CHAPTER 9

Making a coprolite: a pilot experimental study to determine the short-term alterations to excrement

Eleanor Joan Green [University of York and Natural History Museum, London]

> *"The laboratory assistant was then given instructions… to watch, and, if he should be fortunate enough actually to take a dog* in flagrante delicto*, to procure a sample with precise details."* [Brown et al. 1922, 1167]

Abstract: Faeces can be preserved in the archaeological record and the analysis of these specimens presents a rare opportunity to investigate a very short window of time in the past. Archaeological coprolites, as preserved faeces are known, provide a wealth of information pertaining to a depositor. Faeces can persist through time via many different preservation mechanisms but at present, the conditions and even the time required to transform a stool into a coprolite remain elusive. It is thought that mechanisms resulting in faeces preservation must happen relatively quickly, so it is key to understand the short-term alterations to excrement after its deposition. In this exploratory study, a modern dog stool was kept in cool and dark conditions for 20 days to observe the early stages of preservation by desiccation. The changes to the faeces were recorded using both metrics and photography. These data show that the faeces underwent rapid change during the first 6 days following deposition, including shrinkage and exterior darkening. The pace of subsequent changes was slower with a stasis reached at day 15. Over the course of the experiment, the faeces lost ~12 g in weight (~57%) and ~19 ml in estimated volume. This study provides insight into the short-term changes faeces undergo that might ultimately lead to the formation of a desiccated coprolite. Importantly, this study highlights the need for more extensive and systematic investigations – particularly relating to how these changes impact the biomolecular content of faeces.

Introduction

It has been recognised for over 200 years that faeces can be preserved over extended periods – from hundreds to millions of years (Hunt et al., 2012). Studies examining faeces have a surprisingly long history, despite the unsavoury nature of the study material (e.g., Brown et al., 1922). Indeed, in clinical settings, stool samples are often examined to detect ill health (Bennett and Tarr, 2009), such as the identification of SARS-CoV-2 in stool samples (e.g., Xiao et al., 2020). Archaeological investigations of ancient faeces are far less commonplace because faeces only preserve in specific environmental or archaeological contexts. Where these archaeological samples are available, a wealth of information can be determined concerning, amongst other things, the depositor's diet (Shillito et al. 2020). To investigate how robust the identification of dietary foodstuffs is from coprolites, several experimental studies on modern faeces have been undertaken. These experiments have largely focused on human and/or animal participants consuming specified and recorded foods, and the resulting faeces being searched for specific plant remains (Calder, 1977), pollens (Dean, 2006; Kelso and Solomon, 2006) and bones (Jones, 1986 and 1990). Using the same approaches, combined with microscopy, an attempt has been made to create reference collections of ingested microfaunal remains (Crandall and Stahl, 1995). These studies show that whilst many tissues types can survive ingestion and digestion (particularly; keratinous, siliceous, or cellulose-rich materials, pollens and bone tissue) the taphonomic effect of these processes is great, and material recovered from faeces does not reflect the full assortment or proportion of dietary inclusions.

Faeces can be preserved via five different mechanisms – fossilisation, partial mineralisation, carbonisation, freezing and desiccation. Some of the conditions required for these mechanisms to unfold are more clear than others (i.e., mechanisms of fossilisation are well understood (Piepenbrink, 1989), and freezing is an obvious and rapid change in sample conditions). However, fossilised coprolites are not archaeological samples, and frozen faeces are very rarely found in the archaeological record.[1] More commonly recovered are samples which have undergone partial mineralisation, carbonisation and desiccation, but the details surrounding the composition of the faeces, the required environmental conditions, and the timescale for their subsequent transition to coprolites are unclear.

Hollocher and Hollocher (2012) have postulated that the mechanisms which result in faeces being preserved must happen very quickly – perhaps even within days – such that the preservation processes outpace those which lead to decay. Importantly, there is no understanding of how the different mechanisms of decay, which inevitably impact the biomolecular composition of coprolites, alter the organics preserved within faeces; this is of particular interest to my own work as a biomolecular archaeologist with an interest in preserved faeces. Gaining a better understanding of the conditions required for faeces to preserve in the archaeological record could offer insight into the short-term depositional environment of a coprolite. Hence, I devised a pilot experimental study to determine the macroscopic, short-term alterations to faecal deposits. As many of the coprolites which have previously been recovered are desiccated samples found in caves (e.g., Borry et al., 2020; Cano et al., 2014; Hagan et al., 2020; Karpinski et al., 2017; Luciani et al., 2006; Santiago-Rodriguez et al., 2013; Tito et al., 2012, 2008; Wibowo et al., 2021) and these are the most straight-forward conditions to simulate, my attempt focussed on making a desiccated coprolite. Furthermore, many recovered coprolites originate from dogs (e.g., Rampelli et al., 2021; Witt et al., 2021). Conveniently, I have a dog, Malcolm, who reliably produces potential sample material each day. Here, I have simulated the production of a single desiccated dog coprolite and discuss the value of such approaches for informing the bioarchaeological analysis of coprolites.

