.0%), followed by red deer (20.5%), wild boar (3.8%), and chamois (3.2%) (Borić et al. 2019:477-481). Martens (4.9%) are also relatively frequent in the Early Mesolithic assemblage (Cristiani and Borić 2016; Borić et al. 2019). The composition of the faunal assemblage from the later Mesolithic assemblage is similar; ibex is again the most frequently represented species (59.5%), followed by red deer (14.1%) (Cristiani and Borić 2016; Borić et al. 2019). Chamois represents 10.2%, wild boar 2.5%, and martens 9.3% of the identified specimens in the subsequent level (Cristiani and Borić 2016; Borić et al. 2019). Indeterminate fish and bird remains are also common in the Mesolithic layers (Cristiani and Borić 2016).

Seocka Pećina

Located in Southeastern Montenegro near Skadar lake, Seocka Pećina is a relatively small cave situated on a low peninsula surrounded by the Crnojevića river (Mihailović et al. 2014). The cave contains materials attributed to the Mesolithic and Bronze Age. Despite its small size, Seocka Pećina is important because it is the only documented Mesolithic site in the Central Balkans located in a lacustrine environment (Živaljević et al. 2020). Radiocarbon dates indicate that it was inhabited during the Mesolithic around 10.7–9.0 ka BP (Gazivoda et al. 2015; Živaljević et al. 2020). The terrestrial fauna is dominated by red deer, roe deer, chamois, wild boar, beaver, and badger, with some of these remains bearing evidence of butchery (Živaljević et al. 2020).

The faunal assemblage also contains the remains of various fish, notably cyprinid and salmonid species (Živaljević et al. 2020).

Vruća Pećina

Vruća Pećina is located in Southeastern Montenegro between the villages of Bioče and Ubjl in the municipality of Podgorica. The site is relatively small, with deposits dating to the Mesolithic and Neolithic. The material from the Mesolithic layer includes shells, lithics, pottery, and a small assemblage of faunal remains (Mijanović et al. 2024). The lithic assemblages bear some traits associated with the Castelnovian tradition but lack the characteristic microburins (Borić et al. 2021). Radiocarbon dates indicate that the Mesolithic assemblages were accumulated ca. 9.3–7.6 ka BP (Borić et al. 2021). Red deer, roe deer, and ibex are the most common species, with a smaller proportion of fish and pond tortoise (*Emys orbicularis*) (Borić et al. 2019).

Vrbička Cave

Located approximately 18 km from Nikšić, the cave was first identified in 2010 (Mijanović et al. 2024) with formal excavations beginning in 2012 and continuing to the present. The archaeological deposits of the cave range from the Upper Paleolithic to the Bronze age (Borić et al. 2019). Radiocarbon dates obtained from Mesolithic material suggests that the site was occupied ca. 9.0–8.6 ka BP (Borić et al. 2019; Borić et al. 2021). The materials recovered from the Mesolithic layer include chipped stone tools and a bead made from the pharyngeal tooth of a carp (Borić et al. 2019). The faunal assemblage includes red deer, roe deer, chamois, wild boar, and ibex (Mijanović et al. 2024; Borić et al. 2019).

2.4 Crvena Stijena

Crvena Stijena, the site that is the focus of this thesis, is a large rock shelter in Western Montenegro near the village of Petrovići (Ćulafić 2017a). The site is situated approximately 700m a. s. l., and approximately 300m above the Lake Bileća (formerly the Trebišnjica river) reservoir that forms the border between Montenegro and Bosnia and Herzegovina. The rockshelter faces the Southwest, with an approximately 25m opening which extends 15–25m into the cliff face (Baković et al. 2009). The limestone that forms the cliff is stained red from iron oxides and it is this red color that gave the rock shelter its name. Crvena Stijena has a deep stratigraphic sequence of some 18m+ (Baković et al. 2009). This exceptional stratigraphy contains a long sequence dating from the Middle Paleolithic to the Early Bronze Age (Basler 1975; Whallon 2017a), making Crvena Stijena one of the richest and most important prehistoric sites in Europe. The site was initially discovered and excavated by archaeologists in the 1950s-60s (Basler 1975). These early excavations resulted in a deeply excavated sondage along the back wall of the rockshelter, where most finds were recorded. In order to reach the deeper Paleolithic deposits, much of the Mesolithic and Upper Paleolithic deposits were removed during these initial excavations.

Relatively little data have been published regarding the Later Prehistoric deposits at the rockshelter. The Bronze age (Layer I) material includes an iron knife and ceramic material (Baković et al. 2009; Borovinić et al. 2017). The decorated handles of the ceramic vessels are stylistically similar to finds from other contemporary Bronze Age sites in Montenegro (Benac 1975; Baković et al. 2009; Borovinić et al. 2017). Several paired postholes and pits, perhaps used for storage, were also uncovered in this layer (Baković et al. 2009; Borovinić et al. 2017).

The Neolithic assemblages span from the Early (Layer III) to the Middle Neolithic (Layer II). The material assemblages from these strata contain several diagnostic ceramic sherds, lithic tools and debris, bone tools, and faunal remains (Borovinić et al. 2017; Vušović-Lučić et al. 2017). The faunal assemblages from Layer III consist primarily of red deer, with some wild boar, chamois, aurochs, lynx, and wildcat (Borovinić et al. 2017). No domestic taxa were identified in this layer, suggesting that hunting was the primary economic activity of the people that occupied the site during this period (Borovinić et al. 2017). In Layer II, red deer and wild boar are the most frequently represented species, along with chamois, aurochs, fox, and wolf (Borovinić et al. 2017). Domestic cattle and sheep remains have also been identified in this assemblage (Borovinić et al. 2017). Ćulafić (2017) reported several species of terrestrial and marine mollusks in the Neolithic layers. Several fireplaces, hearth features, and ash lenses were identified in the two layers (Borovinić et al. 2017; Vušović-Lučić et al. 2017). The characteristic designs found on the ceramic sherds have been associated with the Impresso ware and Danilo ware technocomplexes (Benac 1975; Baković et al. 2009; Borovinić et al. 2017). While the lithic assemblages from the Early Neolithic deposits show technological continuity with the preceding Mesolithic, the Middle Neolithic assemblage breaks this continuity (Borovinić et al. 2017) There is somewhat more information regarding the Mesolithic deposits (Layer IV) at Crvena Stijena. These deposits are discussed in detail further below.

From the early excavations, limited information is available regarding the Upper Paleolithic material deposits, as these deposits (Levels VIII–V) were largely removed in the early excavations. During these excavations, faunal remains were rarely kept, unlike the lithic artifacts which were largely retained (Mihailović 2009; Mihailović et al. 2017). The available literature suggests that the assemblages contained a variety of taxa, including cervids, aurochs/bison, ibex, wild boar, marmot, and hare (Mihailović 2009). The artifacts from these levels were ascribed to a transitional Early/Late Epigravettian technocomplex (Level IX) and to a Late Epigravettian technocomplex (Level VIII–V) (Mihailović and Mihailović 2007). From the excavations in the early 2000's, only a limited section of the remaining deposits could be ascribed to the Upper Paleolithic (Mihailović et al. 2017). One of these layers—layer X—has been radiocarbon-dated between 28.0/28.9–13.6 ka BP (Mercier et al. 2017).

The lithic assemblages from Layer X have been attributed to the Late Gravettian/Early Epigravettian (Mihailović and Mihailović 2007). Immediately below Layer X is a thick layer of tephra derived from the Y5 Campanian Ignimbrite eruption (Brunnacker 1975; Morley 2007; Morley and Woodward 2011). The material culture from this layer (Layer XI) indicates a mix of both Middle and Upper Paleolithic technocomplexes (Mihailović et al. 2017). The faunal assemblage from layer X mostly consists of red deer and ibex, along with chamois, roe deer, panther, leporids, and marmots (Morin and Soulier 2017). Interestingly, the proportion of small game (leporids and marmots) is appreciable in the assemblage, although no evidence of human intervention has been identified on the specimens (Morin and Soulier 2017). The faunal evidence from fauna in Layer X suggests that the site was occupied during the late spring/summer (Morin and Soulier 2017).

Crvena Stijena is perhaps best-known for its rich Middle Paleolithic deposits, with dates ranging from ca. 40.0–78.3 ka BP for layers XI–XXIV (Morley et al. 2017; Mercier et al. 2017). From this sequence, a wealth of information regarding paleoenvironment and Neanderthal lifeways—including their subsistence strategies and technologies—has been generated (e.g., Mihailović and Whallon 2017; Whallon 2017; Bradák et al. 2021; Monnier et al. 2022; Jambrina-Enríquez et al. 2022). In the latest Middle Paleolithic layers (XII–XIV), artifacts characteristic of both the Mousterian and Uluzzian technocomplexes have been identified (Mihailović and Whallon 2017; Monnier and Tostevin 2023). Several bone retouchers are also found in these upper layers (Morin and Soulier 2017). The lithic artifacts recovered in layers XV–XVIII show affinities with the Micromousterian technocomplex (Monnier and Tostevin 2023). In layers XX–XXII, the lithic artifacts are associated with the Charentian Mousterian and contain artifact types such as transversal scrapers and sidescrapers (Mihailović and Whallon 2017; Monnier and Tostevin 2023). The lowest Middle Paleolithic deposits include tools produced using the Levallois and discoidal methods (Mihailović et al. 2017; Mihailović and Whallon 2017; Monnier and Tostevin 2023).

The faunal assemblages from the Middle Paleolithic layers are all dominated by red deer (Morin and Soulier 2017). In most layers, caprine species are the second most abundant taxa, except for levels XXVI and XXIV, in which large bovids, horses, and rhinoceros are more frequent (Morin and Soulier 2017). Fallow deer are also relatively common, particularly in the upper layers (Morin and Soulier 2017). Carnivore remains and associated taphonomic modifications on specimens are minimal throughout the layers (Morin and Soulier 2017). Small taxa, including tortoises, leporids, and marmots, are present in relatively small proportions throughout the assemblages (Morin and Soulier 2017). Tortoise remains have been identified only in the lowest layer, whereas marmot and leporids are present throughout the Middle Paleolithic sequence (Morin and Soulier 2017). Interestingly, Morin and Soulier's (2017) study found no evidence of significant faunal turnovers across layers X–XXIV, which suggest environmental conditions were relatively stable in the region (Morin and Soulier 2017).

LAYERS (adapted from Basler 1975)	CULTURAL ATTRIBUTIONS/LAYERS DEFINED IN RECENT EXCAVATIONS	AGE (KA BP)
I	Bronze Age	
II	Middle Neolithic (Danilo)	8.4
III	Early Neolithic (Impresso)	
IV	Mesolithic	8.5–10.0
V	*Absent (Late Epigravettian)*	
VI	*Absent (Late Epigravettian)*	11.2
VII	*Absent (Late Epigravettian)*	
VIII	*Absent (Late Epigravettian)*	11.0–13.6
IX	*Absent (Early/Late Epigravettian)*	

LAYERS (adapted from Basler 1975)	CULTURAL ATTRIBUTIONS/LAYERS DEFINED IN RECENT EXCAVATIONS	AGE (KA BP)
X	Late Gravettian/Early Epigravettian	*13.6*–28.0/28.9
XI	Y5 Tephra	39.0
XII (top)	M1 *Uluzzian*	
XII	M2c/M2c1	47.7–48.0
XIII	M3	49.3
XIV	M4	
XV	M5	
XVI	*Absent*	
XVII	*M5 bottom*	
XVIII–XVX	VXIII-XIX	48.3–65.6*
XX	XX	
XXI–XXIII	XXI-XXIII	
XXIV	XXIV	52.2–78.3*

Table 2.1: The stratigraphic sequence at Crvena Stijena (adapted from Morin and Soulier 2017). * Indicates TL/ESR dates. Dates are from Baković et al. (2009), Morley and Woodward (2011), Mercier et al. (2017).

2.4.1 Crvena Stijena Mesolithic Assemblages

The Mesolithic layers uncovered in the early excavations of Crvena Stijena were the first to be discovered in Montenegro (Basler 1975). More recent excavations renewed in 2004 led by a collaborative team of international researchers (Whallon 2017). Although much of the Mesolithic material had been removed during the previous excavations, a remaining pocket of intact Mesolithic layers were discovered and excavated near the opening of the rock shelter (Baković et al. 2009). Beneath a layer of loose, powdery grey sediment with archaeological materials of mixed contexts, several intact, in situ Mesolithic layers were uncovered (Baković et al. 2009). These layers contained several hearth features, ash lenses, as well as a sizeable sample of Mesolithic artifacts (Baković et al. 2009).

