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# Using birds as indicators of Neanderthal environmental quality: Gibraltar and Zafarraya compared

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ABSTRACT

We compare the Middle Palaeolithic sites of Gibraltar and Zafarraya in southern Iberia. We use birds as indicators of environmental quality and demonstrate huge differences between coastal and inland, mountain, sites separated by less than 150 km. We conclude that the Gibraltar sites represented locations of repeated occupation by Neanderthals over tens of millennia whereas Zafarraya represents a site of sporadic visits for particular prey. This is in response to very different climatic conditions. Our results show how important ecological quality is in understanding Palaeolithic sites and metapopulations and how birds are particularly informative in our understanding of the ecology of such sites.



## 1. Introduction

An ecological perspective is central to our understanding of human dispersion, dispersal and extinction in the Pleistocene (Finlayson, 2004). A case in point is the climatically unstable and fluctuating world of the Late Pleistocene, particularly between 50 and 30 thousand years ago (ka), of Eurasia (Finlayson and Carrión, 2007). In Eurasia, this period corresponds to the extinction of the Neanderthals, the arrival of modern humans and the interbreeding of both populations (Callaway, 2015). The distribution of human populations during this period probably took the form of a mosaic across a range of scales in space and time, defying interpretation by tried-and-tested methods available to archaeologists and palaeoanthropologists. The discovery of a new lineage of hominin, based on genetic analysis of an otherwise insignificant finger bone (Krause et al., 2010), is a case in point. Problems of interpretation of spatio-temporal data are heightened in regions of high topographic diversity at small scales (Finlayson et al., 2004). One such region is the south of the Iberian Peninsula. Birds are excellent indicators of ecological conditions, including habitat structure, bioclimate and environmental quality (Finlayson, 2011). In addition, virtually all Pleistocene species are still present today so that their ecological characteristics are well known. For these reasons birds are ideal subjects for studying the ecological characteristics of Pleistocene sites which they occupied (Finlayson, 2006). The two best studied southern Iberian localities in which the Pleistocene bird species have been studied are Gibraltar and Zafarraya. This paper compares, using the recorded Middle Palaeolithic avifauna, the ecological quality of the two sites and argues that we can only begin to understand complex metapopulation processes (Hanski and Gaggiotti, 2004), once a thorough understanding of the local and regional ecology has been reached. Although it will be difficult to answer metapopulation questions from archaeological and palaeontological sites, a better understanding of the ecological characteristics of such sites can be achieved with birds being ideal candidates for use as indicators

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(Finlayson et al., 2011). This paper aims to compare the ecological characteristics, and from that ecological quality (defined as suitability for persistent human occupation and survival), of two closely situated sites but which differ significantly in topographical and bioclimatic features (Jennings et al., 2011).

## 2. The sites

The Rock of Gibraltar has a long history of research related to the Neanderthals which dates back to the 19th Century with the discovery of the Forbes' Quarry skull (Stringer, 2000). It is a 6-km long limestone peninsula which is known to have been occupied by the Neanderthals from at least 127 ka until 32 ka (Finlayson et al., 2006). Nine sites within the peninsula have yielded evidence of Neanderthals, two with fossils. Of these we use four caves in the present study: Gorham's, Vanguard, Ibex Caves and Devil's Tower Rock Shelter. They are the four which have produced significant evidence of birds in association with Neanderthal occupation. Gorham's, Vanguard and Devil's Tower are situated at sea level and Ibex Cave is at 290 m above present sea level (asl).

Zafarraya is a single cave situated inland on a 12-km long limestone ridge, 140 km north-east of Gibraltar. The site is located at 1022 m (asl), 25 km from the nearest coast and only 70 km from the highest peak in the Iberian Peninsula (Mulhacen at 3842 m). Its history is more recent than Gibraltar's, with the discovery of a Neanderthal mandible in 1983 (Barroso Ruiz and de Lumley, 2006).

Gibraltar and Zafarraya are only 140 km from each other (Fig. 1). Bioclimatically, Gibraltar today is situated within the Thermo-Mediterranean, sub-humid, zone while Zafarraya is within the Meso-Mediterranean, sub-humid, zone (Jennings, 2006). The Mean Annual Temperature (T) at Gibraltar ranges between 17 and 19 °C (M, coldest month temperatures fall to between 4 and 100 °C) and at Zafarraya between 13 and 17 °C (coldest month temperatures fall to between −1 and 4 °C). The annual rainfall range (R) is equivalent, between 600 and 1000 mm. In modelled bioclimatic conditions mimicking a glacial (Jennings, 2006; Jennings et al., 2011), Gibraltar retained Thermo-Mediterranean conditions in exposed land due to falling sea-level and the higher areas reached Meso-Mediterranean while Zafarraya became completely Supra-Mediterranean (T 8–13 °C; M −4 to −1 °C). Both sites developed Dry rainfall regimes (R = 300–600 mm). Proximity to the high peaks of the Sierra Nevada and its glaciers had a greater climatic impact on Zafarraya than on Gibraltar where distance from the high peaks and the oceanic tempering climatic influence kept climatic conditions similar to today's with only an increase in annual temperature range of 2 °C during the worse moments (Ferguson et al., 2011).

## 3. The birds

The number of species identified from Middle Palaeolithic contexts at Gibraltar is 151 (Finlayson, 2015a). This is the highest for any Middle Palaeolithic locality in Eurasia (Tyrberg, 1998, 2008). This represents over 29% of the species currently recorded breeding

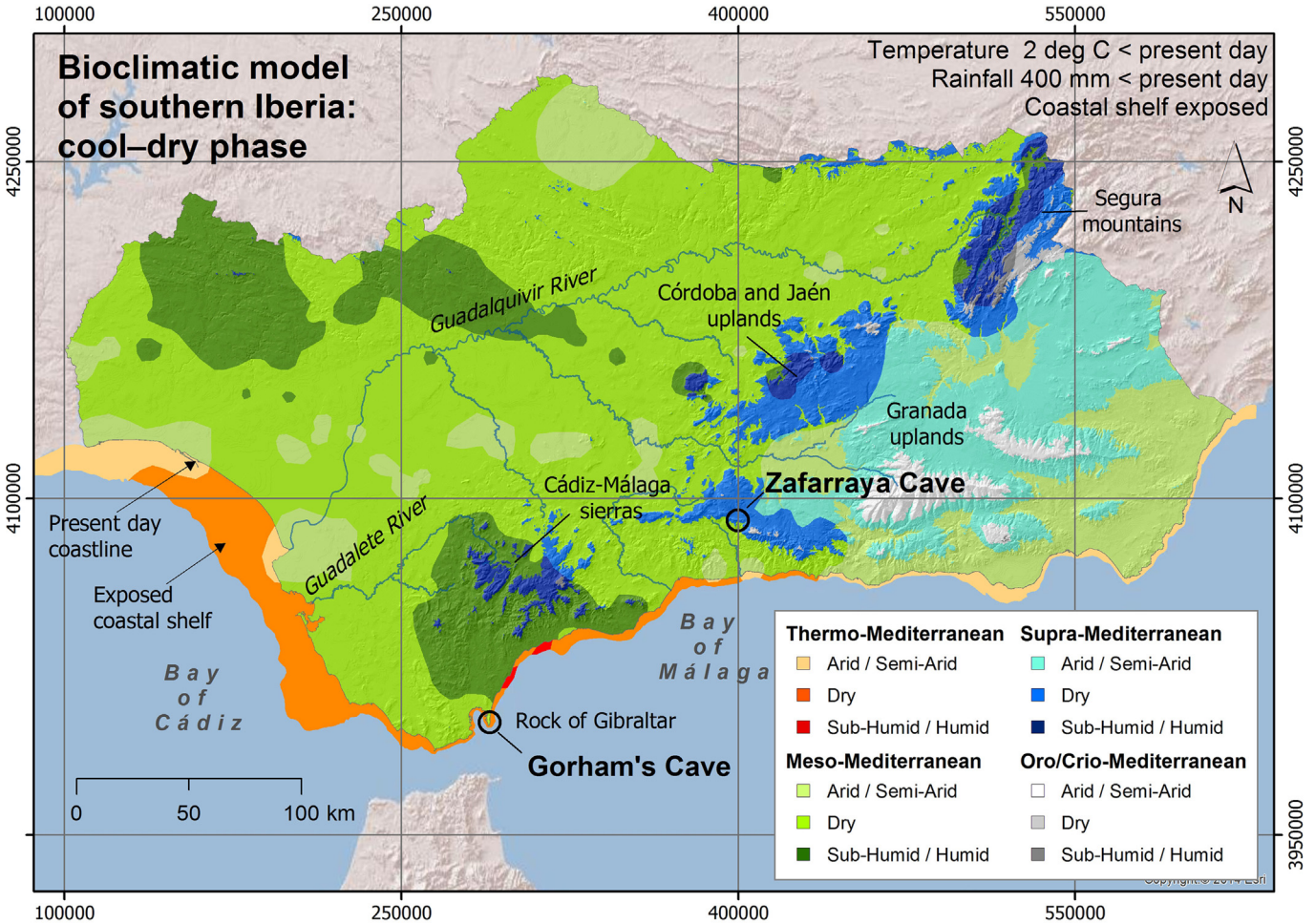


**Fig. 1.** Map of southern Iberia showing bioclimate during a cold and dry phase and indicating the location of Gibraltar and Zafarraya.

