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PIGEONS AND PELAGICS:
INTERPRETING THE LATE PLEISTOCENE AVIFAUNAS OF
THE CONTINENTAL 'ISLAND' OF GIBRALTAR

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Resum

Quatre jaciments espeleològics del Pleistocè tardà (la balma de Devil's Tower i les coves de Gorham, Vanguard i Ibex) han lliurat alguns dels conjunts ornítics més abundants i diversos del Paleàrtic Occidental, incorporant devers 130 taxa. Les associacions d'espècies sense equivalents moderns esdevenen a tots els jaciments, però semblen poder-se atribuir amplament als efectes combinats del temps promig de deposició i a la conducta migratòria, i no a l'existència d'ambients no anàlegs als actuals. S'ha confirmat que un total de 18 espècies han criat a la regió de Gibraltar durant el Pleistocè tardà. A més d'espècies típiques de les comunitats modernes d'ocells ibèrics, incloent *Cyanopica cyanus*, s'han identificat restes immadures de dues ànneres, *Melanitta nigra* i *M. fusca*, que actualment crien a les regions Àrtica i Boreal. La presència com a reproductors d'altres espècies marines nord-atlàntiques, com *Pinguinus impennis*, no s'ha pogut confirmar.
Paraules clau: Pleistocè tardà, Gibraltar, avifaunas, migració, cria, *Melanitta nigra, M. fusca*.

Abstract

Four Late Pleistocene cave sites; Devil's Tower Rock Shelter and Gorham's, Vanguard and Ibex Caves, located on the southern Iberian peninsula of Gibraltar, have yielded some of the most abundant and diverse avifaunal assemblages in the Western Palearctic, incorporating some 130 taxa. Species associations with no modern equivalents occur throughout the sites, but appear to be largely attributable to the combined effects of depositional time-averaging and migratory behaviour and not the former existence of non-analogue environments. A total of 18 species are confirmed as having bred in the region of Gibraltar during the Late Pleistocene. In addition to species typical of modern Iberian bird communities, including *Cyanopica cyanus*, immature remains were identified of two ducks, *Melanitta nigra* and *M. fusca*, that currently breed in Boreal-Arctic regions. Breeding presence of other North Atlantic marine species, including *Pinguinus impennis* cannot be confirmed.
Key words: Late Pleistocene, Gibraltar, avifaunas, migration, breeding, *Melanitta nigra, M. fusca*.

INTRODUCTION

The Late Pleistocene encompasses the last interglacial-glacial cycle, from around 130,000-12,000 years before present (BP). It is a period characterised by rapid climatic fluctuations, culminating in the last glacial maximum and subsequent amelioration between approximately 24,000-12,000BP. Understanding the nature of these fluctuations and their impacts is not only important in terms of understanding possible future climatic changes, but also in coming to understand the development of modern faunal communities. Remains of vertebrates are one source of evidence of both climate change and faunal development. Mammalian faunas have traditionally dominated Late Pleistocene vertebrate research, however more attention is now being given to exploring the palaeoecological potential of other classes. Foremost amongst these are birds, now shedding a widespread reputation of being both scarce and uninformative (cf. Lowe & Walker, 1997; see also Tyrberg, 1998).

Bird remains are in fact regular, if not necessarily abundant, components of Late Pleistocene vertebrate assemblages, and may be found in a wide range of depositional situations, (Tyrberg, 1998; Morales Muñiz 1993). Recovery of Late Pleistocene bird material is frequently associated with the excavation of archaeological sites, whether Neanderthal or Anatomically Modern Human (Tyrberg, 1998). Consequently, there is a strong tendency for interpretation to focus primarily on taphonomic issues, considering them in relation to human activities (cf. Stewart, 2002). However, there is a growing awareness of the intrinsic value of avian assemblages, particularly as palaeoecological proxies.

One key advantage of birds in palaeoecological applications is the availability of a vast modern ornitho-

logical literature, from which detailed analogue information can be drawn for Pleistocene populations (Baird, 1989; Morales Muñiz, 1993). Modern analogues can be used at various levels of interpretation, from examining an individual taxon to comparing the overall species composition of an assemblage with modern biogeographic regions. Where modern equivalents exist, this approach can be very successful (e.g. Tyrberg, 1999). However, a phenomenon widely recognised in Late Pleistocene research is the occurrence of faunal associations with no modern equivalents. Known as non-analogue faunas, these are of considerable interest as possible evidence of environments unknown at the present day (Lowe & Walker, 1997). They are regularly encountered in avian assemblages, where species now characteristic of contrasting habitats or climate are found in association. In the Mediterranean region, such associations have been interpreted as evidence of compression of biomes during the Late Pleistocene, for example of Mediterranean and tundra habitats in southern France (Covas & Blondel, 1998). Whilst non-analogue species associations may undoubtedly represent non-analogue environments, it is also possible that they could be relicts of taphonomic processes, or even reflect certain aspects of avian behaviour. Alternative explanations for their origins must be considered before a non-analogue environment can be invoked.

Modern analogues of bird species are primarily based upon habitat and climate preferences, frequently of species' breeding ranges. Implications of the behaviour of modern species, and the resulting interactions with their environment tend to be given less emphasis. Yet, certain aspects of species' behaviour can have profound implications on the understanding of an assemblage's palaeoecological signal.

Paramount amongst these behaviours is migration, which in birds may occur across a wide range of temporal and geographic scales. However, it is the various seasonal movements of many species which are the most obvious manifestation of the behaviour, and which also have the greatest potential impact on the palaeoecological signal of an assemblage. It should be noted that far from affecting a minority, seasonal migration is in fact demonstrated by the majority of bird species in the Western Palearctic (Alerstam, 1990). As a result, most modern temperate continental avian communities are extremely fluid in their species composition throughout the year. Migratory behaviour represents a particular palaeoecological problem, as a migrant occurring in an assemblage may potentially represent one of several situations: its summer breeding grounds, its wintering grounds or its route of passage. This can have habitat implications, but most importantly it has climatic significance, as the majority of migratory movements primarily reflect seasonal conditions.