Materials and methods

The faeces subject to testing was provided by Malcolm who is a ~12-year-old mongrel (suspected Jack Russell – Whippet crossbreed) (Fig. 1a). Malcolm's diet primarily consists of commercial dog kibble (Royal Canin® Gastrointestinal High Fibre), providing 33% carbohydrate, 23% protein, 21% fibre and 16% fat (Fig. 1b). The stool was produced on 28 May 2023 at approximately 8.00 am.

[1] As a point of interest, even the experimental robustness of knives fashioned from frozen human faeces has been comprehensively tested (Eren et al., 2019). This practice was allegedly witnessed within an Inuit community in the mid 20th century. The story has been recounted widely in ethnographic accounts (Davis, 1998) and popular media. Knives made from frozen faeces do not work (Eren et al. 2019).

a)

b)

KEY VALUES	Per 1000 kcal	Per 100g as fed
Protein	72.62g	23.00g
Fat content	50.52g	16.00g
Carbohydrate (NFE)	104.20g	33.00g
Crude fibre	35.05g	11.10g
Crude ash	23.37g	7.40g
Dietary fibre	65.68g	20.80g
Calcium	3.47g	1.10g
Phosphorus	2.53g	0.80g
Potassium	2.53g	0.80g
Sodium	1.42g	0.45g
Chloride	3.63g	1.15g
Magnesium	0.19g	0.06g
Copper	4.74mg	1.50mg
Zinc	53.68mg	17.00mg
Taurine	0.54g	0.17g
Vitamin A	5683.61 IU	1800.00 IU
Vitamin E	135.78 IU	43.00 IU
Omega 6	10.29g	3.26g
Omega 3	2.40g	0.76g
EPA + DHA	0.98g	0.31g

Metabolisable energy* 316.7kcal/100g as fed

**Calculated according to NRC2006.*

Figure 1. The depositor and a breakdown of his main nutrition. a) Malcolm on a walk during the lockdown of 2020. **b)** The nutritional information for Gastrointestinal High Fibre dry food as provided by Royal Canin®.

For hygiene purposes and the sake of easy manoeuvrability, a base was created for the stool to sit upon throughout the course of the experiment. The base consisted of a sheet of thick clear plastic backed with white paper including a scale bar and the weight of the base (~1 g) was deducted from the recorded combined weight to give the weight of the faeces. The faeces was moved from its original place of deposition in a plastic bag and set upon the base. The base and faeces were then moved to a brick outhouse (which is shaded by surrounding buildings) and were left undisturbed for 20 days.

Each day between 08:00 and 09:00 the temperature of the outhouse was recorded as well as the weight of the faeces. A photographic record was made throughout the experiment to chart the changes in the appearance of the faeces over the course of the experiment. By imposing a digital scale onto the photographs the length and width of the faeces on each day was calculated. Whilst not a perfect metric due to the variation in width along the length of the faeces, the volume of the faeces was estimated each day using the equation to calculate the volume of a cylinder.

To compare changes with the environmental record, the minimum and maximum daily temperature and humidity (recorded between 12.00 and 16.00) were recorded. On Day 14, the temperature of the outhouse was recorded every 2 hours for a 24-hour period; this was taken to represent the typical variation in the outhouse temperature.

Results and discussion

On Day 1 the stool had a smooth outer surface and was a consistent medium-dark shade of reddish brown (Fig. 2), the stool weighed 21 g and had an approximate volume of 33 ml (~6.5 cm in length and ~2.4 cm in width). By the end of the 20 days, the surface of the sample was slightly cracked in some places and had a variable colouration ranging from a dark shade of orangey brown to shades of very dark brown to black (Fig. 2). At the end of the experiment the sample weighed 9 g and had an approximate volume of 14 ml (~5.4 cm in length and ~1.8 cm in width). The outer surface of the stool was hard and brittle, although the sample was robust and could be quite forcibly handled without causing morphological damage. Seemingly, a coprolite had formed, providing support for the theory that mechanisms of preservation must occur rapidly.

The only macroscopically identifiable inclusions on the surface of the faeces were small white hairs (Fig. 2). Malcolm was shedding his coat from the end of May and throughout June 2023. It is likely he had been advancing this process by licking (due to the white colour of the hair, presumably his legs) and had ingested some of it.

A noticeable change in the visual appearance of the faeces was the rapid darkening of the exterior colour within the first week of deposition (Fig. 2). This is likely to be a result of the Maillard reaction. Poinar et al. (1998) identified products of the Maillard reaction – amino acids reacting with reducing carbohydrates – in coprolites and so this reaction is assumed to play a role in faecal preservation. The Maillard reaction is the same as that which occurs when food is cooked, but unlike during cooking, this is not catalysed by high temperatures during coprolite formation. The extensive blackening of the stool