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in Europe (Hagemeijer and Blair, 1997). The main cave in the peninsula is Gorham's Cave with 142 species, followed by Devil's Tower Rock Shelter (77), Vanguard Cave (73) and Ibex (23), (Barton et al., 2012; Finlayson, 2015; present study). In contrast, Zafarraya has a bird species list of only 35 for Middle Palaeolithic contexts (Barroso Ruiz et al., 2006). This observation, in itself, is a clear indicator of the significant ecological differences between the two sites.

### 3.1. Characteristics of the main species recorded in Gibraltar and Zafarraya – general features

Finlayson (2011) has defined the biological characteristics of the 862 species currently occupying the Palaearctic Region. He has used the following criteria: Bioclimatic Tolerance, Latitude Position, Temperature Tolerance, Humidity Tolerance, Range width, Breeding and

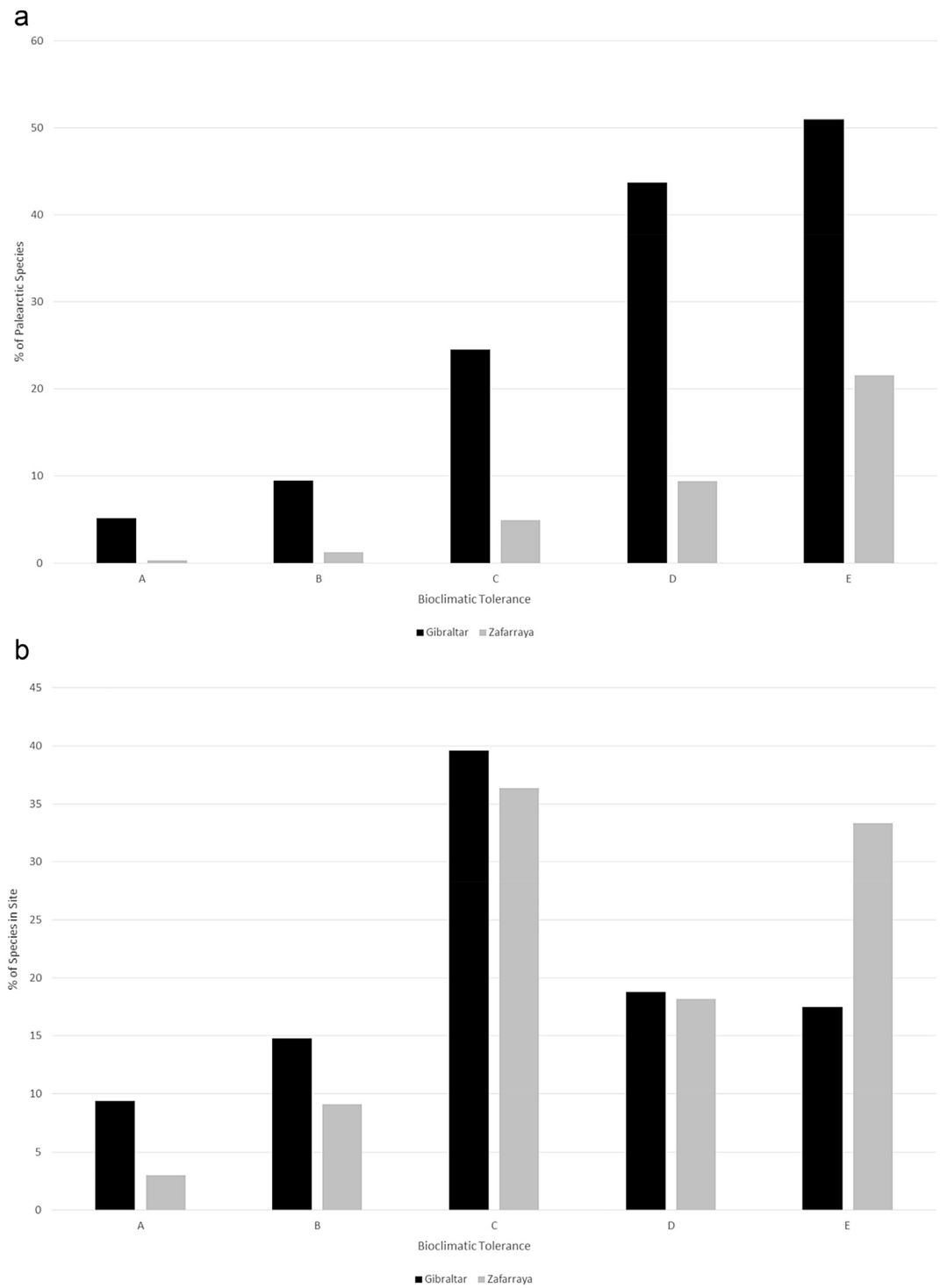


**Fig. 2.** Distribution of bird species recorded at Gibraltar and Zafarraya Pleistocene sites by Bioclimatic Tolerance. (a) Proportion of species out of all Palaearctic species in each category; (b) proportion of species in each category out of total for the site.

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Feeding Habitat, Diet and Migratory behaviour. These characteristics will be used to compare the avifauna of Gibraltar and Zafarraya.

### 3.1.1. Bioclimatic tolerance

Bioclimatic tolerance was ranked as follows: A = Specialist (occupies between 1 and 20% of the bioclimates available); B = Semi-specialist (21–40%); C = Moderate (41–60%); D = Semi-generalist (61–80%); E = Generalist (81–100%). The observed pattern of bird species representation by bioclimatic tolerance was similar for the two sites (Fig. 2a) but with many more species in Gibraltar. The majority of birds present were species with high bioclimatic tolerance, those best able to survive climatic fluctuations without having to move, reaching over half of the Palaearctic species in Gibraltar. In terms of representation within each site (Fig. 2b), species of intermediate tolerance (C) dominated in both sites and there was a greater representation of Category E in Zafarraya than in Gibraltar which had a greater spread of tolerances. Put together, these observations suggest that the Zafarraya birds are a reduced subset of

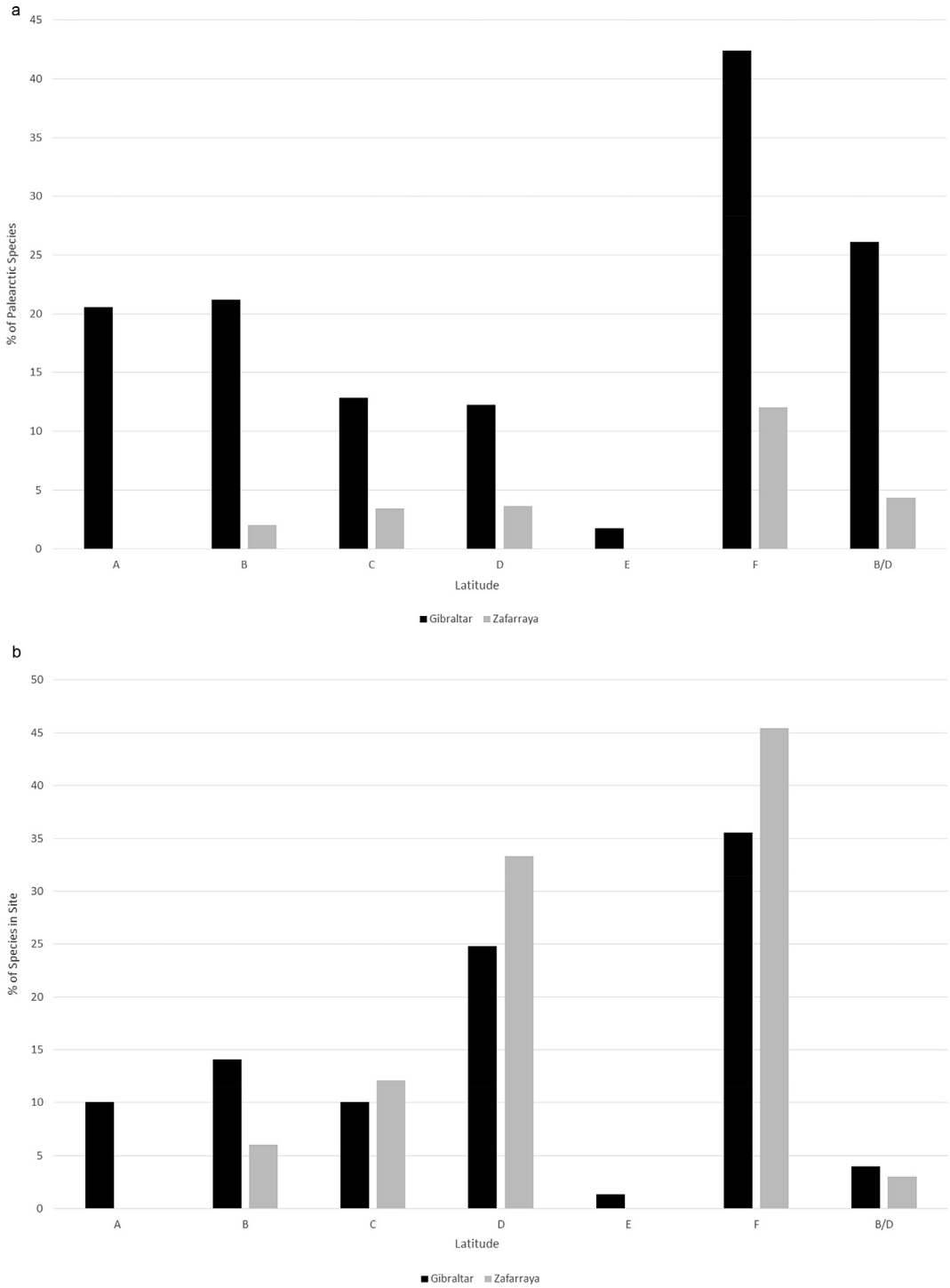


**Fig. 3.** Distribution of bird species recorded at Gibraltar and Zafarraya Pleistocene sites by Latitude. (a) Proportion of species out of all Palaearctic species in each category; (b) proportion of species in each category out of total for the site.

