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Rates of diagenesis of tropical insectivorous bat guano accumulations: implications for potential paleoenvironmental reconstruction

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Abstract: Cave guano deposits are increasingly being recognized as valuable repositories of paleo-climatic and paleo-environmental information. However, that value is constrained by rates of guano decomposition, and these rates have not been previously well-studied. Here we show that field and laboratory studies of deep insectivorous bat guano sequences in the caves of Borneo demonstrate the extreme dependence of decomposition rate on guano water content. Under tropical conditions, moist guanos exhibit decomposition coefficients (*k*) values of ~0.01, implying the loss of most of the organic content on decadal timescales. Under similar temperatures but drier conditions, *k* values drop to ~3 x 10^{-6}, permitting significant organic (chitin) content to persist for tens of thousands of years. One of the implications of these findings for paleo-environmental records older than the limit of carbon dating is that a value for *k* can be calculated based on a single carbon date, which then allows an estimate of likely age at base of deposit.

Keywords: bat guano, *k* factor, guano respirometry, radiocarbon, Sarawak

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INTRODUCTION

Paleo-environmental and paleo-climatic proxy data are increasingly being extracted from cave guano deposits (e.g., Onac et al., 2014). However, age is not necessarily correlated with the overtly-apparent state of decomposition, and simple field observation (without time-consuming and expensive preliminary lab analyses) rarely allows any estimate of the probable age of the deposit and thus its potential value as a proxy. For example, in tropical, and, in some cases, warm-temperate environments, some insectivorous bat species can form very large (10^5 - 10^6 individuals) colonies that deposit huge quantities of guano in their roost caves. These accumulations can reach tens of thousands of cubic meters in volume (e.g., 5 x 10^4 m^3 in the caves of Mona Island, West Indies: Peck & Kukalova-Peck, 1981), 10 m or more in depth, and incorporate material dating back more than 50,000 years (Bird et al., 2007; Wurster et al., 2010). The post-depositional fate of this guano is dependent on cave micro- and macro-environmental parameters, but we hypothesize that it is most especially dependent on the water content of the guano. Under very dry conditions, bat guano may be preserved with little or no diagenesis over thousands of years (e.g., Wurster et al., 2010). Over timescales of 10^4 years, these deposits may generate a range of diagenetic nitrate, phosphate, and sulfate minerals within a stratified, organic sequence (Hill & Forti, 1997; Audra et al., 2021). Conversely, under wet conditions, insectivorous guano may decompose to a residual clay over decadal timescales.

The research literature is notably deficient in studies of guano degradation rates, and of long-term water content. There is a substantial literature on the mineral products of guano decomposition (e.g., Onac & Vereş, 2003; Shahack-Gross et al., 2004; Audra et al., 2021; Merino et al., 2022). Wurster et al. (2015) summarized the final elemental products of these diagenetic processes. However, relatively few studies have quantitatively addressed the processes in the context of *rates of diagenesis* in bat guano accumulations, and none provide empirical data on rates of change.

Here we address the processes of decomposition of insectivorous bat guano, and their rates in varying micro-environmental situations (controlled mainly by temperature and moisture), by means of empirical field and lab studies. These yield estimates of typical "half-lives" of insectivorous guano, providing a tool for

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field researchers in paleo-*chiropterocoprology* – a way to estimate the probability of survival of the record, potentially reducing, or at least focusing, the requirement for expensive and potentially futile lab analyses.

METHODS

The non-chitinous components of bat guano (e.g., protein, fats, waxes) break down rapidly in days or weeks, or are consumed by coprophagous invertebrates (Ferreira, 2019), and thus are not relevant to the paleo-archive. The longer-lived chitinaceous component (i.e., the fragmented insect exoskeleton, which is a complex of the chitin polymer n-acetyl glucosamine, together with a tightly-bound proteinaceous matrix of sclerotin: Moussian, 2019) is eventually degraded by slower-acting microbial metabolism. Survival of this chitinaceous component under different conditions varies with time and specific environmental conditions (Beier & Bertilsson, 2013). The inputs to the process are: 1. guano accumulation (controlled by bat densities); 2. arthropod bioturbation and coprophagy; and 3. bacterial community composition/population (governed by temperature, moisture, and pH). The outputs are water, heat, sulfuric, phosphatic and nitric acids, ammonia, carbon dioxide, elemental nitrogen, hydrogen sulfide, and residual minerals (nitrates, sulfates, phosphates, and clays) (e.g., McFarlane et al., 1995; Onac & Forti, 2011; Lundberg & McFarlane, 2021; McFarlane & Lundberg, 2021; Lundberg et al., 2022).

Study sites

Active decomposition processes were studied in Deer Cave (Gua Payau), Gunung Mulu National Park, Sarawak, Malaysia (4.024° N, 114.825° E, 197 masl), a very large, essentially horizontal cave passage some 1.05 km in length (excluding side passages) with dimensions exceeding 90 m in width and 90 m in height throughout (Fig. 1).

The cave hosts a diverse ecosystem of troglobitic and troglophilic invertebrates (Chapman, 1981, 1982), a significant population of cave swiftlets (*Aerodramus* spp.), and perhaps 12 species of bats (Abdullah et al., 2007), including a large population of the Wrinkle-Lipped bat, *Chaerephon plicata* (Molossidae). The true population size of *C. plicata* at Deer Cave has never been quantitatively measured, and some estimates in the popular media (ranging from 2 million to 3.5 million) are exaggerated, but, by comparison to the known population size of the same species at Gomantong Cave, Sabah (McFarlane et al., 2015), is certainly several hundreds of thousands of individuals. Lundberg et al. (2022) provide the first quantitative (conservative) estimate of total population at 774,828 ± 48,320. The bulk of the *C. plicata* population in Deer Cave today roosts in five distinct areas (Fig. 1), three of which were included in this study (Areas A, C and D).

