Late Pleistocene Avifauna of the Pešturina Cave (Nišava District, SE Serbia) and its Implications for Late Pleistocene Refugia in the Central Balkans

Zlatozar N. Boev¹, Stefan Milošević²

¹ - National Museum of Natural History, Bulgarian Academy of Sciences, 1 Blvd. Tsar Osvoboditel, 1000 Sofia, BULGARIA
² - University of Belgrade, Faculty of Philosophy, Laboratory for Bioarchaeology, Čika Ljubina 18-20, 11000 Belgrade, SERBIA

*Corresponding author: boev@nmnhs.com; zlatozarboev@gmail.com

Abstract. Avian remains presented here were collected from the deposits spanning between late MIS 5 to 3, and give a rare opportunity to observe Last Interglacial/Last Glacial avian succession in the Central Balkans. The Late Pleistocene avifauna from Pešturina cave (Niš District, SE Serbia), comprises 26 taxa from 18 families and 10 orders, 16 of which are reported for the first time from Pleistocene deposits of the Central Balkans. Today, these species live in a variety of habitats – open grassland, forest, rocky, and aquatic habitats. The species from forest habitat were the most abundant. All species (except black grouse) are present in the country’s modern avifauna. The cave provides some examples of “mixed” Pleistocene avifaunas, including species both of Euro-Siberian and Mediterranean/temperate present day distribution. The occurrence of rock sparrow marks one of the northernmost Pleistocene ones in Europe so far, while presence of other species is suggestive for complex mosaic ecosystems, which probably characterized Last Glacial landscapes in the Central Balkans, at least until the LGM.

Key words: Quaternary/Late Pleistocene birds, Late Pleistocene refugia, Central Balkans, avian paleoecology, avian taphonomy, avian zoogeography.

Introduction

Paleontological studies, based on avifaunal remains, are important for understanding the changes in paleoecological settings of the archaeological/paleontological sites. Quaternary record of birds on the Balkan Peninsula is still insufficiently studied. About 20 Pleistocene cave localities so far revealed exhaustive avifaunal complexes (Fig. 1). Pešturina cave (Niš District, SE Serbia) represents a previously unexamined Late Pleistocene site in the region, located in the central part of the Balkan Peninsula. The paper presents results of paleoavifaunal study, with an aim to fill in the Last Interglacial/Early Glacial ecological gap in the Central Balkans, and present the uncovered avifauna and its nature of accumulation. Since studied material comes from an archaeological site, the paleoecological reconstruction is important in assessing the range of habitats also available to Paleolithic humans – late Neanderthals and modern humans of the Gravettian culture. The results are compared with other Late Pleistocene avifaunas from the Balkans, Aegean, and the northern Mediterranean arch. Paleoecological studies of the Late Pleistocene avifaunas throughout Balkans and the Aegean are numerous (MOURER-CHAUVIRÉ, 1981; MLÍKOVSKÝ, 1995a; SÁNCHEZ MARCO, 2004; MICHAELIDIS, 2013; WILCZYNSKI et al., 2016), but do not allow precise ecological division.
between various warm/cold stages of the Late Pleistocene, mostly due to lack of absolute dating. Based on them, it can be established that some taxa occur quite frequently throughout the peninsula – grey partridge, brambling, Eurasian bullfinch and jay, peregrine falcon, and various corvids, while other were so far often encountered in the interior/montane, or Mediterranean (Aegean/Ionian/Adriatic) parts of Balkans (black grouse, Eurasian woodcock and skylark, griffon vulture, common quail). A number of species of the “boreal” avian complex have been found at many of the Late Pleistocene localities in the Balkans: short-eared owl, whimbrel, white-winged snowfinch, horned lark (Wilczyński et al., 2016), red-breasted goose, boreal owl, red knot (Mikhailidis, 2013), redwing (Mourer-Chauvire, 1981). At present, the main parts of their summer (breeding) range lie out of the Balkan region, or northwards from the region of the Pešturina cave. In the same time, a large number of bird species preferring warm climate (swifts, swallows, larks, pipits, orioles, shrikes, warblers, etc.) have been also found at these localities.

Further importance of this material is that the majority of remains come from Last Interglacial (MIS 5) deposits of the site, which are so far rarely observed and studied on Central Balkans, and the Balkans in general. Also, the occurrences of several bird taxa were identified for the first time in the Late Pleistocene record of this region.

