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Carbon and Nitrogen Isotopic Signatures of Bat Guanos as a Record of Past Environments

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Carbon and nitrogen isotope ratios were measured for various ecogeochemical samples relevant to bat guano ecosystems. In particular, *ca.* 800-year-old subfossil guano from Jackson's Bay Cave Compex, Jamaica, yielded ratios similar to the modern guano from other Jamaican bat caves but quite different from modern guano of the same area. Diagenetic change and differences in bat food habits were unlikely explanations for the observation. Instead, insects that feed on C_4 and CAM plants were the main prey for the bats in present Jackson's Bay area, while the ultimate source of organic matter for bats in other Jamaican caves and for the bats that deposited guano in Jackson's Bay Great Cave *ca.* 800 years ago were C_3 photosynthesis. We suggest that the isotopic data indicate that the surrounding environment experienced a significant mesic episode in the recent past. This mesic climate would have supported a large population of bats, which in turn would have accumulated significant quantities of guano. The subsequent return to the more xeric conditions prevailing today would have caused a drastic reduction in bat population size and effectively ended significant guano accumulation. Fossil guano from Carlsbad Caverns, New Mexico, U.S.A., suggested that native C_3 plants might have been more abundant in Wisconsinan than today. Isotope analyses of old guanos from Bat Cave in Grand Canyon National Park, Arizona, U. S. A., found a possible implication that C_4 photosynthesis might have had contributed a little more to the bats' diet in the cave before the construction of Glen Canyon Dam.

1. Introduction

Measurement of the carbon and nitrogen stable isotope compositions of ecogeochemical samples provides significant ecological information. Different types of photosynthetic pathways, food source analysis of animals, the discrimination of marine *versus* freshwater organic matter, and other information can be derived from isotopic data.[1] Isotopic signatures are often less susceptible to environmental variations than other parameters, and the methodology can be extended to studies of past environments because of their stability.

A practicing naturalist would collect animal feces or a part of an animal such as hair and feathers. They are easily available, and readily treated to fit for the isotope measurements. Guano, in particular, appears well suited to isotopic study, and is available in quantity in certain caves. In some cases, the protected environment of caves may preserve stratified guano deposits spanning thousands of

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years.

The isotopic ecogeochemistry of bat guano has the potential to shed much light on the history of local ecosystems, but this potential has been little explored. Though Mizutani *et al.*[2] noted that $\delta^{15}N$ of soil organic nitrogen could be used for evaluating past seabird activity, only recently, he and his colleagues have demonstrated the utility of their idea.[3] Des-Marais *et al.*[4] reported a carbon isotope study of the individual hydrocarbons in bat guano, and showed that the $\delta^{13}C$ values of alkanes in the guano can be related to the feeding behavior of the bat prey as well as the photosynthetic pathways of the local vegetation. Though they noted the potential of the isotopic study of guano for an investigation of the vegetational changes with time, the guano they used was less than 40 years old and could not provide a historical record.

In 1978, members of the Jamican Caving Club, prospecting in the lower, flooded corners of Jackson's Bay Great Cave, discovered a large chamber almost filled with a massive accumulation of composted bat guano.[5] It was an unstratified, homogeneous deposit and named as the Queen Series. Its age was later indirectly dated: A marine gastropod, *Cittarium pica*, commonly transported into caves by terrestrial hermit crabs, was recovered from a depth of 1.2 m in the guano and dated by tandem mass spectrometry radiocarbon techniques at 795± 70 years B.P.[6]

Jackson's Bay Great Cave is one of many caves that together constitute Jackson's Bay Cave Complex, Clarendon, Jamaica. It is a complex cave system located on the south-western edge of the Portland Ridge, a xeric thorn-scrub community in the rain-shadow of the Blue Mountains.[7] Among other caves of the complex are Somerville Cave, Drum Cave, and Water Jar Cave. Quite unlike the Jamaican tropical forests to the north, annual rainfall in the region is 1014 mm with a dry season of 6 to 10 months having less than 100 mm. The seasonality of precipitation as measured by the average monthly rainfall and its standard deviation is 84.5±50.8 mm/month (data from Amity Hall, 91 year average).

All large bat colonies of more than 1,000 individuals presently known from Jamaica are located in mesic environments,[8] where they are presumably sustained by the enhanced productivity. None of the numerous caves described from Portland Ridge[9] support bat colonies large enough to accumulate the estimated 200 m^3 of subfossil guano from the Queen Series deposit. Groups of less than a dozen bats are encountered near various entrances to Jackson's Bay Great Cave, in contrast to some other Jamaican bat caves where enormous legions of bats are found.

It was, therefore, suggested that the guano accumulated at a time when the climate around Jackson's Bay was less xeric and able to sustain a large population of bats.[10] The onset of the present dry conditions sometime in the recent past must have caused the local extinction of this population.

When we measured the carbon and nitrogen isotope ratios of this subfossil guano and fresh guano from Somerville Cave in the same Jackson's Bay Cave Complex, their ratios were quite different. Two explanations would be possible for the result: 1) Diagenetic changes may have shifted the isotopic ratios from their original values, and 2) The diet of the bats