Guano sampling

Guano was sampled (in July 2018 and July 2023) at Area C (Site C) by direct collection from a 75 cm-deep profile excavated in an actively accumulating deposit, and also from Area A (site A2), a 50 cm-deep profile, also in an actively accumulating deposit. Following in-situ temperature (Nicety DT1311 K-type thermistor; ±0.1°C) and pH measurements (Extech PH110; ±0.2 pH), minimally-disturbed samples of approximately 5 cm^3 were collected from the surface and at least every 10 cm, by horizontal insertion of clear plastic centrifuge tubes, which were then sealed and returned to the laboratory. Duplicate samples were collected for DNA analysis, the methods and results of which study are reported in McFarlane & Lundberg (2024, *in press*).

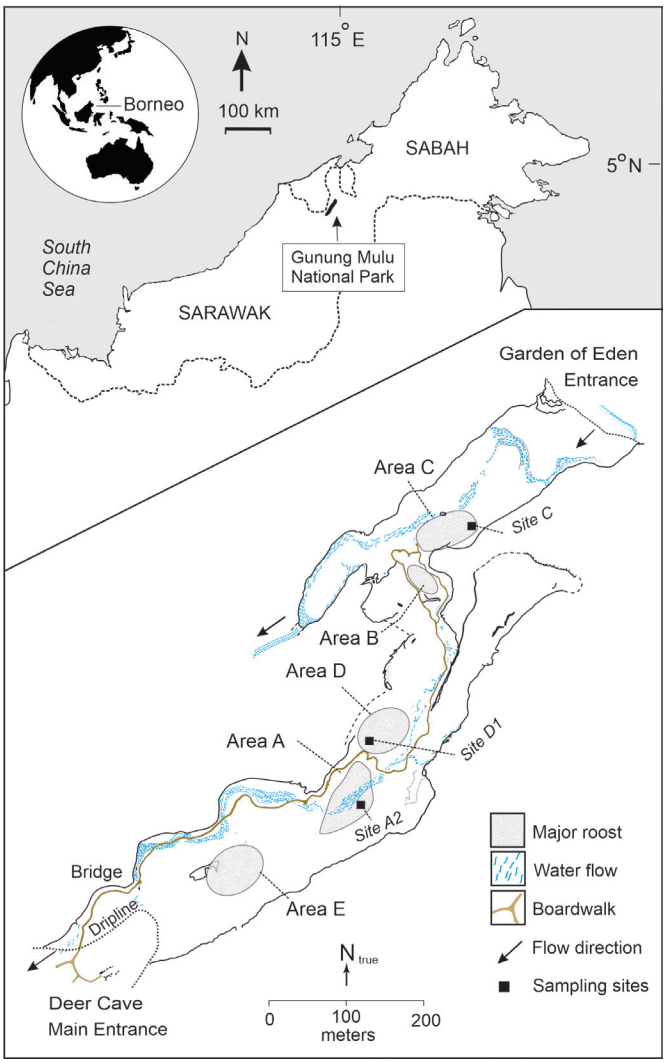

Fig. 1. Location of Gunung Mulu National Park (Sarawak) and Deer Cave main roosts and sampling sites.

The guano samples collected for chitin analysis were weighed, and then oven-dried at 70°C for 24 hr, for the determination of water content, and analyzed for total carbon, nitrogen, and sulfur (CNS) content using an Elementar Vario Micro Cube combustion analyzer (Dept. of Geology, Pomona College and Jan Vizer Stable Isotope Laboratory, University of Ottawa).

Additional sub-fossil guanos from Jamaica, New Mexico, and Arizona were analyzed and dated.

Guano deposition rate

Deposition rate is a necessary component of the respirometry calculation and daily mass decomposition calculations. Guano deposition rates were part of a companion study that is reported in detail by Lundberg

et al. (2022). These are supplemented by additional measures from field work in 2023. Fresh guano falling from roosts was collected over four days in 0.09 m^2 gauze squares (raised to avoid guanophagic insects) distributed over the areas of guano accumulations. Spatial locations and dry guano weights were entered into ArcGIS. Guano fall rate (g of dry guano/m^2/day) was contoured by a standard Krigging algorithm (van Rentergem et al., 2024, *in press*).

Guano respirometry

Aerobic decomposition of organic matter, including chitin, yields carbon dioxide as a by-product. Respirometry thus allows real-time analysis of aerobic guano decomposition. The energy content of fresh guano was determined from a 1 g sample of fresh guano, dried at 70°C for 24 hr, and combusted in a Parr Instruments bomb calorimeter. In the field, Site D1, aerobic metabolism of the surface guano accumulation was measured using a 1.5 dm^3 polyethylene, 12 cm-diameter respirometry chamber (i.e., the enclosed surface area is 113 cm^2), connected to a CO2Meter CM-0056 recirculating CO_2 pump and logging meter, via a desiccant tube to remove water vapor. A vial containing 1.5 ml of phosphoric acid adsorbed onto glass fiber was placed within the chamber to absorb ammonia. The system was allowed to run for 24 hours, sampling at 10-minute intervals. Laboratory analysis of ammonium was performed using Nessler's reagent on a Hanna Instruments 83200 spectrophotometer.

Guano age

Five samples of guano (Site A2) from 0.5, 10, 30, 35, and 46 cm depth in the profile were submitted to the Keck Carbon Cycle Accelerator Mass Spectrometry facility (University of California, Irvine) for radiocarbon analysis. The four upper samples were shown to contain "bomb" radiocarbon, so the sequence was calibrated using the CALIBomb program (Intcal13, NHZ1; Reimer et al., 2013). The other radiocarbon dates were calibrated using CALIB (Stuiver & Reimer, 1993). Two additional samples from Site C, from 35 cm (middle) and 70 cm (base) depth, were radiocarbon dated at Northern Arizona University, Arizona Climate and Ecosystems Isotope Laboratory. Details of the interpretation of the dating results are given in Supplementary information.