In addition to species that migrate along fairly well defined routes, others may disperse very widely from their breeding ranges over a large, generalised area (Wernham et al., 2002). This dispersal migration is characteristic of many pelagic seabirds, whose wanderings may potentially bring them within the range of terrestrial localities far beyond their established breeding range. As a result, in addition to non-analogue climatic

associations, such behaviour introduces potential for extreme contrasts in habitats to occur within a single assemblage (e.g Stewart, 2002).

The aim of this paper is to examine the implications of introducing possible effects of migration and other aspects of avian behaviour into palaeoecological interpretation, using examples drawn from a group of localities in Gibraltar, southern Iberia, where non-analogue species associations are a hallmark of their Late Pleistocene avifaunas.

Located on the north-east coast of the Strait of Gibraltar, the small peninsula of Gibraltar itself lies within a region significant in modern ornithology as the junction of two major migration bottlenecks. Terrestrial species passing north or southwards between the continents of Europe and Africa seek a relatively short sea-crossing over the Strait, only 14 km at its narrowest; marine and coastal species are funnelled through the Strait as they pass east or westwards between the western Mediterranean and the Atlantic. From a palaeontological perspective, the physical geography of the region means that even during Late Pleistocene changes in sea-level or in the precise nature and extent of migration, the Strait of Gibraltar would have remained a bottleneck that migrating birds would have been constrained to use. Both the Strait of Gibraltar and the great limestone outcrop of the Rock of Gibraltar that dominates the peninsula are today classed as Important Bird Areas, in direct recognition of their significance to migrating birds (Heath & Evans, 2000).

Furthermore, Southern Iberia also has biogeographic significance as having been one in a chain of Late Pleistocene temperate refugia located along the southern edge of Europe, characterised by modern associations of largely non-migratory residents with restricted ranges, often including endemic species or subspecies (Harrison, 1982). In a lesser way, the Rock of Gibraltar itself can be regarded as a refugium, providing a montane habitat 'island' within a lowland coastal plain. Although Gibraltar has no endemic birds, it does have an endemic plant species, Gibraltar Candytuft *Iberis gibraltarica* (Cortés & Finlayson, 1988).

The combination of Late Pleistocene refugium and migration bottlenecks have created some of the richest, most diverse and dynamic avian communities in the Western Palearctic. At present, some 75% of Western Palearctic bird species may occur within the region of the Strait of Gibraltar during the course of a year (Finlayson, 1992). This represents a total of some 400 species known from the Strait region, of which 186 are breeding residents or summer migrants; 91 are wintering or passage migrants; and the remainder are accidental vagrants (Finlayson, 1992).

Certain caves on Gibraltar have yielded abundant bird remains from the Late Pleistocene, offering the prospect of detailed proxy evidence of Gibraltar's Late Pleistocene palaeoenvironments. Non-analogue species associations occur regularly throughout the stratigraphic sequences of these sites. However, given the fundamental importance of migration to the region's modern avifauna, the phenomenon must be given due consideration as a possible cause of non-analogue associations, in addition to other taphonomic factors.

MATERIAL AND METHODS

Gibraltar's Late Pleistocene avifaunas have been examined in a number of previous works, most important of which are the original publications on the bird remains from Devil's Tower Rock Shelter, recovered during the 1920s (Bate, 1928) and those from excavations at Gorham's Cave during the 1950s (Eastham, 1968). Whilst no material has been retrieved from Devil's Tower since the original work, a number of excavations have been carried out at Gorham's Cave, adding considerably to knowledge of the site and its fauna (Stringer *et al.*, 2000).

The present paper primarily considers material recovered from Gorham's Cave and the two previously unexplored sites of Ibex and Vanguard Caves during a series of excavations conducted between 1994-1998 under the auspices of the Gibraltar Museum and The Natural History Museum, London (Stringer, 2000; Stringer *et al.*, 2000; Finlayson *et al.*, 2000). Identifications of the avian assemblages were made using the recent comparative collections of The Natural History Museum, Tring, supplemented by the collections of the Museo Nacional de Ciencias Naturales, Madrid and the Institut Mediterrani d'Estudis Avançats, Palma de Mallorca. The recently excavated bird material from Gorham's and Vanguard Caves is now mainly held by the Department of Palaeontology, The Natural History Museum, London; further Gorham's and Vanguard specimens and the entire Ibex Cave assemblage are held by the Gibraltar Museum.

Avian taxonomy used here follows Dickinson (2003). Grid references are given in Universal Transverse Mercator.

RESULTS

In its present form, Gibraltar is a small peninsula, 5.2 km long, 1.6 km wide (natural maximum) and about 6 km² in area. It is dominated by the vast outcrop of Jurassic limestone known as the Rock, which extends roughly 2.5 km along the peninsula, rising to over 400 m at its highest point. At least 143 caves have been discovered within the Rock (Rose & Rosenbaum, 1991), in which varied archaeological and palaeontological assemblages have been preserved. A summary is given below of each site considered here, Gorham's, Vanguard and Ibex Caves, and Devil's Tower Rock Shelter (Fig. 1), in geographic order from north to south.