Figure 2.8: View of Crvena Stijena, entrance to the rockshelter is indicated with an arrow.

The uppermost layer, (GS 1) is made up of a brown sediment with scree, along with a few artifacts from mixed archaeological contexts. In this layer two 7–10cm postholes, and a layer of ash were uncovered at the base of the level. (Baković et al.

2009). According to Baković et al. (2009) and D. Mihailović (personal comm.), this layer was significantly disturbed. The underlying layer (GS 2) is characterized by a thick layer of grey sediment with scree and several ash/charcoal lenses (Baković et al. 2009). Near the base of GS 2, an approximately 70cm-wide hearth containing ash and charcoal lenses was discovered surrounded by other areas of burned earth and ash (Baković et al. 2009). Many bones, snail shells, and lithics were collected in this layer (Baković et al. 2009). Below GS 2, a relatively thin, archaeologically sterile layer (GS 3) of loose scree was removed (Baković et al. 2009). Underlying this sterile layer, GS 4— the lowermost Mesolithic layer— was described as a dark grey to brown sediment with scree of larger size, laid directly over a level of Pleistocene material (Baković et al. 2009). Small amounts of charcoal, ash, shells, lithic material, and bones were recovered in this layer (Baković et al. 2009). The GS 2 deposits are dated to ca. 8.5–8.4 cal ka BP while the GS 4 deposits were dated to ca. 10.0–9.7 cal ka BP (Baković et al. 2009; Mercier et al. 2017).

Much of the research regarding the Mesolithic assemblages from Crvena Stijena has focused on the lithic and bone tool assemblages (Mihailović 2009; Mihailović et al. 2017). In the contact zone between GS 1 and GS 2, two cores, one blade/bladelet, one flake, and two tools were recovered (Baković et al. 2009). The majority of the artifacts recovered during the recent excavations were concentrated in GS 2, near the hearth feature (Baković et al. 2009). In this layer, cores, blades/bladelets, flakes, tools, and one microburin were recovered and attributed to the Castelnovian technocomplex (Baković et al. 2009). GS 4 produced a smaller assemblage of lithic artifacts (Baković et al. 2009). A large assemblage of Epigravettian and Castelnovian lithic and osseous artifacts were recovered from surface and profile cleanings of the excavation area, which likely derive from the Mesolithic or Neolithic layers (Baković et al. 2009; Mihailović 2009, Mihailović et al. 2017). The Castelnovian artifacts recovered at Crvena Stijena are very similar to those found at Odmut cave (Mihailović 2009).

The species list from the 1950-60's excavations include brown hare (*Lepus europaeus*), fox (*Vulpes vulpes crucigera*), badger (*Meles meles*), wild cat (*Felis silvestris*), wild boar, red deer, roe deer, and aurochs (Malez 1975; Mihailović 2009). Dimitrijević (2017) reports on the 2005–2006 assemblages as consisting of abundant mammalian remains, molluscan shells, and a small amount of microfaunal remains (Dimitrijević 2017). Red deer is the most frequently represented animal in all assemblages, followed by wild boar and roe deer (Dimitrijević 2017) (Table 2.2).

TAXA	%NISP GS 2	%NISP GS 4
Cervus elaphus	50.3	31.8
Sus scrofa	12.1	5.0
Capreolus capreolus	18.6	2.3
Ibex ibex	0.0	4.5
Lepus europaeus	11.1	22.7
Lynx lynx	1.0	4.5
Felis silvestris	1.0	0.0
Meles meles	0.0	2.3
Martes martes	0.5	2.3
Martes sp.	0.5	0.0
Vulpes vulpes	4.0	4.5
Ursus arctos	1.0	0.0

Table 2.2: %NISP counts adapted from Dimitrijević (2017).

According to Dimitrijević (2017), red deer comprises 50.3% of the identified fauna in GS 2, followed by roe deer (18.6%), wild boar (12.1%), brown hare (11.1%), and fox (4.0%). Other carnivorous taxa (brown bear, martens, wild cat, lynx) comprise the rest of the assemblage but are never represented by more than 1.0% of the NISP. Red deer are still the most common taxa identified in GS 4, but drop to 31.8% of the identified fauna in the assemblage. Roe deer similarly drops in representation to just 2.3% of the identified fauna in GS 4. Conversely, wild boar and brown hare are better represented in GS 4, at 25.0% and 22.7%, respectively. Notably, Dimitrijević (2017) identifies ibex (4.5%) in the GS 4 assemblage, a species which is not documented in GS 2. An interesting feature noted by Dimitrijević (2017) is the high frequency of ungulate first and second phalanges that have been fractured, a pattern which applies to even the smallest ungulates. This pattern was interpreted as indicative of intensive marrow extraction (Dimitrijević 2017:295).

The malacological assemblages consist of mostly local terrestrial snail species; *Medora contracta*, *Helix secernenda*, *Aegopis acies*, and *Aegopis verticillus* (Ćulafić 2017b). A smaller number of marine snails and shellfish were also recovered in the Mesolithic layers, including *Columbella rustica*, and *Mytilus* sp. (Ćulafić 2017b). The terrestrial shells may represent natural accumulation, but the marine shells were transported to Crvena Stijena by its human occupants (Ćulafić 2017b). Because Ćulafić (2017b) provides NISP counts for all layers combined, it is unclear exactly how many of these specimens were found in the Mesolithic layers. For this reason, it is difficult to draw conclusions on the Mesolithic from these data.

As Crvena Stijena is one of only a few sites in the Balkans containing layers dating to the Early and Late Mesolithic (Mihailović 2017), it is possible to assess subsistence changes during the Early Holocene using these assemblages. The results of the current study, which expand upon the work conducted by Dimitrijević (2017), will be presented in detail in chapters four and five.

Chapter 3 Human Behavioral Ecology and Foraging Theory

3.1 Human Behavioral Ecology

Human Behavioral Ecology (HBE) is a subset of Evolutionary Ecology that studies the fitness-related behavioral trade-offs that humans face under specific environmental conditions (Stephens and Krebs 1986; Bird and O'Connell 2006, 2012). In archaeology, HBE models have been used to test hypotheses regarding past human behavior (Winterhalder and Smith 2000). These models are based on the concept of optimization analysis (Smith 1978) and draw upon Game Theory (Smith 1982). From its inception, HBE has been used primarily to understand past subsistence strategies, although other aspects (e.g., human life history, food sharing, thermoregulation) are increasingly being examined as well (Mace 2000; Winterhalder and Smith 2000; Bird and O'Connell 2006; Nettle et al. 2013; Pelton et al. 2024). In this study, HBE-based models, particularly those drawn from Foraging Theory, will be used to interpret diet breadth and other decisions regarding faunal exploitation.

3.2 Foraging Theory

The theoretical basis of many Foraging Theory (FT) models is the assumption that maximizing the rate of nutrient acquisition enhances fitness, and that a forager should act in a way that optimizes nutrient acquisition (Stephens and Krebs 1986; Bird and O'Connell 2006). FT models address several questions regarding acquisition, time allocation, and spatial organization of foraging resources and their impacts on resource selection and use by foragers (Bird and O'Connell 2012). Foraging Theory operates in an economy of energy (typically measured in calories), with the forager making decisions based on the energetic costs of pursuing certain resources and the energetic gain of procuring those resources; the goal being to maximize caloric gain while minimizing energetic trade-offs. These decisions include what resources to forage for at the expense of others, where to forage for these resources, how much time to spend foraging, and how to process foraged resources (Bird and O'Connell 2012).

A resource in foraging theory may be defined as a species of plant or animal, or a particular subset of that species—referred to as prey types in this approach. Given the limitations imposed by the archaeological record, which obscures detailed assessments of intra-specific variation, prey types are primarily treated in this study as corresponding to animal species. The economic returns of each prey type are primarily defined based on values published by Morin et al. (2022) and other ethnographic accounts. Several FT models are used to assess the dietary breadth and the overall patterns of intensification at the Crvena Stijena, each of which are discussed below.

The Prey Choice Model

The Prey Choice Model (PCM), also known as the 'optimal diet' or 'diet breadth' model, addresses the issue of prey selection (MacArthur and Pianka 1966). Because prey types often differ in their energetic returns and patterns of distribution, a forager can 'rank' prey types based on a cost-benefit analysis. Higher-ranked prey types are those that will provide the forager with the highest energy returns per unit of time handling that prey type. Based on this, assumptions can be made regarding which prey types will be pursued upon encounter, and which should be ignored in favor of higher-ranked prey types (MacArthur and Pianka 1966). The PCM assumes that prey types are encountered randomly, and that a forager will encounter them individually and sequentially. In the model, a forager should always pursue high-ranked prey upon encounter and should ignore lower-ranked prey until encounters with higher-ranked prey decrease. Then, lower-ranked prey types should be pursued in descending rank order until their energetic return is lower than the return for search and handling all higher-ranked prey types (MacArthur and Pianka 1966; Bird and O'Connell 2006, 2012).

The Patch Choice Model

When prey is not encountered randomly relative to their abundance but are aggregated, the forager must decide which patch to exploit and for how long to forage in the patch before moving to another (MacArthur and Pianka 1986; Bird and O'Connell 2006). A patch may be defined as something as small in scale as a single bone or as large as an entire biome (Grayson 1989; Broughton 1999; Burger et al. 2005). The Patch Choice Model (PaCM) is similar to the PCM, as the forager is expected to exploit higher-ranked patches before lower-ranked patches, taking travel costs into account (MacArthur and Pianka 1966; Stephens and Krebs1986; Bird and O'Connell 2012). In the PaCM, travel costs have an impact on forager decision making, as a lower-ranked patch may be exploited simply because of costs associated with travel to a higher ranked patch.

Because animals are often used as bioindicators when reconstructing past landscapes and environments (Lyman 2017; Croft et a. 2018), understanding their ecology can be useful in estimating the kinds of patches that past foragers were exploiting. Red deer, roe deer, and wild boar are among the most frequently identified taxa in regional faunal assemblages. The red deer is generally considered an ecotone species, inhabiting open woodlands and the zone that mark a transition with grasslands (Mitchell et al. 1977; Geist 1998; Schaefer et al. 2008). However, red deer are highly adaptable and are found in a wide variety of landscapes, including heavily forested areas, as well as alpine meadows and slopes at high altitudes (Apollonio et al. 2010; Anderwald et al. 2016; Niedziałkowska et al. 2021). Another common cervid species in archaeological assemblages, roe deer, prefer more heavily forested environments (Mancinelli et al. 2015) but may also be encountered in mixed forest-open grassland environments (Danilkin and Hewison 1996). Similar to red deer, roe deer are also quite ecologically flexible and can inhabit a wide variety of environments, including those at high altitudes (Jepsen and Topping 2004). Wild boars prefer more heavily forested lowlands where they can access energy rich foods like acorns or other tree nuts and shelter from predation (Massei and Genov 2004; Jánoska et al. 2018). In the last several decades, increasing wild boar populations have colonized mountainous habitats and are frequently found feeding in open agricultural land (Baubet et al. 2004; Colomer et al. 2024). While these changes in wild boar habitat use are likely explained by several factors including climate change and changes in agricultural practices (Massei and Genov 2004), they do point to the plasticity of wild boar habitat use—making it possible that open or montane habitats were occupied by the species in the past.

Ibex, one of the most common ungulates found in Mesolithic assemblages in Montenegro, is a montane species, usually living at altitudes between 1,600 – 3,200 m. a.

s. l. today, although ibex remains were found around 300 m. a. s. l. during the Pleistocene (Parrini et al. 2009). Ibex usually avoid woodland areas, preferring open alpine meadows and slopes (Pedrotti 1995; Parrini et al. 2009). The chamois, present only in the Upper Paleolithic assemblages at Crvena Stijena, is also a primarily montane species, but are known to spend time in forested areas, particularly during the winter months (Ballo 2010; Corlatti et al. 2022). Baumann et al. (2005) showed that the chamois occupied both alpine meadows and forest during the Pleistocene. Today, populations in Croatia are reported around 100 – 300 m. a. s. l. (Corlatti et al. 2022). Miracle and Sturdy (1991) suggest that the chamois are well-adapted to the rugged, holokarst landscape and should not always be treated as an alpine species. Marmots, also common in the Upper Paleolithic assemblage, are also mountain dwelling species—preferring open, rocky alpine meadows and slopes (Allainé et al. 1994; Armitage 2000) at similar altitudes to the chamois (Herrero et al. 1994). Leporids, particularly brown hare, tend to prefer temperate savanna or grassland environments, and generally avoid dense woodlands and high altitudes (Tapper 1987; Bock 2020). However, when population densities become high at lower altitudes, brown hares may move to higher altitudes (up to 2000 m.) (Flux 1990). Another hare species, the mountain hare (*Lepus timidus)*, a species present throughout Europe during the Late Pleistocene and the present, tends to occupy dense forests and higher altitudes (Angerbjörn and Flux 1995; Thulin 2003).

