Limestone caves and the Quaternary record of terrestrial tetrapods on islands

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Abstract: The potential for finding Quaternary tetrapod fossils on islands is governed by a combination of biodiversity, geology, fossil preservation, and time span of records. Islands with extensive limestone exposures are particularly well represented at low and middle latitudes, where biodiversity is potentially high, and the caves and karst fissures in these landscapes have proven to be rich reliquaries of the Quaternary fossil record. This is particularly apparent when we contrast limestone islands with volcanic islands in the Lesser Antilles; the latter present a serious deficiency in the fossil vertebrate record and an impediment to understanding the biogeography of the region. Caves and karst fissures are also ephemeral on geological time scales, and few tropical island sites are known that are older than the Last Interglacial. In Britain, important cave sites of Middle Pleistocene age are known, but are rare.

The karst record of Quaternary vertebrates from islands has been accumulating since the 19th century, and has provided magnificent insights into the evolutionary history of such faunas that are largely unobtainable from non-karst contexts. Nevertheless, caves and karst fissures are a distinctly finite resource, and conservation of existing sites together with procedures to identify and protect newly discovered sites are essential.

Scientific interest in the insular records of Quaternary vertebrates has a long history; indeed, it predates the publication of the Darwin–Wallace theory of evolution (Wallace 1858; Darwin 1859) and the birth of the science of geology (Lyell 1830, 1832, 1833). As early as 1823, William Buckland had described Pleistocene bone caves from Britain and Gibraltar in his seminal Reliquiae Diluvianae (Buckland 1823). Within a few years, the apparent but vigorously contested co-occurrence of human remains and artefacts with extinct, ‘Pre-Noachian’ mammals had become a central philosophical debate in the Natural Sciences. Careful excavations at Kents Cavern (Devon, England) by the Rev. J. MacEnery (MacEnery 1859), and later by William Pengelly, were specifically intended to address this question. In the West Indies, Edward Drinker Cope described the extraordinary giant extinct rodent Amblyrhiza inundata from the diminutive islands of Anguilla and St. Maarten (Cope 1869). The importance of these island discoveries was such that Alfred Russel Wallace urged that the caves of Borneo be prospected for fossils (Wallace 1864), although early efforts there were relatively unsuccessful.

By the first decade of the 20th century, the major islands of the West Indies were being intensively prospected for cave deposits of extinct vertebrates, with outstanding results, by H. E. Anthony of the American Museum of Natural History (Anthony 1918, 1919, 1920). A century later, excellent reviews of insular Quaternary vertebrate faunas are available for the world’s major archipelagos, the West Indies (Morgan & Woods 1986; van der Geer et al. 2010) and the Mediterranean islands (van der Geer et al. 2010), and there is a rich literature for major islands including Madagascar (van der Geer et al. 2010), New Zealand (Worthy & Holdaway 2002), the Hawaiian islands (James & Olson 1991; Slikas 2003), and the Mascarenes (Rijssijk et al. 2009; Hume & Middleton 2011). However, obvious questions arise: how complete is this record? What are the prospects for extending it?

The importance of karst to the island record

The preservation and recovery of the vertebrate fossil record of islands is closely correlated with the extent of karst and/or pseudokarst development on the island. In short, islands that lack caves rarely preserve any significant record of their Quaternary faunas. This is well illustrated in the West Indies, where extensive records have been recovered from the karst-rich Greater Antilles and from the ‘limestone caribbees’ of Anguilla (Mcfarlane & MacPhee 1989), Barbuda, Barbados (Turvey et al. 2012), together with Curacoa and Bonaire (Hooijer 1959; McFarlane & Debrot 2001; McFarlane & Lundberg 2002). In contrast, the volcanic islands of the Antilles arc (Dominica, Montserrat and St. Lucia) have produced almost nothing. Our knowledge of these latter Quaternary vertebrate faunas is limited to late Holocene archaeological sites (e.g. Steadman et al. 1984), a single recovery from a lahar deposit on Grenada (MacPhee al. 2000), and a few taxa that survived into the historical era and were collected alive in the late 19th century. Archipelagos that lack significant karst altogether (the Seychelles are an example) generally lack any Quaternary vertebrate record that precedes the Holocene archaeological window. Of course, not all caves are karstic in origin. A few islands that have been surfaced by recent basaltic volcanism have lava tubes that can be important archives of extinct fauna; the native rodent fauna of the Galapagos is known exclusively from such sites (Steadman & Ray 1982), and the extensive lava tubes of the Hawaiian islands continue to add to our knowledge of extinct birds (Olson & James 1982, 1991; Slikas 2003). Unfortunately, lava tubes are often even more ephemeral than limestone caves, as a result of typically thin roofs and burial by subsequent lava flows; few if any lava tube vertebrate fossil records predate the Holocene.