Fig. 1. Sites of the major Late Pleistocene avifaunas of Balkan Peninsula: Pešturina (*); Tylos (1); Mavromori (2); Liko Gumbes C and Gerani complex (3); Kitsos (4); Vraona (5); Elaichoria 3 (6); Mecha Dupka (7); Bacho Kiro (8); Devetashka (9); Temnata and Cave 16 (10); Kozarska (11); Filipovska and Tsareva Tsarkva (12); Razhishkata (13); Kozarnika (14); Smolučka (15); Trebački krš (16); Mališina stijena (17); Crvena stijena; (18) Bijambarska (19); Zelena (20); Velika; (21) Veternica (22); Krapina (24); Šandalja I and II.
Short description of the site
Pešturina cave (Niš District, SE Serbia; N 43° 17'58", E 22° 37'0", 305 m a.s.l.; Fig. 1) is located on the rim of the Nišava river basin, at the transition from mountainous-broken terrain and a canyon entrance to lowlands. It is a small cave, 22 m deep, and 15 m wide. The cave entrance is 3.5 m high.

The main stratigraphic units consist of 3 Pleistocene (layers 2-4) layers, which contained the assemblage for this study, and one Holocene layer (layer 1). Late Pleistocene age is confirmed by C14 dating in cal. BP (ALEX & BOARETTO, 2014; ALEX et al., 2019), and ESR (Blackwell et al., 2014):

1. Layer 2: 15 960 – 16 380 (RTD-7148), 28 990 – 31 270 (RTK-6446), >37 800 (RTK-6445);
2. Layer 3: 32 067 – 33 400 (RTD-7231B), >40 660 (RTK-6449); 36 400 – 41 400 ESR
3. Layer 3/4: >41 100 (RTK-6447), 36 340- 46 330 (RTK-6450);
4. Layer 4: 43 080 – 45 170 (RTD-7149); 81 600 – 105 700 ESR.

The uncovered mammalian fauna is abundant (34 766 specimens) and is characterized by large diversity of species: *Mammuthus* sp., *Coelodonta antiquitatis*, *Bison priscus*, *Equus ferus germanicus*, *Equus hydruntinus*, *Megaloceros giganteus*, *Cervus elaphus*, *Dama dama*, *Capreolus capreolus*, *Capra ibex*, *Rupicapra rupicapra*, *Sus scrofa*, *Lepus europaeus*, *Castor fiber*, *Hystrix vinogradovi*, *Ursus spelaeus*, *Ursus arctos*, *Panthera leo*, *Panthera pardus*, *Crocuta crocuta*, *Canis lupus*, *Vulpes vulpes*, *Felis silvestris*, *Meles meles* (Milošević, 2016; Dimitrijević, in prep.). The site also yielded first Neanderthal remains in Serbia found in secure stratigraphic context (RADOVIĆ et al., 2019).

Nearly a thousand chipped stone artefacts were collected in course of excavations. These are mostly quartzite backed and naturally backed knives, retouched flakes, denticulates, and notches, atypical scrapers, with small proportion of flint products and low levallois index, giving the Mousterian industries from layers 4 and 3 Charentian character rich in denticulates. Layer 2 contained Gravettian artifacts, mostly finished tools among which microgravettes were most numerous (MIHALIĆ & MILOŠEVIĆ, 2013). Description and examination of all artefacts found in the cave remain out of the scope of present paper.

Materials and methods
Presented material was collected in course of systematic archaeological excavations during 2010 – 2013 campaigns from trench spanning over 16 m², and up to the depth of around 2,5 m. The material was collected through the washing and sieving of the excavated sediments on 4 and 2 mm mesh.

A total of 43 bones and bone fragments of birds were collected. All finds are kept in the Laboratory for Bioarchaeology (University of Belgrade, Serbia). Remains were determined using comparative osteological collection from the Vertebrate Animals Department of the National Museum of Natural History (Bulgarian Academy of Sciences, Bulgaria). Avian taxonomy follows del HOYO & COLLAR (2014, 2016). Species’ habitat preferences are after Harrison (1982).