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the Gibraltar birds, with a greater overall emphasis on species capable of surviving wide climatic fluctuations.

### 3.1.2. Latitude range

Species were allocated to the latitude band on which its geographical breeding range was centred: A = Arctic (70°N); B = Boreal (60°N); C = Temperate (50°N); D = Mid-latitude Belt (warm species) (40°N); E = Subtropical (30°N); F = Multi-latitude (species occupied several latitude bands). The main species in Gibraltar and Zafarraya are those which occupy several latitude bands (Fig. 3a, Category F) which is in keeping with the high proportion of bioclimatically tolerant species noted above. Next in both sites are split category B/D species although this category is proportionally more important in Gibraltar than in Zafarraya. These are species which occupy boreal ranges but have relict populations in the mountains of the mid-latitude belt, a legacy of the Pleistocene (Finlayson, 2011). The differences between Gibraltar and Zafarraya (other than the greater number of species in Gibraltar) lie in the

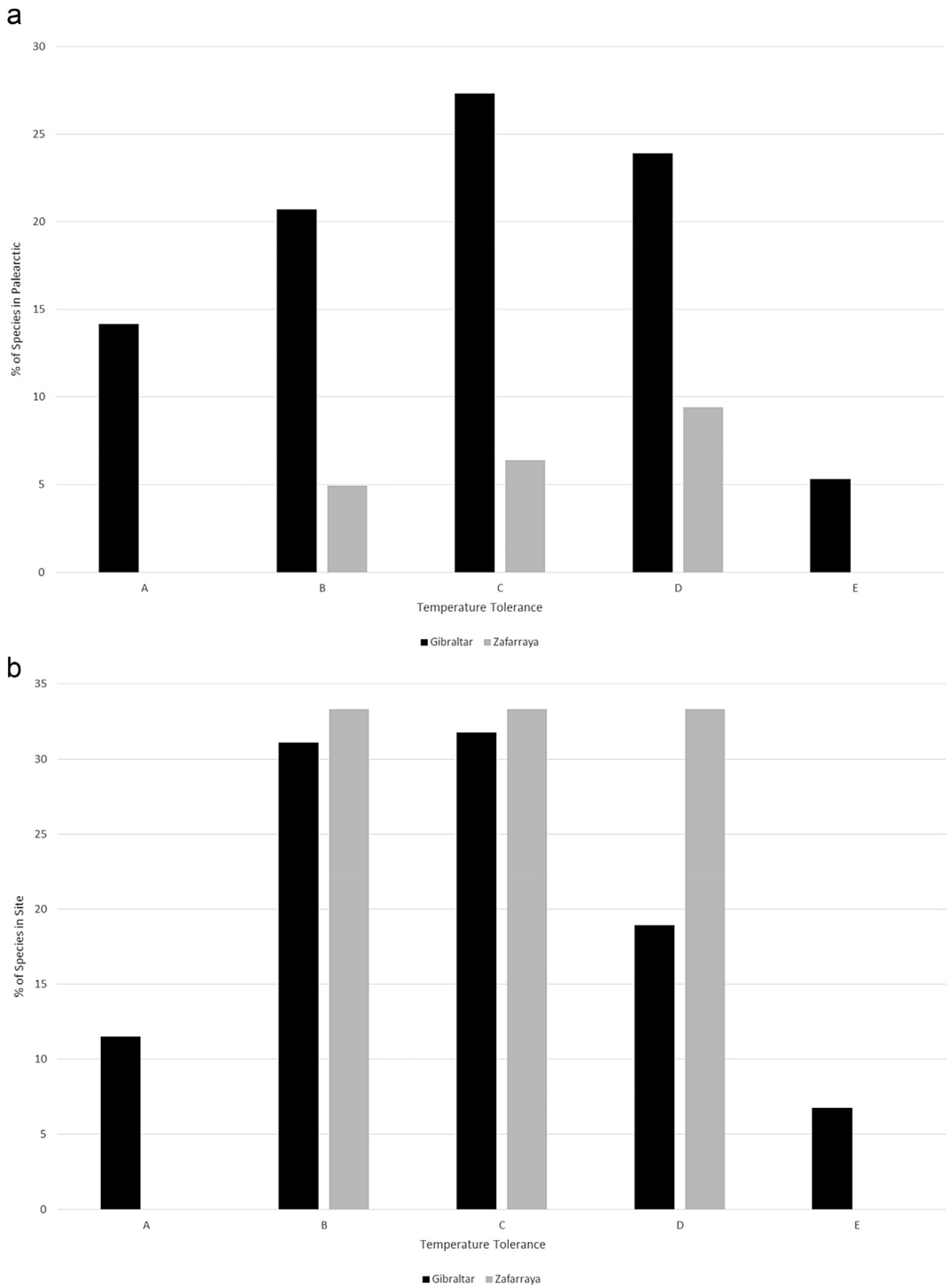


**Fig. 4.** Distribution of bird species recorded at Gibraltar and Zafarraya Pleistocene sites by Temperature Tolerance. (a) Proportion of species out of all Palaearctic species in each category; (b) proportion of species in each category out of total for the site.

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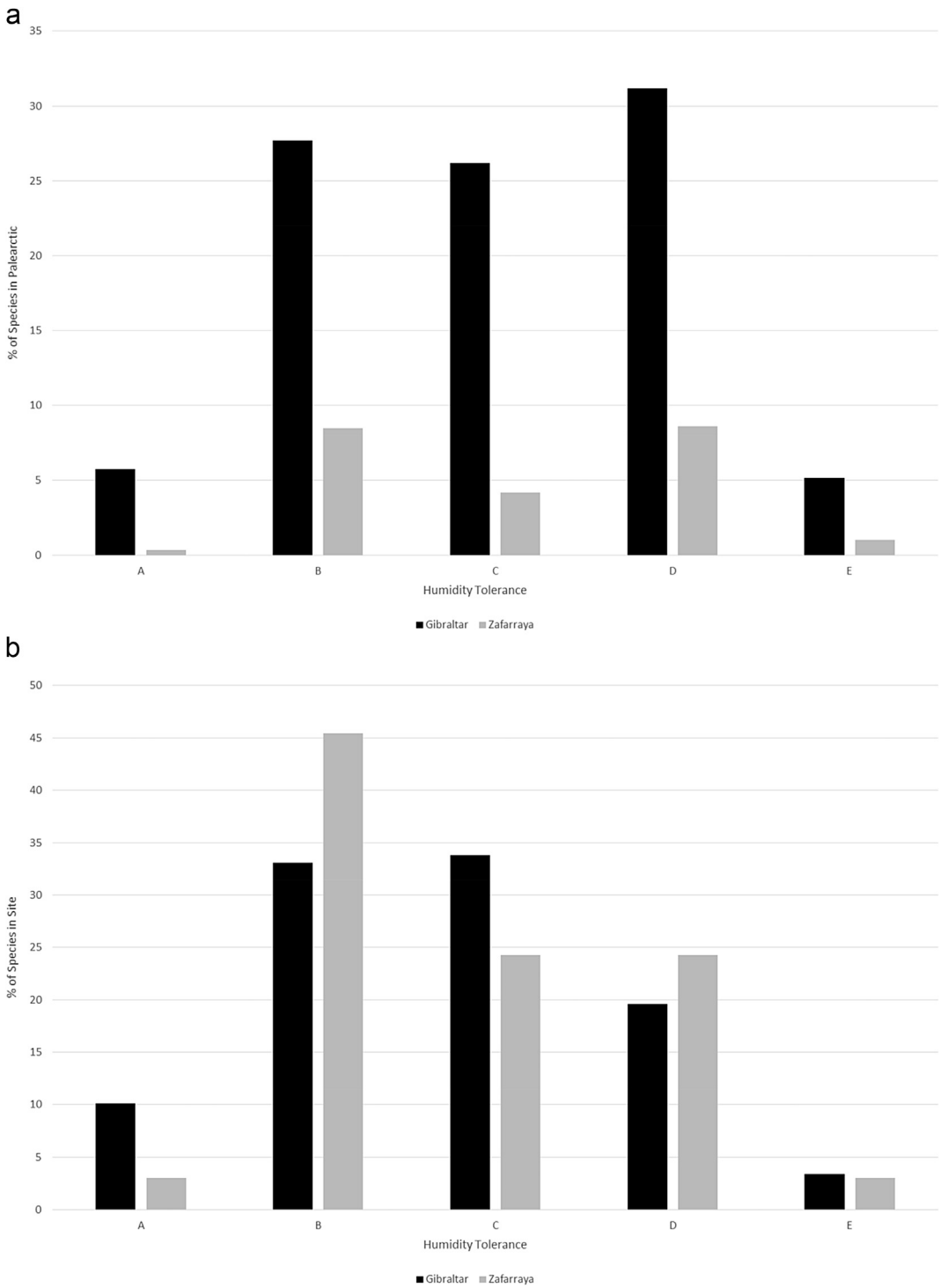


**Fig. 5.** Distribution of bird species recorded at Gibraltar and Zafarraya Pleistocene sites by Humidity Tolerance. (a) Proportion of species out of all Palaearctic species in each category; (b) proportion of species in each category out of total for the site.

greater range of latitude bands represented in Gibraltar. In particular Arctic, Boreal and Sub-tropical species are practically absent in Zafarraya (Fig. 3a). The high representation of Arctic and Boreal species in Gibraltar is almost exclusively due to a marine and coastal component of species, which are thought to have been displaced southwards during southward excursions of the Polar Front (Eynaud et al., 2009; Finlayson, 2011). Within each site multi-latitude and Category D species predominated (Fig. 3b). These are all species whose ranges coincide with the latitude position of both sites. The spread of latitude categories is greater in Gibraltar than Zafarraya, indicating this site's greater diversity of ecological and bioclimatic opportunities.