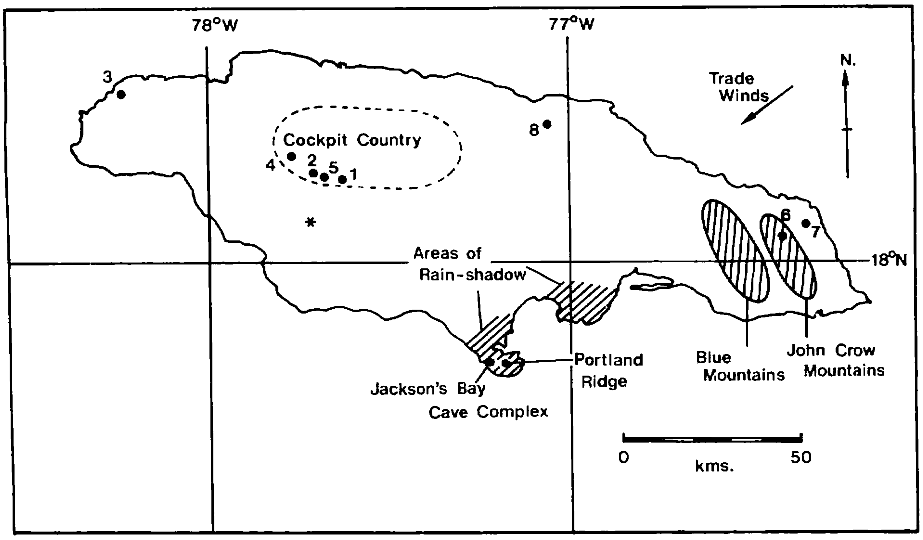

Fig. 1. Map of Jamaican bat caves. Number refers to: 1) Oxford Cave, 2) Falling Cave, 3) Abingdon Cave, 4) Wondrous Cave, 5) Welsch Ratbat Cave, 6) Cornwall Barracks Cave, 7) Brother Frader's Ratbat Caverns, and 8) Mount Plenty Cave. Asterisk indicates the location of the peat bog discussed in "5.3.2 Other evidence for mesic climate in Jackson's Bay area" of the text.

ca. 800 years ago may have been isotopically different from that of bats currently living in the caves. This paper seeks, in general, to explore the extent to which old bat guano may be useful in reconstructing past environments, and, in particular, to examine the possibilities above as an example of ecogeochemical utility of bat guano.

2. Sampling Locations

2.1 Jamaican caves

Figure 1 shows the locations of Jamaican caves, from which guanos were sampled in 1986 to 1988. The Jackson's Bay Cave Complex (17°44′N, 77°13′W) consists of many caves, including Somerville Cave and Jackson's Bay Great Cave, which are hydrologically linked. Somerville Cave and several areas within Jackson's Bay Great Cave have small groups of the Parnell's Mustached Bat (*Pteronotus parnelli*) living in them. The bat is an aerial insectivore and feeds on flying insects, especially small beetles and moths, over dry limestone scrub forest. There is no significant agriculture around Jackson's Bay, besides some sugar fields about 10 km northwest. The bats are unlikely to forage that far, however. Along the coast, there are extensive salt ponds.

Other Jamaican caves from which guanos were collected were Oxford Cave (18°13′N, 77°38′W), Falling Cave (18°12′N, 77°43′W), Abingdon Cave (18°24′N, 78°15′W), Wondrous Cave (18°14′N, 77°47′W), Welsch Ratbat Cave (18°12′N, 77°42′W), Cornwall Barracks Cave (18°04′N, 76°25′W), and Brother Frader's Ratbat Caverns near Cornwall Barracks Cave.

Oxford Cave, Manchester Parish, is a major bat roost located in a disturbed rainforest trasition habitat receiving 2468 mm of rainfall per year. The seasonality of precipitation is 205±115 mm/month (data from Troy, 91 year average). The cave supports four species of insectivorous bats and one insectivore/nectarivore bat.[8] Abingdon Cave is located on the periphery of the Cockpit Country, receiving rainfall comparable to that at Oxford Cave.

The environment in the vicinity of Wondrous Cave and Welsch Ratbat Cave is mesic tropical rainforest. At Welsch Ratbat Cave, both frugivorous and insectivorous bat species are present. The frugivorous bats are the Jamaican Fruit Bat (*Artibeus jamaicensis*) that specializes on figs (*Ficus* sp.). It has a short gut transit time of about 20 min, and void a liquid excrement that is only partially digested fruit juice and pulp, with a few seeds. As a predator avoidance strategy, they often take fruit back to a cave roost before eating them. Their guano, therefore, includes a compost of dropped fruit, leaves, and germinating shoots.

Cornwall Barracks Cave and Brother Frader's Ratbat Cavern, both in the John Crow Mountains, are in an extremely mesic rainforest environment receiving 5368 mm of precipitation per year. The seasonality of precipitation is 447±155 mm/month (data from Moore Town, 91 year averge).

2.2 Some bat caves in other regions

Fresh guano was collected in 1988 from Carlsbad Caverns (32°08′ N, 104°29′ W), Carlsbad Caverns National Park in Eddy County, New Mexico, U.S.A. It is a maternity roost for the Mexican Free-tailed Bats (*Tadarida brasiliensis*) in summer and shelters a population of about 300,000. The bats are a typical high, fast flying aerial insectivore. Its major diet is Lepidoptera, Hymenoptera, Coleoptera, and Homoptera.[11] The Cave Myotis (*Myotis velifer*), an aerial insectivore, feeding opportunistically mainly on Coleoptera and Lepidoptera and less on Homoptera,[11] also occurs in the caverns,[12] but does not contribute appreciably to the guano deposits used in this study. New Cave is a few kilometers apart from Carlsbad Caverns and contains fossil Free-tailed Bat guano, which was sampled in 1988. Earlier, the guano has been subjected to radiocarbon dating three times, all giving infinite ages. The higher sensitivity of the technique at later attempts has given the higher minimum age of 30,000 years.[13, 14] The environment around Carlsbad regions is upper Chihuahuan desert, but bats forage over the riparian margins of the Pecos River[12] bacause of the relatively abundant vegetation of the area.

