Neanderthal exploitation of marine mammals in Gibraltar

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Two coastal sites in Gibraltar, Vanguard and Gorham's Caves, located at Governor's Beach on the eastern side of the Rock, are especially relevant to the study of Neanderthals. Vanguard Cave provides evidence of marine food supply (mollusks, seal, dolphin, and fish). Further evidence of marine mammal remains was also found in the occupation levels at Gorham's Cave associated with Upper Paleolithic and Mousterian technologies [Finlayson C, *et al.* (2006) *Nature* 443:850–853]. The stratigraphic sequence of Gibraltar sites allows us to compare behaviors and subsistence strategies of Neanderthals during the Middle Paleolithic observed at Vanguard and Gorham's Cave sites. This evidence suggests that such use of marine resources was not a rare behavior and represents focused visits to the coast and estuaries.

Middle Paleolithic | seal | mollusks

n the last decade studies focusing on Neanderthals have been providing a different perspective of their subsistence and hunting strategies (1–7). Studies of their diet based on carbon and nitrogen stable isotopes show that Neanderthals, in addition to occasional scavenging, were also active hunters on a regular basis (8–10). Paleontological studies of Neanderthal occupation levels reinforce their capability of hunting a wide variety of fauna (11, 12) and show no evident differences from Upper Paleolithic human hunting behavior (13, 5, 14).

The Gibraltar sites reinforce this hypothesis and together with other suggestive evidence from Italy (3) provide evidence that Neanderthals were exploiting marine mammals and other coastal resources between marine isotope stages (MIS) 5–3. Mousterian technology is firmly associated only with the Neanderthals in Europe (15) and in the Iberian Peninsula. Within Gibraltar, we find indications that Neanderthals had knowledge of the geographic distribution and behavior of their prey. We present here the evidence from Gibraltar sites showing that Middle Paleolithic humans exploited not only mollusks (16, 17), but also seals, dolphins, and fish, through a wide time span. Subsequent Upper Paleolithic human levels of occupation in Gorham's show behavior similar to that of Neanderthals and similarly complex subsistence strategies that allowed them to exploit marine resources (18).

Sites and Their Formation

Vanguard and Gorham's Caves lie on the eastern side of Gibraltar (ref. 19 and Fig. 1). Both of these sites are wide sea caves, \approx 35 m high, with long stratigraphic sequences (\approx 20 m).

The Last Interglacial (MIS 5) is represented on the Rock by several high-stand sea-level deposits and erosive landforms (20), clearly visible on the eastern flank. Many previous caves were widened by wave action, and beach deposits accumulated within them or at the feet of the cliffs. In a clearly regressive phase of

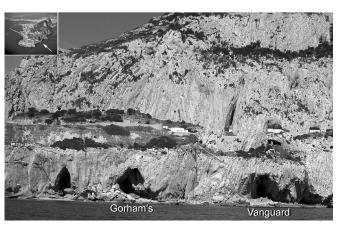


Fig. 1. Photograph from the sea of Governor's Beach, southeast side of the Rock, showing Vanguard Cave (*Right*) and Gorham's Cave (*Left*). (*Inset*) View of the rock and location of the sites.

sea level, with successive fluctuations, the whole sequence of aeolian sands that fill the large caves of Governor's Beach was unconformably deposited. Intercalations of gravitational episodes, rockfalls, and rock avalanches are seen stratigraphically.

The stratigraphic sequence of Governor's Beach, and particularly in Vanguard Cave, begins with a littoral deposit of sandy gravels and abundant remains of shells, with a thickness of up to 4 m, representing facies underneath unit E (Fig. 2) of foreshore and backshore (early MIS 5; ref. 21). The overlying blown sand record was generated during MIS 5 to 3, between 125 and 30 ka, inferred from OSL dates and their geomorphological evolution (20). These aeolian accumulations comprise cliff-front dunes and sand ramps. Vanguard contains reddish-brown clays and silts (associated with periods of human occupation), and interspersed aeolian sand layers, which are sterile (22). The age of the Vanguard Cave material discussed here is >41,800 radiocarbon years, based on a series of dates on charcoal from unit A, near the top of the stratigraphic sequence (23, 24).

