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ORIGINAL ARTICLE

The palynology and entomology of bat faeces at the Zerga Esker of the Mauritanian Adrar

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ABSTRACT

Bat synecology is notoriously hard to comprehend. Here, we propose a method encompassing many aspects of the bat ecosystem, i.e. the combined study of pollen and insects in its faeces (guano) together with vegetation surveys. In 1998-2004, we sampled recent and sub-recent guano of an insectivorous bat, *Rhinopoma microphyllum* (Brünnich 1782), which accumulated in a cave in an Ordovician Esker on the Adrar Plateau of Mauritania at the southern limit of the Sahara. This region is largely unexplored and was closed to field work for many years. The results indicate foraging not only near the esker, but also in small settlements at least 30 km away from their roost, such as in Chinguetti and Atar, as well as in the oases. The entomofauna include species attracted to artificial lights. Pollen analyses reveal that the bats visited both natural and cultivated landscapes including temporary cultivation in grayir. Individual guano samples were often characterised by different pollen taxa, indicating different flowering periods. The bats were thus not only influenced by and dependant on the highly erratic sequences of vegetational development after very irregular precipitation, but also on human activities. Findings of parasites, probably from the bats, provide some additional indication of bat vigour. Our multidisciplinary approach is a powerful tool with which to reconstruct various aspects of a delicate desert ecosystem, on which bats, a service-provider mammal by control of insect populations, closely depends.

* The results of a study on a hyena dropping found in the same cave are provided in supplementary information. Titre, résumé et légendes en français disponibles en matériel supplémentaire.

Highlights

- Many aspects of bat ecosystem covered by joint pollen-insect analysis in guano
- *Rhinopoma microphyllum* guano accumulated in the Zerga Esker, Mauritanian Sahara
- Bats depending on insects around distant light sources
- Bats depending on the highly erratic sequences of vegetational development after very irregular precipitation

INTRODUCTION

Insect-eating bats are endangered animals and, in many places, require protection; due to their nocturnal habits, their behaviour is hard to study; and therefore indirect methods are necessary. Apart from echolocation call recording as a means of identification (Loumassine et al. 2018), a complementary and rewarding approach for ecological purposes is to investigate their faeces, often called guano. Not unlike bird guano, large accumulations of bat guano may form in caves. Guano studies have the significant advantage of avoiding the trauma of net capture.

Pollen and insect studies of modern and ancient bat guano have shown some good results. They reveal not only environment, but also bat and insect behaviour. Palynological studies are relatively frequent on modern and fossil guanos in Europe and Southern Africa (e.g. Carrión et al. 2006 in Spain, Marais et al. 2015 in Namibia). Outside Africa, previous studies have analysed the insect content of bat droppings for ecological purposes with particular reference to behaviour, activity times, prey-selectivity and seasonal variation (e.g. Gamboa & Díaz 2021). Assigning fragments of invertebrates to their taxonomic families and subfamilies in bat guano is generally not difficult and some useful guidance exists (Shiel et al. 1997). The recognition of voided insect remains to a lower taxonomic level, i.e. genera or species, is more demanding and provides additional insights. Thus, the combination of pollen and insects researched in well-identified faeces enables environmental reconstruction and is a powerful tool to grasp many aspects of ecosystems, bat synecology and bat protection.

As far as can be established no pollen or insect studies of insectivorous bat guano and hyena droppings have been made so far in Africa north of the Equator, although potential for study of insectivorous bat guano exists. For example large accumulations of guano have been noted in a cave in Cameroun (Testa 2012).

Several species of bats live in Mauritania (Fig. 1), but allegedly the full diversity is unknown and potentially the number of species of bat may reach thirty (Allegrini et al. 2011). The guano found in the Cave of Zerga (Fig. 1) is regarded as linked to and voided by *Rhinopoma microphyllum* as a live colony was observed in the cave. This insectivorous bat is a well-known desert and semi-desert species in north-west Africa with a distribution extending eastwards to Pakistan (Schlitter & Qumsiyeh 1996, Loumassine et al. 2018). In Mauritania, it was recorded by Poulet (1970) in Akjoujt (190 km west-south-west of Zerga) (Fig. 1) and is regarded as a social forager (Cvikel et al. 2015). GPS tagging of *R. microphyllum* in Israel indicates individual foraging over distances exceeding 90 km in one night (Cvikel et al. 2015). According to Encyclopaedia.com (undated), *Rhinopoma* bats use gleaning and hawking techniques to feed on insects ranging from flying ants and termites to beetles, bugs and moths. Other living vertebrates observed in the area are listed in supplementary materials (SM) Section 3.

Cavities in the esker were opportunistically explored over several successive years (Fig. 1, 2 and Table 1) when *R. microphyllum* bats, bat guano and various animal faeces and remains were found. According to P. Lluch (pers. comm. 2001), animal faeces were especially abundant amongst fragmentation blocks in a rock shelter opening to the south (20° 19’ 30.5” N, 12° 41’ 25.3” W) (Fig. 1B). Based on tentative identifications, he found droppings of hyena, jackal or fox, Felou Gundi (*Felovia*) and Daman (*Hyrax*) as well as a spine from porcupine (*Hystrix*).

The aim of this investigation is to identify and reconstruct the environment in which Greater Mouse-tailed Bats, *Rhinopoma microphyllum* (Brünnich 1782), (Rhinopomatidae, Chiroptera) (gbif undated), were foraging at the southern limit of the Sahara in Mauritania (Fig. 1). This country has been widely unexplored in terms of bat research and has been largely closed for 10 years for fieldwork due to terrorism threats (2007-2017). Our study is based on bat guano samples collected prior to closure in the Cave of Zerga (also known as the Cave of Zarga) in an Ordovician Esker situated between the settlements of Atar and Chinguetti (Fig. 1). The bats environment and diet were reconstructed on the bases of vegetation surveys, pollen analyses (several guano samples) and insect analyses (one guano sample). A hyena dropping collected in the same place was also examined for its pollen content. The results are provided in SM Section 5.

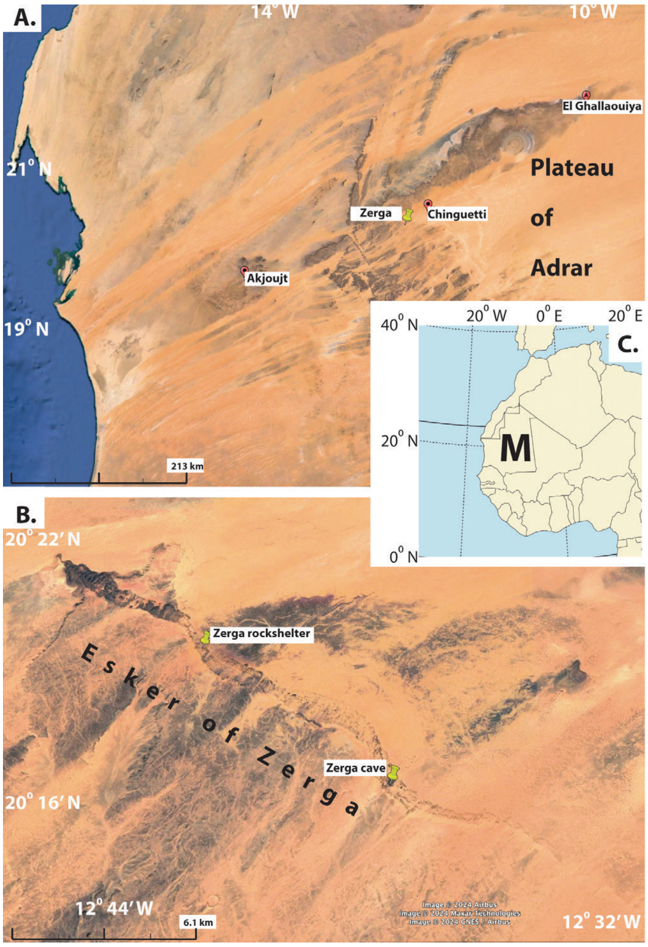

Fig. 1 - **A.** Location of the Adrar plateau in Mauritania; **B.** Location of sampled cave (Zerga guano pointer) and of rock shelter with various scats; and **C.** Inset map: location of Mauritania (M) in N-W Africa. [Légende en français disponible en matériel supplémentaire Section 2]

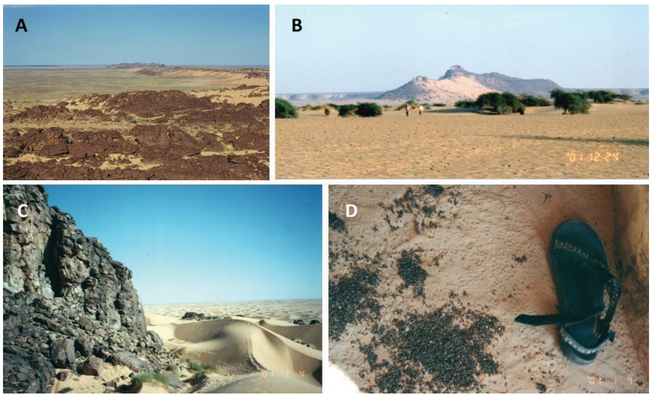

Fig. 2 - **A.** South side of Zerga Esker, 27 January 2004 (Photo: F. Marret); **B.** *Acacia* and *Balanites* trees at the north end of the esker (El Aateg), 24 December 2001, possibly also *Maerua* and *Capparis*, with two persons in the foreground for scale; **C.** Cave of Zerga entrance, view towards the north, 4 January 2001, with footprints for scale; **D.** Bat guano near cave entrance with a sandal for scale, 4 January 2001 (Figures: S. Leroy). [Légende en français disponible en matériel supplémentaire Section 2].