How common are caves?

If we accept that our record of extinct island quadrupeds to a very large extent derives from caves (and infilled karst fissures), then it is useful to consider the question of how plentiful the cave resource may be. The island of Jamaica offers an excellent insight, because it has been uniquely well documented thanks to the pioneering efforts of Alan Fincham (Fincham 1977, 1997) and more recently by Stefan Stewart and the Jamaican caves Organization (www.jamaicancaves.org). At the time of writing, 1043 caves have been described and located (Fig. 1), scattered across an island of c. 10829 km² (some 70% of which is underlain by limestone). These cave sites range from shallow ‘rock shelters’ a few metres in length to the 3.5 km long Gourie Cave and the 10 km Jacksons Bay caves complex. A general characteristic of caves is that they exhibit...
an inverse relationship between the number of sites and their length. Figure 2 demonstrates that this relationship is reliably linear (on log–log axes), and can be extrapolated to predict the expected number of caves in each size class. The predicted total number of caves in Jamaica derived from this approach is \( c \approx 3000 \), of which the majority of predicted but as yet unrecorded cave sites are fairly short. If we use an arbitrary cut-off of 4 m length to distinguish ‘true’ caves (i.e. those deep enough to have a reasonable prospect of preserving fossiliferous sediments) we find that of a predicted 875 caves >4 m, 737 (78%) have already been documented.

**What fraction of caves preserve a Quaternary vertebrate record?**

Of the 737 Jamaican caves >4 m length, some 28 (3.8%) have yielded a publishable vertebrate record (e.g. Morgan 1993) For comparison, it is instructive to compare a non-tropical example, Britain, which has been intensively prospected both for caves (by the sport caving community) and for ‘bone’ caves (by the palaeontological and archaeological communities, with extensive collaboration from cavers) for some 250 years. Cave-bearing limestones total some 3800 km² in Britain, and several thousand caves are known. Hundreds of sites have yielded ossiferous remains, but in the vast majority of cases these comprise isolated teeth or bones of Holocene and modern, and often archaeological, faunas. Significant ‘bone caves’ (which I define here as yielding Pleistocene record of sufficient importance to merit significant publications) total only 28. Plotting the cumulative number of such sites against calendar date (Fig. 3) yields an accumulation curve akin to those used to assay biodiversity (e.g. Ugland et al. 2003), and it is apparent that the rate of discovery of new sites is approaching its asymptote. The karst of Devon, SW England, is particularly interesting because it lies outside the southern margin of the maximum extent of the Pleistocene ice sheets and has preserved a wealth of Pleistocene ossiferous deposits that in other karst areas might have been destroyed by glacial planation. In an area of only 49 km² of limestone, Devon hosts 270 known caves of which 12 (4.4%) have yielded Pleistocene bone deposits (although only four meet the previous criterion of ‘significant’). If we combine the Jamaican and Devon records (which are surprisingly concordant, given the contrasts between tropical and temperate karsts) the mean number of bone caves in the total cave inventory is \( 4.1 \pm 0.4 \). Applying this result to the earlier estimate of the number of 3000 caves in Jamaica gives an expected number of 12.4 bone caves in Jamaica. The Jamaican estimate of 3000 caves (Fig. 2) is thus about ten times lower than the Devon estimate, an extremely significant difference.
undiscovered Jamaican caves, we may postulate that the number of significant bone caves remaining to be found on that island may be as few as 6–9 sites.