Bat Cave is in Grand Canyon National Park, Arizona, U.S.A. and also harbors Free-tailed Bats. In 1988, it provided fresh guano of *T. brasiliensis* and fossil guano of the same species (or its chronospecific ancestor) dated at 7620 ± 70 years B. P. (Beta Analytic 27955). Present agriculture near the cave is on the Indian Reservation to the south. It is unlikely, however, that the bats forage over there, as the cave opens 200 m directly above the Colorado River, which would make an excellent foraging area.

3. Methods

3.1 Guano preparations

Details of the procedures are given elsewhere.[15] The drying procedure of samples was roughly as follows: After arrival of samples at laboratory, vacuum-dry a part of them by a freeze dryer for carbon content and its isotope ratio, and directly put another part to Kjeldahl digestion for

Table 1. Organic Carbon and Kjeldahl Nitrogen Contents of Jamaican and Some North American Guanos, and Their Isotope Ratios

Location	Bat	Organic carbon Content [mgC/(g dry sample)]	Organic carbon Isotope ratio [‰]	Kjeldahl nitrogen Content [mgN/(g dry sample)]	Kjeldahl nitrogen Isotope ratio [‰]	Remarks
Jamaica						
Somerville Cave	P. p.	90.1	−17.8	28.7	20.9	
Jackson's Bay	unknown[c]	31.8	−24.3	5.9	12.4	b, f)
Oxford Cave	P. p.	190	−25.3	65.7	5.1	
Falling Cave	P. p.	31.7	−25.4	6.5	13.0	
Wondrous Cave	P. p.	68.3	−25.5	41.5	5.2	
Welsch Ratbat	A. j.[d]	88.3	−26.5	32.6	4.7	
Welsch Ratbat	A. j.[d]	28.2	−26.1	13.1	5.4	b, f)
Abingdon Cave	unknown	54.1	−27.7	n. a.	n. a.	
Cornwall Barracks	unknown	138	−26.1	55.4	3.8	
Brother Frader's	unknown	192	−25.6	93.2	7.0	
Carlsbad region (New Mexico, U.S.A.)						
Carlsbad Caverns	T. b.	195	−21.6	112	12.7	
New Cave	T. c.[e]	22.3	−21.3	10.4	20.3	a, b, f)
Bat Cave (Arizona, U.S.A.)						
Bat Cave	T. b.	248	−24.4	n. a.	n. a.	
Bat Cave	T. b.	126	−21.5	n. a.	n. a.	b, g)
Bat Cave	unknown	60.6	−22.5	n. a.	n. a.	b, h)

The letters for bats are: P. p. for *Pteronotus parnelli*, A. j. for *Artibeus jamaicensis*, T. b. for *Tadarida brasiliensis*, and T. c. for *Tadarida constantinei*. Letters n. a. signify "not analyzed." All samples were decarbonated by 2 N HCl. Sample that showed an intensive bubbling is marked as [a]. Excepting those marked as [b], all the guanos are modern; estimated ages of old guanos are: 795±70 years B. P. for Jackson's Bay Great Cave guano, unknown for Welsch Ratbat Cave guano, more than 30,000 years B. P. for New Cave Guano, and 7620±70 years B. P. for Bat Cave guano. [c]: Probably guano of P. p.; even if it were of other species, the bats that deposited the guano must be an insectivore, since the guano lacks the heterogeneous mixture of woody remains typical of frugivore guano. [d]: Although Welsch Ratbat Cave also houses a small insectivorous bat species, *Artibeus jamaicensis* appeared to roost separately in the cave and the guanos were very likely of theirs. [e]: It is presumed to have originated from fossil free-tailed bats, *Tadarida constantinei*, whose bones are found in profusion at the same site[16]; and *T. constantinei* may be a chronospecies of *T. brasiliensis*.[17] Excepting those marked as [f], guanos were collected directly from cave floors by scooping into airtight glass vials; Jackson's Bay guano from 1.3 m depth; Welsch Ratbat from 0.3 m depth; and New Cave from a black basal layer exposed in guano mining trenches. [g]: Old guano pellets. [h]: Decomposed guano.

nitrogen content and its isotope measurement; and the dried guano was decarbonated and homogenized to pass a 0.5 mm sieve before subjected to the carbon analysis.

In some cases, decarbonation resulted in an increase in the carbon content; *e.g.*, in case of guanos from Jackson's Bay Cave Complex, the subfossil guano showed an increase from 15.4 to 31.8 mgC/(g dry sample) and the modern guano from Somerville Cave from 21.7 to 90.1 mgC/(g dry sample). Small amount of sample used for the determination and its heterogeneity due to the presence of inorganic matters are presumed to have caused this observation. The $\delta^{13}C$ values, nonetheless, decreased from -22.8 to -24.3‰ for the subfossil guano and from -16.1 to -17.8‰ for the modern guano. The decrease is quite expected because $\delta^{13}C$ for carbonate is normally about zero ‰.

3.2 Determination of organic carbon and Kjeldahl nitrogen contents and their isotope ratios

While details and relevant references are given elsewhere,[15] determination of organic carbon content and Kjeldahl nitrogen content and of their isotope ratios was performed roughly as follows. A sample was combusted, and the amount of CO_2 thus generated was measured manometrically. Orgainc nitrogen was converted to ammonia by Kjeldahl digestion and finally to N_2 gas. The nitrogen content was determined by using an aliquot of ammonium sulfate solution. After purification, CO_2 and N_2 were introduced to either a Hitachi RMU-6R mass spectrometer or a Finnigan MAT-251 mass spectrometer. The carbon isotope ratio was expressed in ‰ deviation from the PDB carbonate standard. The carbon isotope data from the Hitachi RMU-6R were corrected for ^{17}O. Standard deviation of the carbon isotope measurement was less than 0.1‰. The data for nitrogen were expressed as ‰ deviation from atmospheric nitrogen. Standard deviation of the nitrogen isotope measurements was 0.2‰.