### 3.1.3. Temperature tolerance

From global maps used to calculate tolerance, Finlayson (2011) gave each species a position on a temperature gradient that went from cold (1%) to hot (100%): A = Species at the cold end (1–20%); B = 21–40%; C = 41–60%; D = 61–80%; and E (warmest, 81–100%).

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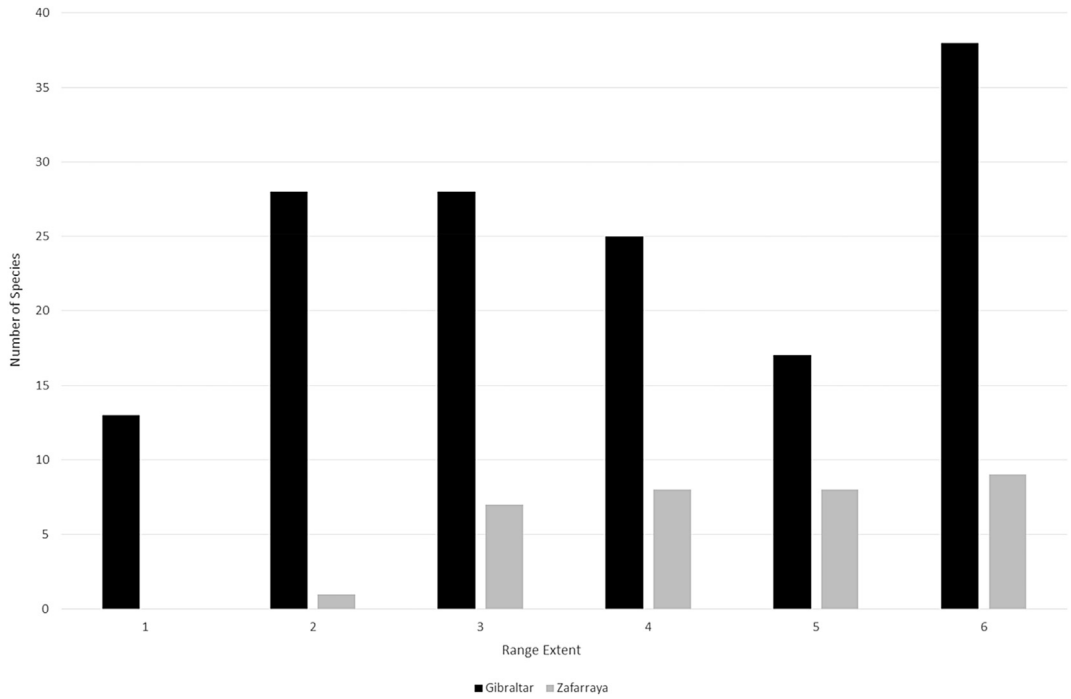


**Fig. 6.** Distribution of bird species recorded at Gibraltar and Zafarraya Pleistocene sites by Range Extent.

Zafarraya is a clear subset of Gibraltar, the latter having species tolerant of the entire temperature range (Fig. 4a) and the former only those at the centre of the distribution. This further supports our observations so far with the presence of a greater spectrum of species in Gibraltar that includes those from the coldest and warmest parts of the gradient. The pattern is repeated when within-site comparisons are made (Fig. 4b).

### 3.1.4. Humidity tolerance

As with temperature, Finlayson (2011) allocated species along a humidity gradient from A (1–20%) at the dry end and E (81–100%) at the wet end of the spectrum. The pattern in both sites is similar (Fig. 5a and b) and suggests that the temperature restriction affecting Zafarraya does not extend as much to humidity.

### 3.1.5. Range extent

One of six scores was allocated to each bird species in accordance to how geographically widespread they were, with 1 being the most restricted ranges and 6 the most widespread. In keeping with earlier observations the main species at both sites, especially Gibraltar, have broad geographical ranges (Fig. 6). They are therefore species that have managed to succeed in many bioclimatic and ecological conditions. The Zafarraya subset is, however, narrower than the Gibraltar one with many more species with narrow ranges also present in Gibraltar. This observation reinforces the previous observations in that Gibraltar offers greater ecological diversity than Zafarraya, permitting specialists (with narrow ranges) as well as generalists.

### 3.1.6. Foraging habitat

The habitat categories used in this and the next sub-sections, following Finlayson (2011) are: F = forest, habitats with a high density of trees; O = open, habitats without trees; M = mixed, habitats between F and O, including savanna, shrubland and mosaics; R = rocky; W = wetland, including all kinds of water habitats, including coastal ones, except marine; Ma = marine; A = aerial. All foraging habitats are represented at both sites except marine and rocky in Zafarraya (Fig. 7a). In keeping with earlier observations Gibraltar has many more species than Zafarraya and they represent a greater spread of habitats. At Zafarraya, the proportion of forest, mixed habitats and wetlands is very low and most species occupying the site were aerial foragers. As these species, which rely on airborne insects, are almost exclusively summer visitors to the region, the observations suggest that summer may have been a key moment of occupation of Zafarraya by birds. When comparing categories within sites (Fig. 7b), open habitat foragers predominate at both sites. Zafarraya retains the aerial component as important. The Gibraltar pattern includes a high contribution of wetland species and, overall, reflects the high habitat diversity available at this site.

### 3.1.7. Nesting habitat

Aerial and marine categories are not represented as there are no species in the Palaearctic capable of nesting in the air or the sea. The rocky habitat, present at both sites in abundance, is the main nesting habitat. In Zafarraya it is virtually the only available nesting habitat, with the exception perhaps of open habitats typical of mountain regions (Fig. 8a and b) and vegetated habitats (forest, mixed) and wetlands are virtually missing. Gibraltar offers a greater nesting habitat diversity than Zafarraya.

### 3.1.8. Diet

Finlayson (2011) describes the following diet categories for Palaearctic birds: O = omnivore, includes plant and animal matter; M = mixed-strategy carnivore, includes a range of animal matter; E = endothermic carnivore, only consumes warm-blooded prey; I = insectivore, only consumes insects and other arthropods; H = herbivore, only consumes plant matter; F = fish; N = necrophyte, eats carrion. Vultures (N) and raptors (E) dominate the species composition in terms of representation of Palaearctic species with 80% and of the Palaearctic vultures and over 50% of Palaearctic raptors in Gibraltar (Fig. 9a). Fish-eaters are an important category in

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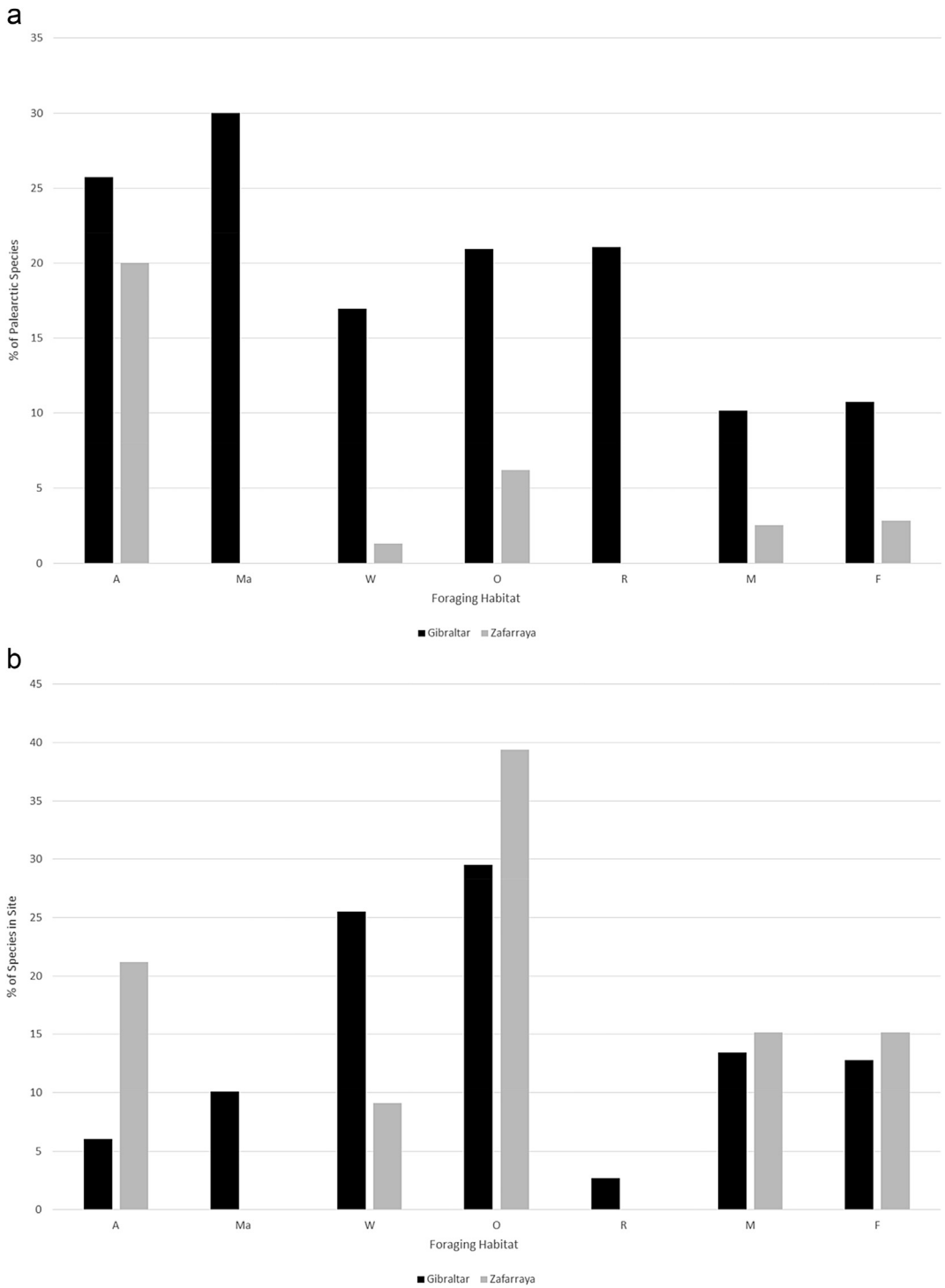