RESULTS

Physical parameters and bacterial components

Temperature, pH, and CO_2 production within the guano sequence are proxies for microbial metabolism and therefore rates of guano decomposition. Temperature and acidity (Fig. 2) show a simple direct relationship, both increasing with depth, to a maximum at about 20-30 cm depth (the zone of maximum decomposition), and both remaining significantly higher than ambient surface conditions. The maximum acidity recorded across all the sites measured was pH 2.8 (maximum acidity at Site C, Figure 2, was 3.82) and the maximum temperature was 34.3°C. Ambient cave air temperature was 25.0°C ±2.5 (six days of data collected for the study reported in Lundberg et al., 2022).

Results of the bacterial DNA study are reported in detail elsewhere (McFarlane & Lundberg, 2024, *in press*). In summary (Fig. 2), the bacterial species and diversity change with depth, and with pH and temperature. The surface, aerobic, zone (of moderate temperature and acidity) has the greatest diversity of taxa with Bacteroidetes co-dominant with Proteobacteria. The number of taxa stabilizes to lower values in the anaerobic middle zone of increasing acidity and temperature, with Proteobacteria dominant. The deepest zone had the lowest diversity, Actinobacteria taking over as dominant.

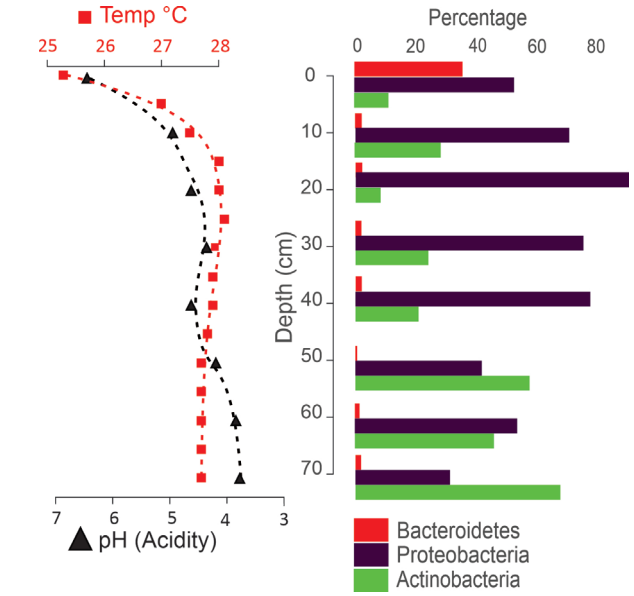

Fig. 2. Changes with depth in guano profile from Site C: acidity, (pH), temperature (ºC), and proportions of major bacterial taxa (*Proteobacteria*, *Bacteroidetes*, and *Actinobacteria*).

Guano deposition rate

Guano deposition rate is highly spatially variable, ranging from <0.1 g dry mass/m^2/day up to ~80 g dry mass/m^2/day in Area A and D, but up to 538 g dry mass/m^2/day in Area C (van Rentergem et al., 2024, *in press*), reflecting the density of roosting bats on the roof above. In some areas, strong diurnal (reversing) air flow (Lundberg et al., 2022) deflects guano fall laterally over tens of metres from its point of origin. Guano accumulation rate at the site of respirometry measurement, Site D, was ~10 g dry mass/m^2/day. The observed guano deposition rate in the area of the profiles (Site A2) was 23 g dry mass/m^2/day, which corresponds to a daily incremental addition of ~1 mm of guano across the surface (using the laboratory-derived density of freshly deposited guano of ~0.25 g/dry mass/cm^3).

Ammonia output

We have previously addressed the dynamics of the nitrogen capital in this cave (Lundberg et al., 2022), and noted that the gaseous ammonia derives largely from urea rather than directly from degradation of the chitin component. The cave discharges ~7 kg N/day in water, and ~0.5 kg N/day in air.

Respirometry results

Production of CO_2 from Area D (Site D1, Table 1) was calculated from a linear regression of the increase in CO_2 against time (Fig. 3), and found to be 2.53 g CO_2/day/m^2 (using standard values of mass of CO_2 at STP). Note that after 14 hours the production of CO_2 levels off, and eventually falls to zero, due to exhaustion of oxygen in the respirometry chamber.

On the assumption that aerobic conditions prevail to no more than 2.0 cm depth in the guano (the limit of visible bioturbation in this area), and using the density of 0.25 g dry mass/cm^3 for fresh, uncompacted guano, the aerobic respiration rate is 5.06 x10^{-4} g CO_2/g guano/day, or 2.38 x 10^{-4} g CO_2/g guano C/day. Aerobic respiration generates 10.9 KJ/g CO_2 produced, so measured aerobic respiration is equivalent to a metabolic output of 2.59 x 10^{-3} KJ/g guano C/day. Calorimetry of fresh guano yields a value of 11.92 KJ/g; thus, aerobic respiration (i.e., decomposition) accounts for some 0.02% of available metabolic energy per day (Table 1).

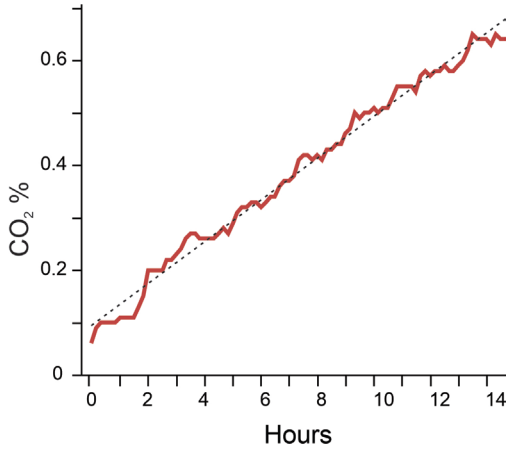

Fig. 3. Cumulative production of CO_2 from guano metabolism, measured in Site D1, Area D.

