Quaternary Science Reviews 143 (2016) 150–174

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Late Quaternary changes in bat palaeobiodiversity and palaeobiogeography under climatic and anthropogenic pressure: new insights from Marie-Galante, Lesser Antilles☆

Emmanuelle Stoetzel [a,*], Aurélien Royer [a,b,c], David Cochard [a], Arnaud Lenoble [a]

[a] PACEA – UMR CNRS 5199, Université de Bordeaux, Bâtiment B18, Allée Geoffroy Saint Hilaire, CS 50023, 33615 Pessac Cedex, France
[b] Biogéoscience – UMR CNRS 6282, Université de Bourgogne-Franche-Comté, 6 Boulevard Gabriel, 21000 Dijon, France
[c] Laboratoire EPHE PALEVO, Ecole Pratique des Hautes Etudes, 21000 Dijon, France

ARTICLE INFO

Article history:
Received 16 October 2015
Received in revised form
28 April 2016
Accepted 10 May 2016

Keywords:
Fossil chiroptera
Blanchard Cave
Late pleistocene
Holocene
Palaeoenvironmental changes
Anthropogenic impact
Bat fauna turnover
West Indies

ABSTRACT

Data on Lesser Antillean Late Quaternary fossil bat assemblages remains limited, leading to their general exclusion from studies focusing on Caribbean bat palaeobiodiversity and palaeobiogeography. Additionally, the role of climatic *versus* human pressure driving changes in faunal communities remains poorly understood. Here we describe a fossil bat assemblage from Blanchard Cave on Marie-Galante in the Lesser Antilles, which produced numerous bat remains from a well-dated, stratified context. Our study reveals the occurrence of at least 12 bat species during the Late Pleistocene and Early Holocene on Marie-Galante, whereas only eight species are currently known on the island. Among these 12 species, six are extirpated and one is extinct. Faunal changes within the Blanchard sequence indicate variations in Pleistocene bat species representation in the Lesser Antilles to have been influenced by climatic conditions, with "northern species" (Greater Antilles) favored during glacial conditions and "southern species" (southern Lesser Antilles) during interglacial events. However, few species disappeared at the end of the Late Pleistocene, with most of the extinction/extirpation events occurring during the Holocene. This pattern suggests human activities in the Lesser Antilles to have played a major role in bat turnover during the late Holocene.

1. Introduction

Untangling the impact of climatic changes and human activities on biodiversity currently represents a key topic for understanding the historical biogeography of species and mechanisms driving their variation over time. While special attention is given to current biodiversity "hot spots", such as the Caribbean islands (Myers et al., 2000; Orme et al., 2005; Ceballos and Ehrlich, 2006), past biodiversity is often poorly documented in these areas. This is primarily due to the scarcity of documented fossil material in these regions, the Lesser Antilles in particular (Morgan and Woods, 1986; Davalos and Russell, 2012).

In the Caribbean, most West Indian terrestrial mammals went extinct in the Late Pleistocene, whereas most bat species survived (Morgan and Woods, 1986; Davalos and Turvey, 2012). An estimated 37% of bat species underwent localized extinction or extirpation on one or more islands, with an overall extinction rate for the entire West Indies reaching 11% (Morgan, 2001). However, other faunal taxa exhibit higher values, for example, between 45 and 70% for herpetofauna (Powell and Henderson, 2005; Bochaton et al., 2015; Bailon et al., 2015) and between 80 and 100% for non-volant mammals (McFarlane, 1999; Morgan, 2001; Davalos and Turvey, 2012). Natural environmental modifications are often considered the main factor driving changes in bat faunas since the last glacial maximum, including climate-induced habitat change (Pregill and Olson, 1981), cave submersion connected to post-glacial sea level rise (Morgan, 1994, 2001) or alterations in

☆ **Individual contribution of authors:** ES studied the fossil bat remains from Blanchard Cave, carried out data analyses and wrote the paper; AR provided unpublished data on isotopic studies at Blanchard Cave, produced the age-depth model in collaboration with AL, and participated in the statistical analyses and article preparation; DC participated in the preparation of the article; AL supervised the study, supplied bibliographic information and participated in article preparation and writing.