**Fig. 7.** Distribution of bird species recorded at Gibraltar and Zafarraya Pleistocene sites by Foraging Habitat. (a) Proportion of species out of all Palaearctic species in each category; (b) proportion of species in each category out of total for the site.

Gibraltar. Herbivores, a rare Palaearctic category (Finlayson, 2011) are missing altogether. The pattern is overturned when within-site comparisons are made. The reason for this is that raptors and vultures are comparatively few in the Palaearctic compared to other birds. As many are in the sites they give a high score in terms of proportion of the Palaearctic species but they are few in comparison with others which then become dominant within the site (Fig. 9b). Omnivores and mixed-strategy carnivores, species able to cope with a variety of foods, are dominant within each site and may be a further reflection of the generalist dominance of the sites, particularly Zafarraya. They include the corvids which are present in many hominin sites (Finlayson and Finlayson, in this volume). The insectivore component is more important in Zafarraya than Gibraltar which is linked to the number of summer-visiting aerial foragers. Vultures and raptors (E and N) are still important but are fewer in comparion to O and M (Fig. 9b).

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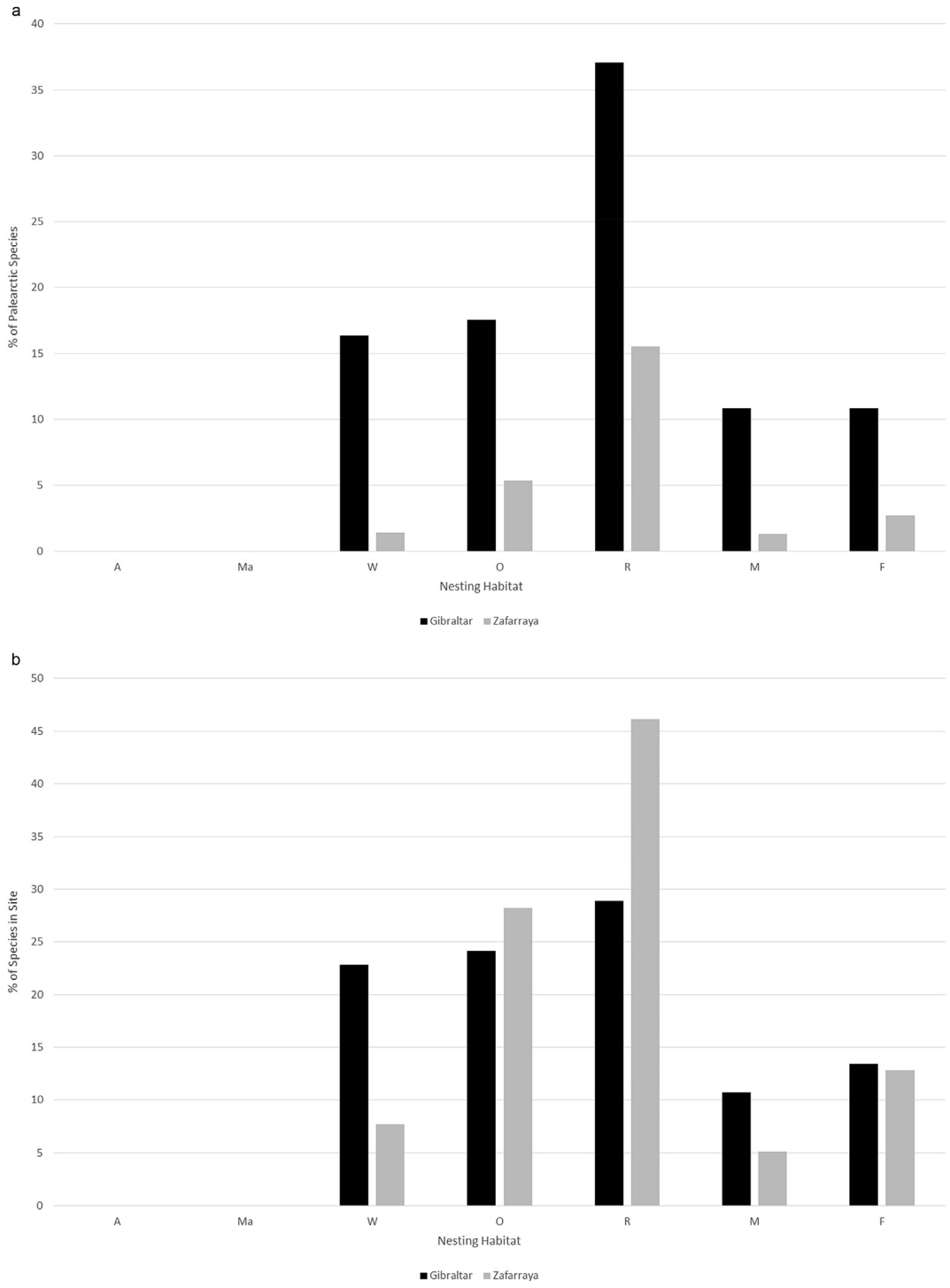


**Fig. 8.** Distribution of bird species recorded at Gibraltar and Zafarraya Pleistocene sites by Nesting Habitat. (a) Proportion of species out of all Palaearctic species in each category; (b) proportion of species in each category out of total for the site.

*3.1.9. Migratory behaviour*

Three categories are used: (S = sedentary; P = partially migratory, some populations of the species migratory); M = migratory. The three categories are represented at both sites (Fig. 10 a and b). The sedentary species are fewest and are generalists able to withstand winter conditions. Importantly, the fully migratory component is dominant in Zafarraya and reflects the component of summer visitors, noted above, and confirming the seasonal nature of the site. This seasonality, as reflected by the importance of migratory birds in each site, is also present in Gibraltar but in a less emphatic manner suggesting that Gibraltar, at sea level, is more seasonally buffered than Zafarraya in the mountains.