MATERIAL AND METHODS

Geology and climate

The study site is located on the Adrar Plateau (650 m to 850 m in elevation) in Mauritania (north-west Africa) in the southern Sahara, near the limit with the Sahel, between the latitudes 19° and 22° N and the longitudes 11° and 14° W (Fig. 1A). Caves and rockshelters occur in the "Cordon de Zerga" at an elevation of c. 700 m on the Adrar Plateau (Fig. 1B). This is a hard sandstone-quartzite time-patinated esker that is intensely eroded, formed during the Ordovician Glaciation (Deynoux 1980, Ghienne & Deynoux 1998). This exceptionally large north-west to south-east orientated esker has an elongate shape and exceeds 30 km in length and one km in width (Fig. 1B) attaining a height of >100 m. The highest point is called Guelb Al-Rawi or Guelb er Raoui. Its name in the local language, i.e. Hassanya, refers to the Barbary Sheep, *Ammotragus lervia*.

The climate of the studied region is Saharan, with summer temperature around 30-35°C and winter temperature 20-22.5 °C (Barry et al. 1987). Precipitation is irregular but 60% of rainfall occurs during August and September when it is less irregular (Ahmedou et al. 2008). These are Monsoon rains. They are more frequent in the south-west of the Adrar. A second minor wet period occurs from December to February as a result of northerly depressions. Annual precipitation is 50-100 mm (Biberson 1969). According to climatic data in Atar (226 m elevation) and Chinguetti (500 m elevation) over the last decades a warming trend is clear; however hardly any trend in precipitation occurs (Yacoub & Tayfur 2020, Meteoblue.com). The annual precipitation in Atar varied widely between 1997 and 2004: i.e. between 12 and 134 mm (Meteoblue.com). Precipitation during 2000 to 2002 was especially low but during 2003 was much higher with 1997 and 1998 closer to average (Fig. 3).

Modern land use, vegetation and palynology

The land-use map (based on LANDSAT imagery September 2013 - November 2014) shows mostly sand dunes north of Zerga and some small patches classified as steppe south of Zerga (OSS 2015). The areas occupied by villages and towns are extremely small. The town of Atar has ~25,000 inhabitants (figure from 2013), the village of Chinguetti ~6700 inhabitants (figure from 2000); some people also live in the oasis of Mhaïreth (or Mhairith) (Fig. 1). The Adrar plateau is a tourist destination especially for hikers. They commonly stop at the Zerga Esker to observe rock paintings outside the cave (Vernet 2020). Farming, pastoralism and tourism combine to add pressure on wildlife.

From the biogeographical point of view, the region lies between the Saharo-Mediterranean and the Saharo-African regions forming an intermediate distinct region as proposed by Monod (Barry et al. 1987). Monod (1952) suggested a clear Saharo-African character influenced by both the Mediterranean and the Sahel. In the Adrar, a north-east to south-west vegetation gradient is recognised as being delimited by the Zerga Esker. In the north-east, Monod (1952) recognised Sahara-Mediterranean influence and in the south-west Sahelian influence associated with summer rainfall. A northerly inflow exists in the north-east of the Adrar following the El Ghallouiya-Chinguetti axis (Fig. 1A).

Although the vegetation of the Adrar is inadequately studied, four main edaphically-controlled plant groups may be recognised *viz.* a rocky substratum (rocky plateaux and screes), a compact substratum (reg or dry desert pavement and dried up silty-clay surfaces or grayir), a soft substratum (unconsolidated sand or erg) and a humid substratum of springs and freshwater pools or gueltas. More information is provided here on the humid substratum which has greater relevance to bats and insects.

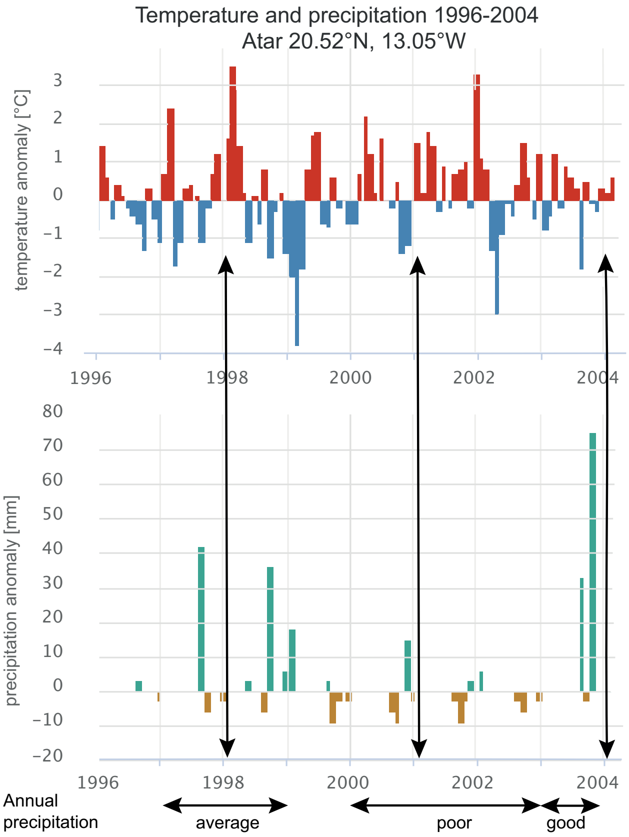

Fig. 3 - Anomalies in monthly precipitation for Atar between 1996 and 2004, as relevant for opportunistic vegetation development following rain. The black double arrowed lines indicate the three sampling periods. Indications of the annual precipitation are given for the years preceding sampling. The Chinguetti data (not shown) are similar. (Source: Meteoblue.com undated). [Légende en français disponible en matériel supplémentaire Section 2]

The vegetation of the Grayir. The grara (Hassanyia word, plural grayir) is a more or less vast basin fed by one or more wadis typically on the plain at the base of a mountain and inundated during floods. In the silty and clayey soils thus formed, the planting of certain crops is temporarily possible. This is a method of cultivation practiced only when it has rained sufficiently. In the past, this was an important farming method, the grayir being cultivated by both gsûr people, i.e. sedentary people living in stone buildings, and nomads. The crops grown there are both local and exotic.

Hygrophilic locations. In the Adrar, a number of sources feed gueltas or freshwater pools which sometimes form small lakes (e.g. El Berbera). Perennial gueltas may have direct pluvial origins or indirect origins through outlets from subterranean flows as, for example, at Amazmaz and Hamdoun. The flora of these privileged locations is very interesting, although often made up of elements from different regions, where edaphic conditions have allowed distinct communities of plants to survive in otherwise desert conditions.

Adam (1962a, 1962b) mentions two flowering periods, a major one after the summer rains and a minor one after the winter rains. According to Bonte (1986), the flowering of trees and other plants in grayir is in spring, when it is still cool enough and when the rare winter rains have kept the soils moist. The period after the summer rains is not favourable to agriculture. The irregular precipitation often results in the sudden erratic appearance of flowering plants.

The cave

The Cave of Zerga is a large vertical cavity near the highest point of the Zerga Esker, i.e. the Guelb er Raoui (elevation c. 700 m) (Fig. 2C and 4). The cave geographic coordinates are 20° 16’ 37’’ N and 12° 37’ 07’’ W. The observations provided by P. Lluch, the cave sampler, are as follows. The height inside the main chamber of the cave does not exceed 20 m, with a relatively narrow width of two to five metres. Air circulates through the two metre wide and 10 m high cave entrance and through a south-east and north-west orientated orifice 0.4 by 0.4 m located at ground level. Most of the bats were attached to the highest draught-free part of the cave roof. Observations in winter between 1997 and 2001 suggest a decrease in colony size, perhaps linked to increased stress associated with tourist interest in the prehistoric cave paintings. It is not known where the bats live in summer. In the same cave, P. Lluch also observed articulated bat leg bones and a bat skull as well as voided pellets of Eagle Owl, *Bubo cinerascens*. The presence of this owl in the cave may suggest predation on bats.