* Corresponding author. Current address: HNHP – UMR CNRS 7194, Muséum national d'Histoire naturelle, Sorbonne Universités, Musée de l'Homme, Palais de Chaillot, 17 place du Trocadéro, 75016 Paris, France.
E-mail addresses: emma_stoetzel@hotmail.com, stoetzel@mnhn.fr (E. Stoetzel).

http://dx.doi.org/10.1016/j.quascirev.2016.05.013
0277-3791/

ecological equilibria linked to a reduction in island land mass (Davalos and Russell, 2012). This contrasts sharply with other taxa for which human impact appears to be the overriding factor leading to their disappearance, particularly when the influence of Amerindian populations is combined with the European colonization of the West Indies (Carlson and Keegan, 2004; Steadman et al., 2005; Fitzpatrick and Keegan, 2007; Davalos and Turvey, 2012; Bochaton et al., 2015). However, it is noteworthy that studies of Antillean Late Quaternary bat assemblages have focused mainly on the Greater Antillean islands or more general evolutionary or biogeographic mechanisms despite the limited number of well-dated fossil assemblages and their broad distribution (Pregill and Olson, 1981; Morgan and Woods, 1986; Hedges, 1996; Rodríguez-Durán and Kunz, 1992; Morgan, 2001; Davalos, 2010; Davalos and Russell, 2012; Davalos and Turvey, 2012; Soto-Centeno, 2013; Soto-Centeno and Steadman, 2015). Orihuela and Tejedor (2012), and Soto-Centeno and Steadman (2015) recently challenged the “classic” climate change hypothesis for the extirpation and extinction of Caribbean bats. Their data demonstrated that the extirpation of several bat species coincided with the first human presence in the neighboring Bahamas, concluding that changes in bat faunas that began in the Late Pleistocene were also heavily impacted by human-induced modifications of the Holocene environment.

The Lesser Antilles experienced significant environmental changes since the Late Pleistocene as well as a considerable alteration of the landscape by human populations during historical periods (Pregill and Olson, 1981; Pregill et al., 1994; Curtis et al., 2001). This region therefore represents an ideal testing ground for evaluating the relative impact of human *versus* natural modifications of the environment on local faunal communities. However, until recently, the only fossil records from the Lesser Antilles were from rare Holocene sites on Montserrat, St. Martin, Barbuda, Anguilla and Antigua (Pregill et al., 1994). Moreover, Burma Quarry on the latter island yielded the only thoroughly analyzed fossil chiroptera assemblage in the region (Steadman et al., 1984; Pregill et al., 1988). Consequently, this limited fossil record led to the exclusion of the Lesser Antilles from discussions concerning the past faunal diversity and biogeographic history of the Caribbean (Davalos and Russell, 2012).

Here we report a new fossil bat assemblage from Blanchard Cave on the island of Marie-Galante in the Lesser Antilles, which fills gaps in our current understanding of Late Quaternary bat communities in the region and provides an opportunity to explore their evolution under both environmental and anthropogenic pressure as well as their relationship with Greater Antillean faunas.

2. Blanchard Cave

2.1. Regional setting

The carbonate island of Marie-Galante, with a maximum elevation of 204 m asl, is a dependency of Guadeloupe. Due to its low relief, the island receives limited precipitation (maximum annual rainfall of around 1500 mm) and the present-day natural vegetation is composed of dry deciduous tropical forest, a large part of which has been transformed into pastures and agricultural fields surrounded by a few patches of secondary forest (Rousteau et al., 1994). This island, separated from Guadeloupe even during glacial lowstands (Fig. 1), has a tropical climate where rainy (June–November) and dry (December–May) seasons alternate with only slight temperature variations (mean annual temperature of 27 °C). Coastal areas are charaterised by a staircase morphology related to slow tectonic movements (Feuillet et al., 2004).