4. Results

The results on Jamaican and some North American guanos are shown in Table 1. Results on all guanos and related matters examined in this study are listed in Appendix 1.

Although the distance between Somerville Cave and Jackson's Bay Great Cave is only 600 m, the guanos from them yielded very different isotope values. While $\delta^{13}C$ and $\delta^{15}N$ for Somerville guano were -17.8‰ and 20.9‰, those from Jackson's Bay Great Cave were -24.3‰ and 12.4‰.

5. Discussion

5.1 Bats as predators of insects in the present Pecos River Valley

Though very little has been reported on the isotope ratios of bat guano, DesMarais *et al.*[4] carried out a laborious work on the $\delta^{13}C$ values for individual hydrocarbons in insectivorous bat guano from a cave in the Carlsbad region and reported the $\delta^{13}C$ values for bulk guano to be -20.1 ± 0.4‰. Most cultivated crops in the area being C_3 plants, they concluded that agricultural pests constitute a major percentage of the bats' diet. The present result of -21.6‰ for the fresh, insectrivorous bat guano from the same region is a little lower. The significance of the bats as predators of agricultural pest insects, therefore, might be a little more at present.

5.2 Isotope ratios of primary producers

To correlate the results of bat guano to palaeoclimate, they have to be first reduced to the level of primary producers. From primary producers to old bat guano, there would be three steps to be considered: 1) From plants to bat food, 2) From food to fresh guano, and 3) Diagenetic change after guano deposition. If the bats are a plant feeder, the first step is inapplicable. The third one is not necessary, when fresh guanos are examined.

For the second step, Mizutani and Wada[18] found insignificant differences in the $\delta^{13}C$ and $\delta^{15}N$ values between the average diet and fresh guano of the Black-tailed Gulls (*Larus crassirostris*). We, therefore, assume that the second step does not change the isotope ratios. And the followings will examine the first and the third steps.

5.2.1 Diet of bats

If the bats are an insectivore, the food chain effect from plant food to insect tissues must be taken into account. It is reported that the whole body of an animal is on average enriched by about 1‰ in ^{13}C relative to its diet.[19] This observation makes it possible to analyze animal's diets in natural environments.[20] A similar enrichment in ^{15}N is also known.[21] The extent of the enrichment varies, but, on the average, is about 3‰.[22)~24)] Although these observations are not universally applicable,[25] we adopt as a first order appoximation the 1‰ enrichment in $\delta^{13}C$ and the 3‰ enrichment in $\delta^{15}N$.

5.2.2 Diagenetic change

5.2.2.a Carbon and nitrogen contents New Cave near Carlsbad caverns yielded fossil guano of more than 30,000 years old. Both carbon and nitrogen contents in the fossil guano were much lower than modern guano in the Carlsbad region (Table 1). In Welsch Ratbat Cave, where the guano from 0.3 m below surface (presumably older than at surface) showed lower carbon and nitrogen contents than the surface guano. And the old guanos from Bat Cave contained orgainc carbon less than the fresh guano from the same cave. These decreases in the contents are likely to be a result of a diagenetic process from bat excreta to old guano. The same tendency is found between guanos from Somerville Cave and Jackson's Bay Great Cave. It, therefore, suggests that a similar process of diagenesis has taken place indeed for the subfossil guano from Jackson's Bay great Cave.

5.2.2.b Carbon isotope ratio When the isotope ratios are looked at, however, a quite different situation emerges (Table 1). Although our study on early diagenetic change in $\delta^{13}C$ and $\delta^{15}N$ for guano from Eagle Creek Cave, Arizona, U.S.A., showed that its rate quite depends on conditions of each cave,[15] the direction of change would still be systematic and predictable, if it ever takes place. The $\delta^{13}C$ values for the Carlsbad guanos appear to remain unchanged during the diagenesis. Old guanos from Bat Cave give higher $\delta^{13}C$ values than the fresh one. Although its age is unknown and probably much younger than the old guanos from the other caves, the guano 0.3 m below surface from Welsch Ratbat Cave showed a little higher $\delta^{13}C$ relative to the fresh guano at surface. Jackson's Bay Cave Complex guanos, Somerville guano (fresh) being higher in $\delta^{13}C$ than Jackson's Bay Great Cave guano (subfossil), appear to behave quite differently, however.

It is known that carbon isotope ratio for total organic carbon in sediments is susceptible only a little to alteration during diagenesis. Ishizuka reported little vertical variation of $\delta^{13}C$ for organic matters in lacustrine sediments.[26] Schimmelmann and Tegner determined the $\delta^{13}C$ values of total organic carbon in Santa Barbara Basin sediment dating into the 15th century, and found that their mean $\delta^{13}C$ value was virtually identical to that from the 19th and 20th centuries.[27] A similar observation was made at the mouth of Tokyo Bay.[28] Examining various factors that would affect the carbon isotopic composition in sedimentary rocks, Mizutani and Wada concluded that the $\delta^{13}C$ change during diagenesis is nearly zero