Abbreviations: (1) anatomical: cmc. – carpometacarpus; dex. – dextra; dist. – distalis; juv. – juvenis; ph. – phalanx; prox. – proximalis; sin. – sinistra; tbt. – tibiotarsus; tmt. – tarsometatarsus; (2) ecological: GS – open grassland; WS – woodland; RS – rocks and rock massifs; AS - aquatic.

Results
Species composition and its paleoenvironmental implications
The established avifauna is rich and varied. The 26 taxa represent 13% of contemporary avifauna in the Balkans part of Serbia (SCI'BAN et al., 2015). Out of them, more than one half of the identified taxa (16) are recorded for the first time in the Late Pleistocene of Central Balkans. Most of the taxa (10) identified at Pešturina cave is stenotypic for forests, followed by those inhabiting grassland and rocky habitats (6), while one is from the aquatic habitat.

Avian remains were at least partly accumulated by large raptor, most probably Eurasian eagle owl (*Bubo bubo*). Bone fragmentation and beak punctures observed on some specimens fully correspond to that species (BOCHENSKI et al., 1993; LAROULANDIE, 2002). Similar avian accumulations have been studied in the region at several Pleistocene sites, both in Serbia and Bulgaria – Smolucka cave (MALEZ & DIMITRIJEVIĆ, 1990) (in Serbia), and Cave 16 (BOEV, 1999), Razhiska cave (BOEV, 2000a), Kozarnika cave (BOEV, 2001a) (in Bulgaria).
Galliformes

Phasianidae

**Perdix perdix** (Linnaeus, 1758)


Habitat: GS.

**Coturnix coturnix** (Linnaeus, 1758)


Remarks: First fossil/subfossil record for Serbia. The species was found in: Bacho Kiro cave, Bulgaria (BOEV, 2000a), Filipovska cave, Bulgaria (BOEV, 2001b), Kozarnika cave, Bulgaria (BOEV, 2001c), Temnata cave, Bulgaria (BOEV, 1994); Devetashka cave, Bulgaria (BOEV, 2001d), Bacho Kiro cave, Bulgaria (BOCHENSKI, 1982), Cave 16, Bulgaria (BOEV, 1999), and Mecha Dupka cave, Bulgaria (BOEV, 1999, 2001d).

Habitat: GS.

**Tetrao tetrix** Linnaeus, 1758


Remarks: Third record in the fossil/subfossil record for Serbia. The black grouse is a species that recently disappeared, both from Serbian and Bulgarian contemporary avifaunas. The species was found in: Velika Pećina, Croatia (MALEZ, 1984), Smolućka cave, Serbia (MALEZ & DIMITRIJEVIĆ, 1990; DIMITRIJEVIĆ, 1998), Zelena cave, Bosnia and Herzegovina (MALEZ, 1973, 1983), Trebjest cave, Montenegro (LENARDIC, 1990), Visoka Pećina, Croatia (LENARDIC, 1990), Vindija, Velika Pećina, Croatia (MALEZ, 1988a, 1997; MALEZ-BAČIĆ, 1975), and Veternica, Croatia (MALEZ, 1963; MALEZ-BAČIĆ, 1975), Filipovska cave, Bulgaria (BOEV, 2001b), Kozarnika cave, Bulgaria (BOEV, 2001a), Devetashka cave, Bulgaria (BOEV, 2001d), and Cave 16, Bulgaria (BOEV, 1999); and Elaichoria 3 cave, Chalkidiki, Greece (MIKOVSKY, 1995a).

Habitat: GS.

Anseriformes

Anatidae

**Anas crecca** Linnaeus, 1758

Material: cmc. sin. prox. (Layer 4). MNI 1


Habitat: AS.

Gruiformes

Rallidae

**Crex crex** Linnaeus, 1758


Remarks: First fossil/subfossil record for Serbia. The species was found in: Kozarnika Cave, Bulgaria (BOEV, 2001a), Temnata Cave, Bulgaria (BOEV, 1994), Devetashka Cave, Bulgaria (BOEV, 2001d), Cave 16, Bulgaria (BOEV, 1999).

Habitat: GS.
Otidiformes

Otididae

*Otis tarda*/*Tetrax tetrax*

Material: (cf.) vertebra cervicalis 9 (Layer 4). MNI 1.