Marine Mammals from Vanguard Cave

As reported (16, 17) the upper units of Vanguard Cave (unit B) contain a well defined layer of ash associated with marine shells,

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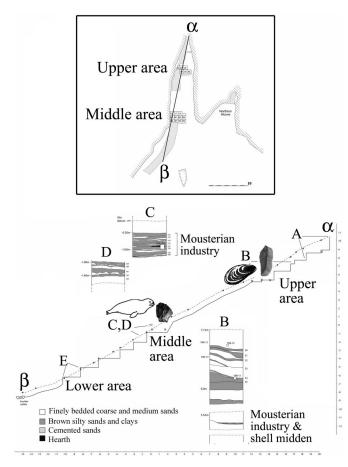


Fig. 2. Plan and profile of Vanguard Cave showing excavation areas along the cross-sections marked on β to α . Unit B (Upper Area), where the mussel unit was uncovered associated with a hearth. Units C and D (Middle Area), where the fossil association of terrestrial and marine mammals has been described here.

dominated by mussels of the species Mytilus galloprovincialis, likely from a nearby estuarine source (17) and a hearth and a concentration of knapping debris and Mousterian stone tools (16), providing clear evidence for the exploitation of marine mollusks by Neanderthals (Fig. 2). This occupation level represents a short period, and it records several activities in the life of the Neanderthal occupants. These activities consisted of selection and collection of mollusks, transport of the gathered mussels to the cave shelter, fire making in the cave, the use of heat to open the shells, consumption of these mollusks, knapping on the hearth embers, and subsequent abandonment of the site (17). This layer increases our knowledge of food availability and behavior of Neanderthals, showing the use and selection of marine resources (25). "Use of these resources is interesting ... because they are very rarely found with any hominine before anatomically modern humans."

Lower in the cave sequence (units C and D) is a series of well defined occupation horizons that contain a central hearth and considerable quantities of bones and Mousterian discoidal core technology artifacts (16) as well as further evidence of the exploitation of marine resources by Neanderthals. The excavation covered an area of $\approx 12 \text{ m}^2$ at the front of the cave entrance (Fig. 2). The hearth has shown microgeomorphological evidence of being reused at least three times (22). A rich species composition of terrestrial mammalian taxa such as ibex (*Capra ibex*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), and bear (*Ursus arctos*), together with marine mammals (seals and dolphins),

Table 1. Marine mammals and \approx 150 marine mollusk shells uncovered from these Mousterian units of Vanguard Cave (units C and D)

Category	NISP	% NISP	MNE	% MNE
Monachus monachus	4	0.47	4	2.13
Delphinus delphis	2	0.23	2	1.06
Family Delphinidae	1	0.12	1	0.53
Tursiops truncatus	1	0.12	1	0.53
Diplodus sargus/vulgaris	1	0.12	1	0.53
Mollusks	149	17.43	*	*
Total marine animals	158	18.48	9	4.79
Cervus elaphus	40	4.68	26	13.83
Capra ibex	121	14.15	72	38.30
Sus scrofa	11	1.29	11	5.85
Total terrestrial herbivores	172	20.12	109	57.98
Canis lupus	2	0.23	2	1.06
Crocuta crocuta	5	0.58	5	2.66
Felis sylvestris	4	0.47	4	2.13
Panthera pardus	7	0.82	6	3.19
Ursus arctos	2	0.23	2	1.06
Total terrestrial carnivores	20	2.34	19	10.11
Unidentified fragments	505	59.06	51	27.12
Total		855		188

*Mollusk MNE is not reliable and has not been included. Specimen (NISP) is an observational unit and counts both complete or fragmented specimens (proximal or distal ends and shafts), whereas an element (MNE) is an analytical unit referred to a single complete anatomical element made up from fragments (38 and A. Currant, unpublished data).

mollusks (Table 1), birds, tortoise, and fish has been recovered from these units.

As well as all terrestrial mammalian taxa, two marine mammal fossils show human-induced damage, both of them monk seal (Monachus monachus). The other Vanguard marine mammals do not show clear evidence of human modification, but they are mixed with terrestrial mammal remains that do and are clearly within Neanderthal occupation horizons. Two groups of cut marks can be distinguished on a proximal phalanx from the hind limb VAN 96 (411) (Fig. 3): one of short and deep marks on the lateral side, transverse to the length of the bone, and the other formed by three parallel cut marks, again transverse to the long axis of the bone, on the ventral side. The fracture on the proximal end of the phalanx shows slight peeling on the broken edge as a result of bending the bone, consistent with disarticulation and detachment from connected muscles and tendons. The juvenile scapula of M. monachus VAN 98 (564) shows a set of long and thin cut marks, divergent from each other and located near the center of the medial surface. The distribution and shape of cuts on the scapula suggest defleshing activity. Based on meat utility of marine mammals, Lyman (26) and Henshaw (27) observed that, in general, axial parts provide important meat values, although appendicular elements have also been found in Inuit occupation and butchery sites in high proportions. Historic ethnographic observations of seal dismemberment by Inuits reports the following procedure: "The flippers are cut off at the joints, and thus the whole skin is drawn off in a single piece... the fore flippers (with the shoulders and the hind flippers) are taken out, the only part remaining being the head, the spinal column, and the rump bone" (27). These anatomical elements found in Vanguard were, therefore, probably not taken arbitrarily by Neanderthals and may reflect primary access to carcasses.