Table 1. Summary of guano respirometry results.

Process	Result
Production of CO_2	2.53 g CO_2/day/m^2
Aerobic respiration rate	2.38 x 10^{-4} g CO_2/g guano C/day
Metabolic output	2.59 x 10^{-3} KJ/g guano C/day
Energy content of fresh guano	11.92 KJ/g
Aerobic decomposition rate	0.02% of available metabolic energy/day

Ages and decomposition rates of profiles (Site A and C)

The calibrated radiocarbon ages (Table 2), using CALIB version 8.2 (Stuiver & Reimer, 1993), data set Intcal 20, provide a basal age for Site A Profile (at 45 cm) of AD 1928.5 ± 12.5. The uppermost four samples showed excess modern C-14, and thus were calibrated using CALIBomb (Reimer & Reimer, 2024), using the geographically appropriate data set NH Zone3 (Fig. 4). This technique is thus shown to be appropriate for dating young guano deposits which are unsuitable for Pb-210 or Cs-137 dating (Johnston et al., 2010; McFarlane & Lundberg, 2021).

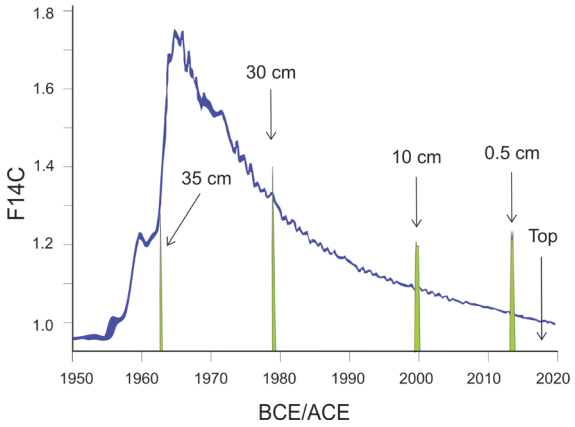

Fig. 4. Guano radiocarbon dates on post-bomb C-14 curve.

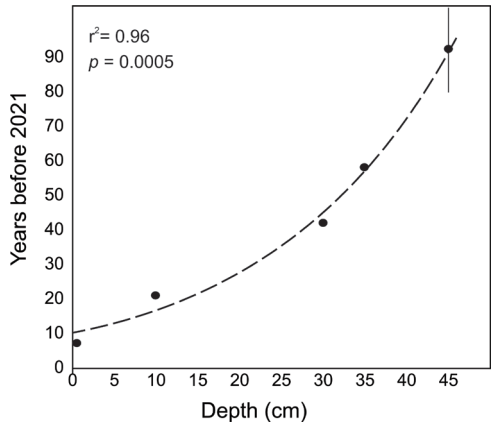

Fig. 5. Exponential model age and depth (age in years before 2021.5 – the year of radiocarbon processing). The age and depth error bars for the uppermost four dates are smaller than the symbol.

Modelling of ages against depth in PAST (Hammer, 2024; Fig. 5) yielded the best fit for an exponential decay curve (r^2 = 0.96, p = 0.0005). The radiocarbon age for the basal sample is 93 years before AD 2021.5 (i.e., the date that C-14 was measured) or 88 years before AD 2016.5 (i.e., the date of original deposition of the guano). The modelled age for the base is 92.5 years before 2021.5 or 87.5 years before 2016.5. That the modelled age is only 0.04 standard deviations from the median radiocarbon age validates the model. All further calculations were based on these 88 years of decomposition for this profile, and dates for interim layers were estimated using the model equation.

Two radiocarbon dates were done for Site C (Table 2), providing a modelled basal (70 cm) age of 130 years of decomposition, and a middle (35 cm) age of 70 years, a rate of decomposition that is consistent with the rate from Site A2, in spite of the rate of guano accumulation being considerably higher at Site C.

Composition of Site A2 and Site C profiles

Chemically-pure chitin has a stoichiometric carbon content of 50.79% (Moussian, 2019). Samples of freshly-falling insect guano in this cave (intercepted before falling to the cave floor), which also includes proteinaceous and wax components, has been determined to have a carbon content of 47.4 ± 0.2%. Similarly, nitrogen values in pure chitin are 7.4%, but in fresh guano have been measured at 12.2 ± 0.1%, reflecting addition of N from non-chitinous components.

Table 2. Carbon-14 data on profiles from Site A2 and Site C.

Profile site	Depth in profile (cm)	Fraction modern ±1 sigma	^{14}C age BP ±1 sigma	CALIB year AD ±1 sigma	CALIBomb year AD ±1 sigma	Years before laboratory measurement
A2	0.5	1.0320 ± 0.0017	Modern	N/A	2013.65 ± 0.25	7.85
A2	10	1.0995 ± 0.0021	Modern	N/A	1999.70 ± 0.3	21.8
A2	30	1.3187 ± 0.0023	Modern	N/A	1978.90 ± 0.1	42.6
A2	35	1.3056 ± 0.0020	Modern	N/A	1962.52 ± 0.05	58.98
A2	46	0.9817 ± 0.0016	150 ± 15	1928.5 ± 12.5	N/A	93
C	35	0.9886 ± 0.15	92 ±12	1897 ± 19	N/A	70
C	70	0.9818 ± 0.15	147 ± 12	1858.5 ± 23.5	N/A	130

Changes with depth in carbon, nitrogen and sulfur contents of Deer Cave guanos from Site A2 and C are presented in Tables 3 and 4. Nitrogen and carbon decrease with depth in a simple and parallel linear trend (Fig. 6), confirming that the profile probably remained undisturbed by mass movement, erosion or flooding for at least 93 years). Nitrogen mobilization (as soluble nitrate) at the base (46 cm depth) is 81% and carbon mobilization is 78%.