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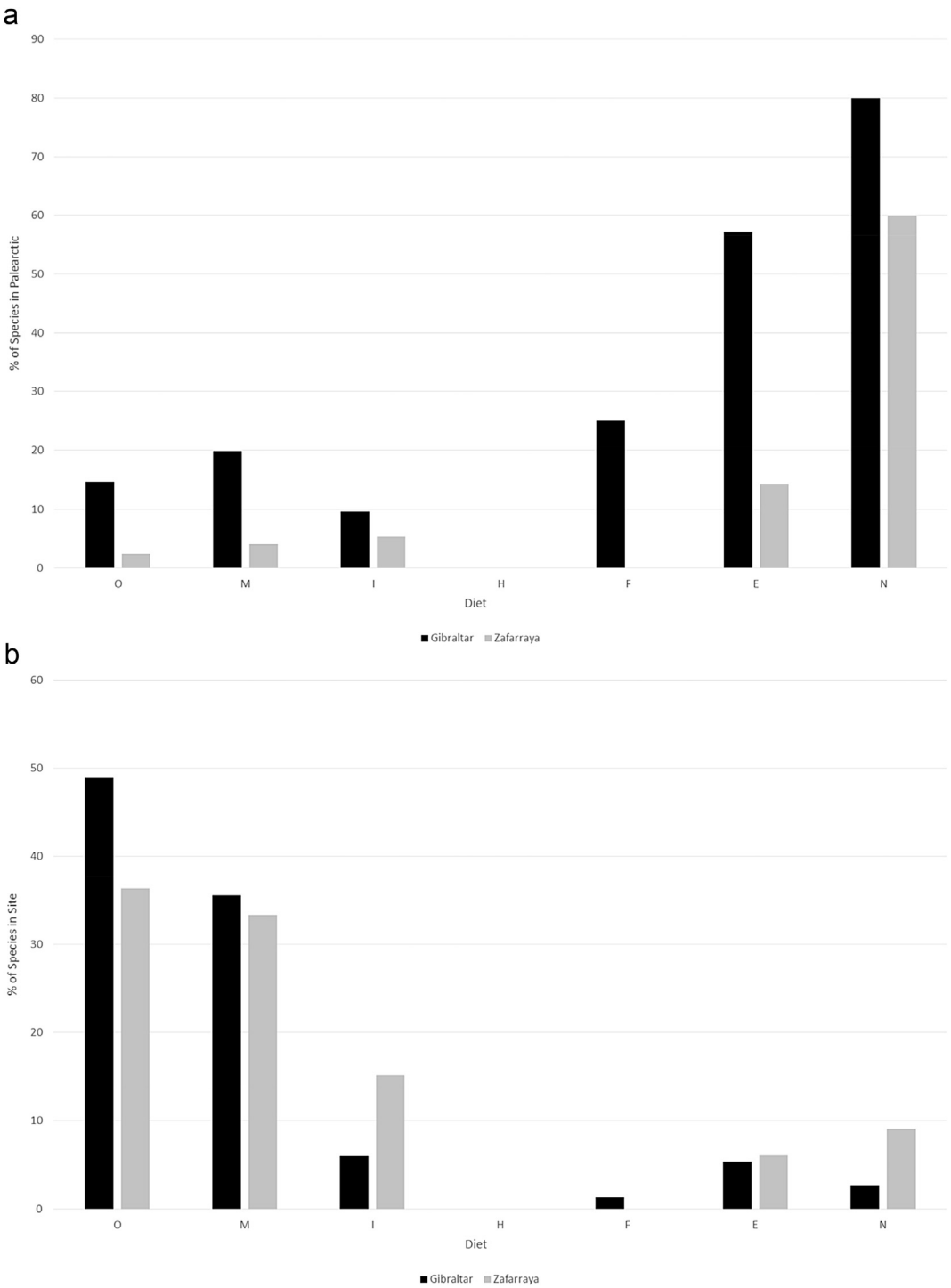


**Fig. 9.** Distribution of bird species recorded at Gibraltar and Zafarraya Pleistocene sites by Diet. (a) Proportion of species out of all Palaearctic species in each category; (b) proportion of species in each category out of total for the site.

### *3.2. Characteristics of the main bird species recorded in Gibraltar and Zafarraya – specific features and within-site breakdown*

In this section we examine some of the specific features that we identified in the previous section as being key to each site. We also split the Gibraltar site into individual cave sites to assess if there are differences within the peninsula itself. We cannot undertake the split for the Sierra de Zafarraya as it only has the one cave.

#### *3.2.1. Cliff-dwelling species*

Table 1 shows that over half of the bird species from Zafarraya are cliff-dwellers. They include an important component of summer-visiting aerial insectivores (swifts and hirundines). This is unsurprising given that the site is located on a long limestone ridge which would have offered plentiful opportunities for such species. We have seen above that the habitat is used preferentially for nesting and not feeding. Although the Gibraltar sites have many more cliff-dwelling species than Zafarraya, the proportion of

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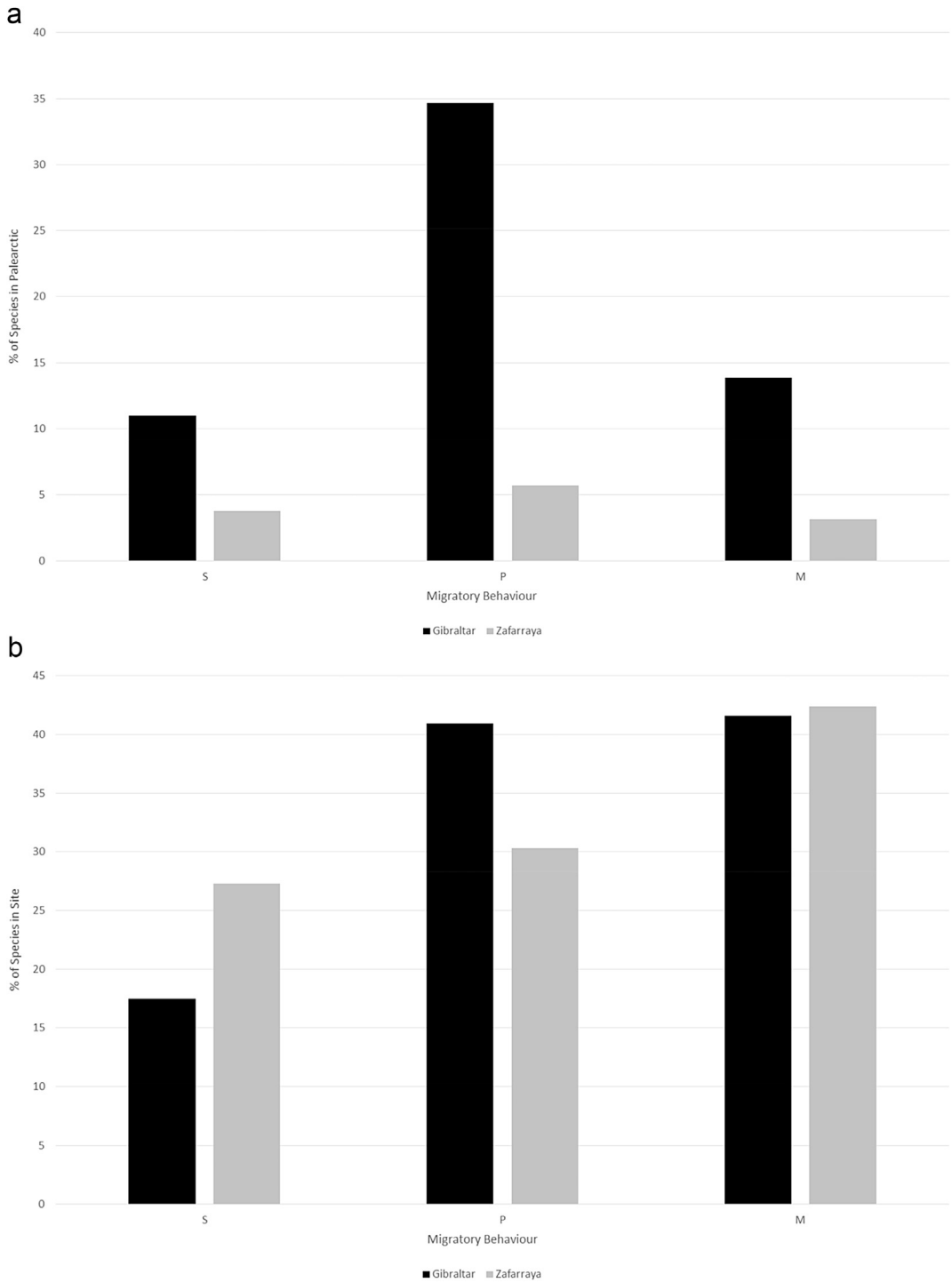


**Fig. 10.** Distribution of bird species recorded at Gibraltar and Zafarraya Pleistocene sites by Migratory behaviour. (a) Proportion of species out of all Palaearctic species in each category; (b) proportion of species in each category out of total for the site.

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the entire assemblage is much lower, between 28 and 38%. The exception is the small rock shelter known as Ibex Cave which is perched high on the Rock at the base of a cliff. Here the total species number was low and most species were cliff-dwellers, resembling the situation in Zafarraya. Gibraltar has an important component of marine species which nest on cliffs, which is absent from Zafarraya.