To understand the relationship and organization of bones and hearths, features at Vanguard were compared with those of Abric Romani (Barcelona, Spain), a site characterized by intensive and recurrent Neanderthal occupations through an extensive period ($39.1 \pm to 70.2 \pm 2.6$ ka; ref. 28) contemporaneous with Vanguard. Abric Romani is especially interesting because of an extensive area of excavation and an excellent preservation

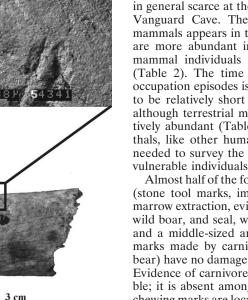


Fig. 3. *M. monachus* proximal hind limb phalanx VAN 96 (411) showing short and deep cut marks on the lateral side. Two groups of cut marks can be distinguished on this seal phalanx, one of short and deep marks on the lateral side, and the other formed by three parallel cut marks, on the ventral side (data not shown). The fracture, on the proximal end of the phalanx, shows slight peeling as a result of disarticulation. Similarly, a juvenile scapula of *M. monachus* VAN 98 (564) shows a set of long and thin cut marks, located near the center of the medial surface. The distribution and shape of these cuts suggest defleshing activity. (*Upper*) SEM micrograph. (*Lower*) Photograph.

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of all types of remains (including wood), with occupations sealed by repeated collapses of the travertine, where a pattern of activities organized around hearths has been distinguished (29, 30). This comparison suggests that the area excavated in Vanguard corresponds to a zone in which primary butchery was undertaken of carcasses brought to the site (31). The hearth found at these levels was not used to cook but to prepare the carcass. Reddish-brown stains are dispersed on the bone surface of monk seals and on terrestrial mammalian bones as well, such C. elaphus and C. ibex. Experimental work has shown that these dispersed stains on the bone surfaces appear when bones are directly exposed to fire (free of meat and skin), and breakage becomes much easier when bones are previously heated, and more advantageous as well, because the marrow solidifies and can be easily removed (32). Bones previously exposed to fire and then broken get a characteristic type of breakage (mixed fracture angles, opposite to oblique, on spiral breaks) (33).

Both marine and terrestrial fossils in units C and D at Vanguard Cave represent immature individuals (64%), and no diagnosable old individuals of any species have been recovered. With regard to marine mammals, this finding would suggest seasonal hunting practices at a time when seals would be vulnerable because of their need to breed on land. Dolphins can be accidentally seasonally beached on the seashore, which may explain their occurrence in the archaeological deposits. The high fat content of these mammals attracts human exploitation (34) but also facilitates rapid decay (35), and this may explain the lack of cut marks on dolphins if Neanderthals were obtaining fat rather than meat. Spatial distribution of this fossil assemblage and refitting of bone fragments (31) seem to distinguish at least three episodes (Fig. 4). Terrestrial and marine mammals, shellfish, and fish are present during all three. Marine mammals are in general scarce at the 12 m² dug at the cave entrance facies of Vanguard Cave. The highest relative abundance of marine mammals appears in the uppermost episode, whereas mollusks are more abundant in the lowermost one. Immature marine mammal individuals are recorded during all three episodes (Table 2). The time span represented by the gaps between occupation episodes is unknown. However, each episode seems to be relatively short as indicated by a long vertical distance, although terrestrial mammals as part of food discard are relatively abundant (Tables 1 and 3). This suggests that Neanderthals, like other humans exploiting coastal habitats, regularly needed to survey the shoreline to locate stranded carcasses or vulnerable individuals.

Almost half of the fossil bones display human-induced damage (stone tool marks, impact marks while opening the bone for marrow extraction, evidence of burning) affecting ibex red deer, wild boar, and seal, whereas <3% of these fossils (mainly ibex and a middle-sized artiodactyl, possibly red deer) have tooth marks made by carnivores. Carnivore fossil bones (including bear) have no damage produced by humans or other carnivores. Evidence of carnivore damage (Table 3) is thus almost negligible; it is absent among marine mammal fossils, and the scarce chewing marks are located in areas and anatomical elements that are not consistent with first access to carcasses, but rather with scavenging. Carnivore tooth marks appear on the tibia, radius, scapula, mandible, and phalanx and are mainly grooves on bones previously exposed to fire (at an incipient stage of burning). Given the lack of evidence of other biological agents (carnivores) or postdepositional/geological disturbances (e.g., storms, water streams) that could bring these marine fossils to the site, we infer that the remains of marine mammals result from Neanderthal transport and activity.