Remarks: As the size of female *O. tarda* overlaps with that of males of *T. tetrax* we prefer to leave identification open. First record in the fossil/subfossil record for Serbia. *O. tarda* and *T. tetrax* were found in the Pleistocene of Šandalja I and Šandalja II, Croatia (*MALEZ & MALEZ-BAČIĆ*, 1974a,b; *MALEZ*, 1993). “*Otis tarda*/*Tetrax tetrax*” was found in the Devetashka cave, Bulgaria (*BOEV*, 2001d), and Vraona, Attika, Greece; (*O. tarda*; *BACHMAYER et al.*, 1989; *MLIKOVSKÝ*, 1995b; *SYMEONIDIS et al.*, 1978).

Habitat: GS.

Charadriiformes

Scolopacidae

*Scolopax rusticola* Linnaeus, 1758


Habitat: WS.

Strigiformes

Strigidae

*Aegolius funereus* (Linnaeus, 1758)


Habitat: WS.

Accipitriformes

Accipitridae

*Gyps fulvus* (Hablizl, 1783)

Material: (cf.) vertebra cervicalis 5 (Layer 4). MNI 1.


Habitat: RS.

Piciformes

Picidae

*Picus canus* Gmelin, 1788


Remarks: First fossil/subfossil record for Serbia. The Grey-headed woodpecker has not been encountered before in the fossil/subfossil record in the Balkans. Pešturina cave is its first Quaternary site.

Habitat: WS.

Falconiformes

Falconidae

*Falco tinnunculus* (Linnaeus, 1758)


Late Pleistocene Avifauna of the Pešturina Cave (Nišava District, SE Serbia)...


Habitat: RS.

Passeriformes

Alaudidae

Alauda arvensis Linnaeus, 1758

Remarks: First fossil/subfossil record for Serbia. The species was found in: Gornja Bijambarska cave, Bosnia and Herzegovina (MALEZ, 1970a), Vindija and Velika Pećina, Croatia (MALEZ, 1975, 1997; MALEZ-BAČIĆ, 1975); Filipovska cave, Bulgaria (BOEV, 2001b), Cave 16, Bulgaria (BOEV, 1999).
Habitat: WS.

Galerida cristata Linnaeus, 1758

Remarks: First fossil/subfossil record for Serbia. The species was found in: Gornja Bijambarska cave, Bosnia and Herzegovina (MALEZ, 1970a), Vindija and Velika Pećina, Croatia (MALEZ, 1975, 1997).
Habitat: GS.

Motacillidae

Anthus trivialis (Linnaeus, 1758)

Material: (cf.) humerus sin. prox. (Layer 3). MNI 1.
Remarks: First fossil/subfossil record for Serbia. The species was found in: Velika Pećina, Croatia (MALEZ, 1975, 1984; MALEZ-BAČIĆ, 1975), and Vindija cave, Croatia (MALEZ, 1988a, 1997), Kozarnika cave, Bulgaria (BOEV, 2001a), Devetashka cave, Bulgaria (BOEV, 2001d); Cave 16, Bulgaria (BOEV, 1999).

Habitat: WS.

Sittidae

Sitta europaea Linnaeus, 1758

Remarks: First fossil/subfossil record for Serbia. The species was found in: Gornja Bijambarska cave, Bosnia and Herzegovina (MALEZ, 1970a), Vindija and Velika Pećina, Croatia (MALEZ, 1975, 1997; MALEZ-BAČIĆ, 1975); Filipovska cave, Bulgaria (BOEV, 2001b), Cave 16, Bulgaria (BOEV, 1999).
Habitat: WS.

Fringillidae

Fringilla coelebs Linnaeus, 1758

Material: (cf.) humerus sin. juv. (Layer 4). MNI 1.
Habitat: WS.

Pyrrhula pyrrhula (Linnaeus, 1758)

Habitat: WS.

Hirundinidae

Ptyonoprogne rupestris (Scopoli, 1769)

Material: (cf.) humerus sin. (Layer 4). MNI 1.
Remarks: First fossil/subfossil record for Serbia. The species was found in: Bacho Kiro...
Cave, Bulgaria (BOCHENSKI, 1982), and Kozarnika Cave, Bulgaria (BOEV, 2001a).
Habitat: RS.

**Passerida**

**Petronia petronia** (Linnaeus, 1758)
Remarks: First fossil/subfossil record for Serbia. The species was found in: Razhishka Cave, Bulgaria (BOEV, 2000).
Habitat: RS.