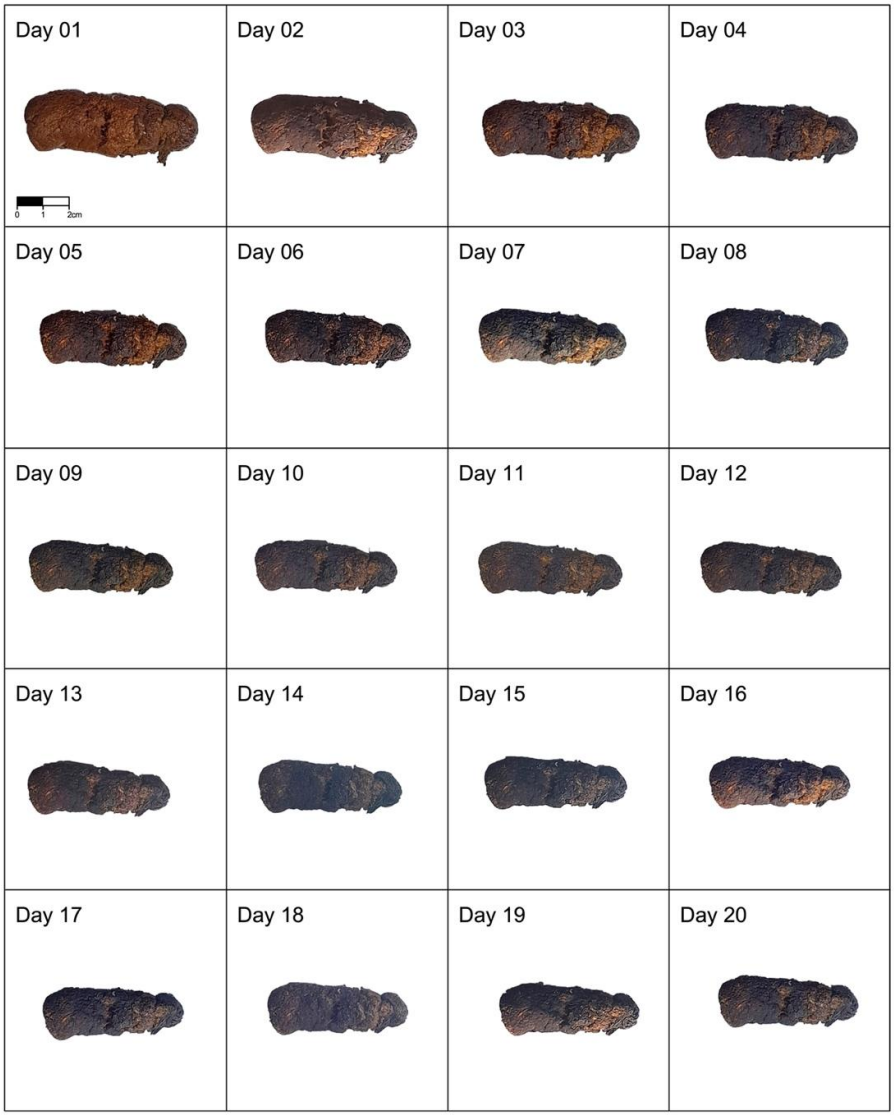

Figure 2. The morphological changes to the faeces over a 20-day period

resembles charring, which is something which should be considered when examining archaeological coprolites. For example, coprolites with blackened surfaces are often assumed to have been charred; heat has a detrimental effect on DNA preservation, so these samples would not be selected for a palaeogenomics study. However, the rapid darkening observed in this study suggests that blackening could occur in the absence of charring and that DNA and other biomolecules may be preserved in blackened coprolites.

As the colour change observed in this study occurred across the entire surface of the coprolite whereas it is plausible that the effects of charring could be localised, in the future, recording the pattern of colouration across a coprolite's surface combined with analysis of recovered DNA, may provide a way to distinguish charring from the Maillard reaction.

In total the faeces lost 12 g in weight and 19 ml of estimated volume (Fig. 3a). The relationship between the cumulative loss of weight and estimated volume was positively correlated ($R^2 = 0.9$) (Fig. 3b), which also reflects that the percentage loss for both weight and estimated volume was both ~57% (Appendix 1). Interestingly, the weight of the stool changed very little in the first 24 hours, but the length, width and volume estimation show there was shrinkage of the sample during this period (Figs. 2 and 3, Appendix 1). After Day 10, the weight and volume of the faeces seemed to stabilise, but a further gram of weight was lost on Day 15 (Fig. 3).

The changes in weight were attributed to a loss of water from the stool. Upon deposition, the water content of faeces has been found to be between 60 – 85% dependent on diet,