Marine Mammals from Gorham's Cave

At Gorham's Cave, marine mammals have been found at the bottom of level IV, associated with a Mousterian industry. The age of these marine mammal remains can be assigned to >30-32ka ${}^{14}C$ BP (1). At level III, seal remains were recovered from the top of the series together with Upper Paleolithic technology. Comparison between level IV (Mousterian) and level III (Upper Paleolithic) shows almost no differences in faunal diversity. Most species are present in both levels, and at Vanguard Cave, with terrestrial mammals that include red deer, ibex, horse, and marine mammals such as phocids (Table 4). An exception is observed with rhinoceroses and suids, absent in level IV at Gorham's (36). However, this could be the result of sampling error because suids and rhinos (Stephanorhinus) were present at Vanguard Cave and in lower horizons at Gorham's Cave (37). Fernandez-Jalvo and Cáceres (38) found a slight difference in small game, with birds appearing to be more abundant in level IV, whereas lagomorphs were more extensively consumed in level III, and human gnawing marks (39) have been recognized on both rabbits and birds in both levels (38). As observed in Vanguard, the Gorham's large and small game assemblages record clear human activity throughout, stone tool-induced modifications with cut marks consistent with

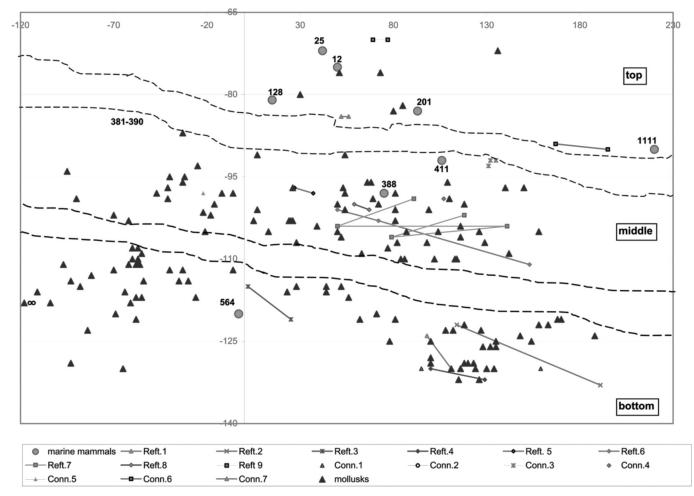


Fig. 4. Longitudinal projection of the fossil distribution of Vanguard Cave, middle area, units C and D, showing three separate episodes. This projection has only considered shells and marine mammal bones. Terrestrial animals are abundant throughout the three episodes, but they have not been plotted to avoid superimposition of fossils and to enable better distinction among these three episodes. Refitting (Reft.) and connection (Conn.) between fossil bones of terrestrial mammals also distinguishes these three episodes. More marine mammals are present in the top and central episodes, whereas shellfish (limpets, barnacles, mussels, and patella) occur more abundantly at the bottom.

butchering/filleting purposes, breakage to extract the marrow (hammerstone anvil, impact and percussion as well as conchoidal scars) and disarticulation (peeling, chop marks, and sawing marks) at the joints. Mixed fracture angles on spiral breaks have also been observed on these fossils, suggesting that bones were previously heated and then broken (32). Carnivore damage is almost absent, and postdepositional taphonomic modifications are very similar between the Middle and Upper Paleolithic levels. Evidence of reworking or even resedimentation was not observed at any level (38).

Ecological Considerations

Overall, the late Pleistocene vertebrate and invertebrate faunas present in Vanguard and Gorham's Cave indicate mild and relatively humid Mediterranean conditions not greatly different from those of southern Iberia today (40). Of the marine mammals, *M. monachus* has a modern geographical range that includes the Mediterranean and Black Seas, and the waters along the northwestern coast of North Africa south to c. 34°N (41). Although found on offshore islands, it prefers rocky coastlines with caves and grottos. However, it is also known to come ashore

Table 2. Marine vertebrate mater	al associated with Mousteri	an industry at Vanguard Cave