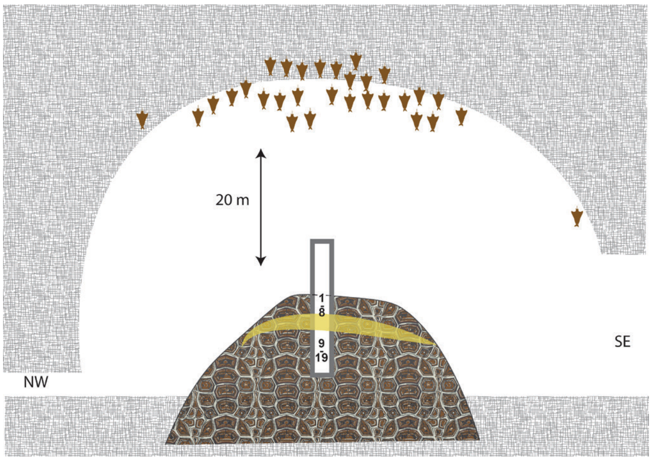

Fig. 4 - Representation of the main guano accumulation in the Cave of Zerga and the position of the 2001 samples (not to scale). [Légende en français disponible en matériel supplémentaire Section 2]

Field sampling

For the purpose of this study, the cave and its surrounding were visited several times between 1997 and 2004 (Table 1).

Samples were taken at three separate times *viz*.: 1) 14 January 1998 after a year of average annual precipitation, 2) 8 February 2001 (following a preliminary visit on 4 January 2001) after a year of low annual precipitation and 3) 27 January 2004 after a year of markedly high annual precipitation (Fig. 3; Table 1).

Sampling of bat guano was by manual scooping in 1998 and 2004. The guano was situated on the surface of the sand at the cave entrance (see photo Fig. 3D).

On 8 February 2001, P. Lluch sampled the main accumulation of guano at the centre of the cave (Fig. 4). The guano was mixed with sand, giving it a somewhat fluid consistency. To maintain stratigraphic constancy, a 100 mm diameter and 50 cm long drain pipe was inserted vertically in the centre of the deposit at its greatest thickness and below the largest bat concentration. Nineteen samples (each a couple of hundred grams) from top to bottom were taken over a thickness of 29 cm. Between samples eight and nine, a pure sand layer, 25 mm thick, was removed (Fig. 4). The lowest sample 19 did not reach the base of the overall aggradation of bat faeces.

The guano accumulation rate is unknown so it is impossible to state how the 1998 sample relates to the 2001 sequence of samples. However, it is clear that the 2004 samples are younger than sample 1 of the 2001 sequence so here the 2004 sample is interpreted together with the 2001 sequential samples.

Table 1 - Dates of the various cave visits and types of sampling. [Légende en français disponible en matériel supplémentaire Section 2]

Year	Day and month	Activity	Type of sample
2004	27 January	Sampling by scooping and photo	Pollen
2001	24 December	Photo	
	24 February	Vegetation surveys	
	8 February	Pipe sampling	Pollen
	4 January	Photo and cave visit	
1998	14 January	Sampling by scooping	Pollen and Insects
1997	Winter	First cave visit	

Vegetation surveys

The surveys followed a larger survey programme of the Mauritanian territory between 1980 and 2000 by one of us either alone or with Th. Monod. The surveys were based either on transects (from a few metres long to a few hundred metres long) or on quadrants (either 10 x 10 m or 100 x 100 m). The dried plants were sent to J.P. Lebrun (at IEMVT , Institut d'Elevage et de Médecine Vétérinaire des Pays Tropicaux, France) for identification and were preserved by Th. Monod at the Muséum d'Histoire Naturelle de Paris. Some zones were visited monthly.

Vegetation surveys were undertaken on 24 February 2001, *i.e.* a fortnight after sampling the bat guano. Rain had promoted plant growth making identification straightforward. The vegetation was surveyed at 16 points including some on and close to the esker (Table 2, Fig. 5 and SM Section 4).

As there is no published Flora of Mauritania, the identifications were made following Ozenda (1983) and a range of specialist articles covering some limited environments, regions, genera or species (e.g. Sauvage 1947, 1949, Maire 1952-1987, Monod 1952, Monteil & Sauvage 1948, 1949, Quézel 1965, Boudet & Lebrun 1986, Lebrun 1998).

Palynological methods

Each guano sample contained several tens of faecal pellets, if not hundreds, thus providing an average of at least several days voidings. Unfortunately, the laboratory extraction details for the nineteen samples of guano taken during 2001 were lost. However, the extraction method had been adapted from a previous study by the same palynologist on guano from a cave in Wales, UK (Leroy & Simms 2006) and the information for the 1998 and 2004 samples was preserved and adapted from the same Welsh study, thus the loss has caused no impact on the data quality. The 1998 guano sample and 2004 samples (i.e. bat guano and hyena faeces) were soaked in Tetrasodium Pyrophosphate, followed by sequential acid treatments: cold HCl, cold HF and cold HCl. The samples were then rinsed with water and sieved through disposable nylon meshes of 125 and 10 µm. The residues were transferred to glycerol in vials and slide preparations were mounted in glycerol. Acetolysis, prior to the acid treatments, was applied only to the 1998 sample after which it was abandoned as this chemical application proved unhelpful. For the 1998 sample after the initial measurement of volume (approx. 1.2 cm^3), one tablet of *Lycopodium* was added in order to get an estimation of pollen concentration. The aim was to count at least 300 terrestrial pollen grains in each sample, but this was not always possible due to the presence of fine sand.

Identification of pollen was made with the support of the atlas of Bonnefille & Riollet (1980) and images in the African Pollen Database (African Pollen Database images undated). The psimpoll software (Bennett 2007) was used for plotting the palynological diagram. The pollen list is organised in five groups: "AP" or arboreal (tree) pollen, "NAP" or non-arboreal (non-tree) pollen, "human indicators" (e.g. crops), "north-east Trade Winds influence" (see wind-transport pollen sources offshore Cape Blanc in Hooghiemstra et al. 2006), "all clumps" (broken stamina, thus groups of identical pollen).

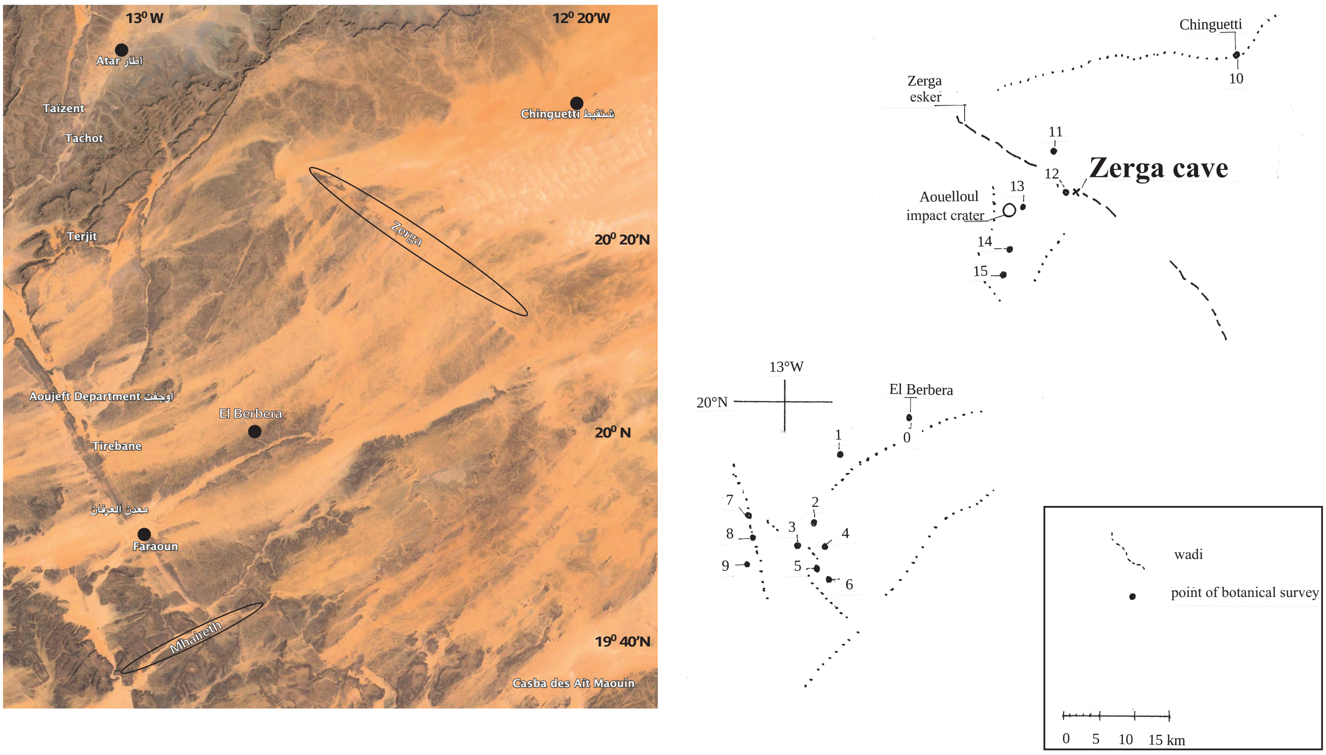

Fig. 5 - Location of vegetation surveys made in February 2001. The numbers 0 to 15 correspond to table 2. [Légende en français disponible en matériel supplémentaire Section 2]