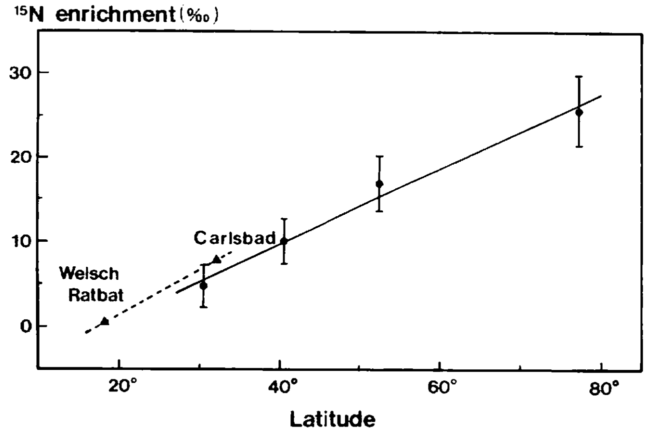

Fig. 2. Latitude of colony locations and ^{15}N enrichment. Closed circle represents the average ^{15}N enrichment at seabird rookeries and the latitude of their location. Closed triangle stands for the ^{15}N enrichment observed for bat colonies. For seabird colonies, the enrichment is the difference in $\delta^{15}N$ between soil Kjeldahl N and uric acid-N in avian droppings, and, for bat colonies, that between old and fresh guanos. The length of vertical bars associated with seabird rookery data indicates the standard deviation ($\pm\sigma$). The oblique, solid straight line was obtained from the linear regression analysis for the four seabird rookeries. The oblique, broken strainght line connects the two datapoints of the bat colonies. Seabird rookery data are from Mizutani *et al.*[37]

‰.[29,30] A laboratory experiment by Fenton and Ritz indicated a ^{13}C enrichment of up to 1‰ in decaying kelp biomass,[31] while the presumed loss of ^{13}C-enriched carbohydrates from sapropelic organic matter in sediment from Mangrove Lake, Bermuda, decreased the $\delta^{13}C$ values of the organic matter up to 4‰ during early diagenesis.[32] In south Florida estuaries, seagrasses and mangroves showed little change in $\delta^{13}C$ during decomposition.[33] DeNiro and Hastorf studied alteration of $\delta^{13}C$ for plants recovered from archaeological sites in Peru, whose age ranging 400 to 4000 years, and found an apparent change in neither carbonized nor uncarbonized plants.[34] Although we must be careful about uncritical comparison among fresh organic matter, decaying organic matter, and diagenetically mature total organic carbon, very large alterations of $\delta^{13}C$ values do not seem to take place during diagenesis. This paper, therefore, assumes no change in $\delta^{13}C$ during guano diagenesis.

5.2.2. c Change in $\delta^{15}N$ and its dependence on latitude The $\delta^{15}N$ values are high in seabird rookeries[21,35] and barnyard and feedlot soils[36] where a large amount of organic nitrogen is deposited. A general mechanism that led to the observation was discussed in the above references. Recently, Mizutani *et al.*[37] reported a linear, latitudinal dependence of ^{15}N enrichment in seabird rookery soils. The enrichment in their study was defined as the difference in $\delta^{15}N$ between soil Kjeldahl N and excreted uric acid-N, the predominant form of metabolized nitrogen in avian droppings. In case of birds, the nitrogen isotope ratio for droppings can be considered the same as that of the metabolized nitrogen, the difference between uric acid-N and bulk avian guano being small.[38] Assuming that this also applies to bat guanos and that the old guanos can substitute for rookery soil, the ^{15}N enrichment at Carlsbad regions would be 7.6‰ and that at Welsch Ratbat Cave 0.7‰. Though the assumptions are admittedly arguable, these enrichments are not very far from what expected based on the latitude of the bat caves and on the linear, latitudinal dependence of the enrichment reported for seabird rookery soil (Fig. 2).

At Eagle Creek Cave whose latitude is similar to Carlsbad regions, no such enrichment was observed for the last 25 years probably because of its extreme aridity and the lack of free circulation of air.[15] As the enrichment may depend on physical and other factors unique to individual cave, the old guano from Carlsbad might be representing the maximum enrichment attainable for caves at its latitude.

We adopt the linear, latitudinal dependence as the expected change in $\delta^{15}N$ for bat guano during diagenesis as long as the relationship gives enrichment: The latitudinal dependence[37] gives ^{15}N enrichment of 6.2‰ at the Carlsbad regions and that of -0.03 to -0.2‰ at Jamaican caves; As the negative enrichment is unlikely to occur through ammonia volatilization, the enrichment in Jamaica would be rather assumed to be zero ‰.

5.2.3 Estimated isotope ratios of primary producers

Table 2 summarizes the overall changes in the isotope ratios from primary producers to bat guano. When these changes are taken into account, estimated isotope ratios of primary producers are obtained and shown in Fig. 3.

Terrestrial plants employ in general two separate photosynthetic mechanisms: 1) C_3 photosynthesis and 2) C_4 photosynthesis. C_3 plants use C_3 photosynthesis and C_4 plants fix CO_2 through C_4 photosynthesis. Although many CAM plants are known to combine nocturnal C_4 fixation and mid-day C_3 fixation, they basically incorporate CO_2 at night into C_4 acids.[39] And carbon isotope ratio separates these two mechanisms. Examining the $\delta^{13}C$ values for plants in the Carlsbad regions, DesMarais *et al.*[4] reported the average of -26.0 ± 2.2‰ for 27 C_3 plants and that of -13.1 ± 1.1‰ for 31 C_4 and CAM plants. The difference due to the photosynthetic pathways was 12.9‰. The shaded areas in Fig. 3 indicate the ranges of these two groups, and most datapoints of estimated primary producers are within the range of C_3 fixation, some being in between C_3 and C_4.

Table 2. Presumed Changes in Carbon and Nitrogen Isotope Ratios from Primary Producer to Bat Guano

Location / Bat food habit / Age of guano	Enrichment (‰)	
	^{13}C	^{15}N
Jamaica		
Frugivore		
Modern	0	0
Old	0	0
Insectivore		
Modern	1	3
Old	1	3
Carlsbad		
Frugivore		
Modern	0	0
Old	0	6.2
Insectivore		
Modern	1	3
Old	1	9.2

Insects are assumed to feed over plants. ^{15}N enrichment for old guano from the Carlsbad regions is a maximum; some caves where little guano decomposition takes place may show a lower value.