Devil's Tower Rock Shelter

Devil's Tower Rock Shelter (approximately TF 89270293) lay at the base of the cliffs of the North Face of the Rock. In addition to the cave chamber itself, a narrow fissure some 1.2 m wide and 4 m deep, the original excavations encompassed the emerging talus slope and the *in situ* deposits it covered (Garrod *et al.*, 1928). A stratigraphic sequence of over 10 m was recorded, comprising various tufas, sands and speleothems overlying a raised

beach. Faunal remains, particularly mammals and birds, were abundant throughout the site. Bate (1928) identified 33 species of bird, but did not appear to have studied the entire collection (Cooper, 1999). Re-examination of the complete Devil's Tower bird assemblage has increased this to some 80 species. Notable avian finds here are various pelagic species, including both *Alle alle* Little Auk and *Pinguinus impennis* Great Auk, and well over a thousand bones of *Tachymarptis melba* Alpine Swift (Cooper, 1999). However, most famous of the fossils unearthed here is the fragmentary skull of a Neanderthal child, found within the cave itself (Garrod *et al.*, 1928). In general though, evidence of human activity was relatively scarce and the site seems to have been used only occasionally. Recent attempts to date material from Devil's Tower have been made difficult by low collagen levels in the bones, but the majority of the sequence does in fact appear to lie beyond the range of radiocarbon (C. B. Stringer, pers. com.).
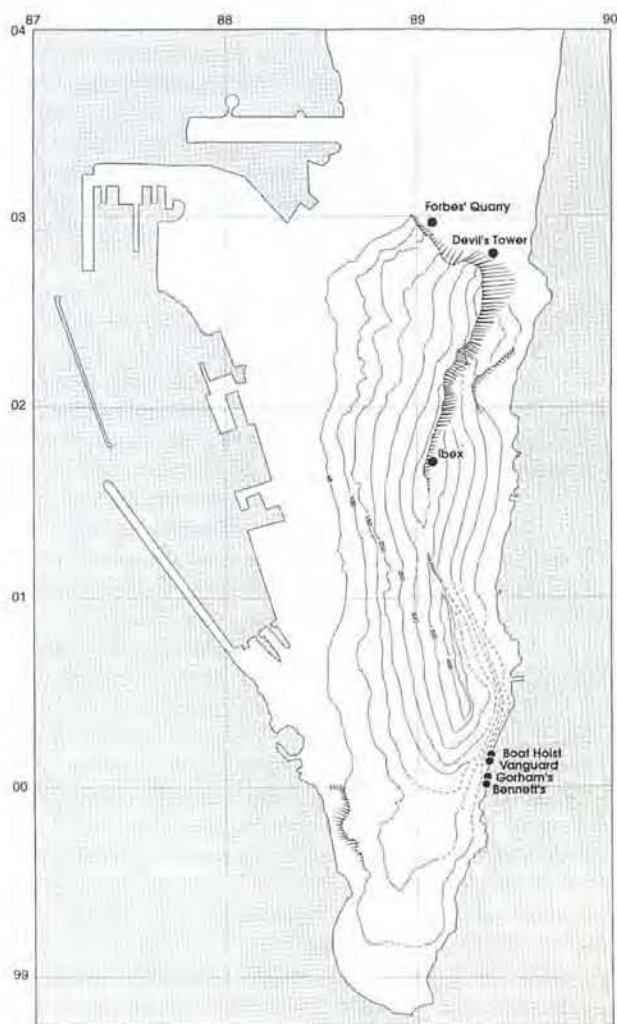

Fig. 1. Map of Gibraltar, southern Iberia, indicating cave sites described in text. Reproduced courtesy of R.N.E. Barton.

Fig. 1. Mapa de Gibraltar, sud de la Península Ibèrica, indicant els jaciments espeleològics descrits al text. Reproduït per cortesia de R.N.E. Barton.

Ibex Cave

Ibex Cave (approximately TF89050172) is located on the eastern side of the Rock, some 250-300 m above sea-level. It is a small cave, about 5 m wide at its mouth and about 5 m deep, lying at the base of limestone cliffs above thick deposits of wind-blown Pleistocene sands. During the only excavation at this site, in 1994, a sedimentary sequence approximately 3 m deep was excavated; this was dominated by silty sands, and included some small blocks of breccia. Despite the relatively small scale of the site, a diverse faunal assemblage was recovered, largely from the single, least disturbed, unit. The assemblage included abundant remains of both large and small mammals, and numerous fragments of tortoise (Fernandez-Jalvo & Andrews, 2000). In terms of birds, some 240 remains were recovered, of which some 75 were identified at least to family, representing at least 25 species (Cooper, 1999; 2000a). These included a complete left femur of *Pinguinus impennis* Great Auk, and an almost complete skull of *Morus bassanus* Northern Gannet (Cooper, 1997, 1999).

A variety of lithics were recovered, predominantly flakes and cores, but these have been interpreted as representing a single episode of human activity at the site, and it is primarily regarded as having been a carnivore den (Barton, 2000; Fernandez-Jalvo & Andrews, 2000).

Electron Spin Resonance dating placed the *in situ* fauna of the undisturbed unit within the mid-last glaciation, approximately between 37,100 ± 3,300 (early uptake model) to 49,400 ± 3,200 (late uptake model) BP (Rhodes *et al.*, 2000).

Vanguard Cave

Vanguard Cave (TF 89360021) is one of a suite of caves that also includes Gorham's Cave, along the eastern coast of the Gibraltar peninsula. It possesses a huge overhanging double entrance and narrow chamber, developed along a fissure, of at least 20 m in length. A second considerably smaller chamber is located to the north of the cave's inner entrance. A total depth of some 16 m of sediments was recorded in the main chamber, consisting mainly of massive coarse sands interspersed with thin units of brown silts and silty sands. Micromorphological examination of the sediments suggests that the cave maintained a relatively dry environment throughout its depositional history (Macphail & Goldberg, 2000). Avifaunal remains were abundant, though not in the quantities found at Gorham's Cave. However, this may reflect the fact that excavations in Gorham's were located relatively deeper within its chamber. Evidence of human activity suggested a relatively low intensity of use, though well preserved discrete hearths were found in several horizons (Barton, 2000).

To date, only the 1995 and 1996 seasons' assemblages have been studied in detail. From an overall collection of some 2,900 remains, about 900 were referable at least to family, with a total of approximately 70 species identified (Cooper, 1999). The pattern of occurrence of bird bones through the sequence revealed a few high-diversity horizons amid units with relatively sparse assemblages. Reflecting the smaller number of recovered specimens in comparison to Gorham's, fewer non-analogue species associations were identified in single horizons, but overall the avifaunas did include species characteristic of both climate and habitat contrasts, such as *Fulmarus glacialis* (Northern Fulmar) and *Coracias garrulus* (European Roller) (Cooper, 1999).