Taxon	Anatomical element	Age	Episode	Label
Delphinus delphis	IV metacarpal Pectoral flipper	Adult	Тор	VAN 96 (12)
Delphinus delphis	Lower thoracic vertebra Epiphysial union	Immature	Тор	VAN 96 (25)
Family Delphinidae	Proximal ulna	Indet.	Тор	VAN 96 (201)
Tursiops truncatus	Vertebra section of vertebral body and fused epiphysis	Immature	Тор	VAN 98 (128)
Monachus monachus	Left hemimandible intact dentition	Immature	Тор	VAN 98 (1111)
Monachus monachus	Proximal hind limb phalanx (human damage)	Adult	Middle	VAN 96 (411)
Monachus monachus	Right premolar	Immature	Middle	VAN 97 (388b)
Monachus monachus	Complete scapula (human damage)	Immature	Bottom	VAN 98 (564)
Diplodus sargus/vulgaris	Part of left dentary of the edible sea bream	Indet.	Middle	VAN 96 (381/390)

Modification	Total	%
Human-induced		
Cut marks	158	22.4
Percussion marks	26	3.7
Flake	17	2.4
Conchoidal scar	6	0.9
Peeling	17	2.4
Adhered flake	6	0.6
Burnt	233	33.1
Carnivore-induced		
Tooth marks	25	3.5
Digestion	1	0.1
Bone licking	1	0.1
Postdepositional		
Trampling	23	3.3
Weathering	14	2.0
Polishing	1	0.1
Root marks	31	4.4
Soil corrosion	3	0.4

Modifications have been grouped as human-induced damage, carnivore damage, and postdepositional damage. Percentages are based on the 704 fossil bones (NISP) represented in this sample (149 sea shells excluded).

on open beaches in northwest Africa. It is only a sporadic visitor to Gibraltarian waters today but is present on the Moroccan Mediterranean coast. *Tursiops truncatus* (bottlenose dolphin) is found primarily in coastal and inshore regions of tropical and temperate waters of the world. Its population density appears to be higher near the shore (41), and it is one of the more commonly stranded species (42, 43). It occurs around Gibraltar, although less abundantly than *Delphinus delphis* (common dolphin), an oceanic species of tropical to warm temperate waters (41). *Diplodus sargus* or *vulgaris* is a fish that often lives near the coast, from <1 m of depth down to >50, among rocks and in sand banks.

Discussion and Summary

Recent isotopic studies on Neanderthals (7–10, 44) suggest that they were heavily dependent on meat from herbivorous terrestrial mammals, whereas Upper Paleolithic humans had a much broader resource base, including regular access to fowling and aquatic resources (44). However, isotopic analyses on Neanderthal bones from coastal environments should also be performed

Table 4. Taxonomic identification of plotted fossils recovered from level III (modern human) and level IV (Neanderthal) of Gorham's Cave (37)

Таха	Gorham's Cave	%	Level III	%	Level IV	%
Cervidae	139	7.9	112	6.4	27	1.5
Equidae	5	0.3	3	0.2	2	0.1
Bovidae	15	0.9	13	0.7	2	0.1
Caprinae	73	4.2	55	3.1	18	1.0
Rhinocerotidae	1	0.1	1	0.1		
Suidae	2	0.1	2	0.1		
Phocidae	2	0.1	1	0.1	1	0.1
Felidae	23	1.3	17	1.0	6	0.3
Canidae	5	0.3	2	0.1	3	0.2
Hyaenidae	24	1.4	5	0.3	19	1.1
Ursidae	3	0.2	1	0.1	2	0.1
Carnivora indet	11	0.6	5	0.3	6	0.3
Leporidae	723	41.1	583	33.2	140	8.0
Aves	182	10.4	70	4.0	112	6.4
Fish	6	0.3	4	0.2	2	0.1
Unidentified	543	30.9	366	20.8	177	10.1
Total	1,757	100.0	1,240	70.6	517	29.4

to test this contrast further (45). Grayson and Delpech (5) showed that Neanderthals and Upper Paleolithic humans did not show significant differences in hunting and butchering behavior in the material studied. Similarly, we have observed that the human occupation levels at Gorham's Cave, first occupied by Neanderthals and then by Upper Paleolithic humans, do not show obvious differences in faunal composition (40). Marine mammals are present in occupation levels associated with Neanderthals at both Vanguard and Gorham's Caves and occur in Upper Paleolithic human occupation levels in Gorham's (38).