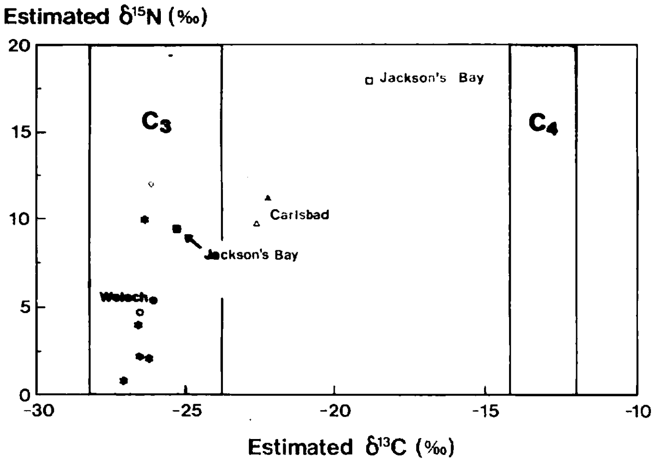

Fig. 3. Estimated carbon and nitrogen isotope ratios of primary producers leading to bats. Guanos of unknown species are assumed to be of insectivores. Symbols used are: triangle, guanos from the Carlsbad regions; square, guanos from Jackson's Bay Cave Complex; circle, guanos from Welsch Ratbat Cave; and asterisk, fresh guanos from other Jamaican caves. Open symbols represent fresh guano and closed ones old guano. The shaded area for C_3 plants and for C_4 and CAM plants cover one-sigma range reported by DesMarais *et al.*[4]

5.3 Jamaican palaeoclimate

5.3.1 Estimated contribution of primary producers

From Fig. 3, it is now apparent that the subfossil guano from Jackson's Bay Great Cave is not a diagenetic product of bat excreta isotopically similar to Somerville Cave guano. Somerville Cave guano and the subfossil guano yielded quite different results in spite of the fact that both came from the same Jackson's Bay Cave Complex, only being separated each other by 800 years in time.

Excepting the modern guano from Somerville Cave, all the Jamaican guanos fit within the one-sigma of C_3 fixation. The food chains that end up to these Jamaican guanos would begin from C_3 plants. On the contrary, the C_3 contribution to the Somerville Cave guano is calculated to be only 36%. In this sense, the guano from Somerville Cave is truly unique not only among *Pteronotus parnelli* modern guanos but also among all the Jamaican fresh guanos, being mostly dependent on C_4 photosynthesis. In other words, the insects that feed on C_4 and CAM plants would be the main prey for *Pteronotus parnelli* in Jackson's Bay area today and the same *Pteronotus parnelli* in other areas consume insects that forage C_3 plants.

What unique about Jackson's Bay today would be its aridity.[40] All other Jamaican modern guanos come from mesic or wet environment. The C_4 and CAM photosynthetic strategies are better suited to sunny, semiarid environments than is C_3 photosynthesis.[41] They are often found in an arid environment; for instance, in the Pecos River Valley, 27 out of 29 grass species are C_4 plants.[4]

Unlike modern guano from Somerville Cave, the estimated $\delta^{13}C$ of primary producers for the *ca.* 800 years old guano from Jackson's Bay area nicely settles within the C_3 range. It is, therefore, suggestive for a humid climate of Jackson's

Bay area at that time period.

5.3.2 Other evidence for mesic climate in Jackson's Bay area

The only previous study of Holocene climate in Jamaica is a report on peat bog core samples by Digerfelt and Enell (*cf.* Fig.1).[42] These authors identify an episode of increased flooding, attributed to increased precipitation, between 1500 and 1000 years B.P., indicating a short-lived episode of the mesic conditions. Speleothem deposits, mostly in the form of dried-out calcite, in Jackson's Bay Caves are a thin surface layer of rather pure flowstone of about 5 cm thickness on the average, also indicating that the mesic conditions were transitory.

Furthermore, Jackson's Bay Cave Complex itself preserves alternative evidence that leads us to suppose that the cave and surrounding environment experienced a significant mesic episode in the recent past.

Wadge *et al.* [5] and McFarlane[7] have drawn attention to the extensive deposits of calcite pearls and dams that cover hundreds of square meters of the Drum Cave floor, though the cave in now located well above the water table. Since the cave pearls form when calcite-containing water falls into shallow pools with regularity, these subaqueous speleothems cannot have formed under present conditions when standing water is present in these passages only briefly during episodes of exceptional precipitation. Once, water must have dripped abundantly from the ceilings of the cave.

A small population of Arawak Indians inhabited near Jackson's Bay Cave Complex in pre-Colombian times. In Water Jar Cave, broken pottery of Arawak origin was found. Though it is now completely dry, standing water must have been present in significant amounts during the period of Arawak occupation and once a source of drinking water for the Indians. Since it is suspected that the Arawaks did not reach Jamaica until about five thousand years ago, the climatic change to aridity took place within the last few thousand years. Furthermore, radiocarbon dating by tandem mass spectrometry was used to date Arawak bone from the Jackson's Bay caves at 710 $\pm$ 60 years B.P.,[13] close to the date associated with the subfossil guano deposit.

5.4 Vegetation in the Pecos River Valley in Wisconsinan

With old guanos from the other locations, we would like to further pursue the ecogeochmical utility of bat guanos. DesMarais *et al.*[4] reported nearly equal numbers of C_3 ($-26.0‰$) and C_4 and CAM ($-13.1‰$) native plant species in the present Pecos River Valley, along which the bats in the regions prefer to feed.[12] Among 29 grass species in the valley, however, 27 including all the dominant 7 are C_4 plants.