Marginal Value Theorem

Marginal Value Theorem (MVT) addresses the issue of time allocation in patches. Once a forager has selected a patch, the MVT can be used to estimate how long a forager will spend exploiting that patch based on the relationship between the marginal energetic gain from the patch compared to the overall foraging return rate, considering that continued within-patch resource exploitation tends to yield decelerated gains (Charnov 1976; Burger et al. 2005). Similar to the PaCM, the MVT can be applied at different scales, from entire biomes to individual skeletal elements. When patches are examined at the scale of anatomical units, the MVT can be applied to carcass processing by establishing potential energy gains from different strategies of carcass exploitation (Burger et al. 2005). Because anatomical units vary in their overall energetic profitability per unit of time, they can be ranked (Jones and Metcalfe 1988; Monahan 1998; Burger et al. 2005). According to Burger et al. (2005), if foragers are less frequently gaining access to prey, they can attempt to maximize their resource gain by spending more time processing carcasses; for instance, by increasing their exploitation of lower-ranked skeletal elements.

3.3 Prey Ranking

Prey body size has often been correlated with prey rank, the rationale being that a larger body size provides higher energetic returns (Broughton 1994a, 1994b; Broughton et al. 2011). However, body size is not the only variable influencing prey rank. Mass collection of small species, especially fish and invertebrates, can generate high net returns (Madsen and Schmitt 1998; Ugan 2005). Mobility may also impact prey rank, as highly mobile prey types may result in lower returns after pursuit and handling costs are factored in (Stiner and Munro 2002; Bird et al. 2009, 2012; Morin et al. 2022).

Morin et al. (2022) calculated estimated return rates for over 300 game species and found that prey body size is a relatively poor predictor of on-encounter return rates, except for glires (lagomorphs and rodents). Thus, Morin et al. (2022) find that pursuit costs are often a critical component determining prey profitability than prey size. In order to assess pursuit costs and prey rank more accurately, one must account for the mode of procurement, technology, and prey behavior (Morin et al. 2022). Additionally, Morin et al. (2022) caution against simply assigning a rank to a species, as this ignores the fact that most species can be encountered in a variety of conditions (i.e., variable body fat composition depending on season, whether the animal is encountered in a herd or not) and pursued by a number of different methods (i.e., with different technologies, mass or solo collecting)—contexts which may significantly shift the rank of a particular taxon (Morin et al. 2022). Morin and colleagues' results support and further explain some of the findings reported by Ugan (2005) who likewise found that body size is not always a reliable proxy for return rates. Small taxa, particularly those that can be mass collected and require minimal processing, can result in very high return rates (Ugan 2005).

Many of the prey rankings used in this study have been adapted from data presented in Morin et al. (2022, 2024), De Vynck et al. (2016), and Ugan (2005). The lowest estimated return rates were used to account for less efficient hunting and fishing technology of prehistoric hunter gatherers compared to modern or historical hunters. Proxy taxa were used to estimate return rates for Mesolithic species that lack published estimates (Table 3.1).

TAXA	COMMON NAME	PROXY	ESTIMATED RETURNS	ESTIMATED RANK	LIVE WEIGHT (KG)
Bison sp.	Bison	*Bison bison* surround (Morin et al. 2024)	16,770	High	700.0
Bos primigenius	Aurochs	*Bison bison* surround (Morin et al. 2024)	16,770	High	700.0
Megaloceros giganteus	Giant deer	*Alces alces* early spring gun (Morin et al. 2022)	26,532	High	485.0
Equus sp.	Horse	*Equus quagga* (Morin et al. 2022)	14,706	High	360.0
Ursus arctos	Brown bear			High	230.0
Cervus elaphus	Red deer	*Cervus canadensis* pike gun (Morin et al. 2022)	23,532	High	200.0
Sus scrofa	Wild boar	*Sus scrofa* pound (Morin et al. 2024)	6,335	Mid	87.5
Capra ibex	Alpine ibex	*Ovis canadensis* (Morin et al. 2022)	17,160	High	74.5
Dama dama	Fallow deer	*Odocoileus virginian*	12,096	High	65.0

TAXA	COMMON NAME	PROXY	ESTIMATED RETURNS	ESTIMATED RANK	LIVE WEIGHT (KG)
		us (Morin et al. 2022)			
Rupicapra rupicapra	Chamois			Mid-Low	52.5
Capreolus capreolus	Roe deer			Mid-Low	25.0
Canis lupus familiaris	Dog			Mid-High	25.0
Lynx lynx	Lynx			Low	25.5
Vulpes vulpes	Red fox			Low	14.0
Meles meles	Badger			Low	12.0
Lepus europaeus	Brown hare	*Lepus californicus* drive low/drive (Morin et al. 2022)	415/1385	Low	4.0
Marmota marmota	Marmot			Mid	3.0
Marten sp.	Marten			Low	1.5
Huso huso	Beluga sturgeon			High	260.0
Acipenser gueldenstaedtii	Russian sturgeon			High	115.0
Cyprinus carpio	Common carp			Mid-Low	15.0 (Borić and Dimitrijević 2006:55)
Silurus glanis	Wels catfish			High	50.0-120.0 (Borić and Dimitrijević 2006:55)
Esox lucius	Pike	Freshwater fish; mixed (Ugan 2005)	3,710	Low	8.0
Scomber japonicus	Chub mackerel	Saltwater fish;	6,065	Mid	1.0

TAXA	COMMON NAME	PROXY	ESTIMATED RETURNS	ESTIMATED RANK	LIVE WEIGHT (KG)
		mixed (Ugan 2005)			
Patella caerulea	Mediterranean limpet	*Scutellastra longicosta* (De Vynck et al. 2016)	2,943	Low	<1.0
Patella rustica	Rustic limpet	*Scutellastra longicosta* (De Vynck et al. 2016)	2,943	Low	<1.0
Phorcus turbinatus	Turbinate monodont	*Oxystele sinensis* (De Vynck et al. 2016)	3,359	Low	<1.0
Helix secernenda	--			Low	<1.0
Aegopis sp.	Glass snails			Low	<1.0

Table 3.1: Late Pleistocene and Early Holocene taxa documented at Crvena Stijena and other sites in the Central Balkans and their estimated prey rank.

Proxies for all ungulate species were assigned based on similar body size, taxonomy, ecology, and behavior. For example, *Alces alces* (Moose or Elk) is assigned as the proxy for giant deer due to its comparable size and taxonomic similarities (Breda 2005). Similarly, bison is assigned as the proxy for aurochs for similar reasons, although ecological differences between the taxa may mean that return rates differed appreciably. The zebra is inferred to be a valid proxy for the horse, as these taxa are closely related and behaviorally and ecologically similar (Rubenstein 1986; King et al. 2016). Wapiti (*Cervus canadensis*) and red deer are taxonomically and behaviorally very similar and were even classified as the same species until relatively recently (Polziehn and Strobeck 2002). Bighorn sheep (*Ovis canadensis*) is used as the proxy for ibex, as the two species inhabit similar biomes, are somewhat gregarious, and are roughly comparable in size. Although whitetail deer (*Odocoileus virginianus*) are somewhat larger than fallow deer, they are used as the proxy taxa due to their behavioral and ecological similarity. The lowest return rate for whitetail deer is used to attempt to control for the differences in size.

In this sample, ungulates tend to produce the highest returns, with the possible exceptions of chamois and roe deer. The large body size of many of these animals can provide foragers with abundant edible tissues and other valuable materials. Seasonal behavioral differences may make some differences in success rates when hunting such prey. For example, during the rut, it may be easier to capture cervid species. During this time cervids, bucks especially, become more active and less cautious; making them more vulnerable to predation (Wilton 1992; Richard et al. 2008; Pépin et al. 2009; Csányi et al. 2022). Cervids, along with many other taxa, seasonally map on to resource-rich patches within the environment, which make them more predictable in their movement (Wilmshurst et al. 1995; Fonseca 2007; Guadry et al. 2015; Siedel and Boyce 2015; Couriot et al. 2018; Kim et al. 2019; Svoboda et al. 2019). Additionally, many species will seasonally migrate between lower and higher elevations, which also increases predictability (Mysterud 1999; Gaudry et al. 2015; Sakuragi et al. 2019). Hunters that are familiar with these behaviors might have used this knowledge to reduce their pursuit costs.

In addition to understanding the ecology of their prey, cooperative social behaviors can also impact success rates for hunting large ungulates. While individual success at hunting large game is low, sharing the resources gleaned from successful hunts can make big-game hunting more rewarding than hunting smaller-bodied taxa (Lupo and Schmitt 2016). Cooperative hunting can increase the success rates of capturing large game, particularly ungulate species due to their sociality and other behaviors (Morin et al. 2024). Likewise, efficient hunting technology can result in higher success rates (Yost and Kelley 1983; Morin et al. 2022, 2024), particularly while hunting ungulates. As suggested by Larsson (1978), Castelnovian technology could have increased the success of Mesolithic foragers hunting in dense forests. Given these observations, it is likely that many of the ungulate species available during the Mesolithic represented high-ranked prey.

While large ungulates may have been most highly valued as food resources, some smaller prey types can be more reliably captured, which increase their caloric returns. For this reason, some small prey types may provide higher returns than anticipated (Lupo and Schmitt 2016). Other species—particularly medium and small carnivore and leporids—could have been valuable for their fur or other raw materials, not necessarily for their meat or other edible tissues. Often, these animals provide relatively low caloric returns, even when procured during coordinated game drives (Morin et al. 2020; Pelton et al. 2024).

The black-tailed jackrabbit (*Lepus californicus*) was selected as the proxy for the leporid species identified in the archaeological assemblages due to its taxonomic, behavioral, and body size similarities to *Lepus* sp. in Europe. Traditionally, small, fast prey like leporids have been assumed to represent low-ranked prey types due to the difficulty of capturing them and the relatively low yields of edible tissue provided by individuals, even when they are mass collected (Morin et al. 2020). Mass collection strategies are best employed when these animals are living at high densities in open areas. Under such conditions, returns from mass-collections of leporids can compare with those generated from hunting lower-ranked ungulates (Morin et al. 2020). However, the rugged terrain and dense forests that were present in the Central Balkans during the Holocene may have precluded mass-collection of these animals. Additionally, *Lepus* sp. tend to be solitary (MacDonald and Barrett 1993), which likely make mass capture more difficult. Therefore, the high-value of rabbit drives likely does not apply to this sample, and these taxa would likely represent a low-ranked resource for the foragers.

The marmots, while similar in size to the hare may represent a higher-ranked resource. Marmots are much slower than hares and rabbits and tend to have a higher body fat percentage (Morin 2012). Additionally, European marmots are known to live in extended family groups (Armitage 2000), which may have made them easier to capture *en masse*. These characteristics likely made marmots more highly ranked prey compared to leporids.

While many carnivores might have been marginal resources in terms of their nutritional utility, these animals possess pelts with dense, soft hairs that trap a layer of air near the skin surface, ideal characteristics for preventing heat loss even in cold conditions (Kitchener et al. 2018; Mota-Rojas et al. 2021). This feature might have made them an appealing prey type, particularly during the colder months when pelts are in their prime (Maurel et al. 1986; Hiller and Vantassel 2022). During the Mesolithic, these furbearing taxa could have included the red fox, hares, lynx, and various mustelids (marten, badger, otter). For example, martens are quite small and are most efficiently captured using specialized trapping technology, which can be quite laborious (Broch 2009). Thus, they likely do not offer much in terms of energy gain. It is possible that during the winter these animals would have been pursued more frequently to obtain their fur when at its peak density.