Table 2 - Vegetation surveys made on 24 February 2001. See Fig. 5 for locations. [Légende en français disponible en matériel supplémentaire Section 2]

	Chinguetti oasis	East of Zerga and Arweitin (plateau and wadi)	Zerga ridge (rocky esker)	Aouelloul / wad Zerga	Tifirt	Wad Tifirt	El Berbera	Wad Dakhla	Plateau and barkhans east of Faraoun	Wad + guelta of Faraoun	plateau of Wagchogda	Gardens of Wagchogda	Aklé wad Wagchogda	Traliessar (forest Acacias and Tamaris)	Aklé south of Maaden	Maaden outskirts and gardens
Location number =>	**10**	**11**	**12**	**13**	**14**	**15**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
ALGAE																
Spirogyra sp.										O						
FUNGI																
Tylostoma			O							O						O
PTERIDOPHYTES																
Adiantum capillusveneris							O									
SPERMATOPHYTES																
Amaranthaceae																
Aerva persica	O	O	O	O	O	O	O	O	O	O	O	O		O		O
Amaranthus angustifolius							O			O		O				
Asclepiadaceae																
Calotropis procera	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
Leptadenia pyrotechnica	O	O	O	O	O	O	O		O	O	O	O		O	O	
Pergularia tomentosa	O	O	O	O	O	O	O		O	O		O				
Boraginaceae																
Heliotropium bacciferum	O	O	O	O	O	O	O		O	O		O		O		O
Trichodesma africanum							O			O		O		O		
Caesalpinaceae																
Cassia acutifolia	O	O	O	O	O	O	O	O		O	O	O		O		O
Capparidaceae																
Boscia senegalensis				O	O	O										
Capparis decidua		O			O		O			O		O				
Cleome arabica	O	O	O	O	O	O	O	O	O	O	O	O				O
Maerua crassifolia	O	O	O	O	O	O	O	O	O	O	O	O		O		O
Caryophyllaceae																
Polycarpaea confusa												O				
Sclerocephalus arabicus		O		O							O					
Amaranthaceae																
Salsola foetida				O								O				
Cistaceae																
Helianthemum lippi		O		O								O				
Combretaceae																
Combretum aculeatum																
Combretum micranthum																
Asteraceae																
Atractylis aristida		O	O	O	O	O	O		O	O	O	O		O		O
Centaurea perrotteti			O													O
Cotula cinerea									O	O		O				
Launaea resedifolia												O				O
Pulicaria crispa												O				O
Convolvulaceae																
Ipomea repens	O	O	O	O			O			O		O				O
Brassicaceae																
Morettia canescens	O	O	O									O				O
Schouwia purpurea	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
Cucurbitaceae																
Citrullus colocynthis	O	O	O	O	O	O	O		O	O		O	O	O	O	O
Cucumis melo	O											O				O
Momordica basalmifera	O						O			O		O				O
Cyperaceae																
Cyperus conglomeratus	O	O	O		O					O		O	O			O
Scirpus lacustris	O						O			O					o	O
Euphorbiaceae																
Chrozophora brocchiana		O		O			O		O	O		O	O	O	O	O
Euphorbia calyptrata	O	O	O	O	O	O	O	O								
Euphorbia balsamifera	O	O	O	O	O	O										
Euphorbia scordifolia	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
Jatropha chevalieri													O			
Ricinus communis												O	O			
Ficoidaceae																
Aizon canariense		O	O								O	O				
Geraniceae																
Monsonia nivea														O	O	
Poaceae																
Aristida acutifolia	O	O	O	O					O							
Cenchrus biflorus												O				
Cymbopogon schoenanthus			O													
Danthonia forskalei	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
Cynodon dactylon																
Panicum turgidum	O	O	O	O	O	O	O	O	O							
Schoenefeldia gracilis				O		O										
Triraphis pumilio				O		O	O									

Table 2 - Vegetation surveys made on 24 February 2001. See Fig. 5 for locations. [Légende en français disponible en matériel supplémentaire Section 2]

	Chinguetti oasis	East of Zerga and Arweitin (plateau and wadi)	Zerga ridge (rocky esker)	Aouelloul / wad Zerga	Tifirt	Wad Tifirt	El Berbera	Wad Dakhla	Plateau and barkhans east of Faraoun	Wad + guelta of Faraoun	plateau of Wagchogda	Gardens of Wagchogda	Aklé wad Wagchogda	Traliessar (forest Acacias and Tamaris)	Aklé south of Maaden	Maaden outskirts and gardens
Location number =>	**10**	**11**	**12**	**13**	**14**	**15**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Juncaceae																
Juncus bufonius							o			o						o
Liliaceae																
Asphodelus tenuifolius			o							o		o				
Hibiscus sp.										o		o				o
Loranthaceae																
Loranthus senegalensis					o									o		
Lythraceae																
Lawsonia inermis							o			o						
Malvaceae																
Abutilon fruticosum										o		o				o
Menispermaceae																
Cocculus pendulus												o		o		
Mimosaceae																
Acacia flava										o						o
Acacia tortilis	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Acacia albida		o														
Acacia seyal								o		o						
Nyctaginaceae																
Commicarpus africanus										o						o
Boerhaavia repens	o	o	o	o	o	o	o			o		o		o		o
Apiaceae																
Pituranthos sp.			o													
Orobanchaceae																
Cistanche phelypaea	o	o			o		o			o		o	o	o		o
Palmae																
Phoenix dactylifera	o						o			o		o				o
Papilionaceae																
Astragalus eremophilus		o					o			o		o				o
Crotalaria saharae		o	o		o		o		o	o		o		o		o
Indigofera semitrijuga							o									
Indigofera sp.							o									
Lupinus pilosus												o				
Rhynchosia memnonia	o						o					o				o
Trigonella anguina		o			o		o					o				o
Plantaginaceae																
Plantago akkensis		o			o		o					o		o		o
Polygonaceae																
Calligonum comosum	o		o													
Emex spinosus										o		o				
Rumex vesicarius	o						o			o		o		o		o
Portulacaceae																
Corbichonia decumbens			o				o									
Resedaceae																
Caylusea hexagyna	o	o					o			o		o				o
Rhamnaceae																
Ziziphus lotus	o	o	o	o		o	o			o		o				o
Neuradaceae																
Neurada procumbens	o	o		o	o		o	o	o	o	o	o	o	o	o	o
Rubiaceae																
Gaillonia reboudiana			o				o			o		o				
Scrofulariaceae																
Linaria aegyptiaca	o	o	o		o		o			o		o		o		o
Balanitaceae																
Balanites aegyptiaca	o	o		o	o		o	o		o	o	o	o	o		o
Solanaceae																
Solanum nigrum			o				o					o				o
Tamaricaceae																
Tamarix sp.	o	o			o		o			o		o		o	o	o
Tiliaceae																
Corchorus depressus	o			o			o			o		o		o		
Typhaceae																
Typha australis							o			o						o
Typha sp							o			o						
Urticaceae																
Forskalea tenacissima	o	o	o				o			o		o				o
Zygophyllaceae																
Fagonia arabica		o	o						o							o
Fagonia olivieri	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Fagonia latifolia			o				o			o						
Fagonia glutinosa							o									
Tribulus terrestris	o	o	o	o	o		o		o	o		o	o	o		o
Zygophyllum waterlotii		o			o		o			o		o				o

Insect remain detection

The 1998 sample was not weighed but did not exceed 15 g of dry matter. It was washed through a 300 µm sieve during 1999 and the residue left to dry. This was composed of thousands of finely macerated insect skeletal fragments, many sub-microscopic. The sample was dry-stored and reviewed again during February 2024. The insects were examined under x80 Nikon trinocular stereomicroscope.

The study of insect remains voided by bats can be daunting, requiring disparate skeletal fragments to be re-associated as a jigsaw of parts in the hope that they will create recognisable genera or species. Identification, when necessary, was supported by consultation with some of the world's leading invertebrate taxonomists. In general, there is a lack of knowledge and reference literature on the desert and semi-desert entomofauna of Mauritania. Problems of identification are here compounded by the often minute size of the fragments.

RESULTS

Vegetation surveys

On 24 February 2001, the soil was wet to a depth of 50 cm resulting in prolific plant seed germination.

The following plants were especially noted. Many pasture species were present at most sampling points, such as *Cucumis colocynthis*, *Schouwia purpurea*, *Euphorbia scordifolia*, *Danthonia* (*Centropodia*) *forskalii*, *Crotalaria saharae*, *Neurada procumbens*, *Fagonia olivieri* and *Tribulus terrestris.* Less abundant were *Chrozophora brocchiana, Euphorbia calyptrata* and *Panicum turgidum. Phoenix dactylifera* and several species of *Tamarix* were present in the wetlands (gueltas and oases) as well as in deep wadis. *Tamarix* marks high soil salinity including the presence of sulphates and chlorides. The presence of many wet clayey basins favoured the development of Poaceae. Note that during later observations on 23-24 December 2001, *Pancratium,* not included in the February listing, was in bloom at the foot of the esker.