Marine mammal exploitation has also been documented in South African Middle Stone Age (MSA) people. Recent publications have shown that at Pinnacle Point (on the south coast of South Africa), they included marine resources in their diet ≈ 164 ka ago (± 12 ka (46). The earliest previous evidence for human use of marine resources and coastal habitats was dated to 125 ka ago in Eritrea (47, 48). Klein et al. (49) claim to find similarities between MSA people and the opportunistic behavior of hyenas in their tendency to patrol the coast year-round, in contrast to Late Stone Age (LSA) groups that focused their coastal visits. Klein et al. (49) also suggested that MSA Africans could have been behaviorally similar to their European Neanderthal contemporaries (50), whereas effective use of coastal resources was a property of LSA people (after 50 ka). We have distinguished in Gibraltar focused coastal visits by Neanderthals repeated during particular times, possibly seasonal. It should be noted that studied LSA sites in South Africa are largely after 20 ka (51, 52) and recent studies suggest that the MSA survived in places until \approx 28 ka (53). This means that the MSA/LSA transition in South Africa may be comparable with the Middle/Upper Paleolithic transition in southwestern Europe (1, 49) and that the LSA focused exploitation of marine resources in South Africa therefore probably postdates that by the Mediterranean Neanderthals.

Vanguard Cave shows that Neanderthals were not only systematically exploiting terrestrial mammals but also marine mollusks, pinnipeds, and cetaceans. Their distribution through the stratigraphy suggests that securing marine mammals was not an accidental or isolated practice, but a focused behavior possibly repeated seasonally or over longer periods. Furthermore, at several Gibraltar Middle Paleolithic sites, coastal wildfowl and seabirds (e.g., the Great Auk Pinguinus impennis), were also likely to have been exploited by Neanderthals (40, 54-56). Significantly, the range of species exploited and the age distribution pattern of the prey strongly indicate that the coastal exploitation of resources by Neanderthals was not a sporadic and isolated occurrence but one that required a knowledge of the life history of prey and its seasonality. Other Middle Paleolithic sites from Portugal (57) and the South of Spain (58, 59) have yielded remains of mollusks, cetaceans, or marine birds. Although evidence of a human role for these marine remains may not be as clear and repetitive as in Gibraltar, their presence should also be considered as reinforcing this behavior in Neanderthals.

This indicates that a wider geographical and ecological range of Neanderthal and Upper Paleolithic human sites will need to be sampled before definitive conclusions can be reached about the extent of behavioral differences between these closely related human groups. Marine resource exploitation provides higher territorial stability (40, 47), and this might have facilitated a late survival of Neanderthals in the South of the Iberian Peninsula (1).