The majority of Vanguard's sequence fell outside the limits of AMS radiocarbon dating, though a few dates in the uppermost levels suggested that the cave had filled by approximately 45,000 BP (Pettit & Bailey, 2000). Additionally, a charcoal sample from a discrete hearth in the side-chamber gave an AMS radiocarbon date of >44,100 BP. To provide a chronology for the main chamber, luminescence dating was applied. Samples from the middle and lowest excavated levels gave ages of 93,380 ± 7,300 BP and 111,850 ± 10,020 BP (Pettit & Bailey, 2000).

Gorham's Cave

Gorham's Cave (TF 89340007) lies adjacent to Vanguard Cave. Of a similar form to its neighbour, it has a very wide, high entrance enlarged by wave-action and tapers back into a passage-like chamber in excess of 40 m length. The 1995-1998 excavations concentrated on deposits lying approximately within the first 20 m of the main chamber.

The exposed sedimentary sequence of some 16-18 m depth, consisted of largely sandy units in the lower sections, with the middle and upper levels dominated by dark, organic rich clays and sandy silts. A particular characteristic of these upper levels was a high degree of local variation in the sediments, with complex relationships between individual units. Also notable was evidence of intense biological activity, including burrowing, human occupation and significant quantities of guano (Macphail & Goldberg, 2000).

A very wide range of palaeontological remains were recorded from this site, including a diverse mammalian assemblage and an abundant herpetofauna in addition to the thousands of bird bones recovered (Currant, 2000; C. Gleed-Owen, *in litt.*). Extensive evidence of human occupation was found, including hearths with charcoal and charred bones, butchered bones and numerous lithics.

Only the avifaunal remains recovered during the 1995 and 1996 seasons have been studied in their entirety. From some 9,000 remains, about 2,600 were identifiable at least to family level, representing approximately 90 species (Cooper, 1999). Typically, bird remains were relatively scarce in most levels, but a few units yielded assemblages of considerable diversity and abundance. Without exception, these units included non-analogue species associations, usually of 'warm' Mediterranean species with 'cold' boreal or arctic species, e.g. *Upupa epops* Hoopoe and *Melanitta fusca* Velvet Scoter, or *Falco naumanni* Lesser Kestrel with *Clangula hyemalis* Long-tailed Duck.

A dating program using AMS radiocarbon targeted the upper levels of the sequence, due to their high archaeological interest. Most dates unfortunately did not coincide with the majority of the bird-yielding units, however one particularly high-diversity unit yielded two dates from charcoal samples; 45,300 ± 1,700 BP from within a hearth and 51,700 ± 3,300 BP at the unit's base (Pettit & Bailey, 2000).

The bird assemblages studied by Eastham (1968) were recovered during excavations directed by John Waechter from 1951-54. However, although this collection still constitutes an important record of birds from Gorham's Cave, Waechter's stratigraphic scheme is now known to be seriously flawed, thus compromising the use of these birds in detailed palaeoecological analyses (Currant, 2000). Consideration of these assemblages is therefore not included here.

DISCUSSION

Together, the combined avifaunal assemblages from Gorham's, Vanguard, Ibex and Devil's Tower Caves represent the richest Late Pleistocene avifauna known from the Iberian peninsula, and one of the richest in the Western Palearctic (cf. Tyrberg, 1998). In total, remains from at least 130 species, in 98 genera from 38 families are now known from the sites (Cooper, 1999). This paper cannot provide a comprehensive review of the complete avifaunal assemblage, but will focus instead on the presence of selected species.

As noted, non-analogue species associations occur throughout the sites, though are most reliably recorded in Gorham's and Vanguard Caves due to the better resolved stratigraphies of these sites. Two broad categories of non-analogue associations can be identified. Firstly, there are juxtapositions of climatic preferences, typified by associations such as *Falco naumanni* and *Melanitta fusca* at Gorham's and secondly, there are contrasts in typical habitat requirements, such the pelagic *Pinguinus impennis* or *Pterodroma* sp. with terrestrial partridges *Alectoris* sp. or *Columba livia/oenas* (Rock/Stock Dove).

The species list of an avian assemblage, be it for an entire site or a single horizon, can be regarded in some ways as the equivalent of a modern regional checklist. All species observed during the period from which records began are included; residents, migrants, vagrants listed together (e.g. Finlayson, 1992: Appendix 1). When using such a list, it is taken as a given that not everything will occur together in time and space, and a good checklist will often include some indication of the seasonal status of each species, and even how frequently it may occur. A fossil species list is simply a checklist without this supplementary data, but is equally as complex (if not more so) and therefore must not be interpreted at face value. To produce this additional, palaeoecological information requires further analysis of the avifauna; the temporal resolution of the site must be examined and each individual species' potential seasonal status considered.

Temporal resolution of an assemblage is dependent on the depositional processes that may have affected its accumulation. Of particular concern are the processes of time-averaging, as they may cause remains from different time intervals to be preserved together, potentially giving rise to palaeoecologically misleading combinations (Kidwell & Behrensmeyer, 1993). The extent of time-averaging will also determine the precision with which an avifauna records climatic fluctuations, which are known to have occurred regularly on a millennial scale throughout the Late Pleistocene (Roucoux et al., 2001).

In Gibraltar, it is noticeable that the high-diversity units in Gorham's and Vanguard Caves are typically more developed humic horizons, which in Gorham's are characterised with considerable organic inputs, especially bird guano (Macphail & Goldberg, 2000). The nature of these levels strongly suggests depositional hiatuses, which would also allow for extended development of their avian assemblages and a corresponding increase in the time-averaging effect. Furthermore, bioturbation is an additional complication evident in the sites. Unfortunately, at present it is not possible to suggest the precise intervals that each of these high diversity units may represent, but it seems likely that temporal resolution in any horizon is potentially on a scale of several millennia or more.