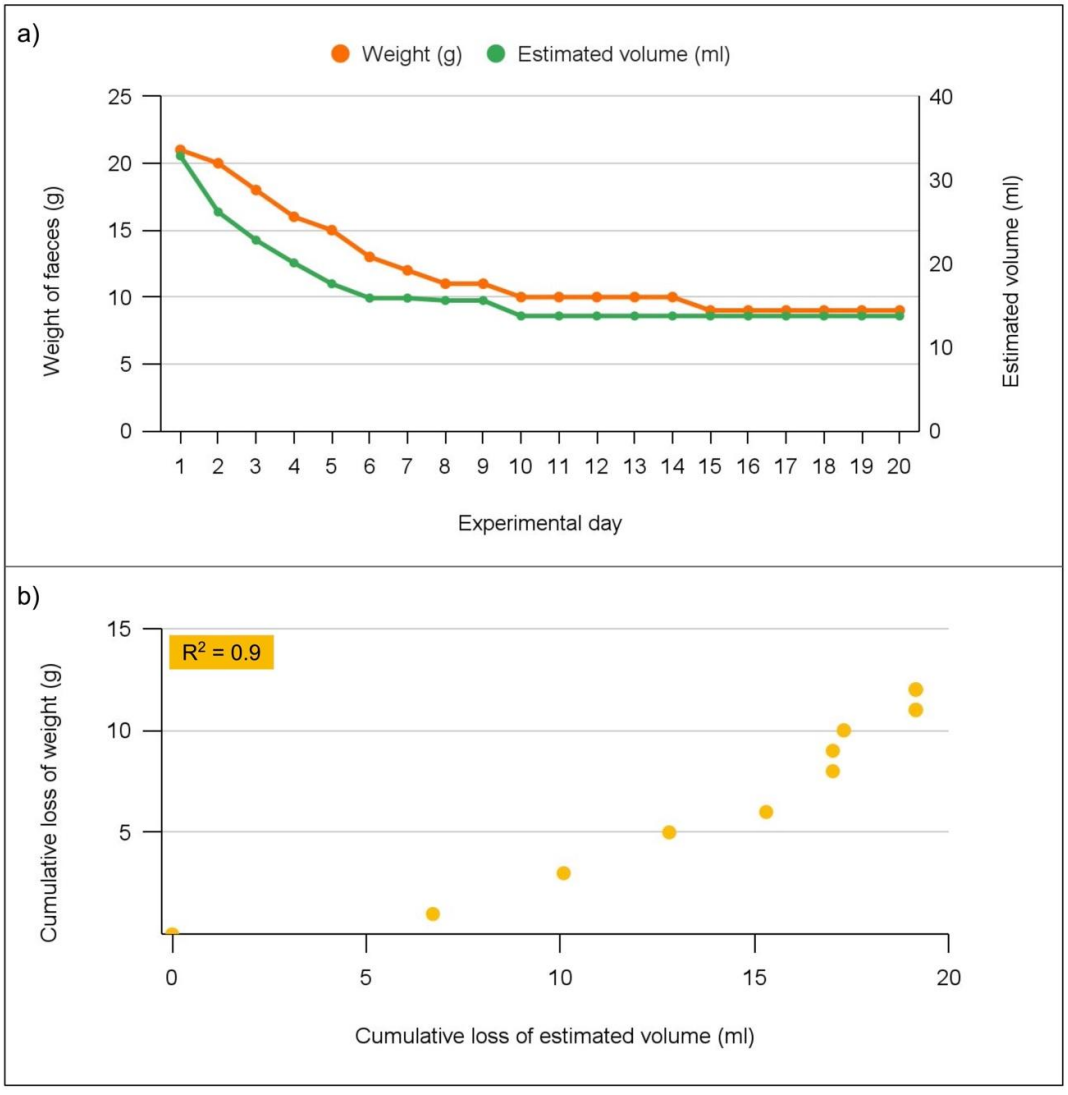

Figure 3. The metric changes to the stool which were observed over a 20-day period. **a)** The loss of weight (orange) and estimated volume (green). **b)** The cumulative loss of weight plotted against the cumulative loss of estimated volume (yellow). Raw data shown in Appendix 1.

individual and time of day (Hill et al., 2011; Nery et al., 2010). Here, the percentage change in weight was 57%. Consistent with previous estimations for the water content of faeces, it is likely that the weight of the sample would continue to slowly decrease until it was completely desiccated.

The temperature of the outhouse stayed fairly constant throughout the 20 days despite the daily exterior temperature fluctuations (Fig. 4). From 08.00 on Day 14 the temperature of the outhouse was recorded every 2 hours for a 24-hour period. Coincidently, Day 14 was the experimental day with the largest difference between high (27°C) and low (8°C) daily temperatures (Appendix 2), even so, the outhouse temperature varied by just 1°C over the period between Day 14 at 08.00 and Day 15 at 08.00 (Fig. 4a). The consistent outhouse temperature demonstrates the environmental stability of the outhouse. Furthermore, as the exterior temperature of Day 14 was the most variable, this suggests that the outhouse temperature was stable throughout the experiment. It is likely that the northwest orientation of the outhouse ensured some environmental stability. The humidity recorded reflects external conditions and varied between 30 and 74% over the course of the experiment (Fig. 4b). The humidity of the outhouse was not measured, but the temperature record suggests the conditions were fairly stable.