Pollen diagram

Pollen in general was well preserved. The amounts were low, especially when sand was present in the treatment residues. Of the 19 samples from the 2001 accumulation, only 11 contained enough pollen grains for significant analyses (more than 100) (Fig. 6). The amounts were especially low or the samples were even barren in samples between six and 15. This corresponds to the field observations concerning pure sand between samples eight and nine with very low levels of pollen in samples also above and below the sand lens. Thus, with the 2014 sample, a time sequence of 12 samples is available. Only one estimation of the pollen concentration is available, namely in the 1998 sample which indicated 5003 pollen grains per cm^3 of guano. Insect fragments were present in all the pollen slides. Sample 18 of 2001 contained less well-intact insect parts, apparently more completely masticated, perhaps due to a mix with droppings from another animal with other chewing/digestive processes.

Guano samples from the 2001 and 2004: Some trends are discernible across the twelve samples, with an increase upwards of *Acacia* (from none to 4%), *Balanites aegyptiaca* (from 1 to 23%), Brassicaceae (from none to 13 %) and Amaranthaceae (from 0.4 to 2%) while Poaceae (including broken parts of stamina) are clearly dominant in the samples below the sand lens, at times reaching extremely high values of > 90%. Fungal spores (22-28%) and indeterminable pollen grains (6%) are more abundant in samples near the sand lens. Some coprophilous spores, such as *Sordaria* and *Sporormiella,* were observed, probably linked to the local presence of herbivorous mammals. *Glomus*, an indicator of soil erosion, is relatively rare. A *Trichuris* egg (a helminth parasite) was found in one sample (2001 sample 18). The Trade Winds indicators (~1%) and the human indicators (<1%) are found in small amounts at all levels in the 2001 samples. Some guano was deposited during specific climatic conditions linked to plant flowering times, e.g. 2001 sample Guano 12 with extremely large amounts of *Euphorbia* pollen (69%) linked to rainfall pattern, or the 2004 guano sample with the unusual presence of *Pancratium trianthum* (3%) and *Borreria* (0.7%) pollen.

The 1998 guano sample contained high *Acacia*, *Ziziphus, Heliotropium*, Brassicaceae and *Rhynchosia* percentages. Besides the occurrence of *Rhynchosia* (13%) unique to this sample and the low percentages of *Balanites* (0.6%), it offers some similarities to the 2001 samples one to nine, mainly above the sand lens. It is not impossible that it is contemporaneous with them.

Insect species list and observations on selected invertebrate fragments

The results from the January 1998 collection indicate that the bats consumed a variety of insects dominated by Hemiptera and Coleoptera some of which have been identified (Table 3). There was an absence of Lepidoptera, Orthoptera and Hymenoptera. The species list confirms that the bats had consumed beetles and true bugs native to the immediate area. Most insects were herbivorous, but not anthophilous.

A significant proportion of the insects consumed remain indeterminate while others are assigned only to subfamily or genus levels.

a. Indeterminate insect fragments

Amongst the innumerable unidentified fragments, Fig. 7 illustrates something of the size and nature of the material. Fig. 7A is a fragmentary elytron with a distinctive rugulose microsculpture comprising uniformly disposed contiguous pits with the epipleural edge bright metallic green. Fig. 7C depicts two hemelytra of an unknown hemipteran, possibly an undescribed cydnid.

b. Hemiptera: Cydnidae

Two head fragments of two different individual phytophagous cydnid or burrowing bugs were identified (Fig. 8A). Images submitted to Dr J. A. Lis, the world authority on this family, were determined (*in litt.,* 25.3.2024) as representing Cydnidae: Cydninae: Geotomini perhaps *Paraethus* Lis, 1994 or *Aethus* Dallas, 1851 both well-known from West Africa.

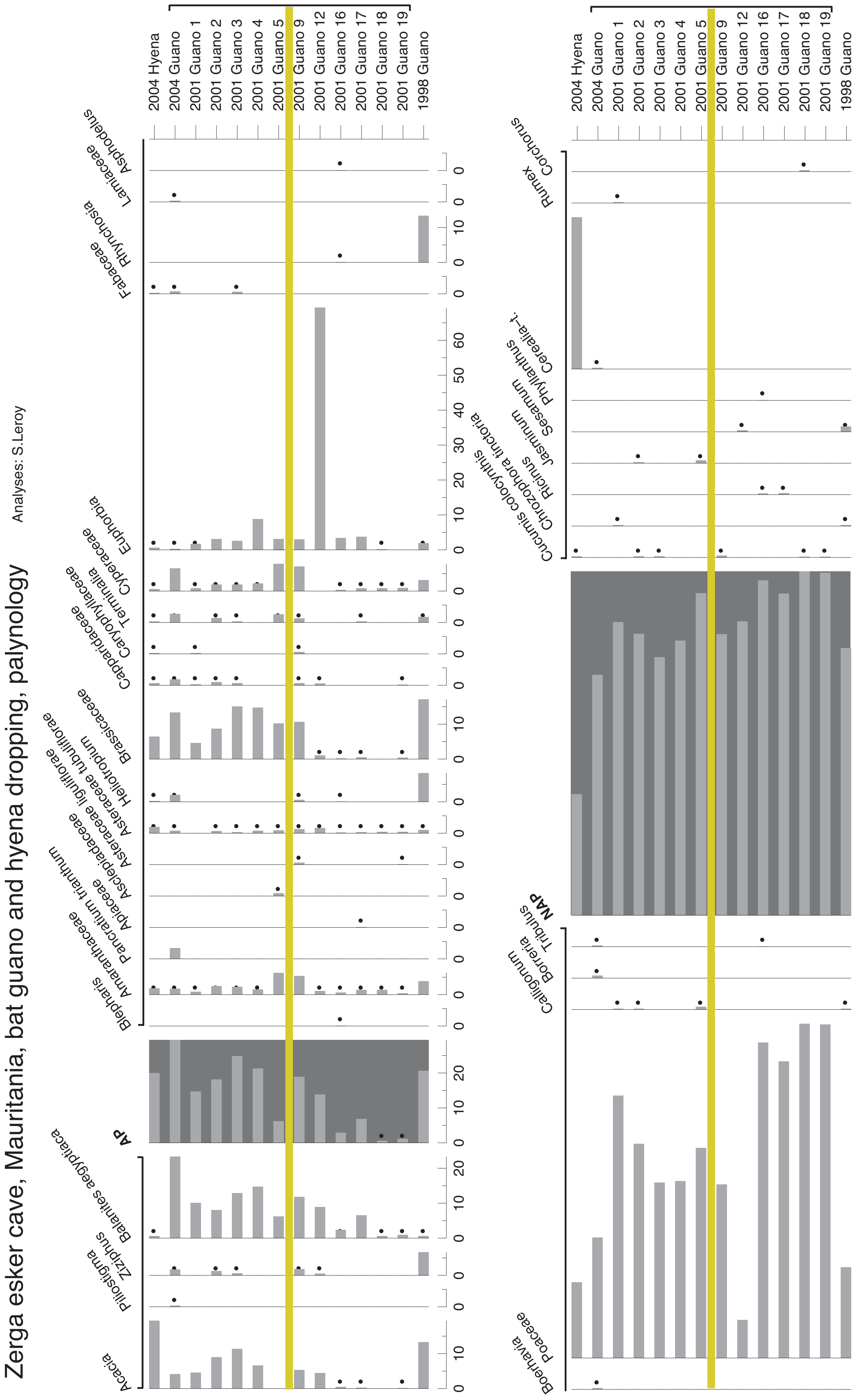

Fig. 6 - Detailed palynological diagram in percentages. Black dot for values lower than 1%. AP: arboreal pollen. NAP: non-arboreal pollen. Thin horizontal black bars lines indicate which taxa are included in the groups. The group names are shown in bold. The thin vertical black line to the right indicates which samples belong to the same guano time sequence (2001 accumulation and 2004 sample). [Légende en français disponible en matériel supplémentaire Section 2].