Therefore the validity of any non-analogue associations must be immediately be suspect, as although birds may have responded sensitively to rapid climatic fluctuations, these events are in fact likely to be represented by a succession of generalised assemblages. Evidence of climatic shifts clearly is preserved by the Gibraltar avifaunas in the occurrence of Arctic and Boreal breeding species such as *Clangula hyemalis*. However, it cannot be determined whether these species would have occurred in close temporal association (i.e. during the course of a year) with Mediterranean migrants such as *Falco naumanni*.

The habit of migration is not considered a recent phenomenon, although the routes and patterns followed by modern birds have probably developed within the past 10,000-5,000 years (Alerstam, 1990). If it is assumed that Late Pleistocene species possessed broadly the same migrational tendencies as their modern counterparts, it is possible to consider the potential seasonal status of Gibraltar's Late Pleistocene birds using a simple deductive technique based on the predicted effects of a southerly retreat in response to climatic deterioration on present Palearctic seasonal distributions. Admittedly, this is rather crude, but it is a useful device for beginning to categorize an assemblage and for identifying potentially valuable indicator species.

Four categories of seasonal status can be defined for Gibraltar Late Pleistocene species as follows:
- Residents: species with non-migratory populations still occurring in southern Iberia.
- Summer migrants: species presently occurring in southern Iberia *only* as summer migrants, and therefore unlikely to have been present outside this season under cooler conditions.
- Probable winterers: species that currently winter well to the north of southern Iberia and are recorded only rarely, if at all, in the Strait region at present.

Species presently wintering in the Strait region and breeding in more northerly territories are classed as indeterminate, as under conditions similar to those at present could have been wintering, or in cooler phases could have been breeding. Also regarded as indeterminate are species which may have a resident population, but also a seasonal migratory population.

Taxa falling into the categories of resident and summer migrant are of great interest, as these would have been part of the region's communities of breeding birds. As far as palaeoecological interpretation of birds is concerned, positive identification of a breeding population is the ultimate achievement for two fundamental reasons. Firstly, it establishes the seasonal status of a given species and secondly, the breeding distributions of modern species can often be more clearly defined in terms of ecological parameters than their wintering regions, therefore giving a more precise signal (e.g. Voous, 1960). Although likely breeding species can be identified on the basis of their predicted seasonal presence, including both summer migrants and residents, physical evidence is obviously preferable to informed speculation. In birds, this may be provided by the remains of juveniles or immatures, medullary bone in adult remains or even eggshells (providing they can be identified).

Some 18 species are represented by positive evidence of breeding in the Gibraltar assemblages (Table 1). Sixteen of these species still breed in southern Iberia at present, reflecting a long-term stability in the region's avifaunas. This stability is also apparent in the mammalian remains and plant macrofossils recovered from Gorham's and Vanguard Caves, which include various characteristic elements such as Spanish Ibex *Capra pyrenaica* and Olive *Olea* sp. (Currant, 2000; Gale & Carruthers, 2000).

If breeding species are ideal palaeoecological indicators, one in particular appears to provide especially strong indications of habitat and climate. Remains of the endemic Iberian subspecies of Azure-winged Magpie *Cyanopica cyanus*, have been found in both Gorham's and Vanguard Caves, including those of immature birds (Cooper, 2000b). The occurrence of *C. cyanus* is interesting for both biogeographical and palaeoecological reasons, and is a good example of the need to avoid overemphasising what could potentially be an anomalous palaeoenvironmental signal.

The modern Iberian population of *C. cyanus* is both sedentary and has fairly specific ecological preferences in terms of vegetation types and climate, suggesting that it would be an ideal source of detailed palaeoecological information (e.g. Finlayson & Pacheco, 2000). However, interpretation of this species in fact requires some careful consideration.

At present, *C. cyanus* has an extremely disjunct distribution, occurring across China, Japan and Korea, and in the Western Palearctic, only in the Iberian Peninsula, with no intervening populations. Previously, its fossil record was confined to China (Tyrberg, 1998), but its origins in Iberia as a relict rather than a recent introduction have been confirmed by the Late Pleistocene Gibraltar finds (Cooper, 2000b). Molecular evidence of the genetic divergence of the eastern and western populations have

Taxon	Status	Devil's Tower	Ibex Cave	Vanguard Cave	Gorham's Cave
Alectoris sp.	R	B/M	—	B	B
Melanitta fusca	W	—	—	—	B
Melanitta nigra	I	—	—	—	B
Gyps fulvus	I	—	—	B	—
Falco naumanni	S	B	—	B	B
Falco cf. *tinnunculus*	I	M	—	—	—
Columba cf. *livia*	R	—	—	—	B
Columba cf. *oenas*	I	—	—	B	—
Columba livia/oenas	I	B/M	—	B	B/M
Columba palumbus	I	—	—	B/M	—
Bubo bubo	R	—	—	—	B
cf. *Strix aluco*	R	B	—	—	—
Tachymarptis melba	S	—	—	B	—
Apus apus/pallidus	S	—	—	B	B/M
Hirundo sp.	I	—	—	B	B
Cyanopica cyanus	R	—	—	B	—
Pyrrhocorax pyrrhocorax	R	B	B	B	B
Corvus monedula	I	—	—	B	—
cf. *Corvus corone/frugilegus*	I	—	—	—	B

Table 1. Bird species in Late Pleistocene Gibraltar represented by positive evidence of breeding. R - predicted resident; S – predicted summer migrant; W – predicted winter migrant; I – indeterminate. B - presence of juvenile or immature bones; M - presence of medullary bone.

Taula 1. Espècies d'ocells al Pleistocè tardà de Gibraltar amb evidència positiva de cria. R – resident predit; S – migrant estival predit; W – migrant hivernal predit; I – indeterminat; B – presència d'ossos immadurs o juvenils; M – presència d'os medul·lar.

corroborated the fossil discoveries (Fok *et al.*, 2002). It seems likely that the absence of its remains from other Iberian sites may be explained in part by taphonomic biases, in that the majority of these sites do not include significant inputs from the woodland situations favoured by *C. cyanus* (Cooper, 1999, 2000b). A second possibility is that its absence from other sites is an indication of a highly restricted range within the refugium area.