**Oriolidae**

**Oriolus oriolus** (Linnaeus, 1758)
Remarks: First fossil/subfossil record for Serbia. The find of “Oriolus sp.” species was found in: Zelena cave, Bosnia and Herzegovina (MALEZ, 1973), Sandalja, Croatia (MALEZ, 1986), and Vindija cave, Croatia (MALEZ, 1988a).
Habitat: WS.

**Corvidae**

**Pyrrhocorax graculus** (Linnaeus, 1766)
Material: tbt. sin. dist.; ulna sin. dist.; humerus sin. (diaphysis part); (cf.) tmt. dex. dist. juv. (Layers 2, 3, 4). MNI 3.
Habitat: RS.

**Garrulus glandarius** (Linnaeus, 1758)
Habitat: RS.

**Corvus monedula** (Linnaeus, 1758)
Habitat: RS.
Late Pleistocene Avifauna of the Pešturina Cave (Nišava District, SE Serbia)


Habitat: WS.

Discussion

Layer and habitat species distribution

The species numbers according to main habitats is as follows: GS – 4(5) species, WS – 10, RS – 6, and AS – 2. The number of GS and WS is almost equal in layers 2 and 3, while in layer 4 GS taxa show the greatest taxonomic diversity.


Layer 4 (105 700 – 81 600) – 17 taxa, 14 species – GS obviously prevail: Gyps fulvus, Perdix perdix, Coturnix coturnix, Crex crex, Otis tarda/Tetrao tetrax, Pyonoprogne rupestris, Petronia petronia, Pyrrhocorax graculus, Corvus monedula. WS: Tetrao tetrax, Scolopax rusticola, Aegolius funereus, Sitta europaea, Fringilla coelebs, Garrulus glandarius. This layer corresponds to the late MIS 5 and perhaps MIS 4 (ca. 110 000 – 70 000 BP).

According to C^{14} dates, it is apparent that stratigraphic mixing occurred at the site, since dates from layer 3 already present infinite C^{14} ages, as well as earlier dates in upper portions of layer 4 compared to some samples from layer 3. However, according to Bayesian model (ALEX et al., 2019), layer 2 is not older than 34 kyA cal. BP, while layer 3 is not older than 45 kyA cal. BP. Also, the dates are not consistent at layer 3 and 4 boundary. Since there are infinite C^{14} ages both from layer 3 and 3-4 layer boundary, it is reasonable to assume the accuracy of ESR for layer 4 – especially since the minimum obtained age ranges from two different samples are 57 500 to 65 600 (BLACKWELL et al., 2012).

In general, the material from layers 2 and 3 refers to Last Glacial, but that of layer 4 reveals avifauna of the Last Interglacial.

The avifauna of Pešturina Cave among other late Pleistocene avifaunas on the Balkan Peninsula and northern Mediterranean

The avifauna of the MIS 3 environment (layers 2 and 3) is represented by some steppe (grey partridge, skylark), and some forest taxa (grey-headed woodpecker, bullfinch, tree pipit). An interesting record is the golden oriole, a species that “is typically a bird of open broadleaf forest”, but also lives in forest steppes (HARRISON, 1982). In context of layer 2 (maximum age of 34 kyA BP), it is interesting to observe a cohabitation species that prefer to feed in broadleaf (golden oriole), coniferous (grey-headed woodpecker), and mixed (bullfinch) forests. Such coexistence probably proves that Balkans were a suitable refugium even in the cool stages of the Late Pleistocene that directly preceded the LGM.

BLONDEL et al. (2010) states that Eurasian jay and common chaffinch (species with very large modern-day distributional ranges) survived in the Balkans during the glacial periods. Records of Pešturina (and other sites such as Krapina, Vindija, and Velika Pećina) fully support the continuity of their persistence in the Central Balkans since the Last Interglacial.

These authors also argue that contemporaneous colonies of Eurasian crag martins “occur near the coast” in the Mediterranean region (BLONDEL et al., 2010: p. 127), but numerous evidences from Pleistocene deposits, including Pešturina, prove its former wider inland distribution. Tree pipit is at present more common in the northern European forests than in the Mediterranean basin, but it was widely spread throughout the Balkans during the temperate/warm stages of Pleistocene.