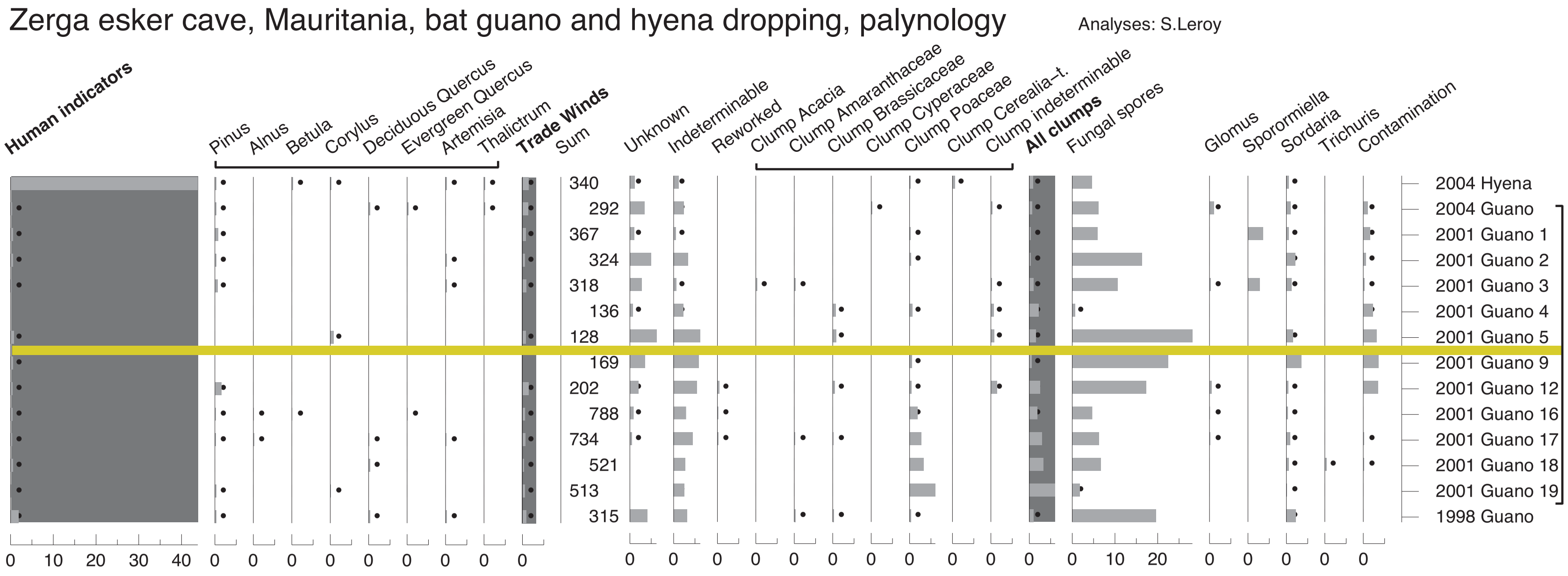

Fig. 6 - Detailed palynological diagram in percentages. Black dot for values lower than 1%. AP: arboreal pollen. NAP: non-arboreal pollen. Thin horizontal black bars lines indicate which taxa are included in the groups. The group names are shown in bold. The thin vertical black line to the right indicates which samples belong to the same guano time sequence (2001 accumulation and 2004 sample). [Légende en français disponible en matériel supplémentaire Section 2].

Table 3 - Invertebrates identified from bat faecal sample from the Zerga Cave, Adrar region, Mauritania, collected on 14 January 1998. [Légende en français disponible en matériel supplémentaire Section 2].

Order	Family	Sufamily/Genus	Species	Comment	Figure
Hemiptera	Cydnidae	*Aethus/Paraethus* spp.	Indeterminate	Two head fragments	8
	Cydnidae	Cephalocteinae: Scaptocorini	Indeterminate	Leg & hemelytra	8
	Cicadellidae	Indeterminate	Indeterminate	*ca* eight head and leg fragments	
Coleoptera	Carabidae?	Indeterminate	Indeterminate	Elytron fragment	7
	Dynastidae	*Podalgus* Burmeister, 1847	*P. cuniculus* Fairmaire, 1895	One individual, aedeagus	9
	Tenebrionidae	*Cheirodes* Géné, 1839	Indeterminate	*ca* eight individuals	
	Chrysomelidae	Galerucinae genus indet.	Indeterminate	Head, one individual	
	Curculionidae	*Entiminae* sp. 1 ?*Phyllobiini* genus indet.	Indeterminate	Alate species, two-three individuals	
	Curculionidae	Entiminae sp. 2 genus indet.	Indeterminate	One individual	11
	Curculionidae	*Menecleonus* Faust, 1904	*M. basigranatus* (Fairmaire, 1868)	One individual	11
Ixodida	Argasidae	*Argas* Latreille, 1795	*A. persicus* (Oken, 1818)	One individual	

Both *Aethus* spp. and *Paraethus* spp. have been observed at artificial light (Rider 2015). Fig. 8B depicts a distinctive metafemora (Fig. 7B) and tibia which associates with an incomplete hemelytron. According to J. A. Lis (*in litt*., 27.3.2024), it may represent Cephalocteinae: Scaptocorini Froeschner, a group that includes obligate psammophilous root-feeders. Of particular interest and relevance is the occurrence of representatives of the scaptocerine genus *Stibaropus* Dallas in Tajikistan bat-caves (Kłys & Lis 2013). Scaptocerine cydnids are also known to fly to artificial light on occasion (J. A. Lis, *in litt*., 30 March 2024).

c. **Hemiptera: Cicadellidae**

Several head fragments and a number of leg fragments can be assigned to this group. Their presence is linked to Poaceae often in significant mass. Representatives of this group frequently appear at artificial night lights.

d. **Coleoptera: Scarabaeidae.** *Podalgus cuniculus* Burmeister, 1847

A widespread psammophilous species distributed in northern and north-west Africa, Asia Minor to Central Asia including the Indian subcontinent (Endrődi 1985) (Fig. 9). The subterranean larvae are rhizophagous and have been recorded in palm plantations; adult beetles, like their close sympatric relative *Phyllognathus excavatus* (Forster, 1771) have a strong attraction to artificial light and are almost certainly crepuscular. In Arabia, this was observed especially during April and May (Krell & Král 2017). Note that the parameres of the single available aedeagus (Fig. 9B) are not strongly expanded.

e. **Coleoptera: Tenebrionidae**. *Cheirodes* Géné, 1839

This beetle is well represented in the faecal sample and many of the sub-microscopic fragments of *ingesta* represent this genus of beetles which, after much consideration is regarded here as specifically indeterminate; further specialist review of the African members of the genus may be desirable (Fig. 10). The asperate elytra are distinctive, the aedeagi are narrow and uniformly attenuated and are illustrated here (Fig. 10 A, C) with the objective of future study. Ferrer (2016) cites *Cheirodes denticulatus* Pic, 1923 and *Cheirodes africanus* Ferrer, 2016 from Mauritania. *C. denticulatus* was regarded by Ardoin (1971) as a typically Sahelian species synonymised with *Cheirodes asperulus* Reitter, 1884 by Ivan & Löbl (2008) but not by Ferrer (2016). The apical spines of the protibiae of *C. asperulus* are somewhat more elongate than in the present species, so it may well be that the *Cheirodes* fauna of Mauritania holds more taxonomic revelations. The genus is widespread in Africa, the Middle East and southern Europe and examples frequently fly to artificial night lights (Pisano & Leo 1984, Ferrer 1996, 2004); for the bats, taxonomy is not a consideration and it may well be that they were able to take advantage of significant light-assembled gatherings.

The larval ecology of *Cheirodes* may not be well understood; Soldati & Guérin (2008) attested to the coprophilous affinity of *Cheirodes brevicollis* (Wollaston, 1864) on Sardinia. The possibility that *Cheirodes* at Zerga Cave are attracted directly to bat faeces is only likely to

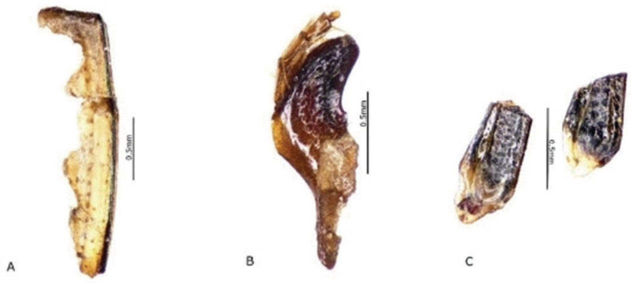

Fig. 7 - Ingesta of *Rhinopoma microphyllum*, Zerga Cave, Mauritania, 14 January 1998 sample. **A.** A distinctive elytral fragment of a beetle, possibly an unknown carabid. **B.** Galea, lacinia and palpi from the right maxilla of a scarabaeid beetle possibly *Podalgus cuniculus*. **C.** Hemelytra of an unknown hemipteran. [Légende en français disponible en matériel supplémentaire Section 2]

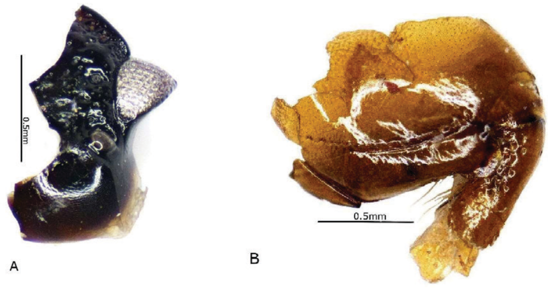

Fig. 8 - Cydnid bugs ingested by *Rhinopoma microphyllum*, Cave of Zerga, Mauritania, 14 January 1998 sample. **A.** Head fragment of *Paraethus* or *Aethus* spp. **B.** Metafemoral and tibial fragment of a possibly undescribed species within subfamily Cephalocteinae tribe Scaptocorini Froeschner. [Légende en français disponible en matériel supplémentaire Section 2]