Within Iberia, the species seems to have quite a narrow set of ecological preferences, but in its considerably larger eastern range, its requirements are somewhat different. It still favours open woodlands, particularly broadleaf ones, but is less restricted by climate, occurring in areas with deep winter snow (Cramp & Perrins, 1994). It is also worth noting that if *C. cyanus* once had a range across the entire Palearctic, it must have been a reasonably adaptable species. When compared with the species' overall characteristics, the more restricted preferences of the present Iberian population seem somewhat atypical. It therefore seems possible that the present Iberian population's ecological needs have been altered through isolation. The extinction of all intervening populations suggest that the species came under severe environmental pressure in its western territories,

	Devil's Tower	Ibex Cave	Vanguard Cave	Gorham's Cave
Procellaridae				
Fulmarus glacialis	—	—	1	1
Pterodroma sp.	—	—	4	31 (4)
Calonectris diomedea	8 (3)	—	—	2
Puffinus ? mauretanicus	2	—	2	3
Hydrobatidae				
Hydrobates pelagicus	—	—	1	4 (2)
Alcidae				
Pinguinis impennis	1	1	—	1
Alle alle	1	—	—	—
Uria aalge	3	—	2	—
Alca torda	1	—	2	3
Fratercula arctica	1	—	9 (2)	3

Table 2. Number of identified specimens of Petrels, Shearwaters, Storm-petrels and Auks (Families: Procellaridae, Hydrobatidae and Alcidae) in Late Pleistocene sites, Gibraltar. Figures in brackets indicate minimum number of individuals (MNI), where MNI >1.

Taula 2. Nombre d'espècimens identificats de petrells, baldritges, virots, aus de les tempestes i alques (Famílies: Procellaridae, Hydrobatidae i Alcidae) als jaciments del Pleistocè tardà de Gibraltar. Les xifres entre parèntesi indiquen el nombre mínim d'individus, quan MNI >1.

	Devil's Tower	Ibex Cave	Vanguard Cave	Gorham's Cave
Anatidae (marine species only)				
Tadorna tadorna	—	—	—	1
cf. *Aythya fuligula*	1	—	—	1
Somateria sp.	1	—	—	2
Melanitta nigra	10 (3)	—	—	6
cf. *Melanitta nigra*	—	—	—	7
Melanitta fusca	—	—	—	3 (2)
cf. *Melanitta fusca*	—	—	—	1
Clangula hyemalis	1	—	1	19 (4)
cf. *Clangula hyemalis*	1	—	2	26 (9)
Mergus cf. *merganser*	2	—	—	—
Mergus cf. *serrator*	1	—	—	—

Table 3. Number of identified specimens of marine ducks (Family: Anatidae) in Late Pleistocene sites, Gibraltar. Figures in brackets indicate minimum number of individuals (MNI), where MNI >1.

Taula 3. Nombre d'espècimens identificats d'ànneres marines (família: Anatidae) als jaciments del Pleistocè tardà de Gibraltar. Les xifres entre parèntesi indiquen el nombre mínim d'individus, quan MNI >1.

leaving a small remnant population – perhaps even confined to a single refugium. The degree of isolation and environmental pressure may have had a bottleneck effect on the relict population, causing both ecological and morphological divergence from the original ancestral population. As a result, although its survival in Iberia is an indication that ecological conditions have remained within certain parameters, as once extinct it could not have re-colonised the region, it is misleading to identify those parameters too closely with the needs of the modern population (cf. Finlayson & Pacheco, 2000). Nevertheless, it can be regarded as a certain indicator of open woodlands in the Gibraltar region during the Late Pleistocene, alongside other species from the Gibraltar assemblages rarely found on Iberian sites such as *Dendrocopos* ?*major* and *Picus viridis* (Cooper, 1999; Cooper, 2000b). From such an example, the benefits of including ecological analogues from multiple species can be appreciated.

In the absence of positive evidence of breeding, determining seasonal status becomes more subjective. In my view, it then becomes critical to consider not only the habitat and climatic preferences of a given species, but also its behaviour; again, drawing on modern populations as analogues. Perhaps the best illustration of this can be found in the interpretation of the continental occurrence of pelagic species, i.e. birds that spend the majority of their lives at sea, normally only returning to land to breed. This is an area that has generated some controversy, with particular attention paid to the implications of Pleistocene finds of the extinct, flightless *Pinguinus impennis* (Cooper, 1997; Mourer-Chauviré, 1999; Stewart, 2002). It is a debate to which the Gibraltar assemblages can make an important contribution, as between them the four sites record one of the most diverse assemblages of pelagic species known from the Late Pleistocene. Auks (Family Alcidae) and petrels, shearwaters and storm-petrels (Families Procellaridae and Hydrobatidae) are particularly well represented, with a total of 10 species present in the sites' combined fossil record (Table 2). In addition to *P. impennis*, notable recoveries included the first Pleistocene Northern Hemisphere continental records of as yet unidentified species of gadfly petrel, *Pterodroma* sp. (Tyrberg, 1998; Cooper, 1999).

In addition to the offshore species, a range of sea-ducks were also recovered (Table 3). Together with certain other marine species, these constitute the most critical avian evidence of the climatic fluctuations of the Late Pleistocene. Climatic deterioration is not similarly recorded in the terrestrial avifauna; finds identified by Eastham (1968) as *Nyctea scandiaca* (Snowy Owl) have proved to be referable to *Bubo bubo* (Eurasian Eagle Owl) (Cooper, 1999).

Therefore, from a palaeoecological perspective it is extremely important to try and establish whether these northern marine species were present in breeding colonies, as this would have markedly different climatic implications than records of wintering individuals.