Hunting larger carnivores like brown bear may have provided high yields of meat and other edible tissues (Roll and Deaver 1978). Brown bears are also a species with a high percentage of body fat relative to other wild game species, particularly just before and in the early days of their hibernation period (Rigano et al. 2017; Ugarković et al. 2020). 'Bear grease', or rendered fat, was utilized by Indigenous North Americans in a number of ways, including in culinary applications, cosmetics, medicine, and the manufacture of various items (Battle 1922; Wallace 1949; Schaeffer 1966; Baker 2018). Obtaining this rich source of fat was often the primary goal of hunters, and bears were more likely to be pursued when at their peak fatness (Waselkov 2020 and references therein). Bear pelts were also considered a valuable resource (Bailey 1973). Despite these high potential gains, hunting these animals can be extremely dangerous, with the risks of pursuit outweighing the potential benefits of capturing such prey. The risks of hunting bear may be minimized during the winters when these animals are in a state of torpor in their dens (Waselkov 2020). When encountered in such conditions, hunters may have been more likely to pursue such large carnivores.

In ethnographic and historical records, dogs have served as companion animals, cooperative hunters, animals of spiritual or ritual significance, beasts of burden, and sometimes as food sources for cultures throughout the world. In this analysis, the value of dogs as a food source and as a contributor to more efficient capture of other food sources is assessed, with the recognition that the complex roles that dogs play in human societies likely means that this assessment is far from complete. Eating canids (dogs and dingoes) has been considered taboo by some Indigenous Australians (Meehan et al. 1999). Feral canids were eaten only during times of famine by some Indigenous Australians, and even then, the meat was not highly prized (Hamilton 1972; Tindale 1974). In groups living in what is today Russia (Nenets, Khanty, and Mansi) ethnographic reports show that the consumption of dog meat was rare and often restricted to periods of significant nutritional stress (Losey et al. 2018 and references therein). Additionally, dogs in some Indigenous American foraging societies were relied upon as food sources during times of starvation (Rowlandson 1682; Vimont 1898; Teit 1906; Allen 1920). For other North American Indigenous societies, dogs were more regularly consumed, particularly during feasts or other ritual events (Stewart and Finlayson 2000; Dorian 2012).

Dogs can be highly effective at hunting a variety of prey—large and small (Roberts 2017; Pacheco-Cobos and Winterhalder 2021; Koungoulos and Brumm 2024). Hunting high-ranked prey like large ungulates with dogs likely resulted in higher efficacy, as dogs could more easily locate and pursue the animals, although they can represent nuisance when hunting some species (Roberts 2017; Lupo 2017). Their utility as effective hunting companions may have meant that they were more valuable to foragers alive, and thus not often used as food sources. However, when necessary, their trusting behavior and the low costs of pursuit could make them appealing prey in the absence of other, more highly-ranked targets.

Traditionally thought of as a low-ranking resource, marine mollusks have been demonstrated to be important and highly valued resources for foragers, especially those with reduced mobility (Meehan 1982, 1983; Bird and Bliege Bird 1997, 2000; De Vynck et al. 2016). Shellfishing represents a more reliable resource base to foragers than other subsistence activities like hunting (Marlowe 2007). In addition to being reliable, shellfish can be mass-collected with little to no specialized technology, and provide important nutrients such as iodine and omega-3 fatty acids (Kyriacou 2017).

De Vynck et al. (2016) found that foraging for intertidal shellfish could result in relatively high return rates, but only for about one third of the days in a month when tidal and weather conditions facilitated the collection of such resources. Larger species made up the bulk of the forager's intake, while smaller species—like limpets and topshells—tended to be ignored, which suggests that these species were low-ranked resources (De Vynck et al. 2016). Duck's foot limpet (*Scutellastra longicosta*) and pink-lipped topshell (*Oxystele sinensis*) were selected as proxies for the marine shellfish found in assemblages in the Central Balkans based on their similar taxonomy and size. Because these species are found in South Africa, where tidal conditions are more variable than in the Adriatic, their value as a proxy is possibly limited. Thomas (2007) reports that efficient foraging of intertidal resources can only be accomplished during extremely low diurnal tides, as it is during these times that the shellfish are most accessible. The tidal fluctuations in the Adriatic are quite minimal, which would have limited the accessibility to these resources. This suggest that shellfish were likely low-ranked resources compared to those in other regions.

Perhaps less reliably encountered than marine molluscs, terrestrial snails are more randomly distributed throughout the landscapes. Similarly to shellfish, no specialized technology is needed to collect terrestrial snails, and they can be easily picked up while searching for other prey types. Given their very small size and their sparse distribution, it is likely that land snails represented low-ranked resources for the Mesolithic foragers.

When they were present in the region during their spawning migrations, anadromous sturgeons (*Huso huso* and *Acipenser gueldenstaedtii*) would have likely been high-ranked prey. Both the Russian and Beluga Sturgeon grow around 2-3m in length, weigh around 100 kg, with some Beluga weighing as much as 1000 kg (Bartosiewicz et al. 2008). The river conditions surrounding the sites in the Danube Gorges could have facilitated the capture of these species, as the current drives the fish in such a way that they can be directed into nets or weirs (Srejović 1972).

Sturgeon species are known to gather and spawn in hard-bottomed, fast-moving, shallow waters— sometimes as shallow as .5–5.5m (Peterson et al. 2007; Falahatkar and Shakoorian 2011; Kuhajda 2014; Baril et al. 2017). These shallow waters can act as a natural trap, making sturgeons vulnerable to human predation when they are in such locations (Needs-Howart 1996). Antonović (2006) and Živaljević (2013) propose that stone mallets recovered from Mesolithic sites in the region could have been used to stun fish trapped in such conditions. Clubbing or stunning sturgeon is well documented in the ethnographic record (Holzkamm and Waisberg 2014 and references therein); and Živaljević (2013) cites a similar technique being used in the Danube until the early 20th century. The gregarious nature of sturgeon spawns also means that a number of individuals could be captured at the same time, yielding copious amounts of meat, oil, and other valuable resources (Kroeber and Barret 1960).

Wels catfish can reach sizes comparable to sturgeon and are available year-round in the Danube (Kottelat and Freyhof 2007; Rees 2013). These fish could have been obtained using the same methods used to capture sturgeons and their presence in the river throughout the year could mean that foragers could reliably encounter these fish. While the construction and maintenance of weirs and nets may have been costly, it is clear that such technology could generate high returns when used to capture large fish like sturgeon and catfish. Harpoon and clubbing technology might have offered useful implements for capturing large fishes (Cristiani and Borić 2016; Antonović 2006; Živaljević 2013). While no preserved canoes, weirs, or netting has been recovered in Mesolithic archaeological assemblages in the Central Balkans, such technologies are documented in other contemporaneous communities throughout Europe (Andersen 1985, 1995; Kooijmans 1987; McQuade and O'Donnell 2007; Kozłowski 2009; Benjamin et al. 2011; Koivisto 2017) and were possibly used by foragers in the Balkans to obtain large fishes.

Chapter 4 Methodology

4.1 Taphonomy

In order to make inferences regarding subsistence, it is first necessary to evaluate the integrity of the assemblages and identify the agents responsible for their accumulation. Many anthropic and non-anthropic processes may alter faunal remains in the times prior to, during, and after their initial deposition, each with the potential to distort interpretations of subsistence at the site. Therefore, correctly identifying and understanding the taphonomic processes at Crvena Stijena is critical for any investigation of diet breadth.

4.1.1 Identifying Anthropic Modifications to Bone Surface

Humans exploit animal carcasses to obtain a variety of resources—meat, fat, marrow, sinew, hides, etc. (Lyman 1987). Fortunately for the archaeozoologist, these activities may leave identifiable traces on the surface of bones in the form of cutmarks, percussion notches, and burning, among other features. However, it is possible to confuse anthropic modifications with the results of natural processes such as trampling, carnivore ravaging, and chemical staining. Careful observations of the surface of each identified specimen from the Crvena Stijena assemblages were made under 30X/60X magnification to aid identifying whether modifications to the faunal remains were of anthropic origin.

Cutmarks

Cutmarks are an unambiguous marker of human action in an archaeological assemblage and are indicative of many different butchery goals such as skinning, disarticulation, and meat removal (Lyman 1994c). It can be difficult to differentiate cut marks from other taphonomic signatures; for example, trampling of faunal remains in abrasive sediments can leave traces on the surface of bone which appear similar to cutmarks (Behrensmeyer et al. 1986, Olsen and Shipman 1988, Fernández-Jalvo et al. 2022). One consideration which may be useful in identifying cutmarks is their location on the bone surface. Cutmarks may occur more frequently in certain areas, such as around epiphyses (Binford 2001, Domínguez-Rodrigo et al. 2009, Costamagno et al. 2019), where a forager needs to cut through tough tissues to dismember a carcass or harvest tendons and ligaments. However, cutmarks may also occur on long bone shaft surfaces in a non-predictable manner, meaning that the location of marks is not always a reliable signature (Soulier 2021).Orientation of marks may also aid in differentiating cutmarks from trampling marks, as experiments have shown that cutmarks are more frequently oriented perpendicular to the axis of the bone whereas trampling marks tend to be oriented randomly relative to the axis of the bone (Behrensmeyer et al. 1986; Olsen and Shipman 1988). While a longitudinal orientation may be helpful in differentiating between trampling marks and cutmarks, it may not always be reliable as trampling marks may also be oriented perpendicularly to the axis of the bone (Domínguez-Rodrigo et al. 2009).

Domínguez-Rodrigo et al. (2009) have defined a series of morphological features to differentiate between cut marks and trampling marks using low level magnification (10X-40X). They found that cutmarks tend to follow a straight trajectory, with continuous micro-striations and a deep, narrow V-shaped base (Domínguez-Rodrigo et al. 2009).

Likewise, Lupo and O'Connell (2002) and Costamagno et al. (2019) have summarized various methods that are useful in identifying and interpreting cut marks on archaeological remains. In the present study, the morphological indicators defined by Domínguez-Rodrigo et al. 2009 were used to identify cutmarks on faunal specimens ≥2 cm.

Burning

The presence of burned specimens in an assemblage also provides compelling evidence of human accumulation at an archaeological site (Stiner et al. 1995; Villa et al. 2004). Burned remains can be indicative of several anthropic activities including cooking and refuse disposal. Burned bone is typically identified based on surface color, ranging from shades of brown to black (carbonized) to white or grey (calcined) (Stiner et al. 1995). Burnt specimens can be difficult to differentiate from chemically stained specimens, as minerals such as manganese or iron oxides may similarly alter the bone surface color (Shahack-Gross et al. 1997; López-González et al. 2006). In this study, burned specimens were identified by color and texture of the bone surface.

Marrow Procurement

Research has demonstrated that bone marrow provides an important source of fat and nutrients and is often among the most desirable animal products in foraging societies (Binford 1978, Morin 2007). In order to access the bone marrow stored in the medullary cavity of long bones, humans often use tools to break through the cortical surface. These tools can leave diagnostic notches on the bone surface in the form of percussion marks (Johnson 1985; Blumenschine and Selvaggio 1988, 1991; Alcántara García et al. 2006;

Pickering and Egeland 2006). These notches are morphologically similar to lithic flake scars. However, anthropic percussion notches can be confused with those produced by the static loading of carnivore teeth as they chew (Bunn 1989). Identification of anthropic percussion marks was based on the morphological characteristics defined by Blumenschine and Selvaggio (1991) and Blumenschine et al. (1996). These morphological indicators include: i) a position near or on the fractured edge, ii) a high breadth:depth ratio without evidence of crushing on the internal surface, and iii) a transverse orientation of the notch to the long axis of the bone.

4.1.2 Identifying Non-Anthropic Modifications to Bone Surface

Chemical Staining

Bone surfaces can be altered by a variety of chemical factors including decomposition, soil chemical and fungal composition, heating, and aerial exposure (Bradfield 2018). Humic acids in soil often give bone surfaces a dark brown color (Dupras and Schultz 2014). As mentioned above, mineral oxides and other chemicals present in the depositional substrate can discolor the surface of bone in ways reminiscent of burning (Shahack-Gross et al. 1997; Šebela et al. 2015). Manganese can stain bone surfaces a dark brown-black color, whereas iron oxides can result in reddish-brown staining (Dupras and Schultz 2014). At Crvena Stijena, manganese and iron oxides are present in the geological system and give the rockshelter its red and black streaked appearance. Chemically stained bones were identified based on the texture, color, and distribution of stained bone surfaces.