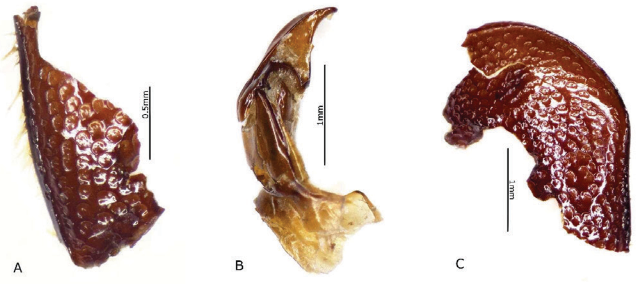

Fig. 9 - Ingesta of *Rhinopoma microphyllum*, Cave of Zerga, Mauritania, 14 January 1998 sample. Coleoptera: Scarabaeidae: *Podalgus cuniculus*. **A.** Fragment of elytron. **B.** Aedeagus lateral aspect. **C.** Fragment of pronotum. [Légende en français disponible en matériel supplémentaire Section 2]

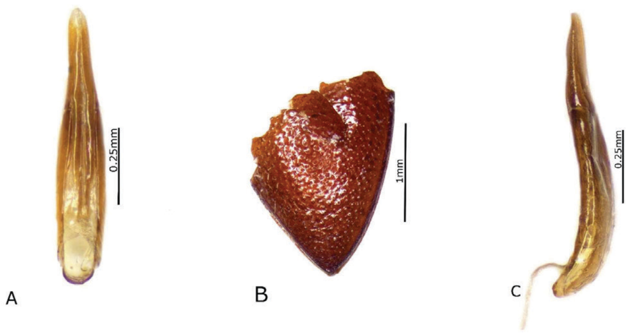

Fig. 10 - Ingesta of *Rhinopoma microphyllum*, Cave of Zerga, Mauritania, 14 January 1998 sample. Coleoptera: Tenebrionidae: *Cheirodes* sp. **A., C.** Aedeagus **A.** Ventral aspect, **C.** Lateral aspect. **B.** Apex of elytron, many such elytral fragments were recovered. [Légende en français disponible en matériel supplémentaire Section 2]

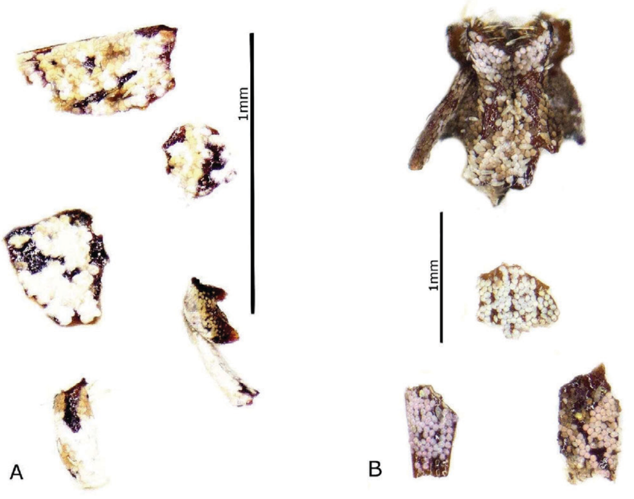

Fig. 11 - Ingesta of *Rhinopoma microphyllum*, Cave of Zerga, Mauritania, 14 January 1998 sample. Coleoptera: Curculionidae. **A.** *Menecleonus cf. basigranatus* skeletal fragments depicting imbricate scaling and distinctively setaceous mesofemora (lower left). **B.** Entiminae genus *indet*., head and elytral fragments of a small robust species with orbicular white, beige, pink and mauve scales. [Légende en français disponible en matériel supplémentaire Section 2]

be confirmed by extended on-site study. According to Advani (1991), the bat colonies are easily detectable from a distance due to the strong and unpleasantly characteristic smell emanating from the bats and their faeces.

f. **Chrysomelidae: Galerucinae**

A single head and antenna represent an unknown genus of chrysomelid ‘leaf’ beetle.

g. **Curculionidae: Entiminae**. Indeterminate species 1

The single example of this small flightless weevil is densely ornamented with white, pink and grey orbicular scales as an adaptation to the desert environment (Fig. 11B). It almost certainly has rhizophagous larvae probably living within the environs of the cave. Quite how a bat might locate such a small slow-moving flightless insect is a point of interest (*vide infra*).

h. **Curculionidae: Entiminae.** Indeterminate species 2

This weevil has been ascribed provisionally to Phyllobiini and is invested with metallic green and yellow orbicular scales. It is alate and volant, i.e capable of flight. Phyllobiini are dominantly Palaearctic in range, and this may be a distinctively Sahelian species. African semi-desert species of *Scythropus* seen by the author do not have such heavily scaled scapes as in these examples.

i. **Curculionidae: Cleoninae:** *Menecleonus cf. basigranatus* (Fairmaire, 1868) *determinavit* Dr M. Meregalli (*in litt.,* 18 March 2024)

According to Meregalli (2017), *M. basigranatus* is the only cleonine presently recorded from Mauritania. The single example is densely scaled and the setiferous mesofemora can be observed in Fig. 11A.

j. **Ixodida, Argasidae**. *Argas persicus* (Oken, 1818) *determinavit* Dr M. Ševčík (*in litt*., 17 March 2024).

A single example of this cosmopolitan temperate climate soft tick, often associated with domestic fowls, was recovered. According to Sonenshine et al. (2019), the genus *Argas* is worldwide in distribution, mostly in xeric environments, dry caves or in otherwise humid environments mostly parasitic on bats or birds.

DISCUSSION

How do the pollen and the insects get into the faeces?

Pollen found in bat guano has multiple sources, the three main ones in decreasing order of importance are: 1) when the bats are grooming and removing pollen collected adventitiously in flight, 2) from insects eaten by the bats (note that flower-visiting insects do not form part of the bat 1998 sample diet, the insects are mostly herbivorous) and 3) by wind-transport of pollen into the cave. It is likely that the sand layer found inside the cave is linked to periods of very strong winds. These mechanisms operating here are thus slightly different from those in the Welsh Cave of Ogof Draenen; for which it was suggested that the insects were visiting flowers, such as *Acer*, *Ilex, Hedera* and somewhat *Salix* (Leroy & Simms 2006). In that case study, fine fragments for Culicidae, known to visit flowers for nectar and thus act as pollinators, were found.

The faecal pollen spectra are clearly different from the regional lacustrine mud and soil spectra dominated by wind-transported and wetland plant pollen, such as Amaranthaceae, Cyperaceae and *Typha* (Lézine et al. 1990, African Pollen Database undated).

Some of the insects consumed are habitually crepuscular or nocturnal and include a significant component that is routinely attracted to artificial light sources. They include Hemiptera, scarabaeid beetles and especially species of the tenebrionid beetle genus *Cheirodes*. It is therefore feasible that these bats were conserving energy by consuming insects massed at artificial light even if that involved distance flying. The closest significant lights are over 30 km distant, but this is not an issue for *R. microphyllum* (Cvikel et al. 2015). It could perhaps be argued that the availability of electricity has positively impacted on the success of *R. microphyllum* in semi-desert regions. Advani (1981) regarded *R. microphyllum* as an anthropophilic species found both "in the midst of human habitations" and in the remotest rural areas. According to Advani (1981), the wide range of habitats covered by the bats influences their feeding ecology, particularly in determining the taxonomic range of *ingesta*.

Which time lapse is incorporated in the faeces samples and what food did they eat?

Concerning the 1998 guano sample studied for its insect content, the entire content of this sample is contemporaneous and, based on beetle periodicity, was probably voided during April to May 1997. No precipitation anomaly preceded the date of sampling (Fig. 3). There is alignment here with statements on *R. microphyllum*, which assert that in Israel a diverse range of food items available in May after the bats arrive at their summer roosts is dominated by beetles (Carabidae, Scarabaeidae, Tenebrionidae and Curculionidae) and some Lepidoptera which later disappear from the spectrum of *ingesta*. Working on the stomach content of three *R. microphyllum* from Akjoujt, Poulet (1970) found a similar taxonomic spectrum of ingested beetles. In South-West Iran, Sharifi & Hemmati (2002) also found that beetles formed a significant component of the intake of *R. microphyllum*. Advani (1981) analysed the stomach content of *R. microphyllum* in the Rajasthan Desert of India and found that beetles formed a large part of the bat intake. Studies in deserts in Israel also indicate a preference for Coleoptera (Hackett et al. 2013).

It is hypothesised that during the periods when plants are more dormant or absent (e.g. when it is too dry) few insects would be present and the droppings would contain a significantly larger amount of air-borne pollen grains of both local and distant origins. This may be, at least partially, the case for the 2001 samples five and nine containing more Amaranthaceae and Cyperaceae pollen than the other spectra. It should be noted however that many of the insects consumed by the Zerga Cave bats are rhizophagous as larvae or nymphs and in common with similar warm-temperate xeric species elsewhere their appearance may well be connected to the onset of rain, even if not flower-visiting.