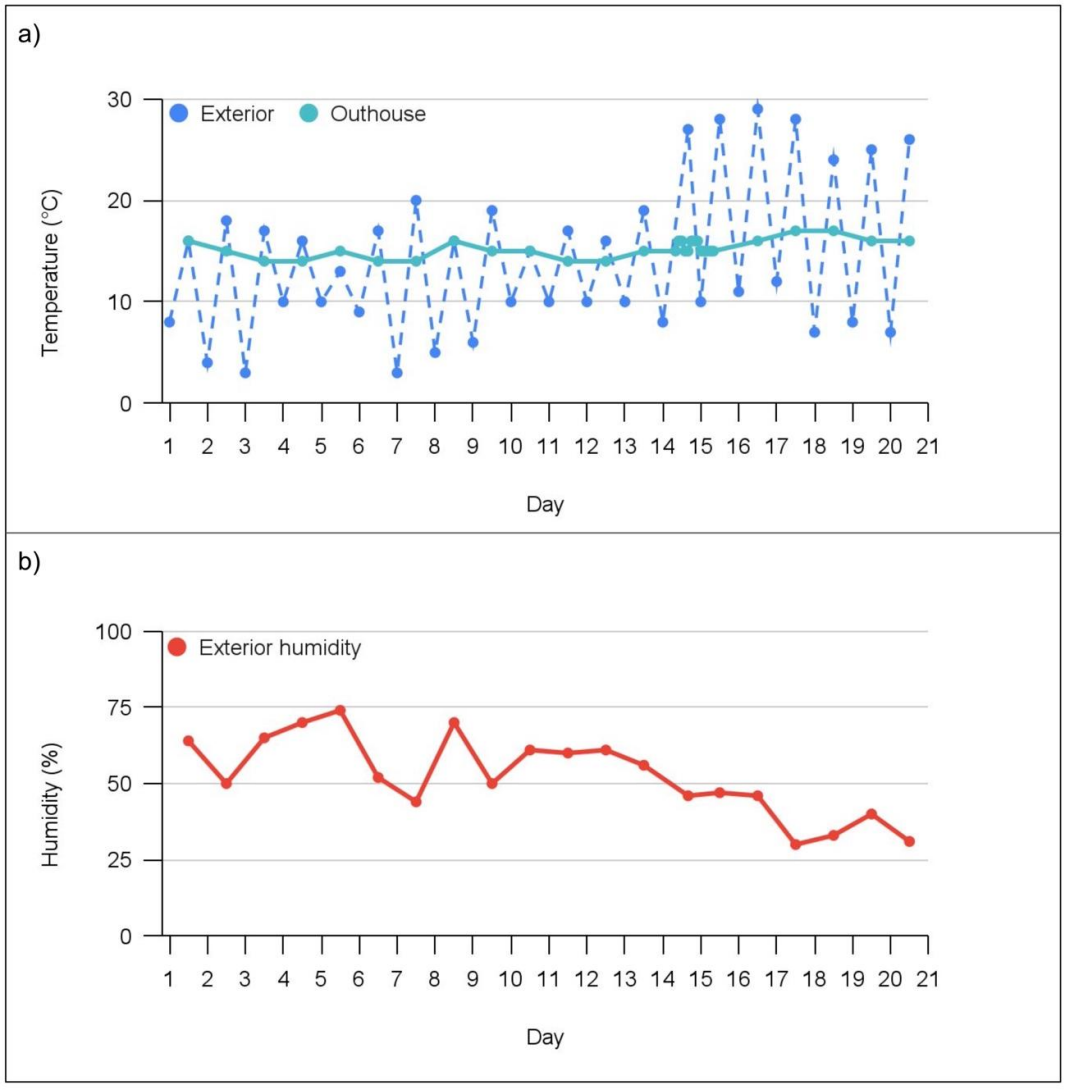

Figure 4 The daily environmental conditions during the experimental period in York. Raw data shown in Appendix 2.

a) The daily minimum and maximum temperature in York is shown by the dashed dark blue line. The temperature recorded in the outhouse between 08.00 and 09.00 is shown by the solid light blue line. Beginning on Day 14 at 08.00 the temperature was recorded every 2 hours for a 24-hour period. **b)** The daily variation in external humidity recorded between 12.00 and 6.00 is shown in red. Raw data are shown in Appendix 2, the environmental data were gathered from the Topcliffe Royal Air Force Base Weather Station which is 20.9 miles away from York and 14 m higher (compared to sea level) than York. This data was made available online via CustomWeather {https://customweather.com/}.

Experimental caveats

Before this experiment, Malcolm was not subject to a change in his regular diet (the components of which can be seen in Fig. 1b). He was not fed a "palaeodiet" or so-called marker foodstuffs to track his bowel movements like many other experimental participants before him (Calder, 1977; Crandall and Stahl, 1995; Eren et al., 2019; Jones, 1986). Therefore, there was no attempt to produce a stool representative of an archaeological dog's faeces and diet inevitably affects the likelihood of faecal preservation (Chin, 2002; Hollocher and Hollocher, 2012). It is very difficult specifically to determine the macronutrients of past dog diets, especially as it is not always clear how much dogs were actively being fed, or scavenging for food, or a mixture of the two.