The fossil-bearing site of Blanchard Cave (15°52′56″N; 61°14′01″W) lies 200 m from the current southern shoreline of Plio-Pleistocene age neritic limestone (Bouysse et al., 1993). The cave opens at the base of the lower cliff line bordering the littoral plain on the southeastern coast of Marie-Galante (Fig. 1). This coastal karst morphology is conducive to the preservation of several fossil-bearing caves (Lenoble et al., 2009), such as Cadet 2 and Cadet 3, approximately one hundred meters to the west of Blanchard Cave (Stouvenot et al., 2014; Bochaton et al., 2015), and Blanchard 2, a few meters higher on the same cliff (Mallye, 2014). The present-day coastal plain, as well as the adjacent relic cliff bordering it landward, were shaped during the marine high-stand of the last interglacial, as indicated by coral dating (Feuillet, 2000). The marine notch at the entrance of the cave shows Blanchard to have opened at least 125 ka ago.

2.2. Site description

The Blanchard site is a single-room cave with a 5 m wide entrance and 2 m high and 20 m long corridor opening onto a 15 m wide and 8 m high main chamber. Hygric measurements indicate Blanchard Cave to be a dry cave throughout the year, with air circulation driven by lower exterior temperatures, the subsequent arrival of cold air in the cave, and an interruption in the thermic stratification of air flow (Lenoble et al., 2015). These micro-climate parameters demonstrate Blanchard Cave to be a “cool chamber” (Silva-Taboada, 1979; Rodríguez-Durán, 1998, 2010).

Blanchard Cave is currently home to 10 to 15 individuals of Jamaican fruit-eating bats (*Artibeus jamaicensis*) roosting in ceiling pockets at the entrance (Masson et al., 1990a), with a variably-sized Antillean fruit-eating colony (*Brachyphylla cavernarum*) intermittently occupying the main chamber. Ten years of research in the cave have shown the size of the *Brachyphylla cavernarum* colony to vary from several hundred to around ten thousand individuals during the rainy season when a nursery forms in the cave. The current occupation of the site by *Artibeus jamaicensis* near the entrance and *Brachyphylla caveranum* in the main chamber is in keeping with the pattern of cave use by bats documented throughout the region (Rodríguez-Durán, 2010).

2.3. History of discovery and excavations at Blanchard Cave

Blanchard Cave is a prominent feature on the island and has been known by several different names, including *Grotte Madame Lionel* (Lasserre, 1961) or *Voûte à Quinquins* (Rodet, 1984). *Quinquin* is a creole word for fruit bat (Phyllostomidae), and the name *Voûte à Quinquin* not only indicates that the cave contains bats but also that this site supplied bats for traditional creole hunting and cooking (Masson et al., 1990b). The site's archaeological interest was probably known for some time, as suggested by another name for the cave, *Grotte Caraïbe*, mentioned by Barbotin in his book describing the pre-Columbian archaeology of the island (Barbotin, 1987). Nevertheless, evidence of the Amerindian occupation of the cave was only revealed by a test-pit at the cave's entrance area in 2005 that unearthed a Late Ceramic period burial (Stouvenot, 2005). In addition to archaeological work, natural fossil-bearing deposits preserved within the cave were identified in 2007 (Lenoble et al., 2009) and test-pits in the cave in 2008 revealed a thick Pleistocene fossil-bearing deposit overlain by a thin archaeological level. Further archaeological excavations were conducted in 2012 over a 25 m^2 area close to the rear wall of the cave (Courtaud et al., 2014). Palaeontological excavations subsequently carried out in the spring of 2013 and 2014 over a surface of 20 m^2 in the same location revealed a 4 m deep stratified natural deposit lying directly on the bedrock (Goetz et al., 2014, Fig. 2). Preliminary results were obtained from a limited number of faunal remains from the 2007 and