In the absence of a historical chronology for the 2001 samples, it is difficult to ascertain whether the shift from Poaceae to *Acacia*-*Balanites*-Amaranthaceae assemblages (Fig. 6) corresponds to a sub-seasonal change in the plants visited by insects or a multi-year climatic trend. Two hypotheses may be considered, *viz*. 1) if the guano accumulation formed in a short time over successive flowering periods, the vegetation change may be interpreted as a drying trend explained by less annual and more perennial plants or 2) if, on the contrary, the guano accumulation formed during several decades, centuries or even millennia, then the vegetation trend may represent a change from desert to savannah, thus a wetting trend requiring time for trees to grow under a different climatic regime.

For comparison, one may look at the results of sequential radiocarbon dating of guano accumulations of other bat species from other locations. In the cave of Ogof Draenen (Wales, UK) with a collapsed entrance, samples from nine to 11 cm depth provided a radiocarbon date of 1835 ± 30 calibrated years before present or yr cal. BP (Leroy & Simms 2006). In the Arnhem Cave in Namibia, the age of the bat guano 36 cm deep was 1540 yr cal. BP (Marais et al. 2015). In two Romanian caves, radiocarbon dating of guano heaps 50 to 80 cm thick provide sequences covering the last four to five centuries (Cleary et al. 2019). Thus, the second hypothesis, a wetting trend, may afford the best explanation of the chronology and sequential development of the accumulation of faeces sampled in 2001 and 2004.

Which environments are visited by the bats?

Vegetation

Because of long-distance foraging by the bats (Cvikel et al. 2015), their guano will contain information not only on the environment near the esker but also from further away. Hence, the bats may have obtained food from the natural and anthropogenic environments near the esker and/or from gardens and oases in nearby small towns and villages, the nearest of which are 32 to 53 km away.

Crops grown in grayir (Bonte 1986) may mature in winter. Small temporary wetlands, which may be cultivated as grayir, have been identified along the south-west flank of the esker and a Landsat image of September 2003 (on Google Earth historical imagery) shows two pools at the north-western end of the esker. A larger and well-established one, Grar Legjar, occurs about eight km north of the esker (map Chinguetti NF-28-VI in OSS 2015 and Fig. 9 in Vernet 2017). Colocynths (*Cucumis colocynthis*) and cereals are the two main crops in grayir and both were represented in the guano pollen spectra. Amongst the cereals, Sorghum (*Andropogon sorghum*) is the most common with millets, oats and wheats more rarely planted. A small bean *Vigna unguiculata* (Bonte 1986) may be grown. The latter was not found in the pollen spectra but pollen of *Rhynchosia* was present, belonging most likely to *R. memmonia,* a fabaceous herb observed in the vegetation surveys. Some species *Rhynchosia* are wild but *R. memmonia* is cultivated as animal forage. Occasional pollen grains from other cultivated plants are present such as *Chrozophora tinctoria* that is used as a blue-purple colorant.

Studies in the Arava Desert, Israel, indicate the importance of *Acacia* for many insectivorous bat species attracted to this tree due to the abundance of arthropods (Hackett et al. 2013). Specifically, *R. microphyllum* was seen most often near artificial sites such as village gardens, date plantations and irrigated plots, while sites with densely packed green *Acacia* followed in preference. Moribund or desiccated *Acacia* trees were hardly visited. These observations fit easily with our interpretation of foraging both near the esker with its *Acacia* and *Balanites* (Fig. 2B), and in the villages >30 km away.

Insects and the dietary intake of bats

Our findings include species of insects that are crepuscular and attracted to artificial night lights such as may occur in the settlements of Chinguetti, Mhaireth and Atar (Fig. 1, 5 and 11). The bats fed opportunistically on available flying insects but at least one bat was able to locate and consume terrestrial apterous beetles using feeding techniques close to or on a land surface. The insects suggest that the regional perennial herbaceous vegetation included grasses, perhaps in quantity, and Amaranthaceae. Larvae of the scarabaeid beetle *Podalgus cuniculus* are known to consume the roots of woody plants.

Although the bats may have visited artificial light sources and almost certainly did, it is of interest that some insects, normally diurnal and heliophilous in the adult stage, were consumed. These include flightless curculionid beetles which must have been collected by bats during the day not necessarily through echolocation; it is noted that individuals of *R. microphyllum* have large eyes (Schlitter & Qumsiyeh 1996). These diurnal insects (Fig. 11) are scarcely represented in the sample and could originate from a single foraging event.

The entomofauna disentangled here (Table 3) is one of highly adapted xerophily that characterises the semi-desert of the Adrar region, some elements of which may extend into the Sahel fringe. Some of the diurnal curculionid beetles are heavily invested in light-reflective scales (Fig. 11) even on the legs and antennae. Areas of biennial or perennial herbaceous vegetation occur in the environs of the cave. The larvae of entimine weevils are generally root-feeders while semi-desert cleonine weevils (Fig. 11) are frequently associated with the roots of Amaranthaceae. Some cydnid bugs (Fig. 8B) are subterranean feeders on the roots of Poaceae during their nymphal stages.

An ecosystem

Social foraging by *R. microphyllum* is more frequent when resources are more ephemeral as observed in Israel (Egert-Berg et al. 2018). Ephemeral food resources are especially true in desert and semi-desert environments, e.g. marked or limited seasonality and availability of particular insects; short plant life cycles and accelerated reaction to erratic rainfall explaining why some samples have an over-representation of some pollen types. For example, the many *Euphorbia* pollen grains in 2001 sample 12 is reminiscent of how bees select one type of plant for nectar and remain faithful to it until depletion.

Parasites

As part of the ecosystem, parasites including helminth worms and ticks are recorded, most likely from the bats. The presence of the tick, *Argas,* in a faecal sample could be fortuitous as occasionally happens with ixodids (Ševčík et al. 2010). It could have been transported facultatively on a bat or it could have originated from a tick population within the cave itself (Sonenshine et al. 2019). *R. microphyllum* are known to have nematode infections (Kazemirad et al. 2020) which could explain the presence of a *Trichuris* egg in 2001 guano sample 18.

Limitations, challenges and opportunities

Although our data are >20 years old and derive from only three sampling seasons they remain very important and merit publication due to the scarcity of information from this part of the world. In Mauritania, prior to our study, no significant investigations of bats and certainly none on their faeces, have been conducted. In relation to the vastness of the Sahara Desert we believe that our study is seminal.

Field work in Mauritania was almost prohibited for 10 years from 2007 to 2017 due to terrorist activity. The death of the cave explorer P. Lluch during 2016 also impacted on our ongoing research. In the context of the natural history of north-west Africa, it is vitally important to use recent archival data to understand the present.

Radiocarbon dating works quite well on guano as shown by Libby (Byrne et al. 1979) who in 1949-1950, used it effectively early on in the development of this method. When funding recently became available for dating of the guano heap, our original samples which had been kept in a fridge had already been disposed of due to the COVID scare of 2020-2021. In order to obtain a better grasp of the accumulation rates of Zerga guano as well as bat population changes over time, it would be necessary to return to the cave and sample more extensively with the objective of obtaining radiocarbon dates.

More recent guano studies often include the following methods. Firstly, genetics (*R. microphyllum* colonies in Walker et al. 2016) is used to clarify species assemblages in roosts, disease impacts on communities and to identify individuals. Secondly, stable isotope ratios are applied to the reconstruction of the feeding ecology, e.g. on an insectivorous bat (Wurster et al. 2007). It would be beneficial to develop these guano studies in Mauritania and the Sahara, alongside palynology and entomology, as all four methods avoid bat capture.

CONCLUSIONS

Pollen analysis indicates that the bats *R. microphyllum* visited not only natural areas but also ephemeral crops in cultivated landscapes. The diversity of pollen spectra indicates that the bats opportunistically visited areas precisely at the appearance of pollen-bearing flowers. Our investigations confirm previous observations that dry-habitat bats are opportunistic foragers inhabiting areas with highly variable food resources finely demarcated in time and space (Sharifi & Hemmati 2002). Additionally, it was established that insects consumed by the bats included species that are crepuscular and that bats are almost certainly attracted to artificial night lights such as may occur in the settlements of Chinguetti and Atar at least 30 km distant. It seems therefore that the bats were not only benefitting from and adapted to erratic rainfall patterns, but also from human impacts and activities.

Guano analyses highlight many aspects of bat synecology including the significance of different types of vegetation, flying and flightless insects and parasites. Entire bat-regulated ecosystems need to be positively conserved in their entirety because of the strong inter-dependence of their various elements confirmed in this study. In general, bats are poorly known and often neglected. However, the role of bats in the management of insects, including species impacting crops and deleterious to human health, is of paramount importance.

Ultimately it is hoped that this new knowledge, illustrating the inter-relationships of animals including humans, vegetation and climate, may be used for the protection of this delicately poised desert ecosystem and elsewhere in the world.

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