As stated, at the height of the cool stages, “no arboreal vegetation persisted north of … the Carpathians” in Southeastern Europe (BLONDEL, 1997: cxxiv), the broad-leaved forests in the Balkans (including those in the region of Pešturina) were refugia for Eurasian jay, tree pipit, grey-headed woodpecker, golden oriole, common chaffinch, woodcock, bullfinch, etc. Data from layer 4 in Pešturina show that: (1) Typical steppe species occur

8
in layer 4: *Perdix perdix*, *Coturnix coturnix*, *Crex crex*, *Otis tarda/Tetrao tetrix*; (2) typical boreal forest species occur in layer 4: *Tetrao tetrix*, *Scolopax rusticola*, *Aegolius funereus*, *Sitta europaea*, *Fringilla coelebs*, *Garrulus glandarius*; (3) typical broad-leaf forest occur in layers 3 and 2: *Picus canus*, *Pyrrhula pyrrhula*, *Oriolus oriolus*, *Anthus trivialis*.

The “steppe” taxa most widespread in the interglacial environment (after HARRISON, 1982) were grey partridge, common quail, corncrake, bustards, rock sparrow, or “forest” (HARRISON, 1982) taxa - black grouse, woodcock, boreal (Tengmalm’s) owl, Eurasian nuthatch, common chaffinch, and Eurasian jay. The presence of the crag martin suggests relatively high summer temperatures, allowing it to hunt abundant small flying dipteran insects. Well-represented steppe and woodland species confirm the mosaic forest-steppe landscape in this region of the Central Balkans, similarly to those already observed in the eastern part of the Balkan Peninsula, i. g. Bulgaria (BOEV, 1999, 2001a, 2006).

All species, except black grouse, found in the Quaternary deposits of the Pešturina cave are present in the recent avifauna of the country (SCIBAN et al., 2015).

In general, the species composition partially corresponds to the Late Pleistocene avifaunas from some of the neighbouring regions in the Balkans – Croatia, Bosnia, Montenegro, and Western Bulgaria where most of the species encountered at Pešturina have been registered so far (BOEV, 1994, 1999, 2000a, b, 2001a, b, c, d, 2006a, b, c). All of them confirm their wider distribution throughout the Central Balkans during the Late Pleistocene. This is best illustrated over the example of Late Pleistocene avifauna from Kozarnika cave (NW Bulgaria, around 70 km away from Pešturina; Gravettian, 26000-19 000 B.P), which show striking similarity (BOEV, 2001a). The 14 common bird species from Pešturina cave (total taxa/species – 26) and Kozarnika cave (total taxa/species – 43; BOEV, 2001a) represent 51.8 % in the Pešturina cave and 32.6 % in the Kozarnika cave respectively. These are: *Anas crecca*, *Falco tinnunculus*, *Tetrao tetrix*, *Perdix perdix*, *Coturnix coturnix*, *Crex crex*, *Aegolius funereus*, *Anthus trivialis*, *Pionoprogne rupestris*, *Fringilla coelebs*, *Pyrrhula pyrrhula*, *Garrulus glandarius*, *Pyrrhocorax graculus*, and *Corvus monedula*.

In comparison to other contemporaneous Late Pleistocene avifaunas in the Balkans (Krapina cave, NW Croatia, around 580 km away from the Pešturina cave), we also found common species. The 3 common bird species from Pešturina cave (total taxa/species – 26) and Krapina cave (total taxa/species – 10; MALEZ & MALEZ, 1988; MALEZ, 1970b) represent 11.1 % and 30.0 % respectively. These are: *Gyps fulvus*, *Perdix perdix*, and *Garrulus glandarius*.

The refugia character of Central Balkans, as suggested by avifaunal remains discussed here, could also had impact of other faunal communities, as well as Paleolithic humans. Various warm adapted terrestrial fauna may have found favourable paleoecological conditions here, both from Mediterranean in course of Last Interglacial, and Danube corridor and Central Europe during the Last Glacial. These may have given the rise of specific mosaic environments rich primarily in species diversity, and perhaps shifts in their population density at various stages of the last Ice Age as well. This may opened up the possibility for Paleolithic humans to choose from a wider array of habitats in which they could establish successful subsistence. At least when the site of Pešturina is concerned, there are no marks of sharp changes in the habitats presented by avifauna, and no true boreal species, although the abrupt paucity in taxonomic representation from the Last Glacial deposits is evident in comparison with the Interglacial assemblage.