At the core of the debate is the proposition that pelagic species would only be available to terrestrial predators and scavengers when they return to land to breed. Therefore, it is argued, terrestrial fossil finds can be equated with former breeding distribution. In the case of *P. impennis*, this argument has been extended to implicate prehistoric humans in the disappearance of former breeding colonies on the Mediterranean and Portuguese coastlines (Mourer-Chauviré, 1999; Mourer-Chauviré & Antunes, 1991). Whether or not humans were involved, the underlying issue remains whether or not breeding colonies were present.

Most modern populations of the pelagic species represented show a marked preference for breeding on off-shore islands, often in substantial colonies. Historically, this is also known to apply to *P. impennis* (Montevecchi & Kirk, 1996). This strong tendency towards isolation is in no small part the result of the vulnerability of such colonies to mammalian predators, the impacts of which are extremely well documented. Petrels and shearwaters are particularly vulnerable; *Pterodroma* species notoriously so, with a global record of many populations driven either extinct or close to it by mammalian disturbance (BirdLife, 2000, Worthy & Holdaway, 2002).

Whilst modern populations can provide direct comparisons for extant species, alternative sources are required for extinct species, such as *P. impennis*. Montevecchi & Kirk (1996) reviewed historical and Holocene archaeological evidence of *P. impennis* in the north Atlantic, but did not conclusively identify mainland breeding sites. Indeed, it was concluded that remoteness from mainland mammalian predators was one of the most important factors governing the location of the species' breeding sites. Why this should be the case, is easily demonstrated by a comparison from the Southern Hemisphere; that of the interaction of penguin rookeries with mammalian predators, as the ecologically convergent penguins are an excellent analogue for the large, flightless *P. impennis*. In both New Zealand and Australia, penguin colonies are preyed upon by cats, foxes, dogs, rats, pigs, ferrets and even goats; adults, chicks and eggs are all taken. Some colonies in farmed regions on New Zealand's South Island of *Megadyptes antipodes* (Yellow-eyed Penguin), similar in size and weight to *P. impennis*, have experienced annual chick mortality in excess of 90% due to mammalian disturbance (Marchant & Higgins, 1990). These examples refer to the impact of introduced predators on 'naïve' prey; they nevertheless serve to demonstrate the great potential vulnerability of accessible breeding colonies of large, flightless marine birds to mammalian predation. However, it may be further noted that in South Africa, breeding colonies of the endemic *Spheniscus demersus* (African Penguin), which has evolved its breeding strategies in the presence of mammalian predators, are predominantly located on offshore islands. Where predators have reached such colonies, e.g cats on Dassen Island, they represent a significant problem (del Hoyo *et al.*, 1992).

Many of the predators listed above, and others, were present in the Gibraltar region during the Late Pleistocene (Currant, 2000). Undoubtedly, accessible breeding colonies of pelagic birds would have represented a significant source of easily caught prey to Gibraltar's mammalian predators, human or otherwise. The fossil evidence of exploitation of such colonies has been found on many sites throughout New Zealand, with the bones of pelagic species present in significant quantities, including those of juveniles (Worthy & Holdaway, 2002).

The scale of archaeological New Zealand 'mutton-birding' undoubtedly surpasses what might have been possible in Late Pleistocene Europe, but does serve to demonstrate in particular what occurs when a resourceful human population encounters a ready supply of attractive prey. Another taphonomic comparison comes from Holocene archaeological sites in North America and northern Europe, where numerous remains of *P. impennis* have been found as evidence of human exploitation of offshore breeding colonies (Montevecchi & Kirk, 1996).

Within the Gibraltar sites' pelagic assemblage, each taxon is represented by only very low numbers of identified specimens and correspondingly low minimum numbers of individuals. None of the Gibraltar auks, petrels or shearwaters are represented by any juvenile or immature remains. The fossil signature of known exploitation of pelagic colonies seems a complete contrast to the pelagic fossil record found in the Gibraltar sites. Therefore, in my view, if both taphonomic and behavioural evidence are taken into account, on the basis of current evidence the Gibraltar remains cannot be interpreted as representing predation on mainland breeding colonies of auks, petrels or shearwaters and an alternative explanation should be considered.

It is noticeable that most of the marine species present are regularly found washed upon European beaches. Additionally, sea-ducks such as *Somateria mollissima* (Common Eider), *Melanitta nigra*, *M. fusca* and *Clangula hyemalis* and a variety of waders are affected by beaching and all may be found in the Gibraltar assemblages (Heubeck, 1987; Granadeiro *et al.*, 1997; Cooper, 1999). Occasionally, beached casualties may be found in considerable numbers as a wreck event, which can occur over a geographically very wide area and may be related to extreme weather conditions (Avery, 1989). Fossil remains of wrecked migrant pelagics, notably Procellaridae, have been identified from a number of dune deposits in New Zealand, though formerly some had been interpreted as evidence of breeding (Worthy & Holdaway, 2002).

If wreck events occurred in the Strait of Gibraltar during the Late Pleistocene, they would have represented important carrion bonanzas for local scavengers. Humans are also known to have exploited beached birds as a food resource (Avery & Underhill, 1986). The balance of fossil evidence, both in Gibraltar and from comparative localities, combined with behavioural habits of pelagic species strongly suggests that the remains of such birds in the Gibraltar sites represent scavenging of occasional beached carcasses.

Taking into account their modern distribution patterns, the majority of these remains are probably those of migrant birds wintering in the Strait region. However, it is clear that at least two boreal-arctic aquatic species were breeding relatively close to Gibraltar at some point during the Late Pleistocene. One tarsometatarsus each of *Melanitta nigra* and *M. fusca* were recovered from Gorham's Cave, both in a relatively late stage of fusion (Fig. 2). Though *M. nigra* is a regular winter presence in the Strait (Finlayson, 1992), the majority of both species' populations presently breed above 55ºN (Cramp & Simmons, 1977). The Gibraltar finds represent the most southerly direct evidence of breeding of *Melanitta*

species, but juvenile specimens of *M. nigra* and also *Clangula hyemalis* are known from Portugal (Mourer-Chauviré & Antunes, 2000). Together, these specimens constitute irrefutable evidence of major southerly displacements in breeding distribution. The Gibraltar remains may represent breeding grounds within the Strait region, but there remains the possibility that they might have been from individuals already at sea (cf. Stewart, 2002).