Trampling

Trampling may have an effect on bone surface preservation, fragmentation, and spatial displacement of elements in an archaeological site (Lyman 1994c). As mentioned above, trampling marks may be confused with cutmarks in archaeological assemblages. Trampling marks were distinguished from cutmarks in this study using the criteria set by Domínguez-Rodrigo et al. (2009). According to these criteria, trampling marks tend to have a more sinuous or curvilinear trajectory, with a shallower and broader cross-section than cutmarks (Domínguez-Rodrigo et al. 2009).

Root Damage

As skeletal remains are deposited, the roots of plants may secrete acids as they grow over them which break down the surfaces of the bone. This leaves diagnostic dendritic, grooved patterns visible on bone surfaces (Behrensmeyer 1978, Morlan 1980, Lyman 1994c). Extensive root etching is problematic as it can preclude the identification of other taphonomic signatures. However, root etching can be distinguished from other taphonomic signatures as a result of these unique dendritic patterns.

The surface preservation of each identified specimen was assessed and recorded according to the degree to which the surface had been modified based on criteria established by Morin (2012) (Table 4.1).

STATE OF SURFACE PRESERVATION	CRITERIA
Intact	Bone surface intact; surface features present are clearly identifiable

STATE OF SURFACE PRESERVATION	CRITERIA
Slightly damaged	Slight damage to surface; modifications identifiable over majority of the surface; some localized damage.
Significantly damaged	Some intact surface present, but most surface features are not visible or eroded.
Extensively damaged	Extensive damage of cortical surface; few to no visible surface features.

Table 4.1: Levels of surface preservation and defining criteria (adapted from Morin 2012).

4.1.3 Impacts of Excavation and Collection Methods

Recovery methods are known to have an impact on both body part and taxonomic representation at archaeological sites (for impact on body part representation, see Klein 1989; Turner 1989; Stiner 2002'; Pickering et al. 2003; for impact on taxonomic representation, see Payne 1972; Shaffer 1992; Graesch 2009). More thorough sampling and collection methods should result in a fuller representation of the original faunal assemblage. A detailed report on the exact excavation and collection strategies used during the 2005–2006 excavations at Crvena Stijena is not available. However, the small proportion of specimens ≤2 cm in the assemblages suggests that fine sieving was not systematically applied to the sediments. This likely led to an inflated representation of largest parts and species which could result in an interpretation favoring a narrower dietary breadth than was present during the Mesolithic occupations. This issue will be considered further in chapter six.

4.2 Measures of Quantification and Abundance

One line of evidence that archaeologists draw upon to make inferences regarding past subsistence activities are the relative abundances of parts and species at a site (Voorhies 1969; Binford and Bertram 1977; Bayham 1979; Binford 1984; Grayson 1984; Lyman 1994a, 1994b, 2008). At Crvena Stijena, faunal remains were quantified using standard zooarchaeological quantification units. When a secure taxonomic identification could not be ascribed to a specimen, the remains were assigned to broader class-level identifications (i.e., Mammalia, Aves, Pisces) and to a body size class (i.e., small, medium, large, Table 4.2).

SIZE CLASS	WEIGHT (kg)	EXAMPLES
Large	≥100	Bison, aurochs, giant deer, horse, brown bear, red deer, panther, beluga sturgeon, Russian sturgeon
Medium-large	60–99	Wild boar, ibex, fallow deer, Wels catfish
Medium	20–59	Chamois, roe deer, lynx, dog
Small-medium	10–19	Red fox, badger, conger eel
Small	1–9	Brown hare, marmot, marten, white-tailed eagle, European pike, common carp, chub mackerel, Mediterranean moray
Very small	≤1	Limpet, sea snail, land snail

Table 4.2: Table depicting body size classes and examples of corresponding taxa.

4.2.1 Number of Identified Specimens (NISP)

The NISP is defined as the number of skeletal remains, including fragments, identified to skeletal element and taxon (Lyman 2008). NISP counts form the core of the abundance indices (discussed below) that were used in this study to assess changes in diet at the site. NISP is negatively impacted by several issues, the most severe problem being the potential interdependence of fragmented specimens, whereby the multiple specimens could be derived from the same element or individual (Grayson 1984, Lyman 2008). In order to overcome the issue of interdependence, NISP was used in conjunction with NDE and other quantification measures.

4.2.2 Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI)

The MNE is calculated by tallying the number of distinct skeletal parts representing each element for each taxon (Lyman 2008). The MNI is calculated using the highest MNE value representing a specific taxon. MNE and MNI control for the potential interdependence of fragmented specimens as it considers that multiple fragments may belong to the same skeletal element and individual. However, MNE and MNI can be impacted by sample aggregation, and must be used in conjunction with other quantification measures in order to produce a more accurate representation of the initial abundances at the site (Grayson 1984, Plug and Plug 1990, Lyman 2008).

4.2.3 Number of Distinct Elements (NDE)

The NDE tallies the number of times a diagnostic landmark (≥ 50 % of cortical surface of the defined feature) is represented in a sample (Morin et al. 2017, 2019). NDE can be used to estimate both skeletal and taxonomic abundance (Morin et al. 2017). Morin et al.'s (2017) system of standardized landmarks make NDE a reproducible quantification method than MNE or MNI. In this study, the NDE was used to compare skeletal part frequencies and to control for interdependence when measuring taxonomic frequencies.

4.2.4 Abundance and Diversity Indices

Changes in dietary breadth may be recognized by changes in the relative abundances of the low-ranked and high-ranked taxa in a faunal assemblage. These changes can be measured using abundance and diversity indices (Bayham 1979; Grayson and Delpech 1998; Grayson and Cannon 1999; Nagaoka 2001). Abundance indices provide a simple way to visualize the relative abundances of distinct types of fauna in an assemblage. These indices have been used to assess changes in dietary breadth and to assess the impact of environmental conditions on samples of different prey types (Broughton 1994b; Broughton et al. 2008, 2011). In this study, the relative abundance of high ranked taxa was calculated to assess their level of inclusion in the diet using the following formulas:

$$\Sigma\ high\ rank\ terrestrial\ taxa\ /$$
$$\Sigma\ (high\ rank\ terrestrial\ taxa\ low\ rank\ terrestrial\ taxa).$$

$$\Sigma\ high\ rank\ aquatic\ taxa\ /\ \Sigma\ (high\ rank\ aquatic\ taxa\ +\ low\ rank\ aquatic\ taxa)$$

Prey rankings as determined in Table 3.1 were used in the calculation of these indices. In addition, Simpson’s Reciprocal Index was used to estimate changes in diet breadth by assessing the species richness (diversity) and evenness (proportional representation) of the faunal assemblages. This index was chosen over others (i.e., Shannon's Index) due to its increased performance at detecting changes in small and incomplete samples (Faith and Du 2018).

4.3 Age and Sex Determination

4.3.1 Age Determination

Age determination of archaeological faunal remains can offer insight into prey choice and hunting strategies by providing information on the varying presence of juvenile, prime-age, and older individuals in a sample (Discamps and Costamagno 2015). Dental remains are often used by archaeologists to estimate age at death. Because teeth erupt, wear, and are replaced according to relatively regular schedules throughout an animal's life, these patterns can be used to estimate the age at death of animals at a variety of phases in their life histories. At Crvena Stijena, age estimations focused primarily on the cervid remains, especially red deer, as they are abundant at the site. Patterns of dental eruption and wear schedules of red deer are well documented (Mariezkurrena 1983; Brown and Chapman 1991; Azorit et al. 2002; Azorit 2011; Calderón et al. 2019; Marín et al. 2024). The eruption sequence of mandibular teeth in red deer as reported by Azorit et al. (2011) and Marin et al. (2024) were used in the present analysis (Table 4.3).

AGE	RED DEER
0–5 months	Dp^2, Dp^3, Dp^4, M^1* Di_1, Di_2, Di_3, Dc_1, Dp_2, Dp_3, Dp_4, M_1*
6 months–1.5 years	Dp^2, Dp^3, Dp^4, M^1, M^2 I_1, I_2, Di_3, Dc_1, Dp_2, Dp_3, Dp_4, M_1, M_2
1.5 years–2.5 years	(Dp^2, Dp^3, Dp^4)***, M^1, M^2 I_1, I_2, I_3, C_1, (Dp_2, Dp_3, Dp_4)***, M_1, M_2

AGE	RED DEER
2.5 years–4.5 years	(P^2, P^3, P^4)**, M^1, M^2, M^3** I_1, I_2, I_3, C_1, (P_2, P_3, P_4)**, M_1, M_2, M_3**
4.5 years–6.5 years	P^2, P^3, P^4, M^1, M^2, M^3 I_1, I_2, I_3, C_1, P_2, P_3, P_4, M_1, M_2, M_3
6.5 years–12 years	P^2, P^3, P^4, M^1, M^2, M^3 I_1, I_2, I_3, C_1, P_2, P_3, P_4, M_1, M_2, M_3
>12 years	P^2, P^3, P^4, M^1***, M^2, M^3 I_1, I_2, I_3, C_1, P_2, P_3, P_4, M_1***, M_2, M_3

Table 4.3: Red deer eruption and wear schedule adapted from Azorit 2011 and Marín et al. 2024. * Tooth is barely erupted, crown still largely beneath the gums. ** Tooth is beginning to show initial signs of wear/replacement. *** Tooth is in final stages of wear.

Another approach used to estimate ages at death focuses on the rates of epiphyseal fusion. This approach is most useful when considering fetal and juvenile remains, as the skeletal elements of prime-age adult or older adult skeletons are often fully fused. As different bones fuse at various times during the life of a young animal, it is possible to estimate their age at death based on the degree of epiphyseal fusion (Reitz and Wing 2008). Calderón et al. (2019) suggest that full skeletal maturity in red deer takes place between 3.5–4.5 years (42–54 months), with hinds typically reaching skeletal maturity earlier than bucks (Table 4.4).

SKELETAL ELEMENT	8 MONTHS	20 MONTHS	32 MONTHS
Scapula	*Tuber scapulae* unfused.	*Tuber scapulae* fused, often the fusion line is still visible.	*Tuber scapulae* fused.
Humerus	Proximal epiphyses (head + lesser tubercle and greater tubercle) unfused; distal epiphysis fused in about half of specimens, but with a visible fusion line.	Proximal epiphyses (head + lesser tubercle and greater tubercle) unfused; distal epiphysis is fused; the fusion line is only slightly visible in a few specimens.	Proximal epiphyses (head + lesser tubercle and greater tubercle) are fused together but remain unfused to the diaphysis; distal epiphysis is fused with no fusion line visible.

SKELETAL ELEMENT	8 MONTHS	20 MONTHS	32 MONTHS
Radius	Proximal epiphysis fused in most specimens; radial tuberosity not fully developed; distal epiphyses unfused.	Proximal epiphysis fused and radial tuberosity is well developed, distal epiphysis unfused.	Distal epiphysis remains unfused.
Ulna	Proximal (olecranon) and distal (styloid process) unfused.	Proximal (olecranon) and distal (styloid process) unfused.	Proximal (olecranon) and distal (styloid process) unfused.
Metacarpal	Distal condyles unfused.	Distal condyles unfused.	Distal condyles unfused.
Pelvis	Acetabulum divided between three bones, not fully fused; Pubic symphysis unfused.	Acetabulum is fused; pubic symphysis unfused.	Pubic symphysis remains unfused.
Femur	Proximal epiphyses (head and greater trochanter) and distal epiphysis unfused.	Proximal epiphyses (head and greater trochanter) and distal epiphysis unfused.	Proximal epiphyses (head and greater trochanter) and distal epiphysis unfused.
Tibia	Proximal and distal epiphyses unfused; tibial crest underdeveloped.	Proximal epiphysis unfused with an underdeveloped tibial crest; distal epiphysis fused in about half of specimens, with a visible fusion line.	Proximal epiphysis unfused with an underdeveloped tibial crest; no visible fusion line at distal epiphysis.
Calcaneus	Calcaneal tuberosity unfused.	Calcaneal tuberosity unfused.	Calcaneal tuberosity unfused.
Metatarsal	Distal condyles unfused.	Distal condyles unfused.	Distal condyles unfused.
Phalanges (1&2)	Proximal articular surfaces unfused.	Most proximal articular surface fused with a visible fusion line.	Proximal articular surfaces fused with no visible fusion line.

Table 4.4: Epiphyseal fusion schedule for red deer adapted from Mariezkurrena (1983).