Table 3. Changes with depth of guanos in profile from Site A2.

Site A Depth (cm)	N%	C%	S%
0	12.3	47.6	0.5
5	12.2	47.3	0.5
10	9.2	39.6	1.0
15	8.1	36.7	1.0
20	6.9	32.0	1.1
25	5.2	24.1	1.0
30	6.4	28.9	1.1
36	4.8	21.9	0.7
41	4.8	21.2	0.6
46	2.3	10.3	0.4

Table 4. Changes with depth of guanos in profile from Site C.

Site C Depth (cm)	N%	C%	S%
0.5	12.1	47.2	0.6
10	9.6	38.2	0.5
20	10.0	37.3	0.5
30	11.6	44.7	0.6
40	10.9	43.7	0.4
50	6.2	24.3	0.1
60	9.6	37.0	0.3
70	3.2	11.3	0.04

One of the major diagenetic products of guano decomposition is gypsum (Audra et al., 2021). Unfortunately, the ultimate origin and systematics of sulfur input to the system remains largely unstudied. Here we simply note that the sulfur data reflect this mobilization and stratified re-deposition within the guano.

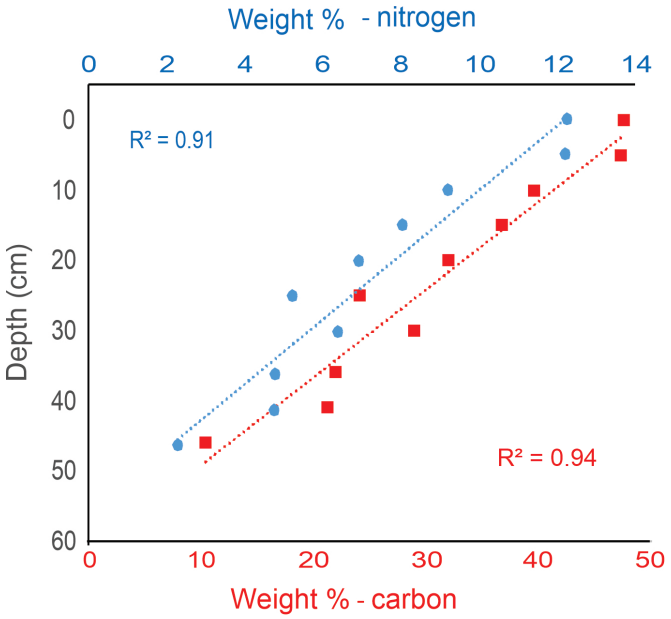

Fig. 6. Changes in carbon and nitrogen content with depth, Site A2.

Applying *k* value coefficients to guano

In the soil science literature, decomposition is frequently measured in terms of the decomposition coefficient *k* (e.g., Janssen, 1984; Manzoni et al., 2012; Krishna & Mohan, 2017). Values of *k* have been shown to decrease with time as rate of decomposition slows with time (Edmonds, 1984), with decreasing temperature, increasing latitude, and with decreasing precipitation (Zhang et al., 2008). Zhang et al. (2008) note also that, although no single variable explains all the variation in k values, the most important variables are total nutrient content, and especially C:N ratio.

Soils show a rather simple relationship of decomposition rate with depth, largely controlled by availability of organic carbon and minimally affected by temperature or oxygen availability (Kirschbaum et al., 2021). However, the insect chitin in bat guano is quite resistant to decomposition. Therefore, *k* values might not follow similar patterns to those in soils, and peak decomposition might not be expected to be at the top of the sequence.

The decomposition coefficient, *k*, has been calculated by Makkonen et al. (2012) as

$$k = -\frac{ln\left(\frac{M_t}{M_0}\right)}{t} \qquad \text{Eq. 1}$$

where M_0 is mass at start of decomposition and M_t is mass at later stage of decomposition. In applying this equation to degradation of chitin in our guanos, M_t is

% carbon content at the basal layer, M_0 is % carbon at the active surface, and t is the basal age. This can equally be applied to nitrogen decomposition rates, allowing a comparison of the potentially differing rates of decay for the carbon ($k_{yr.C}$) versus the nitrogen component ($k_{yr.N}$).

For the 88 years of decomposition of the Site A profile, the integrated annual decomposition rate constant for carbon, $k_{yr.C}$, is 0.0174, and for the 119 years since original deposition in 2016 at Site C profile, $k_{yr.C}$ is 0.0120. The value for nitrogen ($k_{yr.N}$) for Site A is 0.0181 and for Site C is 0.0108.

Change in k values (for carbon and for nitrogen) with depth in profile reveal the zones of differing decomposition rates (Fig. 7). For the uppermost few centimeters of loosely-packed, bioturbated guano decomposition rate is low. However, a rapid increase is apparent below about 5 cm, and decomposition peaks at around 25 cm depth, declining towards the base of the profile. The nitrogen and carbon change in tandem but the nitrogen is mobilized more rapidly. Note that this pattern of changing k values with depth matches well with the pH, temperature and bacterial variations with depth shown in Figure 2.

The k values were also calculated for a set of geographically diverse, ancient insectivorous bat guanos preserved under different moisture regimes. These results are summarized in Table 5.