The modern and fossil guanos from the Carlsbad regions estimate the $\delta^{13}C$ values for primary producers to be $-22.6‰$ and $-22.3‰$, respectively. When DesMarais *et al.*'s results[4] were adopted as endpoint values for the two groups of vegetation, the relative contribution of C_3 photosynthesis to bat food chain would be 74% for modern guano and 71% for fossil guano.

Because the bats at present frequent not only the area where native plants grow but also cultivated crop fields where alfalfa and cotton, both C_3 plants, dominate, the major C_3 contribution is understandable. However, the similar proportion more than 30,000 years ago in the absence of anthropogenic agriculture is somewhat unexpected. And its potential implication to the past flora and insect fauna is intriguing, though the estimate is very much tentative, and though more detailed analysis requires a better knowledge of the isotopic behavior along food chain.

Carlsbad locates in the southwestern U.S.A. and it is known that the area lagged behind the beginning of nonglacial climates in the north. The age of 30,000 years for the fossil guano is a minimum based on the infinite ^{14}C dates, and the true age would be probably 30 to 50 thousand years B. P., which is in between early and late Wisconsinan. The climate then would have been a little cooler. Packrat middens with radiocarbon dates from 11,000 to more than 40,000 years B.P. record woodland plants in the area.[44] Though not exactly the same area, Cole reported that the plant species along the Colorado River were generally distributed *ca.* 800 m lower in elevation and *ca.* 550 km further down-river during late Wisconsinan than present.[45] While C_4 plants now dominate grasses in the Pecos River Valley, the low, calculated contribution of C_4 and CAM plants might indicate that, without C_3 agricultural species, native C_3 plants were more abundant in the bat feeding ground at that time.

5.5 Bat Cave guanos from the Colorado River

The $\delta^{13}C$ values of *ca.* 7600 years old guanos from Bat Cave in Grand Canyon give on the average an estimated $\delta^{13}C$ value of $-23.0‰$ for primary producers, while that of fresh guano results in a lower estimated value of $-25.4‰$. This would indicate that the bats now forage mostly C_3 plants and that plants which employ C_4 photosynthesis constituted a small portion of their diet in the past.

The bats in the Bat Cave are likely to forage over the Colorado River. The vegetation in the area about 7600 years ago does not seem to be well documented, but would not be very different from today excepting a possibly more extensive, open juniper woodland at lower elevation than present.[46] This possibility works against the higher $\delta^{13}C$ for the old guano, however. Rather, the present, high C_3 contribution might have resulted from more recent event: Due to flood control of the Glen Canyon Dam, the riparian vegetation in the canyon is more extensive today.[47] In the past, severe spring flooding would have regularly flushed out the canyon, and desert vegetation of the canyon walls would have merged directly into annual herbs growing on temporary mudbanks. Today, trees and woody shrubs have been able to establish themselves along the river margins. This change in vegetation along the river might be reflected in the larger contribution of C_3 fixation to the bats' diet today.[48]

6. Conclusions

The subfossil guano in Jackson's Bay Great Cave accumulated about 800 years ago. In view of the extensive guano deposition that took place at this time, the Jackson's Bay environment must have sustained a much larger bat population than now exists in the area. The isotopic data presented here clearly point to significant environmental differences *ca.* 800 years ago. We propose that the bats of Jackson's Bay at *ca.* 800 years B. P. were top predators in an ecosystem sustained by C_3 photosynthesis. These conditions currently exist in other Jamaican localities with a mesic, rainforest flora. The subfossil guano, therefore, appears to have accumulated at a time when a more mesic environment supported a significantly larger bat population than is now sustainable in Jackson's Bay Cave Complex.

The fossil and modern guanos from the Carlsbad regions showed the relative contribution of C_3 fixation to bat diet to be about the same. The present C_3 contribution presumably comes from crop fields in the Pecos River Valley where C_3 plants are principally grown. In the absence of agriculture some 30,000 or more years ago, the past contribution might have come from more abundant native C_3 plants in the valley at that time.

Guanos from Bat Cave suggested that the bats there fed on a little more of C_4 plants about 7600 years ago than today. The flood control of the Glen Canyon Dam is thought to be relevant to the observation through an establishment of trees and shrubs along the Colorado River margins.

Although many uncertainties remain to be cleared, we are confident that the $\delta^{13}C$ differences among the primary producers are systematic and large enough to produce signals in old guano that may be interpreted palaeoclimatically, in spite of various ecogeochemical and diagenetic changes. The present study should facilitate the application of stable isotopes of carbon and nitrogen to palaeoclimatic investigations, offering an opportunity to sample bat guanos available in certain caves and to look into the palaeoenvironmental conditions and palaeoecology through their isotope ratios.