However, a second tarsometatarsus from Gorham's of *M. nigra* with an unfused proximal epiphysis (Fig. 2) is strongly suggestive of breeding grounds somewhere within the immediate Gibraltar region. Unfortunately, this specimen was found in the cave's superficial sediments and its original stratigraphic and temporal context cannot be assessed.

Southerly displacement of these and other 'cold' marine species reflects regular extensions of Boreal water masses, at least in colder months, into the latitude of the Strait region, and possibly even into the western Mediterranean. Arguably, certain of these specimens may well record the impact of Heinrich Events on the avifaunas of the North Atlantic. At least four of these ice-rafting episodes are known to have occurred during the accumulation of the deposits in Gorham's and Vanguard Caves (Roucoux *et al.*, 2001). Part of the stratified immature specimen of *Melanitta nigra* was recovered from the unit underlying the base of the high-diversity unit dated by AMS radiocarbon to $51,700 \pm 3,300$BP (Cooper, 1999; Pettit & Bailey, 2000). This may suggest a correlation with a Heinrich Event at approximately 57,000BP (Roucoux *et al.*, 2001) but further analysis is required.

Fig. 2. Immature tarsometarsi of *Melanitta fusca* (left - 'Gor 1996, sample 276') and *Melanitta nigra* (centre - 'Gor 1996, sample 92' |proximal| and 'Gor 1995, sample 293' |distal|; right - 'Gor 1996, sample 5') from Gorham's Cave, Gibraltar. Photo: The Natural History Museum, London.

Fig. 2. *Tarsometatarsos immadurs provinents de la cova de Gorham, Gibraltar, de* Melanitta fusca *(esquerra - 'Gor 1996, mostra 276') i* Melanitta nigra *(centre - 'Gor 1996, mostra 92' [proximal] i 'Gor 1995, mostra 293' [distal]; dret - 'Gor 1996, mostra 5'). Fotografia: The Natural History Museum, London.*

Conclusions

The Late Pleistocene avifaunas of Gibraltar are amongst the richest and most diverse avian assemblages of this age known from the Western Palearctic. The combined assemblages from the four sites investigated; Devil's Tower Rock Shelter and Ibex, Gorham's and Vanguard Caves, are characterised by a succession of generalised, superficially unchanging avifaunas, including frequent examples throughout of non-analogue species associations, both of habitat and climatic contrasts.

However, the sites appear to demonstrate relatively poor temporal resolution. Although birds could have responded rapidly to the brief, sharp climatic fluctuations known to have occurred during the accumulation of the Gibraltar assemblages, deposition at the sites could not record anything but the broadest of distributional changes. For the most part, the non-analogue associations must be regarded as taphonomic relicts.

Migration further complicates the interpretation of the Gibraltar avifaunas, as to resolve any palaeoecological signal requires some assessment of each species' seasonal status – which might have changed over time. Whilst predicting possible status by deduction can be helpful, only positive evidence of breeding can confirm a species' presence in a particular season. Identification of breeding ranges, which may be either of residents or summer migrants, must therefore be given priority.

In Gibraltar, 16 out of 18 known Late Pleistocene breeding species still breed in the region, including the endemic Iberian subspecies of *Cyanopica cyanus*, reflecting the region's role as a temperate refugium. However, even with reliable evidence of breeding, it is important not to over-emphasize the importance of any single species, such as *C. cyanus*, thus avoiding the danger of skewing interpretations with potentially anomalous ecological indications.

The stability of the terrestrial species contrasts with the presence of various boreal-arctic marine taxa throughout the assemblages, indicating the impacts of climatic fluctuations and associated oceanic changes, on the distributions of North Atlantic birds. The remaining two species represented by juvenile or immature specimens, *Melanitta nigra* and *M. fusca*, both presently breed in boreal-arctic regions, and are incontrovertible evidence of significant displacement of their breeding ranges into southerly latitudes by as yet unspecified periods of climatic deterioration. However, a tentative correlation may exist between one specimen of *M. nigra* and a Heinrich Event at approximately 57,000 BP. By contrast, remains of other pelagic and coastal species, including *Pinguinus impennis* and *Pterodroma* sp., cannot be taken as evidence of former breeding grounds. Instead, comparison of Gibraltar's fossil finds with the behaviour of modern pelagics and other fossil assemblages of such birds, strongly suggests that the Gibraltar finds represent occasional wrecks, probably of wintering individuals.

Gibraltar's location on the converging major migration routes of the Strait of Gibraltar does mean that the effects of migration on its Late Pleistocene avifaunas may be exaggerated. Each site has been influenced by a unique set of depositional processes that may or may not be similar to those encountered elsewhere. However, given that non-analogue species associations are recorded throughout Late Pleistocene assemblages in the Mediterranean and beyond, issues of interpretation raised by the Gibraltar avifaunas are certainly of wider relevance. It is apparent though, that significantly different situations do exist. Gibraltar's non-analogue associations are primarily contrasts between aquatic and terrestrial species; elsewhere non-analogue associations of only terrestrial species occur (Tyrberg, 1998). It is my view nevertheless, that any associations involving one or more species of known migratory habits must be considered with extreme caution.

Increasingly, birds are being used in modern studies as environmental indicators, and there is a growing understanding of their response to climatic change (e.g. Wernham *et al.*, 2002; Butler, 2003). This body of knowledge is a valuable resource for enhancing our understanding of the Late Pleistocene fossil record of birds, offering insights into avian behaviour that may shape future palaeornithological research. Equally, modern ornithologists should be encouraged to refer more frequently to palaeontological and archaeological works (e.g. Harrop, 2004), as remains of Late Pleistocene birds are the physical evidence of species and communities during this critical period in the biogeographic history of modern avifaunas. Only by this two-way flow of information can the full palaeoecological potential of Late Pleistocene birds be explored.

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