4.3.2 Sex Determination

The sex of a specimen can be estimated by comparing morphological features of skeletal elements that are known to be sexually dimorphic (i.e., the pelvis, canines, antlers) between male and female skeletons (Klein and Cruz-Uribe 1984). Due to the highly fragmented nature of the faunal remains at Crvena Stijena, assessing sex was difficult for most specimens. Sex estimation in this study is primarily focused on cervid remains, using the presence or absence of antlers and/or pedicles as a sex indicator.

4.4 Differentiating Between Wild and Domestic Fauna

In some Late Mesolithic contexts, researchers have proposed that domesticated species (e.g., pig and dog) were present (i.e., Geddes 1985; Krause-Kyora et al. 2013; Crombé et al. 2020), a possibility that is disputed (Binder 2000; Dinu et al. 2006; Rowley-Conwy and Zeder 2014). Dogs are known domesticates in the Central Balkans during the Mesolithic, and evidence suggests that they were included in the diet (Dimitrijević 2008). Domesticated pigs have been claimed to have been present in the region (Boroneanţ 1973), although this proposition seems poorly supported (Dinu et al. 2006).

4.4.1 Morphological Identification of Domesticated Taxa

It remains unclear just how morphologically distinct early domesticated suids were from their wild counterparts, making it difficult to differentiate between early domesticated pigs and wild boar (Rowley-Conwy et al. 2012). Despite this, research has shown that the morphology of molariform teeth vary between domestic and wild *Sus scrofa* populations, with wild populations having larger molariform teeth compared to domesticated populations (Evin et al. 2015). The well preserved suid molariform teeth in the Crvena Stijena assemblages were measured using protocols adapted from von den

Driesch (1976) and assessed according to the references provided in Rowley-Conwy et al. 2012, Owen et al. 2014, and Evin et al. 2015. Differentiating between early dogs and wolves can also prove challenging, as the two groups are morphologically similar. Janssens et al. (2019) report that mesio-distal size reduction of P4 is a reliable characteristic to differentiate between wolves and early dogs, along with the mesio-distal reduction of M1, this last criterion being less useful. Because of this, dental remains, particularly carnassial teeth, were chosen to differentiate between wolf and dog remains in the assemblages following Janssens et al. (2019) protocol.

4.5 Determining Seasonality

Understanding patterns of site occupation is critical for understanding subsistence, as certain resources may only be available at specific times during the year. There is evidence that exploitation of dietary resources became more seasonal during the Mesolithic (Crombé and Robinson 2014). A simple method to estimate seasonal occupation is the presence or absence of certain seasonally available species (Monks 1981). Archaeologists can also use physiological lines of evidence such as dental eruption and replacement, antler growth, and other physiological events reflected in the skeleton to estimate seasonality (Monks 1981; Lubinski and O'Brien 2001).

Red Deer

Red deer is the most frequent mammal represented in the Mesolithic assemblages at Crvena Stijena. Red deer are synchronous birthers, with the calving season of red deer in Europe taking place in early summer from late May to early June (Clutton-Brock and Guinness 1975; Clutton-Brock et al. 1982). The hind typically births one calf a year

(Guiness et al. 1971; Clutton-Brock and Guinness 1975; Clutton-Brock et al. 1982). In this study, red deer dental and fetal remains were used to estimate seasonal occupation at the site.

Roe Deer

Roe deer is one of the most common taxa in the Mesolithic assemblages at Crvena Stijena. Like red deer, roe deer are synchronous birthers, with most births occurring in the late spring to early summer (Linnell and Andersen 1998; Gaillard et al. 1993). Roe deer typically birth one to three calves at a time, and those calves follow a regular pattern of dental eruption and replacement after birth (Tomé and Vigne 2003; Høye 2006; Garel et al. 2014; De Marinis et al. 2018). Age estimates derived from roe deer dental remains were used to estimate seasonal occupation at Crvena Stijena.

Chapter 5 Results

5.1 Description of the Faunal Sample

The faunal assemblages associated with the early Holocene/Mesolithic occupations at Crvena Stijena contain 2,297 specimens (Table 5.1), of which 1,106 are identified to at least taxonomic class. Of those specimens, 800 are identified to either genus or species. The remaining specimens are quantified using the *Number of Specimens of Uncertain Taxonomic Status* (NSUTS) (*sensu* Morin 2012:67). The 1,191 remains that are taxonomically undiagnostic are recorded either as long bone shaft fragments (LBN) or indeterminate remains (non-identified specimens or NID).

	GS 1*	GS 2	GS 4	Mixed/ Unclear Context
NISP	60	378	89	274
NSUTS	6	165	42	92
LBN	33	359	134	215
NID	61	188	79	122
Total	160	1,090	344	703

Table 5.1: Overview of Mesolithic faunal assemblages from Crvena Stijena. * Due to the mixed nature of the GS1 deposit, it is not included in any of the analysis, results, or interpretations discussed below.

5.2 Taphonomic Analyses

5.2.1 Overall Bone Surface Condition

The Early Holocene faunal assemblages generally display a poor to fair preservation of bone surface with many specimens covered in thick, ashy concretions, which occasionally completely obscure the surface of some specimens. In the total NISP sample (*n* = 800), the bone surface of most specimens is slightly to significantly damaged (Figure 5.1). The most common surface modifications are burning, concretions and root etching. These obstructions frequently made detailed observations of bone surfaces difficult.

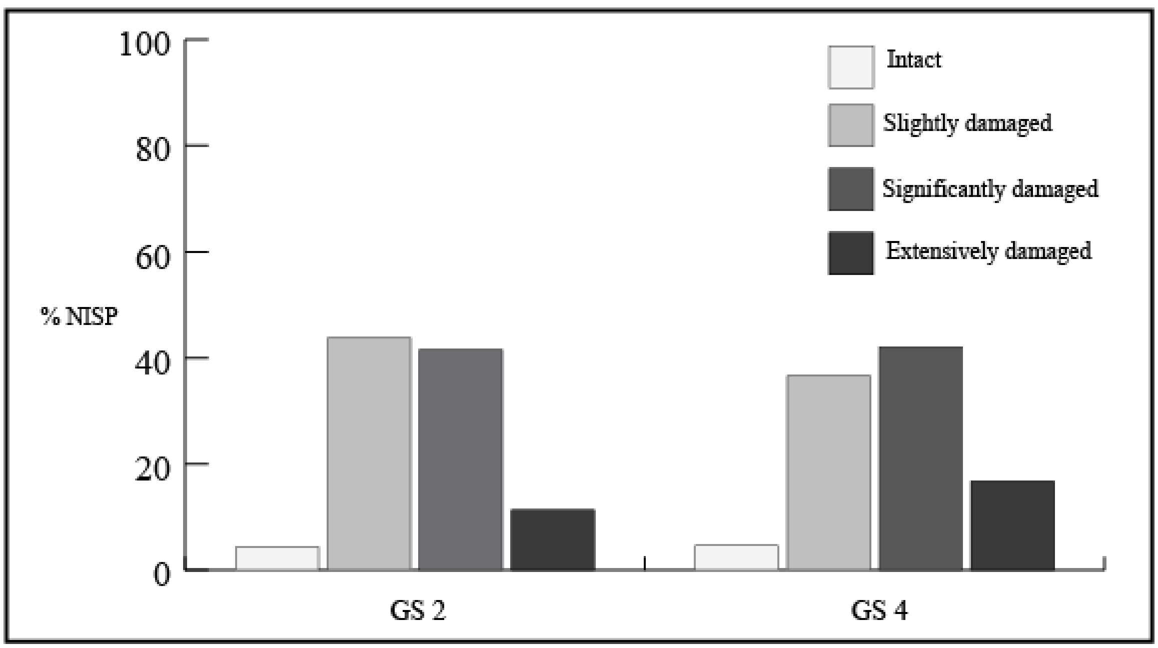


Figure 5.1: Surface state of specimens throughout the assemblages.

5.2.2 Fragmentation

The Early Holocene assemblages at Crvena Stijena are all highly fragmented. Only 3.9% of the remains represent complete elements; these are primarily short bones (i.e., carpals, tarsals, phalanges). The relatively low frequency (6.5% TNSP) of specimens ≤ 2 cm suggests that the material was incompletely recovered, potentially favoring the representation of larger skeletal elements and species. In the combined GS2-GS4 sample, 89.6% of the specimens are fragmentary. Green bone fractures are relatively common, being observed on 39.1% of the identified remains. As noted by Dimitrijević (2017), the first and second phalanges of ungulates are often fragmented, with some of these phalanges (n = 17) also bearing impact notches.

5.2.3 Natural Agents

Concretions

Many of the bones in the Early Holocene assemblages are partially to fully coated in thick, often ashy, calcareous sediments. Throughout the sequence, 56.4 % of the identified faunal remains are covered to varying degrees by concretions. These concretions have made it difficult to fully assess the extent of taphonomic modifications such as cutmarks in the assemblages. The ashy nature of the concretions is not surprising, as many of the remains were recovered in direct or close association with a hearth feature in GS 2.

Root Etching

Plants had an impact on the faunal assemblages at Crvena Stijena as 22.4 % of the identified remains show evidence of root etching. This suggests that the bones remained in the active root zone for some time before being buried sufficiently deep enough to avoid the damage of plant roots and fungi.

Soil and Chemical Staining

Manganese and other dissolved chemicals can stain and/or coat the surfaces of bones as they become exposed to water permeating the cave sediments (López-González et al. 2006). Some of the faunal remains from Crvena Stijena have been stained a dark black color from manganese oxides which occur naturally in the excavation zone. Overall, the impact of manganese on the Mesolithic assemblages seems to be limited. The proportion of manganese-stained bones decreases through the levels, from 1.8% NISP GS 2 to .8% NISP GS 4. However, as many bone surfaces are obscured by thick concretions, the impact of chemical staining on the assemblages is possibly underestimated.

Carnivore Activity

Only 1.3% of the Mesolithic remains show signs of carnivore gnawing or tooth pitting. Only one specimen with crenulated edges from carnivore gnawing was recovered in GS 4. The GS 2 assemblage provided the most abundant evidence of carnivore presence, with several specimens bearing tooth marks, mostly on rabbit remains ($n = 4$). Based on the size of the tooth marks, this damage was likely produced by a medium-sized carnivore such as fox or lynx. However, it is known that Mesolithic populations in the Central Balkans had dogs, and while there are no identified *Canis* remains in the Mesolithic assemblages from Crvena Stijena, the action of this species cannot be excluded.

5.2.4 Human Agents

Burning

Fire appears to be one of the most significant taphonomic agents at Crvena Stijena. Overall, about 32.0% of the Mesolithic specimens show signs of thermal modification. Within the sample of NISP and NSUTS remains, the proportion of thermally modified specimens is lower at 23.0%, while 39.0% of the NID and LBN remains are burned or calcined. The frequency of burned specimens increases significantly from 25.0% in GS 4 to 37.2 % in GS 2. In GS 2, many specimens were found near a hearth feature, which may account for the higher proportion of burned bone in this level. Of the NID sample from GS 2 (NSP = 186), 15.6% of specimens are burned spongy bone, 31.7% are burned compact bone.

Cutmarks and scrape marks

Throughout the assemblages, unambiguous cutmarks are few (*n* = 39). Most cutmarks are observed on red deer remains (*n* = 24), particularly on mandibles and meat-bearing long bones (i.e., femur: *n* = 6, mandible: *n* = 4). Cutmarks are also observed on roe deer (*n* = 5), wild boar (*n* = 3), and caprine (*n* = 1) remains. Cutmarks also appear on medium- (*n* = 1), medium-large- (*n* = 3), and large-mammalian (*n* = 1) specimens. In GS 2—the layer with the highest frequency of cutmarks—3.1% of identified specimens have cutmarks. Only 1.5% of identified specimens in GS 4 have cutmarks. Scrape marks are also present throughout the assemblages, although at a low frequency (*n* = 5).

Impact Notches

A number of specimens throughout the assemblages have impact notches (*n* = 56). These percussion marks are particularly common on the first and second phalanges (*n* = 18) and on long bone fragments of ungulates (*n* = 36). Of all ungulates at the site, 88.8% of first and second phalanges are represented by fragmented/incomplete specimens. When considering only giant deer, red deer, and wild boar, 97.9% of first and second phalanges are represented by fragmented/incomplete specimens. Even the roe deer—the smallest ungulate species at the site—follows this pattern (57.7% of the specimens are incomplete). Twenty-six specimens in GS 2 have impact notches. Of these, 18 occur on red deer remains. Seven specimens in GS 4 have impact notches, all but one occurred on the long bones or phalanges of red deer.