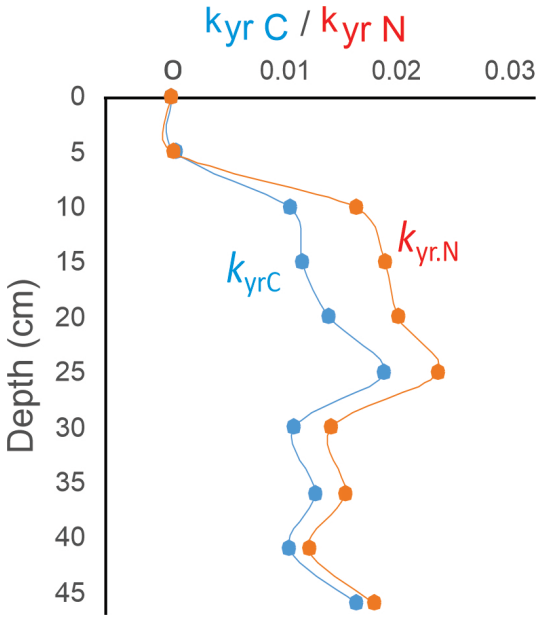

Fig. 7. Changes in k values for C and N with depth in profile, Site A2.

Table 5. Dates, %C at depth of sampling (i.e., M_t; M_0 of fresh insect guano is 47.2%), k values and regional PET ratios for geographically diverse sites (note that "PET ratio" is the ratio between mean annual rainfall and potential evapotranspiration).

Location	years BP	%C	k	Regional PET ratio and Humidity province
Deer Cave, site A2 base 46 cm deep	88	10.315	0.0174	1.33, Humid
Deer Cave, site C base 70 cm deep	119	11.333	0.0120	1.33, Humid
Aden Crater, New Mexico	3066	47.148	3.3E-06	0.19, Arid
Niah Cave, Pit, 1.2 m deep	29597	6.595	6.7E-05	1.33, Humid
Bat Cave, GCNP, Arizona, 1.3 m deep	12468	22.504	6.0E-05	0.10, Arid
Bat Cave, GCNP, Arizona, surface	5688	2.679	5.0E-04	0.10, Arid
Potoo Hole, S. Jamaica, 85 cm deep	2102	6.599	9.7E-04	0.52, Semi-arid
Drum Cave, S. Jamaica	12048	7.206	1.6E-04	0.52, Semi-arid
Fowl House Cave, N. Jamaica	20434	16.388	5.0E-05	0.88, Sub-humid

DISCUSSION

Metazoans generally lack the enzymatic capability to break down chitin directly, but prokaryotes degrade it by one of two pathways. Chitinases randomly cleave the chitin molecule into chitobiose, which is further degraded to N-acetylglucosamine by the action of N-acetylglucosaminidases (Glavina Del Rio et al., 2010). An alternative pathway involves deacetylation by deacetylases to chitosan and then degradation to chitobiose by chitosanases (Davis & Everleigh, 1984). In either case, the penultimate decomposition product is glucosamine, a readily-soluble amino sugar which is rapidly deaminated to ammonia and fructose (Wolf et al., 1956).

Microbial chitin degradation occurs under both aerobic and anaerobic conditions, although the latter has been less studied (Beier & Bertilsson, 2013). In soil and aquatic sediments, the degradation of chitin occurs mainly close to the surface, where aerobic bacteria dominate (Sturz & Robinson, 1985). Soil bacteria able to degrade chitin include species of the genera *Flavobacterium*, *Bacillus*, *Cytophaga*, *Pseudomonas*, whilst chitin-degrading fungi include *Aspergillus*, *Mucor*, and *Mortierella* (Schlegel, 2006; Glavina Del Rio et al., 2010). As Figure 2 demonstrates, the zone of maximum microbial activity, as indicated by high temperature and acidity values, correlates with the peak of Proteobacteria, a phylum that exhibits a range of tolerance to oxic conditions (Moon et al., 2018).

Freshly deposited insectivorous bat guano consists primarily (>98%) of the finely divided chitinous exoskeletons of arthropods, together with smaller quantities of lipids and fatty acids (e.g., Sperry, 1926), and urea from the associated urine fall (e.g., Herrera et al., 2006; Lundberg & McFarlane, 2009). Insect chitin is a β-1,4-glycosidic linked homopolymer of N-acetyl-D-glucosamine. Global chitin bio-production is enormous – in excess of 10^{10} tons per year (Beier & Bertilsson, 2013; Brzezinska et al., 2014) but long term or significant accumulation is absent from most environments (Gooday, 1990) due to efficient decomposition. Arid cave environments are an

exception to this rule, commonly accumulating huge deposits of guano and preserving them over tens of thousands of years (Hutchinson, 1950; Wurster et al., 2015; McFarlane & Lundberg, 2022). In contrast, as this research demonstrates, in warm, moist environments, guano deposits can fully decompose over decadal timescales (e.g., roughly a century for complete decomposition of guanos in Deer Cave). Conversely, at Niah Great Cave, Sarawak, the external environment is essentially identical to that of Deer Cave, but better drainage and cave microclimate produce much lower water content in the guanos. Some of those guanos are preserved in excess of the radiocarbon limit (McFarlane & Lundberg, 2022). Guano decomposition under these much drier conditions, calculated from a radiocarbon-dated sequence, is equivalent to a *k* value 3 orders of magnitude lower.

As is apparent from Table 5, surface PET values correlate only loosely with guano diagenesis rates. In cases of extreme in-cave aridity, as at Aden Crater fumarole in New Mexico, 3000 year-old guano is essentially indistinguishable from freshly deposited guano. Scanning electron microscopy of the freshly deposited guano collected in Deer Cave (Fig. 8A) shows finely preserved exoskeleton fragments, with essentially unmodified insect scales and setae. In comparison, the 3000 year-old guano from Aden Crater (Fig. 8B) reveals a remarkable similarly: it retains fine details of insect exoskeletons (and a bat hair in the upper right). In contrast, the guano from the base of Deer Cave, Site C (Fig. 8C), only 119 years old, is so far decayed that no insect fragments can be identified, chitin is completely degraded, and the sample is dominated by residual gypsum crystals (showing the same interesting "open book" morphology remarked upon by Lundberg & McFarlane, 2021).