Archaeological dog coprolites often contain lots of bone fragments, and for coprolites found in waterlogged sites the mineral component of bone (calcium and phosphate) contributes to the mineralisation process (Hollocher and Hollocher, 2012). It is unlikely that the presence of these minerals affects desiccation, nevertheless, Malcolm's diet included calcium (1.1%) and phosphorous (0.8%) (Fig. 1b). The majority of Malcolm's calories come from carbohydrates (33%). Ancient dogs have been shown to have an increased amylase gene copy number compared to wolves (Ollivier et al., 2016). Amylase (specifically Amy2B) is an enzyme involved in the digestion of starches and carbohydrates, therefore this increase in copy number was concluded to be a result of dog diets becoming more synchronous with the diets of farming humans (Ollivier et al., 2016). This is to say that whilst Malcolm's diet may seem a far cry from a Viking dog's diet, perhaps the differences are not as large as initially expected.

Assuming that the rate of desiccation is dependent on depositional environmental conditions, the base created for the stool to sit upon must be considered. The plastic base ensured the sample could be easily and hygienically weighed every day and the photographs taken over the course of this experiment could be scaled appropriately. However, the utilisation of this base meant that the stool did not desiccate on a natural surface. The impermeable plastic base may have resulted in the retention of water. Coprolites which have desiccated in a natural environment are in contact with the ground which facilitates the sequestering of water from the stool.

Moreover, the placement of the stool on top of the plastic base meant that the stool was not exposed to the usual colonisation of environmental species, including coprophilous insects, bacteria and fungi (Rowland, 1975). The assessment of the source of different bacterial profiles from archaeological coprolites has shown that the microbial community can quickly be transformed by colonising bacteria (Witt et al., 2021; Yarlagadda et al., 2022). These microbes will inevitably change the course of faecal preservation – a factor which is not accounted for in this study. It appears that the conditions in the outhouse did protect the stool somewhat from environmental contaminants, as there was no indication of fungal colonisation over the 20 days. Fungal colonisation does occur commonly on undisturbed faeces (Pouliot, 2018). However, the lack of observable growth may also relate to the time of year and the environmental conditions – fungi thrive in moist environments. The outhouse was chosen as it maintained a fairly constant temperature despite the variety in the daily temperature fluctuations and humidity (Fig. 4; Appendix 2).

Recommendations for creating experimental coprolites in the future

Even with the caveats discussed above, this experiment is a rudimentary first step towards understanding the short-term, post-depositional changes to faecal material. More work needs to be carried out before these results can be considered archaeologically informative.

If this experiment was to be repeated, four improvements and extensions to the study are suggested. The first improvement is to increase the sample size. The recording of more stools in the same systematic way would enable an assessment of the effect of stool variation in similar environmental conditions. This should ultimately be expanded to include faecal samples from additional dogs with differing diets. An improved experimental design would include a number of dog diets of varying compositions which would be fed to dogs of differing sizes and breeds. Some of these diets could be based on what we know from archaeological samples. This would better inform on whether the diet, the depositor, the depositional environment or a combination of all three are important factors for faecal preservation. Due to the extensive scale of such an experiment, perhaps this could be an interesting citizen science project.

The second suggested improvement concerns recording technology. Taking photographs using a more powerful lens would record macroscopic differences more accurately and the ability to record temperature and humidity at regular intervals would provide a more accurate tracking of the environmental conditions. To improve the accuracy of tracking water loss, a scale should be used which has the precision to measure milligrams. The rate at which water is lost from the sample is also likely to be affected by the stool size – a smaller stool will have a greater surface area to volume ratio compared to a large stool and therefore it is assumed water loss will be more rapid in smaller stools. This could be investigated if the first improvement was implemented.

Thirdly, the experiment presented here has investigated only preservation by desiccation, but there are four other mechanisms of faecal preservation, three of which are relevant to the archaeological record – mineralisation, carbonisation and freezing. Desiccation was selected for this study as the required conditions were relatively simple to simulate. Arguably the formation of mineralised coprolites is far more complex than the desiccation of a faecal sample, as multiple factors have an impact on the preservation including dietary content, groundwater minerals, and bacteria-mediated mineralisation (Hollocher et al., 2010). Most of the coprolites which have been recovered from archaeological sites in temperate regions are formed in this way. These conditions will be very difficult to recreate (even in a laboratory setting), especially in a manner that facilitates the regular monitoring of changes to a sample. If the construction of an environment with such conditions can be conceived of, the investigation of the mechanisms involved in the mineralisation of faeces would be of significant interest.

Finally, and crucially, tracking the decay of biomolecules through different phases of preservation would be particularly useful information in obtaining and interpreting data from archaeological substrates. Moreover, this would further the understanding of biomolecular preservation within these substrates, allowing for a better appreciation of the taphonomic processes which faeces undergo during the transition to a coprolite. Does the biomolecular decay reach a stasis as macroscopic changes do? Investigating this question further would be the most beneficial extension of the experiment for future bioarchaeological investigations of coprolites. Whilst the experiment reported here is a rudimentary first step, it has provided sufficient information to indicate that additional experiments incorporating the suggestions made above would be hugely beneficial for selecting promising archaeological samples.