As many other Pleistocene localities on the Balkans, Pešturina cave provides interesting examples of the s. c. „mixed” avifaunas: *Tetrao tetrix* and *Oriolus oriolus* (Fig. 2), *Pionoprogne rupestris* and *Scolopax rusticola* (Fig. 3). At the present, breeding ranges of these species are more or less widely separated, but in the mosaic forest-steppe landscapes of Pleistocene they coexisted in the vicinities of the cave.

As FINLAYSON (2011) writes, the glaciations cold did not affect the Palearctic’s birds [dramatically], because the cold seasonality could be dealt with through migration, while sedentary species simply shifted geographical position. Among those that found refuge on the southern peninsulas, and other cryptic refugia, were the sedentary and partially migratory.
bioclimatic tolerants. The boreal birds returned north too, but also left prisoners, this time trapped around the mountains of the mid-latitude belt (s. c. glacial relicts). (p. 236). This author accepts the western Balkans, and to a lesser degree the Alps and the Italian mountains, as “the major European refugia for broadleaved trees during the last glaciation”. (p. 29).

Fig. 2. Present day ranges of Tetroa tetrix (after Schmitz, 1997) and Oriolus oriolus (after Wassmann, 1997) in Europe, with the position of Pešturina indicated. The areas of overlapped ranges are given in grey color.

Fig. 3. Present day ranges of Ptyonoprogne rupestris (after Sackl & Sere, 1997) and Scolopax rusticola (after Hoodless & Saari, 1997) in Europe, with the position of Pešturina indicated. The areas of overlapped ranges are given in grey color.

Pešturina cave reveals distribution of 5 present long-distance migratory birds, which are summer visitors in the Balkans. These belong to 3 orders – C. coturnix, A. trivialis, O. oriolus, P. rupestris, and C. crex. One species (P. petronia) deserves special attention, as its present day (summer) range lies far south of the location of the Pešturina cave (Mingozzi & Onrubia, 1997). This is the one of the northernmost occurrences of the rock sparrow in Pleistocene Europe.


Acknowledgements

Excavations at Pešturina cave are funded thanks to the Serbian Ministry of Culture grant No 177023, as is the study of presented Pešturina osteological material for one of the authors PhD (SM). We thank National Museum of Natural History in Sofia, Bulgaria, for avifauna comparative material, and Vesna Dimitrijević and Laboratory for Bioarchaeology at Faculty of Philosophy in Belgrade and its study collection. Special thanks to two anonymous reviewers of the manuscript for their helpful suggestions and remarks.

References


Blackwell A. B., Chu S., Chatty I., Huang Y. E. W., Mihailović D., Roksandić M.,


BOCHENSKI Z., TOMEK T., BOEUF Z., MITEV IV. 1993. Patterns of bird bone fragmentation in pellets of the Tawny Owl (Strix aluco) and the Eagle Owl (Bubo bubo) and their taphonomic implications. Acta zoologica cracoviensia, 36: 313-328.


BOEUF Z. 2006b. Middle Pleistocene birds from the Morovitsa Cave (Lovech District, NC Bulgaria). In: ZHALOVAI, I., DAALEV I. (Eds.), Proceedings of Jubilee Scientific Conference “75 years of organized speleology in Bulgaria”, Bulgarian
Late Pleistocene Avifauna of the Pešturina Cave (Nišava District, SE Serbia)...


Dimitrijević V., in prep. Key addition to faunal sequence of Middle-Late Pleistocene of Serbia: Remains of mammals from the deposits of the cave Pešturina (Jelašnica, Eastern Serbia).


Malez M. 1983. Ornitofauna iz gornjeg pleistocena Bosne i Hercegovine. RAD
Zlatozar N. Boev, Stefan Milošević

Jugoslavenske akademije znanosti i umjetnosti, 44: 7-37.


Late Pleistocene Avifauna of the Pešturina Cave (Nišava District, SE Serbia)...


Radović P., Lindal J., Mihailović D., Roksandic, Mirjana. 2019. The first Neanderthal specimen from Serbia: Maxillary first molar from the Late Pleistocene of Pešturina Cave. *Journal of Human Evolution* 131: 139-151.


Accepted: 21.03.2020
Published: 15.04.2020