How deep is the insular record?

It has already been noted that on islands without caves, the fossil record of quadrupeds is chronologically very shallow, a consequence of the generally short-lived nature of most of the alternative sites of fossil preservation such as ponds and bogs. Caves provide a greater chronological depth because the caves themselves are generally long-lived. However, on geological time scales, limestone caves are nevertheless ephemeral. Caves and fissures are destroyed by valley down-cutting, unroofing, and collapse. Even when caves themselves survive, capture of surface drainage can result in rapid erosion of their fossil-bearing sediment deposits, and anthropogenic damage ranging from guano extraction to uncontrolled archaeological excavation can destroy deposits. It is therefore unsurprising that frequency of fossil deposits in caves and karst fissures is inversely proportional to their age. Figure 4 plots the age of the oldest, securely dated ossiferous deposits from 14 important British bone caves against their frequency, yielding an exponential decay curve with an ‘equivalent half-life’ of 106 ka. In other words, approximately half the fossil record is lost every 100 ka. Given the rarity of these significant bone caves overall, it is unsurprising that two and a half centuries of intensive research have yielded only a handful of British cave sites that are demonstrably older than 200 ka.

An analysis of dated Quaternary vertebrate cave deposits from Jamaica yields a similar pattern, albeit from a small dataset, with an ‘equivalent half-life’ of c. 195 ka (Fig. 5). This value is likely to be biased by a focus on dating indurated breccias containing distinctively old faunas; if the dataset includes additional sites listed by Morgan (1993) that are undated but presumed Holocene on faunistic evidence, the ‘equivalent half-life’ falls to c. 125 ka. Similar metrics have not been developed for other karst areas around the world, but anecdotal summaries suggest similar patterns, notwithstanding great differences in geology and climate. For example, Australia’s richest Quaternary vertebrate cave site, the Naracoorte cave system, has yielded radiometric ages no older than Marine Isotope Stage 11 (Moriarty et al. 2000; Grün et al. 2001). (True cave sites should not be confused with exhumed palaeokarst ‘cave’ deposits, such as those at Riversleigh, Australia, which are much older. Fossiliferous palaeokarst fissures and ‘caves’ are known from Britain from as far back as the Mesozoic (Savage 1993) but cannot be considered ‘cave deposits’ within the usual meaning of that term.)

Discussion

Bone caves (i.e. caves and fissures that preserve records of ancient quadrupeds) are a scarce resource. This observation applies not only to intensively investigated islands of modest karst resources such as Britain, but also to less well-studied islands such as Jamaica (and the other limestone West Indies). The reality is that most of the significant sites on many islands may already have been found. Those that remain to be found will probably be discovered by cavers (including cave divers), not palaeontologists, which places a high premium on maintaining good relationships between these communities. Moreover, the scarcity of the resource demands that every effort be taken to preserve what we already have. Recent re-investigations of some of the most important British sites from the 19th century (e.g. Lundberg & McFarlane 2007; Lundberg et al. 2010) have yielded new interpretations of these deposits through the application of state-of-the-art dating technologies, but these advances can continue only if the sites are themselves adequately conserved. Sites such as Victoria Cave, Yorkshire are nominally protected by national legislation, but in practice continue to deteriorate through the actions of uncontrolled casual visitors. Most sites in the West Indian islands are completely unprotected. It is likely that much of the future advancement in our understanding of the Pleistocene history of quadruped faunas on islands will derive from reanalyses of existing sites, and the realistic protection of these sites must become a priority.

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Fig. 4. The number of ‘significant’ Quaternary bone caves known from Britain versus the maximum age of their palaeontological records.

Fig. 5. The number of ‘significant’ Pleistocene bone caves known from Jamaica versus the maximum age of their palaeontological records.
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