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Appendix 1. Organic Carbon and Kjeldahl Nitrogen Contents of Bat Related Samples from Various Regions and Their Isotope Ratios

Bat species involved Class Secimen/Location	Organic carbon Content [mgC/(g dry sample)]	Organic carbon Isotope ratio [‰]	Kjeldahl nitrogen Content [mgN/(g dry sample)]	Kjeldahl nitrogen Isotope ratio [‰]	Remarks
Macrotus californicus					
Insect food in Roosevelt Mine, U.S.A.					
Grasshopper		−22.2		3.6	a)
Grasshopper		−22.7		1.9	b)
Katydid		−21.3		4.3	c)
Moth, body		−27.2		18.2	d)
Moth, wing		−25.1		6.2	d)
Guano					
Roosevelt Mine	211	−24.9			
Tadarida brasiliensis					
Bat tissue in Arizona, U.S.A.					
Hair		−19.9		9.6	e)
Bone		−18.1		9.3	e)
Wing skin		−22.5		11.9	f)
Guano					
Devil's Hole	188	−23.0			
Bat Cave	248	−24.4			
Bat Cave	126	−21.5			h)
Carlsbad Caverns	195	−21.6	112	12.7	
New Cave	22.3	−21.3	10.4	20.3	#, h, l, m)
Pteronotus parnelli					
Guano					
Oxford Cave	190	−25.3	65.7	5.1	
Oxford Cave	229	−25.1			g)
Somerville Cave	90.1	−17.8	28.7	20.9	
Somerville Cave	21.7	−16.1			g)
Wondrous Cave	68.3	−25.5	41.5	5.2	
Falling Cave	31.7	−25.4	6.5	13.0	
Myotis sp.					
Guano					
Coon Springs Cave	165	−23.4	93.6	6.2	
Coon Springs Cave	186	−22.9	95.5	5.8	g)
Myotis velifer					
Guano					
California Mine	216	−25.5	108	9.6	
California Mine	267	−24.6			g)
Desmodus rotundus in Costa Rica					
Bat tissue					
Body skin	413	−15.9	113	6.3	
Brachyphylla cavernarum					
Guano					
Cavannagh Cave	101	−25.5		#	
Artibeus jamaicensis					
Plant food found in Mount Plenty Cave					
Fig, berry skin		−26.5		3.9	j)
Fig, sprout stem		−24.9		0.4	j)
Fig, berry		−25.8		−1.0	j)
Fig, leaves		−26.8		1.7	j)

Appendix 1 (Continued)

Bat species involved Class Secimen/Location	Organic carbon		Kjeldahl nitrogen		Remarks
	Content [mgC/(g dry sample)]	Isotope ratio [‰]	Content [mgN/(g dry sample)]	Isotope ratio [‰]	
Guano					
Welsch Ratbat	88.3	−26.5	32.6	4.7	
Welsch Ratbat	28.2	−26.1	13.1	5.4	h, m)
Leptonycteris nivalis					
Plant food in Arizona					
Yucca schotti, leaf	249	−24.6	35.5	5.3	k)
Yucca schotti, stem	236	−25.6	28.1	5.8	k)
Bat tissue in Mexico					
Body skin	414	−18.3	122	10.5	
Unknown species of fruit bat in the Philippines					
Guano					
unknown	14.7	−27.9			#,h)
unknown	30.6	−26.6			h)
Unknown species					
Guano					
Jackson's Bay	31.8	−24.3	5.9	12.4	h, i, m)
Jackson's Bay	15.4	−22.8			g, h, i, m)
Brother Frader's	192	−25.6	93.2	7.0	
Cornwall Barracks	138	−26.1	55.4	3.8	
Abingdon Cave	54.1	−27.7			
Penthouse Cave	20.6	−28.2	7.9	18.4	h)
Bat Cave	60.6	−22.5			#,h)

Blank space indicates "not analyzed." *Macrotus californicus* is an insectivore that hunts large insects on the ground and on low vegetation. The common vampire bat (*Desmodus rotundus*) feeds in Costa Rica on cattle which feed on pasture in areas of cleared rainforest. *Brachyphylla cavernarum* switces diet from insects to fruit and nectar, according to seasonal availability. Long-nosed Bats (*Leptonycteris* sp.) are committed flower feeders,[49] and a kind of agave, *Yucca schotti*, is an important food plant for them. Roosevelt Mine, Mule Mountains, Riverside County, California, is in the Mojave desert. Devil's Hole is in St. Maarten, Netherlands Antilles. Coon Springs Cave, Arizona, is about 100 km distant from Eagle Creek Cave and houses *Myotis* sp. California Mine, Riverside County, California, U.S.A., is located approximately 200 m from the Colorado River. Cavannagh Cave is in Anguilla, British West Indies. Penthouse Cave (18°12′ N, 77°43′ W) near Welsch Ratbat Cave houses no bats today, but contains an organic rich deposit of unkown origin and age; Thouh it lacks positive identification as old bat guano, it is common practice to call any dark, apparently organic layers in cave sediments as bat guano, which has been shown incorrect in several cases; The current state of knowledge in guano diagenesis is not sufficient to tell decomposed guano from other organic rich deposits; In particular, tropical caves receive a large amount of organic matters from flood water, hurricane blown vegetation, and other causes. a): unknown species (Family: Acridae); b): Pallid-winged Grasshopper (*Trimeritropis pallidipennis*); c): *Capnobotes fuliginosus*; d): White-lined Sphinx Moth (*Celerio lineata*); e): collected near Eagle Creek Cave; f): collected near Bat Cave; Guano samples marked as g) were not decarbonated by 2 N HCl; Excepting those marked as h), all the guanos are modern; i): probably guano *Pteronotus parnelli*; j): samples (*Ficus* sp.) had been stored in 70% ethanol; k): air-dried specimen collected along highway I-10, 50 km east of Tucson, Arizona, U.S.A.; l): presumed to be the guano of *Tadarida constantinei*, chronospecies of *Tadarida brasiliensis*; m): sampled from depth (*cf.* Table 1); and samples that showed an intensive bubbling are marked as #. In addition, our separte paper in this issue gives carbon and nitrogen isotope data of a stratified guano core from Eagle Creek Cave, Arizona, U.S.A.[15]: one gram of the dried guano contained 256±30 mg of organic carbon with $\delta^{13}C$ of −21.9±1.5‰ (17 samples) and 169±9 mg of Kjeldahl nitrogen whose $\delta^{15}N$ was 6.9±1.0‰ (19 samples).