5.3 Faunal Analyses

5.3.1 Taxonomic Composition of the Mesolithic Assemblages

GS 2

TAXA	NISP	MNI
Cervus elaphus	233	4
Capreolus capreolus	66	3
Sus scrofa	27	2
Lepus europaeus	23	5
Vulpes vulpes	12	1
Megaloceros giganteus	5	1
Capra ibex	5	1
Lynx lynx	4	1
Martes sp.	2	1

Ursus arctos	1	1
Total	378	20

Table 5.2: NISP and MNI counts for GS 2.

The faunal assemblage from GS 2 is dominated by ungulates, representing 88.9% of the identified specimens in the layer (Table 5.2). Red deer is the most frequently represented taxa, comprising 61.6% of the identified assemblage. Roe deer also comprises a large proportion of the assemblage, with 17.5% of the identified specimens. Wild boar and brown hare are also fairly common, comprising 7.1% and 6.1% of the sample, respectively. Various carnivores—including the lynx, fox, martens, mustelids, and brown bear—account for 5.0% of the total.

GS 4

TAXA	NISP	MNI
Cervus elaphus	48	2
Lepus europaeus	15	2
Sus scrofa	11	1
Capreolus capreolus	4	1
Capra ibex	4	1
Lynx lynx	2	1
Vulpes vulpes	2	1
Megaloceros giganteus	1	1
Martes sp.	1	1
Meles meles	1	1
Total	89	12

Table 5.3: NISP and MNI counts for GS 4.

Like GS2, the faunal assemblage from GS 4 largely consists of ungulates (76.4%, Table 5.3). Red deer is the most abundant species, comprising 53.9% of the GS 4 identified specimens. The brown hare is the second most common species (16.9%). Wild boar is also relatively abundant in the GS 4 assemblage, with a prevalence of 12.4%. Other ungulates present in the layer include roe deer, giant deer, and ibex. Together, these constitute 10.1% of the total. Small- and medium-sized carnivores, including the lynx, fox, badger, and martens, are uncommon in the assemblage (6.7%).

TAXA	GS 2	GS 4
Cervus elaphus	1.34	-1.34
Capreolus capreolus	-3.08	3.08
Sus scrofa	-1.62	1.62
Lepus europaeus	-3.34	3.34
Vulpes vulpes	0.46	-0.46
Megaloceros giganteus	0.15	-0.15
Capra sp.	-1.96	1.96
Lynx lynx	-0.90	0.90
Martes sp.	-0.63	0.63
Ursus arctos	0.49	-0.49
Meles meles	-2.06	2.06

Table 5.4: Adjusted standardized residuals from χ2 test. Lightly highlighted cells signify a high positive residual; darkly highlighted cells signify a significant negative residual.

To evaluate if there are differences between the Mesolithic layers, a chi-squared test was run. The result showed some significant differences with a small effect size (χ^2 = 31.13, $p < .001$, Cramer's V= .26). To understand which taxa are statistically over- or under-represented in the assemblages, the adjusted standard residuals were calculated (Table 5.4). Values ≥ +/- 1.96 (α = .05) are considered significant. Some interesting patterns emerge. In GS 4, brown hare and badger are overrepresented, whereas roe deer are underrepresented. Conversely, roe deer are significantly overrepresented in GS 2, while brown hare and badger are under-represented.

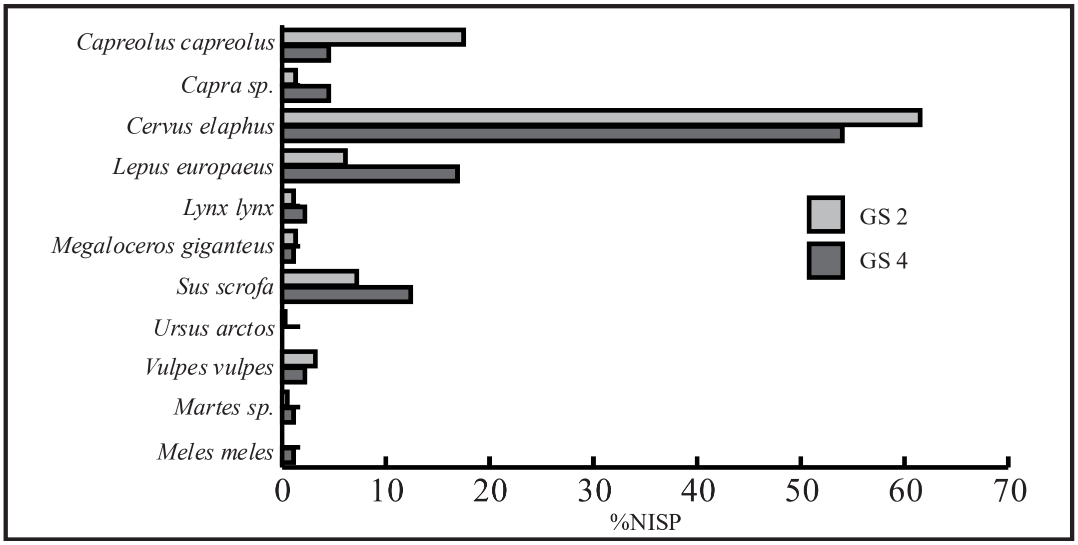


Figure 5.2: NISP frequencies in GS 2 and GS 4.

5.3.2 Presence of Domesticated Animals and Seasonal Occupation

No domesticated taxa were identified in the Mesolithic assemblages. While none of the specimens in the GS 4 assemblage could be used to assess seasonality, in GS 2, a fetal tibia and a mandible fragment from red deer point to a mid-fall to mid-winter occupation during the Late Mesolithic.

5.3.3 Sample Diversity and Abundance Indices

Simpson's Reciprocal Index was used to assess change in species diversity in the Mesolithic assemblages (Table 5.5). Overall, species diversity is relatively low in both samples. To test for evidence of subsistence intensification during the Mesolithic and during the Pleistocene-Holocene transition, abundance indices were calculated to assess the changes in the use of high-ranked prey types (Table 5.5). The values from the two levels are nearly identical, with a relatively high proportion of high-ranked prey in the assemblages.

LAYER	∑NISP	Simpson's Reciprocal Index (1 / D)
GS 2	378	2.4
GS 4	89	3.0
	Abundance index (terrestrial)	
GS 2		.72
GS 4		.72

Table 5.5: (Upper) Sample diversity in the Mesolithic layers as measured by Simpson's Reciprocal Index. (Lower) The lowest value for this index is 1; the highest value is equal to the number of species in a sample. The higher the value, the greater the diversity of the sample. (Lower) Abundance indices for the terrestrial prey types. Values closer to 1.0 represent a predominance of high-ranked taxa, values closer to 0.0 represent a predominance of low-ranked taxa.5.4 Comparisons with the Upper Paleolithic Assemblages.

5.4.1 Taxonomic Composition of Layer X

TAXA	NISP
Cervus elaphus	20
Capra ibex/caucasica	16
Lepus sp.	6
Marmota marmota	3
Panther sp.	2
Capreolus capreolus	1
Sus scrofa	1
Rupicapra rupicapra	1
Total	50

Table 5.6: NISP counts from X. Adapted from Morin and Soulier (2017).

The Mesolithic faunal assemblages were compared with the Late Gravettian/Early Epigravettian layer (X) to assess whether there are any differences in taxonomic composition between the Late Pleistocene and Early Holocene diet. According to Morin and Soulier (2017:293), ungulate taxa represent 78.0% of identified specimens in layer. Red deer comprise 40.0% of the assemblage, followed by caprines (32.0%). Chamois, roe deer, and wild boar each represent 2.0% of the assemblage (Table 5.6). Leporids and marmots comprise 12.0% and 6.0%, respectively. The only carnivore taxa identified inthe layer are panthers, representing 4.0% of the sample.

	GS 2	*GS 4*	*X*
Cervus elaphus	2.60	-0.90	-2.75
Capreolus capreolus	4.06	-2.78	-2.54
Sus scrofa	-0.57	1.89	-1.56
Lepus sp.	-3.26	3.10	0.93
Vulpes vulpes	1.08	-0.29	-1.24
Megaloceros giganteus	0.57	-0.04	-0.81
Capra sp.	-6.14	-0.16	9.42
Lynx lynx	-0.36	1.05	-0.81
Martes sp.	-0.25	0.74	-0.57
Ursus arctos	0.61	-0.46	-0.33
Meles meles	-1.65	2.20	-0.33
Rupicapra rupicapra	-1.65	-0.46	3.06
Panthera sp.	-2.34	-0.65	4.33
Marmota marmota	-2.86	-0.79	5.31

Table 5.7: Adjusted standardized residuals from χ2 test. Lightly highlighted cells signify a high positive residual; darkly highlighted cells signify a significant negative residual.

A chi-squared test show that there are some significant differences in the species represented between the two periods, with a large effect size ($\chi^2 = 185.58$, $p < .001$, Cramer's V= .42). The adjusted standard residuals (Table 5.7) indicate that red deer and roe deer are overrepresented in the Late Mesolithic layer (GS 2), while the same species are significantly underrepresented in the Upper Paleolithic layer. Leporids are significantly underrepresented in GS 2, but overrepresented in GS 4. Caprines show the largest differences, being disproportionally abundant in layer X compared to all other layers— especially GS 2.

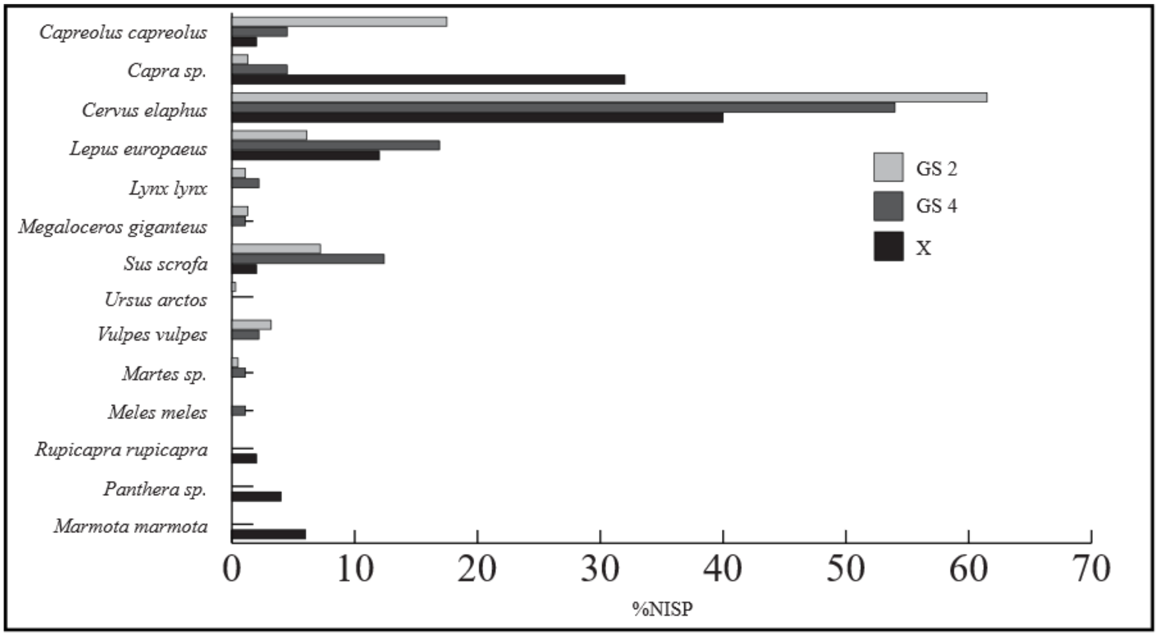


Figure 5.3: NISP frequencies in GS 2, GS 4, and X.

5.4.2 Sample Diversity and Abundance Indices

Simpson's Reciprocal Index was used to assess the diversity of the species in the assemblages (Table 5.8). Overall, diversity is low in all layers, although somewhat higher in layer X. The abundance index was used to assess the proportion of high-ranked prey types in the faunal assemblages. Values are high in all layers, which implies a large proportion of high-ranked prey in the assemblages.