Conclusions

The short-term changes to dog faeces that occur in an undisturbed, dark cool environment have been carefully recorded in this study. Although desiccated coprolites are hundreds, sometimes thousands of years old, this experiment offers insight into the initial period of faecal desiccation. The recording of biomolecule preservation alongside the physical changes occurring during the desiccation of multiple dog stools produced by different individuals with different diets over a longer period will be an informative exercise. If experimental conditions can be achieved which will allow the formation of mineralised coprolites, this would be of great value to coprolite studies from waterlogged sediments.

Appendix 1a, 1b

Day	Total weight (g)	Weight of faeces (g)	Loss (g)	Cumulative loss of weight (g)
1	22	21	0	0
2	21	20	1	1
3	19	18	2	3
4	17	16	2	5
5	16	15	1	6
6	14	13	2	8
7	13	12	1	9
8	12	11	1	10
9	12	11	0	10
10	11	10	1	11
11	11	10	0	11
12	11	10	0	11
13	11	10	0	11
14	11	10	0	11
15	10	9	1	12
16	10	9	0	12
17	10	9	0	12
18	10	9	0	12
19	10	9	0	12
20	10	9	0	12

Day	Approx length (cm)	Approx width (cm)	Approx radius (cm)	Estimated volume (ml)	Estimated loss (ml)	Cumulative ~ loss of volume (ml)
1	6.7	2.5	1.25	33	0	0
2	6.3	2.3	1.15	26	7	7
3	6.0	2.2	1.10	23	3	10
4	5.8	2.1	1.05	20	3	13
5	5.6	2.0	1.00	18	2	15
6	5.6	1.9	0.95	16	2	17
7	5.6	1.9	0.95	16	0	17
8	5.5	1.9	0.95	16	0	17
9	5.5	1.9	0.95	16	0	17
10	5.4	1.8	0.90	14	2	19
11	5.4	1.8	0.90	14	0	19
12	5.4	1.8	0.90	14	0	19
13	5.4	1.8	0.90	14	0	19
14	5.4	1.8	0.90	14	0	19
15	5.4	1.8	0.90	14	0	19
16	5.4	1.8	0.90	14	0	19
17	5.4	1.8	0.90	14	0	19
18	5.4	1.8	0.90	14	0	19
19	5.4	1.8	0.90	14	0	19
20	5.4	1.8	0.90	14	0	19

Appendix 2

Date	Exterior Temperature		Outhouse temperature		Humidity (%)
	Low	High	°C	Time	12 - 6 pm
28/05/2023	8	16	16	~8.30 am	64
29/05/2023	4	18	15	~8.30 am	50
30/05/2023	3	17	14	~8.30 am	65
31/05/2023	10	16	14	~8.30 am	70
01/06/2023	10	13	15	~8.30 am	74
02/06/2023	9	17	14	~8.30 am	52
03/06/2023	3	20	14	~8.30 am	44
04/06/2023	5	16	16	~8.30 am	70
05/06/2023	6	19	15	~8.30 am	50
06/06/2023	10	15	15	~8.30 am	61
07/06/2023	10	17	14	~8.30 am	60
08/06/2023	10	16	14	~8.30 am	61
09/06/2023	10	19	15	~8.30 am	56
10/06/2023	8	27	15	8:00 am	46
			16	10:00 am	
			16	12:00 pm	
			15	2:00 pm	
			15	4:00 pm	
			16	6:00 pm	
			16	8:00 pm	
			16	10:00 pm	
11/06/2023	10	28	15	12:00 am	47
			15	2:00 am	
			15	4:00 am	
			15	6:00 am	
12/06/2023	11	29	16	~8.30 am	46
13/06/2023	12	28	17	~8.30 am	30
14/06/2023	7	24	17	~8.30 am	33
15/06/2023	8	25	16	~8.30 am	40
16/06/2023	7	26	16	~8.30 am	31

References

Bennett, W.E., Jr and Tarr, P.I. (2009). Enteric infections and diagnostic testing. *Current Opinion in Gastroenterology*, 25(1), 1–7.

Borry, M. et al. (2020). CoproID predicts the source of coprolites and paleofeces using microbiome composition and host DNA content. *PeerJ*, 8, e9001.

Brown, H.C., Stammers, G.E.F. and Balfour, A., 1922. Observations on canine faeces on London pavements: Bacteriological, Helminthological, and Protozoological. *The Lancet*, 200(5179), 1165-1167.

Calder, A.M. (1977). Survival properties of organic residues through the human digestive tract. *Journal of Archaeological Science*, 4(2), 141-151.

Cano, R.J. et al. (2014). Paleomicrobiology: revealing fecal microbiomes of ancient indigenous cultures. *PLoS One*, 9(9), e106833.

Chin, K. (2002). Analyses of coprolites produced by carnivorous vertebrates. *Paleontological Society Papers*, 8, 43–50.

Crandall, B.D. and Stahl, P.W. (1995). Human digestive effects on a micromammalian skeleton. *Journal of Archaeological Science*, 22(6), 789–797.

Davis, W. (1998). *Shadows in the Sun: Travels to Landscapes of Spirit and Desire*. Island Press.