**Table 1**
Cliff-dwelling bird species found in Middle Palaeolithic contexts at Gibraltar and Zafarraya.

| Species | GOR | VAN | IBEX | DEV | GIB | ZAF |
|---|---|---|---|---|---|---|
| *Fulmarus glacialis* | 1 | 1 | | 1 | 1 | |
| *Pterodroma* sp | 1 | 1 | 1 | | 1 | |
| *Hydrobates pelagicus* | 1 | | | | 1 | |
| *Puffinus mauretanicus* | 1 | 1 | | 1 | 1 | |
| *Puffinus puffinus* | 1 | | | | 1 | |
| *Calonectris diomedea* | 1 | | | 1 | 1 | |
| *Morus bassanus* | 1 | | 1 | 1 | 1 | |
| *Phalacrocorax aristotelis* | 1 | 1 | | 1 | 1 | |
| *Phalacrocorax carbo* | | | | 1 | 1 | |
| *Geronticus eremita* | 1 | | | | 1 | |
| *Aquila chrysaetos* | 1 | | 1 | 1 | 1 | 1 |
| *Aquila fasciata* | 1 | | | 1 | 1 | |
| *Haliaeetus albicilla* | 1 | 1 | | 1 | 1 | |
| *Gyps fulvus* | 1 | 1 | | 1 | 1 | 1 |
| *Gypaetus barbatus* | 1 | | 1 | | 1 | 1 |
| *Neophron percnopterus* | 1 | 1 | | | 1 | 1 |
| *Falco naumanni* | 1 | 1 | 1 | 1 | 1 | 1 |
| *Falco tinnunculus* | 1 | 1 | 1 | 1 | 1 | 1 |
| *Falco peregrinus* | 1 | | 1 | 1 | 1 | 1 |
| *Falco eleonorae* | | | | 1 | 1 | |
| *Larus argentatus* | 1 | 1 | | 1 | 1 | |
| *Larus marinus/hyperboreus* | 1 | | | 1 | 1 | |
| *Rissa tridactyla* | 1 | 1 | | | 1 | |
| *Pinguinus impennis* | 1 | | 1 | 1 | 1 | |
| *Alle alle* | | | | 1 | 1 | |
| *Uria aalge* | | 1 | | 1 | 1 | |
| *Alca torda* | 1 | 1 | | 1 | 1 | |
| *Fratercula arctica* | 1 | 1 | | 1 | 1 | |
| *Columba livia* | 1 | 1 | 1 | 1 | 1 | 1 |
| *Bubo bubo* | 1 | 1 | 1 | 1 | 1 | |
| *Athene noctua* | 1 | 1 | | 1 | 1 | 1 |
| *Tyto alba* | 1 | | | | 1 | |
| *Apus apus/pallidus* | 1 | 1 | | 1 | 1 | |
| *Tachymarptis melba* | 1 | 1 | 1 | 1 | 1 | 1 |
| *Prunella collaris* | | | 1 | | 1 | |
| *Hirundo rustica* | 1 | 1 | | | 1 | 1 |
| *Hirundo daurica* | | | | | 0 | 1 |
| *Delichon urbica* | 1 | | | | 1 | 1 |
| *Ptyonoprogne rupestris* | 1 | 1 | | | 1 | 1 |
| *Monticola* sp | 1 | 1 | 1 | | 1 | |
| *Oenanthe leucura* | 1 | | | | 1 | |
| *Phoenicurus ochruros* | 1 | 1 | | | 1 | |
| *Pyrrhocorax pyrrhocorax* | 1 | 1 | 1 | 1 | 1 | 1 |
| *Pyrrhocorax graculus* | 1 | 1 | | 1 | 1 | 1 |
| *Corvus monedula* | 1 | 1 | | 1 | 1 | 1 |
| *Corvus corax* | 1 | 1 | 1 | | 1 | 1 |
| **Total** | **40** | **27** | **15** | **29** | **45** | **18** |
| **%** | **28.17** | **36.99** | **65.22** | **37.66** | **29.80** | **51.43** |

### 3.2.2. Carrion-feeding species

It is clear from Table 2 that many of the Zafarraya species are regular carrion feeders. This is also true for the Gibraltar caves although proportionately lower probably given the wider range of species there. Nevertheless, at Vanguard and Ibex Caves the proportions resemble Zafarraya.

**Table 2**
Carrion-feeding bird species found in Middle Palaeolithic contexts at Gibraltar and Zafarraya. Note that non-corvid passerine species included (*Motacilla alba* to *Sturnus* sp.) are regular at carcasses in the winter, feeding on fat, maggots and other insects attracted to the rotting flesh.

| Species | GOR | VAN | IBEX | DEV | GIB | ZAF |
|---|---|---|---|---|---|---|
| *Milvus migrans* | 1 | 1 | | 1 | 1 | |
| *Milvus milvus* | 1 | 1 | | 1 | 1 | |
| *Buteo buteo* | 1 | 1 | 1 | | 1 | |
| *Buteo lagopus* | 1 | | | | 1 | |
| *Aquila chrysaetos* | 1 | 1 | 1 | | 1 | 1 |
| *Haliaeetus albicilla* | 1 | 1 | | 1 | 1 | |
| *Aegypius monachus* | 1 | 1 | | 1 | 1 | |
| *Gyps fulvus* | 1 | 1 | | 1 | 1 | 1 |
| *Gypaetus barbatus* | 1 | | 1 | | 1 | 1 |
| *Neophron percnopterus* | 1 | 1 | | | 1 | 1 |
| *Accipiter gentilis* | 1 | 1 | | 1 | 1 | |
| *Larus argentatus* | 1 | 1 | | 1 | 1 | |
| *Larus marinus/hyperboreus* | 1 | | | 1 | 1 | |
| *Larus ridibundus* | 1 | 1 | | 1 | 1 | |
| *Motacilla alba* | 1 | | | | 1 | |
| *Erithacus rubecula* | 1 | 1 | | | 1 | |
| *Phoenicurus ochruros* | 1 | 1 | | | 1 | |
| *Turdus* sp | 1 | 1 | 1 | 1 | 1 | 1 |
| *Parus major* | 1 | | | | 1 | |
| *Fringilla coelebs* | 1 | 1 | | 1 | 1 | |
| *Passer* sp | 1 | | | | 1 | |
| *Sturnus* sp | 1 | 1 | | | 1 | |
| *Pyrrhocorax pyrrhocorax* | 1 | 1 | 1 | 1 | 1 | 1 |
| *Pyrrhocorax graculus* | 1 | 1 | | 1 | 1 | 1 |
| *Corvus monedula* | 1 | 1 | | 1 | 1 | 1 |
| *Corvus corone* | 1 | | 1 | 1 | 1 | 1 |
| *Corvus corax* | 1 | 1 | 1 | | 1 | 1 |
| *Cyanopica cooki* | 1 | 1 | | | 1 | |
| *Pica pica* | 1 | 1 | | | 1 | 1 |
| **Total** | **29** | **22** | **7** | **15** | **29** | **11** |
| **%** | **20.42** | **30.14** | **30.43** | **19.48** | **19.21** | **31.43** |

### 3.2.3. Wetland species

The richness of the Gibraltar sites is clear from the wetland species assemblage (Table 3). There is a virtual absence of wetland species in Zafarraya and the situation is similar at Ibex Cave, contrasting with the high proportion of species at the other Gibraltar sites.

**Table 3**
Wetland bird species found in Middle Palaeolithic contexts at Gibraltar and Zafarraya.

| Species | GOR | VAN | IBEX | DEV | GIB | ZAF |
|---|---|---|---|---|---|---|
| *Podiceps auritus* | 1 | | | | 1 | |
| *Plegadis falcinellus* | 1 | | | | 1 | |
| *Branta bernicla* | | 1 | 1 | | 1 | |
| *Tadorna* sp | 1 | | | | 1 | |
| *Clangula hyemalis* | 1 | 1 | | 1 | 1 | |
| *Melanitta nigra* | 1 | 1 | | 1 | 1 | |
| *Melanitta fusca* | 1 | | | 1 | 1 | |
| *Mergus merganser* | | | | 1 | 1 | |
| *Mergus serrator* | 1 | | | 1 | 1 | |
| *Somateria* sp | | | | 1 | 1 | |
| *Anas acuta* | | | | | | 1 |
| *Anas strepera/acuta* | 1 | | | | 1 | |
| *Anas platyrhynchos/strepera* | 1 | | 1 | 1 | 1 | |
| *Anas querquedula* | | | | | | 1 |
| *Anas crecca/querquedula* | 1 | | | 1 | 1 | |
| *Aythya fuligula* | 1 | | | 1 | 1 | |
| *Aythya ferina/marila* | 1 | | | | 1 | |
| *Fulica atra* | 1 | | | 1 | 1 | |
| *Rallus aquaticus* | 1 | | | | 1 | |

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**Table 3** (*continued*)

| Species | GOR | VAN | IBEX | DEV | GIB | ZAF |
|---|---|---|---|---|---|---|
| *Porzana porzana* | 1 | 1 | | 1 | 1 | |
| *Glareola pratincola* | 1 | | | | 1 | |
| *Himantopus himantopus* | 1 | | | | 1 | |
| *Charadrius* sp | 1 | 1 | | | 1 | |
| *Vanellus vanellus* | 1 | 1 | | 1 | 1 | |
| *Pluvialis squatarola* | 1 | 1 | | | 1 | |
| *Gallinago* sp | | 1 | | | 1 | |
| *Limosa limosa* | 1 | 1 | | 1 | 1 | |
| *Numenius arquata* | 1 | | | | 1 | |
| *Tringa totanus* | 1 | 1 | | 1 | 1 | |
| *Calidris canutus* | 1 | | | | 1 | |
| *Caldris alba/alpina* | 1 | 1 | | | 1 | |
| *Phalaropus fulicaria* | 1 | 1 | | | 1 | |
| *Chlidonias niger* | 1 | | | | 1 | |
| **Total** | **27** | **12** | **2** | **14** | **31** | **2** |
| **%** | **19.01** | **16.44** | **8.7** | **18.18** | **20.53** | **5.72** |

### 3.2.4. Coastal species

The pattern observed for wetland species is exaggerated for coastal species (Table 4). Clearly, there are none in Zafarraya which lies well inland but, curiously, the proportion at Ibex Cave is also very low. This suggests that the gradient of coastal species richness is steep away from the coast and that most species are lost very quickly.