Layer	∑NISP	Simpson's Reciprocal Index(1 / D)
GS 2	378	2.4
GS 4	89	3.0
X	50	3.7

	Abundance index (terrestrial)
GS 2	.72
GS 4	.72
X	.78

Table 5.8: (Upper) Sample diversity in the Mesolithic layers as measured by Simpson's Reciprocal Index. (Lower) The lowest value for this index is 1; the highest value is equal to the number of species in a sample. The higher the value, the greater the diversity.

Chapter Six Discussion and Concluding remarks

6.1 Taphonomic Impacts on the Mesolithic assemblages

6.1.1 Intensive Carcass Processing

The taphonomic evidence all suggest that the faunal assemblages of the Mesolithic at Crvena Stijena were accumulated as a result of human subsistence practices. The high degree of fragmentation of skeletal elements, particularly of long bones and other marrow-bearing skeletal elements suggests that the exploitation of marrow was an important subsistence activity. It is well known that the exploitation of fat stored in bones is quite common in forager populations (i.e., Levin and Potapov 1964; Binford 1978; Speth 1983; O'Connell and Hawkes 1988). Fat is a necessary part of the diet, as it provides easily metabolizable energy, and facilitates the absorption of important vitamins A, D, E, and K (Sanders 2024). Additionally, the caloric value of fats is far greater than that of proteins or carbohydrates (Sanders 2024). Fats or carbohydrates are also necessary to avoid protein poisoning, and ethnographic accounts show that hunters would seek out fat sources especially during the lean season (Speth and Spielmann 1983). The fats stored in bones offer a reliable source of fat, even when animals are lean or starved (Peterson et al. 1982; Davis et al. 1987). It is likely that the high degree of fragmentation of skeletal elements in the Mesolithic samples is due in large part to the targeted exploitation of fats stored in the bones.

Skeletal elements can be ranked in terms of their economic utility, particularly by the amount and type of fat stored in the bone marrow and grease (Binford 1978; Jones and Metcalfe 1988; Bar-Oz and Munro 2007; Morin 2007). According to the Marginal Value Theorem, the highest ranked elements (e.g., tibia, femur) should be processed before those of lower rank (e.g., first and second phalanges) (Charnov 1973; Burger et al. 2005).

Dimitrijevic (2017) noted the particularly high degree of fragmentation of the first and second phalanges of ungulates at the site, a pattern which is supported by this study. the majority of first and second phalanges of ungulates at the site, including the very small phalanges of roe deer, have been cracked for marrow. The intensive breakage of these skeletal parts suggests that the Mesolithic populations at Crvena Stijena were periodically facing subsistence stress. Because body fat composition varies seasonally in wild animals (Holand 1992; Ballard 1995; Peréz-Serrano et al. 2020; Stanisz et al. 2023), seasonal occupation of Crvena Stijena may have encouraged foragers to seek additional fat from the phalanges at times.

6.1.2 Burning

Because many burned specimens were recovered near a hearth feature in GS 2, the question of whether bone was used as fuel during this occupation arises. Because lipids are highly flammable, bone can be uses as an effective source of fuel (Morin 2010). Experimental data have shown that spongy epiphyses, especially distal epiphyses, generally are more efficient to burn compared to compact diaphyses due to the lipids released from the spongy matrix, which produce a more prolonged burn (Costamagno et al.1999, 2005; Théry-Parisot et al. 2005). Costamagno et al. (2005) have argued that a high portion of burned epiphyseal bone relative to the portion of burned compact bone in an archaeological assemblage provides evidence for the use of bone as fuel. In the GS 2 assemblage, burning is more frequently recorded on compact bone than spongy bone fragments. Additionally, regional paleoenvironmental data suggest that it is likely that the Mesolithic occupants of Crvena Stijena had access to forested areas where they could gather plenty of wood or other vegetal matter to more efficiently burn in their hearths (Willis 1994; Aufgebauer et al. 2012; Cagliero et al 2023; Schmidhauser et al. 2024). However, it is possible that unsystematic collection methods have led to an under-representation of small spongy bone fragments, particularly fragile, burnt specimens. Therefore, the use of bone as fuel cannot conclusively be ruled out.

Based on the available evidence, there is no clear pattern demonstrating that the occupants of the rockshelter were selectively using spongy bone as fuel. Rather, the relatively high occurrence of burned bone observed throughout the assemblages could be explained as a product of refuse disposal. Studies have attributed high frequencies of burnt bone in assemblages which do not appear to have been used as fuel to the hygienic disposal of organic waste (Cain 2005; Yravedra and Uzquiano 2013). Other studies have also emphasized the symbolic or ritual aspects of such deposition (Nolde 2020). In the case of the Crvena Stijena Mesolithic assemblages, it is very difficult to assess the occupants' motivations and several interpretations are plausible.

6.2 Foraging Strategies

6.2.1 Patch Use

Based on the species frequently found in the assemblages, it seems that the Mesolithic occupants at Crvena Stijena foraged primarily within a deciduous forest patch, perhaps at lower altitudes such as the valley bottom, where they could more reliably encounter cervids, leporids, and wild boar. As a secondary patch, they perhaps exploited a more open, higher elevation patch where they could have encountered ibex. The higher frequency of ibex remains in GS 4 compared to GS 2 is perhaps suggestive of a more open environment surrounding the site during the Early Mesolithic compared to the Late Mesolithic, going along with a slightly higher reliance of those areas in foraging activities. However, ibex remains occur at relatively low frequencies of each Mesolithic assemblage, and its presence could alternatively be explained by opportunistic encounters at lower elevations along with the other species.

In the Upper Paleolithic assemblage, patterns of patch exploitation appear similar, although perhaps accompanied with an increased reliance on the more open or higher-altitude patch where ibex and alpine marmot could be encountered. These potential changes in patch exploitation could be related to changes in the local environment around the site. It seems that during the Upper Paleolithic/Late Pleistocene occupations at Crvena Stijena, the environment may have been less densely forested than during the Mesolithic/Early Holocene occupations, which is largely in accordance with known environmental changes that took place in the region during the Pleistocene-Holocene transition (Willis 1994; Aufgebauer et al. 2012; Cagliero et al 2023; Schmidhauser et al. 2024).

6.2.2 Diet Breadth

Based on taxonomic data, subsistence at the site appears focused on exploiting medium and large ungulates as the core of the diet, suggesting a relatively narrow subsistence strategy. Red deer is by far the most frequently encountered animal in both Mesolithic assemblages and represents one of the highest-ranked prey available to the foragers. The substantial proportions of lower and mid-ranked prey types such as hare and roe deer perhaps suggest that at times, lower-utility resources were pursued. Furbearers (fox, lynx, and various mustelids) may have been consumed during the Mesolithic, although they might have been captured primarily for their pelts. The estimated occupation of Crvena Stijena during the Late Mesolithic coincides with the season during which these animals' pelts are at their peak. If the furbearer remains were also accumulated during this time, they could have been pursued to take advantage of this quality.

Values for the abundance indices are nearly identical between the two layers, suggesting that throughout the Mesolithic, no significant changes in subsistence intensification occurred. Diversity is also relatively similar between the assemblages, although somewhat higher in GS 4 compared to GS 2. However, the small sample sizes, especially in GS 4, means that sampling error cannot be excluded. Diet breadth is also narrow in the Upper Paleolithic layer, X, a level where red deer and caprines are dominant. However, there is a slight decrease in the values from abundance indices between the Upper Paleolithic and Mesolithic occupations—.78 and .72, respectively (Table 5.8). This could point to some intensification in subsistence strategies during the Pleistocene-Holocene transition.

Variations in species recorded between the Mesolithic and Upper Paleolithic assemblages are likely indicative of changes in local environment rather than changes in human subsistence behavior. For example, the decreasing frequency of caprine remains through time at the site is possibly related to the population decline and eventual disappearance of ibex from the region during the Early/Middle Holocene due to habitat contraction and hunting pressure (Geskos 2012), an idea also put forth by Dimitrijević (2017). The decline in the frequency of marmot, another open-slope dwelling species, through the Pleistocene-Holocene occupations at the site is probably attributable to environmental changes as well. As the region became more heavily forested during the Holocene, the preferred open habitats of these taxa may have contracted significantly, making them less frequently available to foragers.

Overall, it appears that there is no robust evidence to suggest any intensification in the use of animal resources within the Mesolithic occupations. However, there may be evidence of a somewhat broader subsistence pattern during the Mesolithic compared to the Upper Paleolithic. It is unclear whether these patterns of dietary breadth observed at the site are reflective of the overall subsistence pattern or the result of some specific attribute of site-use at Crvena Stijena. As discussed previously, the relatively small sample sizes and the problem of unsystematic collection make it possible that the subsistence base was in fact wider than suggested by the current analysis.

6.3 Subsistence at Crvena Stijena and Other Mesolithic Sites in the Central Balkans

The available faunal data from other Mesolithic sites in the Central Balkans shows that the foragers in this region were often successful at capturing high-ranked prey types. During the Mesolithic throughout the Central Balkans, red deer and wild boar consistently are consistently well represented in the faunal samples. In the more rugged, open landscapes of the inland Adriatic zone, ibex was commonly procured as well. Along the Danube River, these terrestrial resources were consumed along with large aquatic taxa such as sturgeon and catfish. Unfortunately, many of these sites from the inland Adriatic and Iron Gates regions were excavated and curated during times when faunal remains were not fully collected. Therefore, it is possible that the diet breadth of foragers at these sites was broader than has been interpreted.

Sites along the Adriatic coast are possible exceptions to this regional pattern of the exploitation of primarily high-ranked prey, as they show frequent use of marine gastropods. However, faunal data from this region are sparse, and it is possible that with more research a different foraging pattern may emerge. It is also possible that the more intensive subsistence practices along the Adriatic coast were implemented only seasonally or temporarily, during periods when higher ranking prey was not readily available to foragers. Such patterns of seasonal intensification—particularly increased reliance on marine invertebrates—have been inferred at other coastal Mesolithic sites in other regions along the Mediterranean rim (Prendergast et al. 2016).

Gendered foraging behavior may also explain the higher frequencies of shellfish in the Adriatic assemblages. Societies with a gendered division of labor, in which women forage primarily for prey types which are traditionally considered 'low-ranking' (i.e. small game, shellfish) are well-documented in the ethnographic record (e.g. Hurtado and Hill 1990; Bliege Bird 1999; Marlowe 2007; Bliege Bird and Bird 2008; Kelly 2013). When there are more women in a foraging group, women are spending more time foraging, or women are encountering certain prey types more frequently, the abundance of 'low-ranked' resources in the diet increases. Thus, the high frequency of shellfish remains in coastal Mesolithic assemblages could be reflective of changes in the demographic make-up of foraging groups, or to changes in the foraging behavior of the women in the group—not necessarily to decreased encounters with other 'high-ranking' prey. Overall, the subsistence patterns observed in the Mesolithic occupations at Crvena Stijena are consistent with those of most other contemporaneous site throughout the inland regions of the Central Balkans.

6.4 Concluding Remarks

The faunal data at Crvena Stijena and other inland sites of the Central Balkans suggest that the local diets mostly focused on highly-ranked prey types. While more marginal animal resources were occasionally exploited at these sites, prey types with high return rates appear to dominate the assemblages. Groups living along the Adriatic coast may have subsisted on a wider range of resources, but additional analyses from this area are needed to support that this was due to overall subsistence intensification. Specifically, further research on the impacts of weather and tidal conditions on shellfish foraging in this region would be useful to better understand the position of marine invertebrates in local optimal foraging economies.

At Crvena Stijena, there appear to be only minimal changes in the range and types of prey exploited between the Early and Late Mesolithic. More significant changes are recorded between the Early Holocene and Late Pleistocene occupations at Crvena Stijena, which may represent some intensification of subsistence strategies between the two periods. Along with this, changes in species representation are more likely related to local environmental changes. The taphonomic analyses show that the occupants of Crvena Stijena were intensively processing carcasses of their prey, perhaps in response to some level of nutritional stress, in ways that are consistent with what is reported for the Middle and Upper Paleolithic at the site (Morin and Soulier 2017).

Ongoing research in the Central Balkans will generate larger and more extensively collected faunal samples to be analyzed, allowing the interpretations made in this study to be refined or revised. Hopefully, future studies will continue to assess the economic roles that animal prey types played in local Mesolithic foraging economies, alongside further studies regarding the social importance of animal prey. To more fully understand prehistoric subsistence, it will be important for future studies to incorporate multiple lines of evidence when interpreting the foraging decisions made by prehistoric hunter gatherers.

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