Dean, G.W. (2006). The science of coprolite analysis: the view from Hinds cave. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 237(1), 67–79.

Eren, M.I. et al. (2019). Experimental replication shows knives manufactured from frozen human feces do not work. *Journal of Archaeological Science: Reports*, 27, 102002.

Hagan, R.W. et al. (2020). Comparison of extraction methods for recovering ancient microbial DNA from paleofeces. *American Journal of Physical Anthropology*, 171(2), 275–284.

Hill, R.C. et al. (2011). Water content of faeces is higher in the afternoon than in the morning in morning-fed dogs fed diets containing texturised vegetable protein from soya. *The British Journal of Nutrition*, 106 Suppl 1, S202–5.

Hollocher, K. and Hollocher, T.C. (2012). Early processes in the fossilization of terrestrial feces to coprolites, and microstructure preservation. In Hunt A.P. et al. (Eds.), *Vertebrate Coprolites: Bulletin 57*. New Mexico Museum of Natural History and Science, pp. 93–98.

Hollocher, K.T., Hollocher, T.C. and Rigby, J.K. (2010). A phosphatic coprolite lacking diagenetic permineralization from the upper Cretaceous Hell Creek formation, northeastern Montana: importance of dietary calcium phosphate in preservation. *Palaios*, 25(1/2), 132–140.

Hunt, A.P. et al. (2012). Vertebrate coprolite studies: status and prospectus. In Hunt, A.P. et al. (Eds.),*Vertebrate Coprolites*. Albuquerque: New Mexico Museum of Natural History and Science, pp. 5–24.

Jones, A. (1986). Fish bone survival in the digestive systems of the pig, dog and man: some experiments. In. Brinkhuizen, D.C and Clason, A.T. (Eds.), *Fish and archaeology: studies in osteometry, taphonomy, seasonality and fishing methods*. BAR International Series, 294, pp. 53–61.

Jones, A. (1990). Experiments with fish bones and otoliths: implications for the reconstruction of past diet and economy. In Robinson, D.E. (Ed.), *Experimentation and Reconstruction in Environmental Archaeology*. Oxford: Oxbow Books, pp. 143–146.

Karpinski, E., Mead, J.I. and Poinar, H.N. (2017). Molecular identification of paleofeces from Bechan Cave, southeastern Utah, USA. *Quaternary*, 443, 140–146.

Kelso, G.K. and Solomon, A.M. (2006). Applying modern analogs to understand the pollen content of coprolites. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 237(1), 80–91.

Luciani, S. et al. (2006). Molecular characterization of a pre-Columbian mummy and in situ coprolite. *American Journal of Physical Anthropology*, 129(4), 620–629.

Nery, J. et al. (2010). Influence of dietary protein content and source on fecal quality, electrolyte concentrations, and osmolarity, and digestibility in dogs differing in body size. *Journal of Animal Science*, 88(1), 159–169.

Ollivier, M. et al. (2016). Amy2B copy number variation reveals starch diet adaptations in ancient European dogs. *Royal Society Open Science*, 3(11), 160449.

Piepenbrink, H. (1989). Examples of chemical changes during fossilisation. *Applied Geochemistry*, 4(3), 273–280.

Poinar, H.N. et al. (1998). Molecular coproscopy: dung and diet of the extinct ground sloth *Nothrotheriops shastensis*. *Science*, 281(5375), 402–406.

Pouliot, A. (2018). *Allure of Fungi*. Csiro Publishing.

Rampelli, S. et al. (2021). The gut microbiome buffers dietary adaptation in Bronze Age domesticated dogs. *iScience*, 24(8), 102816.

Rowland, J. (1975). Some ecological aspects of animal excrement. *The American Biology Teacher*, 37(3), 154–157.

Santiago-Rodriguez, T.M. et al. (2013). Microbial communities in pre-columbian coprolites. *PloS One*, 8(6), e65191.

Shillito, L.-M. et al. (2020). The what, how and why of archaeological coprolite analysis. *Earth-Science Reviews*, 207, 103196.

Tito, R.Y. et al. (2008). Phylotyping and functional analysis of two ancient human microbiomes. *PloS One*, 3(11), e3703.

Tito, R.Y. et al. (2012). Insights from characterizing extinct human gut microbiomes. *PloS One*, 7(12), e51146.

Wibowo, M.C. et al. (2021). Reconstruction of ancient microbial genomes from the human gut. *Nature*, 594(7862), 234-239.

Witt, K.E. et al. (2021). Integrative analysis of DNA, macroscopic remains and stable isotopes of dog coprolites to reconstruct community diet. *Scientific Reports*, 11(1), 3113.

Xiao, F. et al. (2020). Evidence for gastrointestinal infection of SARS-CoV-2. *Gastroenterology*, 158(6), 1831–1833.e3.

Yarlagadda, K. et al. (2022). Geographically diverse canid sampling provides novel insights into pre-industrial microbiomes. *Proceedings of the Royal Society B: Biological Sciences*, 289(1974), 20220052.

E-mail: eleanor.green@york.ac.uk

Last updated: 24.x.2024