**Table 4**
Coastal bird species found in Middle Palaeolithic contexts at Gibraltar and Zafarraya.

| Species | GOR | VAN | IBEX | DEV | GIB | ZAF |
|---|---|---|---|---|---|---|
| *Gavia stellata* | 1 | | | | 1 | |
| *Podiceps auritus* | 1 | | | | 1 | |
| *Branta bernicla* | 1 | 1 | 1 | | 1 | |
| *Tadorna* sp | 1 | 1 | | | 1 | |
| *Clangula hyemalis* | 1 | 1 | | 1 | 1 | |
| *Melanitta nigra* | 1 | 1 | | 1 | 1 | |
| *Melanitta fusca* | 1 | | | 1 | 1 | |
| *Mergus merganser* | | | | 1 | 1 | |
| *Mergus serrator* | 1 | | | 1 | 1 | |
| *Somateria* sp | | | | 1 | 1 | |
| *Anas strepera/acuta* | 1 | | | | 1 | |
| *Anas platyrhynchos/strepera* | 1 | | 1 | 1 | 1 | |
| *Anas crecca/querquedula* | 1 | | | 1 | 1 | |
| *Aythya fuligula* | 1 | | | 1 | 1 | |
| *Aythya ferina/marila* | 1 | | | | 1 | |
| *Haematopus ostralegus* | 1 | | | 1 | 1 | |
| *Himantopus himantopus* | 1 | | | | 1 | |
| *Numenius phaeopus* | 1 | 1 | | | 1 | |
| *Numenius arquata* | 1 | | | | 1 | |
| *Vanellus vanellus* | 1 | | | 1 | 1 | |
| *Pluvialis squatarola* | 1 | 1 | | | 1 | |
| *Charadrius* sp | 1 | 1 | | | 1 | |
| *Gallinago* sp | | 1 | | | 1 | |
| *Tringa totanus* | 1 | 1 | | 1 | 1 | |
| *Limosa limosa* | 1 | 1 | | 1 | 1 | |
| *Calidris maritima* | 1 | | | | 1 | |
| *Calidris canutus* | 1 | 1 | | | 1 | |
| *Calidris alba/alpina* | 1 | 1 | | | 1 | |
| *Phalaropus fulicaria* | 1 | 1 | | | 1 | |
| *Larus argentatus* | 1 | 1 | | 1 | 1 | |
| *Larus marinus/hyperboreus* | 1 | | | 1 | 1 | |
| *Larus ridibundus* | 1 | 1 | | 1 | 1 | |
| *Sterna* sp | 1 | | | 1 | 1 | |
| *Chlidonias niger* | 1 | | | | 1 | |
| **Total** | **31** | **15** | **2** | **17** | **34** | **0** |
| **%** | **21.83** | **20.55** | **8.7** | **22.08** | **22.52** | **0** |

### 3.2.5. Marine species

There is, as expected, a complete absence of marine species from Zafarraya and the proportion of species at Gibraltar is lower than for the other groups examined (Table 5). There is, nevertheless, a good representation of species. The number of species in Ibex is small but proportionately comparable to the other Gibraltar sites. This may be evidence that these marine species were nesting on the cliffs high up on the Rock of Gibraltar from where they could have accessed the marine environment easily.

**Table 5**
Marine bird species found in Middle Palaeolithic contexts at Gibraltar and Zafarraya.

| Species | GOR | VAN | IBEX | DEV | GIB | ZAF |
|---|---|---|---|---|---|---|
| Fulmarus glacialis | 1 | 1 | | 1 | 1 | |
| Pterodroma sp | 1 | 1 | 1 | | 1 | |
| Hydrobates pelagicus | 1 | | | | 1 | |
| Puffinus mauretanicus | 1 | 1 | | 1 | 1 | |
| Puffinus puffinus | 1 | | | | 1 | |
| Calonectris diomedea | 1 | | | 1 | 1 | |
| Morus bassanus | 1 | | 1 | 1 | 1 | |
| Phalacrocorax aristotelis | 1 | 1 | | 1 | 1 | |
| Phalacrocorax carbo | | | | 1 | 1 | |
| Haliaeetus albicilla | 1 | 1 | | 1 | 1 | |
| Larus argentatus | 1 | 1 | | 1 | 1 | |
| Larus marinus/hyperboreus | 1 | | | 1 | 1 | |
| Larus ridibundus | 1 | 1 | | 1 | 1 | |
| Rissa tridactyla | 1 | 1 | | | 1 | |
| Stercorarius parasiticus | 1 | | | | 1 | |
| Sterna sp | 1 | | | | 1 | |
| Chlidonias niger | 1 | | | | 1 | |
| Pinguinus impennis | 1 | | 1 | 1 | 1 | |
| Alle alle | | | | 1 | 1 | |
| Uria aalge | | 1 | | 1 | 1 | |
| Alca torda | 1 | 1 | | 1 | 1 | |
| Fratercula arctica | 1 | 1 | | 1 | 1 | |
| **Total** | **19** | **11** | **3** | **15** | **22** | **0** |
| **%** | **13.38** | **15.07** | **13** | **19.48** | **14.57** | **0** |

### 3.2.6. Other species

The remaining species found are species associated with different types of vegetation. A number are migratory and may reflect the importance of Gibraltar as a migration site, between Europe and Africa, in the Middle Palaeolithic as it is now. Some species in Zafarraya are worthy of comment. The Grey Partridge (*Perdix perdix*) is a species which today has its southern limit in the mountains of northern Spain (Finlayson, 2011). Its presence so far south is unusual. The species is absent from Gibraltar. If the identification of this species is correct, then it is indicative of the cooler conditions that reached down to Zafarraya but never had an impact on coastal sites, as at Gibraltar. The other species of interest is the Red-footed Falcon (*Falco vespertinus*). This is a continental species which is a summer visitor to Europe. Although it may be observed in Iberia on passage it is mainly a species of eastern Europe and beyond, typically associated with dry climatic steppic conditions (Finlayson, 2011). Its presence may reflect the extent of arid continental conditions in Iberia during cold periods, once again a situation not reflected at the coastal sites.

## 4. Discussion

Our results clearly contrast the ecological conditions at Zafarraya and Gibraltar, only 140 km apart. Zafarraya has an impoverished avian assemblage relative to Gibraltar which has more than four times as many species. Importantly, the assemblage at Zafarraya is dominated by generalist sedentary or specialised migratory species, particularly cliff-dwellers many of which are also scavengers. Curiously, tree nesting scavengers (e.g. Cinereous Vulture, *Aegypius monachus*) are absent from Zafarraya but not Gibraltar. Cliff-nesting and scavenging birds are also important at Gibraltar but they are embedded within a wider assemblage of species that

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includes important components of wetland, coastal and marine species. Here there is a greater diversity of species, including generalists but also specialists. In our opinion, this diversity is indicative of ecological quality. Finlayson and Finlayson (in this volume) have drawn attention to the close relationship between Neanderthals and scavenging birds.

The picture is reflected in other taxa (Barroso Ruiz and de Lumley, 2006). Among mammals, the presence of Stoat (*Mustela erminea*) and Chamois (*Rupicapra pyrenaica*) in Zafarraya reflects a similar situation to that noted for the Grey Partridge and is indicative of the impact of cold continental conditions which are not recorded at Gibraltar. The presence of Dhole (*Cuon alpinus*) and the ass (*Equus hydruntinus*) reflects arid conditions, as with Red-footed Falcon, not observed on the coast. The relative impoverishment of the amphibian and reptile fauna (sensitive to cold temperatures and arid conditions) compared to Gibraltar (Blain et al., 2011) further strengthens the observations made in this paper.

The vegetation recorded from charcoal at Zafarraya (Barroso Ruiz and de Lumley, 2006) indicates a strong component of cold-arid climate species, ranging from meso-Mediterranean to oro-Mediterranean bioclimates with a small representation of warmer species, presumably during milder climate phases. The pattern is in complete contrast with the situation at Gibraltar which harbours a wide diversity of largely thermo-Mediterranean vegetation throughout (Carrión et al., 2008), a phenomenon well-established for the Strait of Gibraltar (Rodriguez-Sanchez et al., 2008).

The suggestion has been made that most of the lithics excavated in Zafarraya were stone tools made outside and brought to the site (Barroso Ruiz and de Lumley, 2006). This would suggest that Zafarraya was a place of sporadic visitation, presumably in search of particular prey targets such as ibex and horse. In this regard, Ibex Cave in Gibraltar most resembles Zafarraya (Shipton et al., 2013) and also has a similar avian assemblage pattern. It contrasts with sites of repeated occupation over millennia, such as Gorham's Cave, where the richness and abundance of resources, exemplified in this paper by birds, permitted the establishment of long-term populations. Ibex Cave in Gibraltar should therefore be seen in the context of a peripheral site to the main occupation caves, one that was visited occasionally with the specific objective of hunting Ibex. It further emphasises in interpreting human occupation sites, this time at local scale, the importance of understanding the nature and function of each occupation site.

## 5. Conclusions

In order to understand the dynamics of human metapopulations, we need to understand the function and use of individual sites in the landscape and not treat them all as equivalent. Each site has specific ecological characteristics which characterise their use by humans. In particular attempts should be made to categorise sites by metapopulation status. Source populations generate more offspring than the environment can support and thus contribute surplus individuals to other populations. In contrast, sink populations, with a negative reproductive balance, are maintained by immigration from source populations. Finlayson (2015b) made a first attempt to categorise Palaeolithic sites as sources or sinks at a global level. This paper follows by examining two sites that are within the same region but differ significantly in ecology.

Birds reveal a high ecological diversity in Gibraltar, supporting earlier publications using a variety of taxa. Zafarraya is revealed as a very specific subset of the Gibraltar site, dominated by cliff-dwellers, scavengers and omnivores, and a summer component of cliff-nesting aerial insectivores. It is not very different from the avian assemblage which would be expected today if there had been no human interference leading to species loss. Zafarraya resembles Ibex Cave in Gibraltar. The latter was a specific, seasonal, Neanderthal hunting site for Ibex. In spite of the proximity of Ibex Cave to the other Gibraltar sites, its avian assemblage resembles that of Zafarraya which we suggest was also a specific, probably seasonal, hunting station.

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