The implication is that regional surface climate (PET) is not so significant as very local cave microclimate. Even relative humidity measured in the cave passage is not very useful because it does not tell us directly about moisture conditions in the guano itself (which relate to drainage conditions, air flow, temperature, etc.). Although Deer Cave is generally very moist, a relatively dry, high-level passage within a few hundred meters of our 88 year-old profile, has lenses of well-preserved guano 2150 ± 30 radiocarbon years in age (McFarlane et al., 2020).

It should be noted that these decomposition rates are averaged over the age of the deposit; examination of the site A guano sequence demonstrates that decomposition rates are significantly faster early in the life of the deposit (Fig. 7), and of course would be expected to change if the moisture regime varies with time.

Although regional climatic conditions obviously have some impact on cave conditions, cave environments are often very different from the surface environments and thus *k* values vary by almost three orders of magnitude and may not correlate with the regional (surface) PET ratios. Drum Cave, Jamaica is dry and dusty; Potoo Hole which is poorly ventilated and moist, with standing water, lies only a few hundred meters away. Both caves are in the arid Portland Ridge of southern Jamaica which experiences a PET ratio of 0.52, but their dry versus moist guanos differ in decomposition rate by a factor of 6.

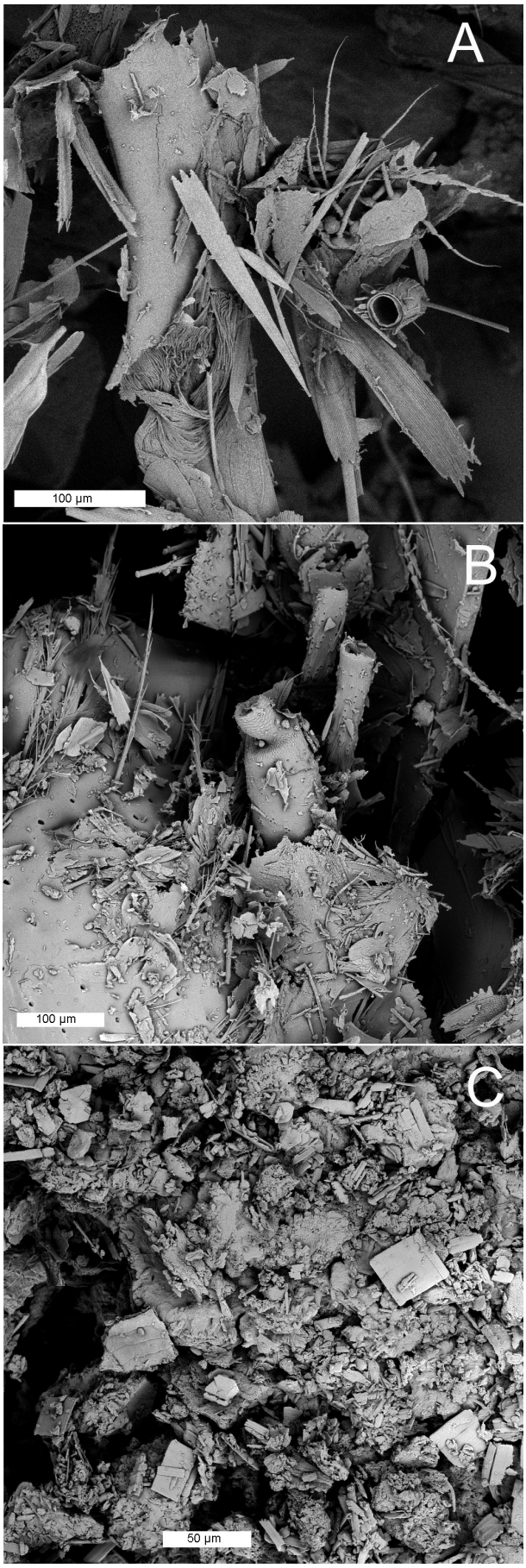

Fig. 8. Comparative states of decomposition of guanos. A. Deer Cave Site A, fresh guano. B. Aden Crater, 3000 years old. C. Deer Cave base of site C, 119 years old.

In contrast to cave guanos, the regional climatic conditions are significant for rates of soil degradation: for example, in warm, wet, tropical evergreen forest soils of Thailand Thaiutsa and Granger (2024) report a *k* of 2.28, with complete mineralization within 1.8 years. In hot, dry desert scrub soils of northwest Mexico Ariaga & Maya (2007) report *k* values from 0.0027 up to 0.0201 varying with soil moisture conditions. Values of *k* = 0.032 for cool but wet arctic soils, are given by Gholz et al. (2000). Cave guano *k* values (Table 5) range from 0.01 to 3 x 10^{-6}; Deer Cave wet guano, at a *k* value of 0.01, is at least two orders of magnitude less than tropical rain forest soil reported by Thaiutsa & Granger (2024), and are in the general range of wet arctic soils. Dry cave guanos have *k* values that are many orders of magnitude lower than the slowest decomposing soils.

Chitin survival

The implication of using *k* values is that the Eq. 1 can be modified such that time can be calculated for survival of chitin to different levels (10%, 50%, etc.)

$$t = -\frac{ln\left(\frac{M_t}{M_0}\right)}{k} \qquad \text{Eq. 2}$$

Figure 9 shows the graphical results of the calculations of age to survival of chitin for the guanos studied (i.e., the guanos in Table 5). Our aerobic decomposition rate of surface guano was measured at 0.02% per day of the available energy content. This rate obviously applies only to the couple of centimeters of surface bioturbated guano. Anaerobic decomposition is significantly lower, as reflected in the *k* values and calculations of chitin survival (Fig. 9).