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- 1. Finlayson C, et al. (2006) Late survival of Neanderthals at the southernmost extreme of Europe. Nature 443:850–853.
- Stringer C, Gamble C (1993) In Search of the Neanderthals (Thames and Hudson, New York).
- 3. Stiner MC (1994) Honor Among Thieves (Princeton Univ Press, Princeton).
- Gaudzinski S, Roebroeks W (2000) Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. J Hum Evol 38:497–521.
- Grayson BK, Delpech F (2003) Ungulates and the Middle-to-Upper Paleolithic transition at Grotte XVI (Dordogne, France). J Archaeol Sci 30:1633–1648.
- Burke A (2004) The ecology of Neanderthals. Int J Osteoarchaeol 14:155–161.
 Bocherens H, Drucker D, Billiou D, Patou-Mathis M, Vandermeersch B (2005) Isotopic evidence for diet and subsistence pattern of the Saint-Cesaire I Nean-
- derthal: Review and use of a multisource mixing model J Hum Evol 49:71–87.
 8. Bocherens H, et al. (1991) Isotopic biogeochemistry (¹³C, ¹⁵N) of fossil vertebrate collagen: Application to the study of a past food web including Neandertal man. J Hum Evol 20:481–492.
- 9. Fizet M, et al. (1995) Effect of diet, physiology, and climate on carbon and nitrogen stable isotopes of collagen in a late pleistocene anthropic palaeoecosystem: Marillac, Charente, France. J Archaeol Sci 22:67–79.
- Richards MP, Pettitt PB, Stiner MC, Trinkaus E (2001) Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic. Proc Natl Acad Sci USA 98:6528–6532.
- Gaudzinski S (2004) A matter of high resolution? The Eemian Interglacial (OIS 5e) in north-central Europe and Middle Palaeolithic subsistence. Int J Osteoarchaeol 14:201–211.
- Stewart JR (2004) Neanderthal-modern human competition? A comparison between the mammals associated with Middle and Upper Palaeolithic industries in Europe during OIS 3. Int J Osteoarchaeol 14:178–189.
- Burke A (2000) Hunting in the Middle Palaeolithic. Int J Osteoarchaeol 10:281– 285.
- Bar-Yosef O (2004) Eat what is there: Hunting and gathering in the world of Neanderthals and their neighbours. Int J Osteoarchaeol 14:333–342.
- 15. Mellars P (1996) The Neanderthal Legacy (Princeton Univ Press, Princeton).
- Barton RNE (2000) Neanderthals on the Edge: 150th Anniversary Conference of the Forbes' Quarry Discovery, Gibraltar, eds Stringer CB, Barton RNE, Finlayson JC (Oxbow Books, Oxford, UK), pp 211–220.
 Fernández-Jalvo Y, Andrews P (2000) Neanderthals on the Edge: 150th Anni-
- Fernández-Jalvo Y, Andrews P (2000) Neanderthals on the Edge: 150th Anniversary Conference of the Forbes' Quarry Discovery, Gibraltar, eds Stringer CB, Barton RNE, Finlayson JC (Oxbow Books, Oxford, UK), pp 171–182.
- Fa D (2008) Where the Last Neanderthals Lived, eds Finlayson C, et al. (Oxbow Books, Oxford, UK), in press.
- Stringer CB, Barton RNE, Finlayson JC, eds (2000) Neanderthals on the Edge: 150th Anniversary Conference of the Forbes' Quarry Discovery, Gibraltar (Oxbow Books, Oxford, UK), p 267.
- Rodríguez-Vidal J, et al. (2007) Contributions to the Quaternary Period Studies (Contribuciones al Estudio del Periodo Cuaternario), eds Lario J y Silva (AEQUA, Avila), pp 215–216.
- Rodríguez-Vidal J, Cáceres LM, Abad M, Ruiz F, Martínez-Aguirre A (2007) Morphosedimentary evidences of the last interglacial maximum on the coast of Governor's Beach, Gibraltar. Geogaceta 42:107–110.
- Goldberg P, MacPhail R (2000) Neanderthals on the Edge: 150th Anniversary Conference of the Forbes' Quarry Discovery, Gibraltar, eds Stringer CB, Barton RNE, Finlayson JC (Oxbow Books, Oxford, UK), pp 93–108.
- RNE, Finlayson JC (Oxbow Books, Oxford, UK), pp 93–108.
 Bronk Ramsey C, Higham THF, Owen DC, Pike AWG, Hedges REM (2002) Radiocarbon dates from the Oxford AMS system: Archaeometry Datelist 31. Archaeometry 44(35):1–149.
- Pettitt PB, Bailey RM (2000) Neanderthals on the Edge: 150th Anniversary Conference of the Forbes' Quarry Discovery, Gibraltar, eds Stringer CB, Barton RNE, Finlayson JC (Oxbow Books, Oxford, UK), pp 155–162.
- 25. Gamble C (1999) Gibraltar and the Neanderthals 1848–1998. J Hum Evol 36:239– 243.
- Lyman RL (1994) Vertebrate Taphonomy (Cambridge Univ Press, Cambridge, UK).
- Henshaw A (1999) Location and appropriation in the Arctic: An integrative zooarchaeological approach to historic Inuit household economies. J Anthropol Archaeol 18:79–118.
- 28. Bischoff J, Julià R, Mora R (1988) Uranium series dating of the Mousterian occupation at Abric Romaní, Spain. *Nature* 332:68–70.
- Carbonell E, et al. (1996) The Last Neanderthals: The First Anatomically Modern Humans. Cultural Change and Human Evolution: The Crisis at 40 ka BP, eds Carbonell E, Vaquero M (Universitat Rovira i Virgili, Tarragona), pp 385–434.
- Vaquero M (1999) Intrasite spatial organization of lithic production in the Middle Palaeolithic: The evidence of the Abric Romaní (Capellades, Spain). Antiquity 73:493–504.
- Caceres I, Fernandez-Jalvo Y (2008) Gibraltar Neanderthals in Context: A Report of the 1995-1998 excavations at Gorham's and Vanguard Caves, Gibraltar, eds Barton RNE, Stringer CB, Finlayson JC. Monograph Series, Oxford Committee for Archaeology (Oxbow Press, Oxford, UK), in press.

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- Caceres I, Bravo P, Esteban M, Exposito I, Saladie P (2002) Current Topics on Taphonomy and Fossilization, eds de Renzi M, et al. (Ayuntamiento de Valencia, Valencia) pp 471–479.
- Villa P, Mahieu E (1991) Breakage patterns of human long bones. J Hum Evol 21:27–48.
- 34. Muñoz AS (1996) Exploitation of pinnipeds in the Atlantic coast of Tierra del Fuego (translated from Spanish) *Arqueologia* 6:199–222.
- 35. Malakoff D (2001) Scientists use strandings to bring species to life. Am Assoc Adv Sci 293:1754–1757.
- 36. Riquelme JA (2008) Where the Last Neanderthals Lived, eds Finlayson C, et al. (Oxbow Books, Oxford, UK), in press.
- Currant A (2000) in Neanderthals on the Edge: 150th Anniversary Conference of the Forbes' Quarry Discovery, Gibraltar, eds Stringer CB, Barton RNE, Finlayson JC (Oxbow Books, Oxford, UK), pp 201–205.
- Fernandez-Jalvo Y, Caceres I (2008) Where the Last Neanderthals Lived, eds Finlayson C, et al. (Oxbow Books, Oxford, UK), in press.
- 39. Fernandez-Jalvo Y, Andrews P, Caceres I (2008) When humans chew bones. J Hum Evol, in press.
- Marean CW, et al. (2007) Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. Nature 449:905–908.
- 41. Walter RC, et al. (2000) Early human occupation of the Red Sea coast of Eritrea during the last interglacial. *Nature* 405:65–69.
- 42. Erlandson JM (2001) The archaeology of aquatic adaptations: Paradigms for a new millennium. J Archaeol Res 9:287–350.
- Klein RG, et al. (2004) The Ysterfontein 1 Middle Stone Age site, South Africa, and early human exploitation of coastal resources. Proc Natl Acad Sci USA 101:5708–5715.
- Klein RG, Cruz-Uribe K, Halkett D, Hart T, Parkington JE (1999) Paleoenvironmental and human behavioral implications of the Boegoeberg 1 late Pleistocene hyena den, Northern Cape Province, South Africa. Q Res 52:393–403.
- 45. McBrearty S, Brooks AS (2000) The revolution that wasn't: A new interpretation of the origin of modern human behavior. *J Hum Evol* 39:453–563.
- Finlayson C (2005) Biogeography and evolution of the genus Homo. Trends Ecol Evol 20:457–463.
- Soriano S, Villa P, Wadley L (2007) Blade technology and tool forms in the Middle Stone Age of South Africa: The Howiesons Poort and post_Howiesons Poort at Rose Cottage Cave. J Arch Sci 34:681–703.
- Finlayson G (2006) Climate, vegetation, and biodiversity: A multiscale study of the south of the Iberian Peninsula. PhD thesis (Anglia–Ruskin University, Cambridge, UK).
- Jefferson TA, Leatherwood S, Webber MA (1993) FAO Species Identification Guide to Marine Mammals of the World (United Nations Environment Programme, Food and Agriculture Organization of the United Nations, Rome).
- 50. Fraser FC (1969) Guide for the Identification and Reporting of Stranded Whales, Dolphins and Porpoises on the British Coasts (British Museum of Natural History, London).
- Sabin RC, Jepson PD, Reid RJ, Deaville R, Patterson IA (2001) Trends in Cetacean Strandings on the UK Coastline and Marine Mammal Postmortem Investigations for the Year 2000: Report No. ECM 516F00/01 (Natural History Museum, London).
- Richards MP, Jacobi R, Cook J, Pettitt PB, Stringer CB (2005) Isotope evidence for the intensive use of marine foods by Late Upper Palaeolithic humans. J Hum Evol 49:390–394.
- Pearson JA (2007) Hunters, fishers and scavengers: A review of the isotope evidence for Neanderthal diet. *Before Farming* 2:1–16.
- 54. Eastham A (1967) The avifauna of Gorham's cave, Gibraltar. Bull Inst Archaeol London 7:37–42.
- Finlayson C, Giles-Pacheco F (2000) in Neanderthals on the Edge: 150th Anniversary Conference of the Forbes' Quarry Discovery, Gibraltar, eds Stringer CB, Barton RNE, Finlayson JC (Oxbow Books, Oxford, UK), pp 139–153.
- Cooper J (1999) Late Pleistocene avifaunas of Gibraltar and their palaeoenvironmental significance. PhD thesis (Univ London, London).
- 57. Antunes M (1992) The Man of Figueira Brava cave (ca. 30000 BP) (translated from Portuguese). *Memoria Acad Cienc Lisboa* 31:487–536.
- 58. Cortés M, Simón MD (2001) Cave Bajondillo (Torremolinos, Málaga, Andalucia): News of the transition between the Middle and Upper Paleolithic in the South of Iberian Peninsula. Trabalhos de Arqueologia. 17. Les Premiers hommes modernes de la Péninsule Ibérique. Actes du Colloque de la Commission VIII de l'UISPP Vila Nova de Foz Côa, octubre 1998 (Instituo Portugues de Arqueologia, Lisboa).
- Cortés M (2005) The Neandertal far west: The Middle Paleolithic at the South of the Iberian Peninsula (translated from Spanish). *Museo Altamira Monografías* 20:55–74.