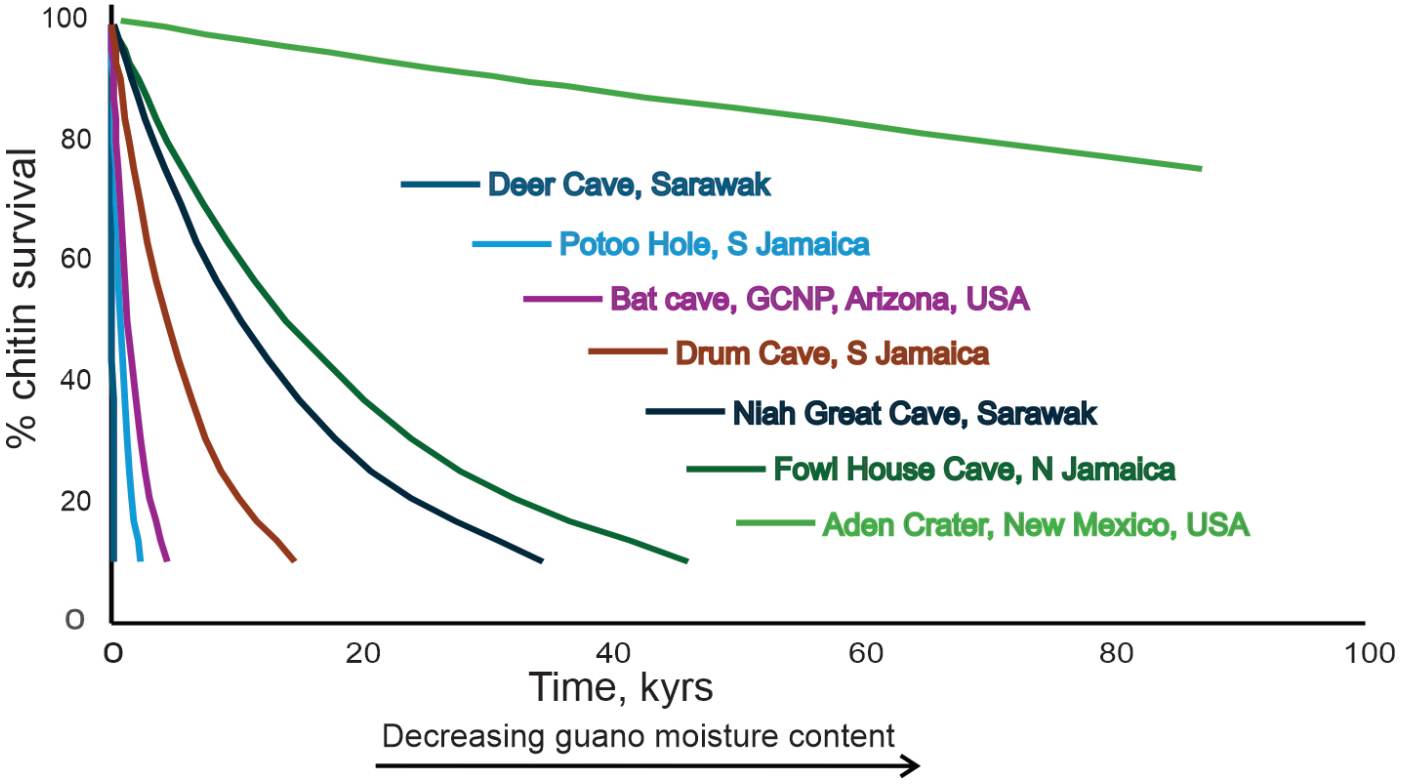

Fig. 9. Time required for degradation of chitin for the studied sites, the legend showing the names placed in decreasing order of *k* values.

The key conclusion is that under near ideal conditions, such as we see in the desert cave of Aden Crater, the potential survival of paleoclimatically useful chitin is of the order of 600-700 thousand years. Several caves are known with guanos that survive beyond the radiocarbon limit, including Niah Cave, Borneo (McFarlane & Lundberg, 2022; potentially of the order of 100,000 years) and Slaughter Canyon Cave, New Mexico (Lundberg & McFarlane, 2007; >200,000 years). The fact that no older guanos have yet been reported probably reflects the likely life span of the caves.

The determination of *k*-values in a cave guano deposit provides a potential tool for age approximations in very old deposits. If *k* is determined for a radiocarbon-datable portion of a deposit, an approximate age for guano layers beyond the radiocarbon limit can be found by extrapolation of the decomposition curve (Eq. 2).

The *k* values also have implications for potential rates of guano-mediated limestone dissolution (Lundberg & McFarlane, 2012) – the higher *k* values producing the more aggressive solvents.

CONCLUSIONS

The research reported here is the first to quantitatively address the processes of insectivorous guano degradation in the context of rates of diagenesis, and to provide empirical data on rates of change. The results demonstrate that the overwhelming control on potential preservation is guano moisture content, more than age, temperature, or depth of accumulation.

It is also the first publication of respirometry measurements in insectivorous bat guano, and of applying the concept of *k* values from soil science decomposition literature to guano diagenesis.

The resultant estimates of typical "half-lives" of insectivorous guano offer a tool to paleoenvironmental researchers hoping to use guano sequences older than the limit of carbon dating.

In summary, the main findings are:

- Bomb radiocarbon dating provides an appropriate technique for dating young guano sequences that are unsuitable for Pb-210 or Cs-137 dating;
- Energy content of fresh guano is 11.92 KJ/g;
- Aerobic respiration of fresh guano is 2.53 g CO_2/day/m^2;
- Aerobic decomposition rate is 0.02% per day of the available energy content;
- In tropical, wet guano, maximum acidity, temperature, and *k* values occur at depths of ~10-30 cm;
- Guano moisture level is the most significant control on *k*;
- Guano *k* values can have an enormous range – from 0.01 in wet tropical caves, down to 3 x 10^{-6} in extremely dry caves;
- SEM studies demonstrate that 3000-year old guano in extremely dry conditions is essentially unaltered;
- Chitin survival under favorable conditions can thus be extrapolated to timescales of 10^5 years.

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