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What goes in does not always come out: The impact of the ruminant digestive system of sheep on plant material, and its importance for the interpretation of dung-derived archaeobotanical assemblages

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Abstract
On archaeological sites where livestock dung was a major fuel source, plant material that survives digestion intact may well be preserved in the remnants of dung-fuelled fires. Preserved plant remains which were derived from dung relate to the diet of animals, and thus provide a way of investigating the agro-pastoral economies of the past. In order to improve our understanding of the taphonomic processes to which plant material is exposed to during digestion, we applied archaeobotanical methods to the analysis of dung from sheep fed a known diet of cereal and wild plant material. Two clear patterns emerge from these investigations. First, cereal material (grain or chaff) survives digestion poorly and was rarely found in the dung analysed. Second, large proportions of seeds of various wild species survive digestion in an identifiable form, probably due to their small size and/or protective coating. These findings are crucial for reliable interpretation of dung-derived plant material in archaeological settings.

Introduction
A primary source of information regarding the use of plants in past societies, particularly in arid and semi-arid regions, comes from the remains of crops, weeds and wild plants preserved by charring. Investigation of this material generally starts with the assumption that they reflect aspects of human plant consumption. There is, however, a growing awareness that the charred plant remains record may, in certain regions, include a substantial proportion of material derived from the burning of animal dung as a fuel source, which calls such interpretations into question (Bottema 1984; Miller and Smart 1984; Miller and Gleason 1994; Miller 1996; 1997; Charles 1998; Reddy 1998; Valamoti and Charles 2005). Indeed, the relatively low temperatures of dung-fuelled fires provide excellent conditions for charring of plant remains. Secure identification of dung-derived material opens up avenues of archaeobotanical research, including the study of animal husbandry and its associated land use practices and agro-pastoral systems (Riehl 1999; Charles and Bogaard 2005; Derreumaux 2005; Miller 2009; Charles et al. 2010).

An essential first step in any archaeobotanical investigation is the attempt to determine, as far as possible, the sources of the plant material, both in terms of on-site activity and off-site land use. This may be a relatively straightforward process when dealing with primary use deposits, such as grain storage features in a burnt building. In other contexts – especially where there is systematic sampling and large-scale flotation – charred plant material does not necessarily represent a single, transparent source. Thus, plant material routinely charred in domestic ovens and hearths may incorporate remains from multiple activities, such as crop processing, cooking and fuel use. Without identification and, where possible, separation of the difference sources that contributed to an assemblage, the interpretation of such remains is limited or even misleading.

Under certain conditions, such as those found in arid regions of Western Asia, the burning of animal dung was, and still is, a major source of fuel. Consequently, where plant material is able to survive digestion and subsequent charring in an identifiable form, it may make a significant contribution to a site's charred archaeobotanical assemblage. This provides the potential for the botanical content of dung to be used as a means to infer animal diet. As there is a delay between the consumption and excretion of plant material, information can be derived about the potentially wide range of plant habitats accessed by livestock that roam over large distances. Furthermore, plant material used as fodder, possibly out-of-season, could also be identified. Given that dung-derived plant remains are a consequence of animal consumption patterns, they must be interpreted differently to other types of plant remains (e.g. crops, weeds and collected wild plants). The presence of dung or dung-derived material has been suspected or identified at a number of early western-central Asian sites including Ali Kosh (Helbaek 1969), Malyan (Miller and Smart 1984), Selenkahiye (van Zeist and Bakker-Heeres 1985, 1988), Kom el-hisn (Moens and Wetterstrom 1988), Gonur Depe (Miller 1993), Deer Alla (Neef 1989), Abu Salabikh (Charles 1998), Tell es-Sweyhat (Miller 1997), Tell Leilan (Wetterstrom 2003) and Jeitun (Charles et al. 2010).

Preserved and intact animal dung, most typically in the form of individual pellets of ovi-caprines, are occasionally observed in archaeological deposits (Charles 1998; Karg 1998; Akeret et al. 1999; Oeggl et al. 2009; Charles et al. 2010; Linseele et al. 2010). Where this is the case, the contents of the pellets may be inspected to provide unambiguous information on animal diet. More usually, however, dung is seen as broken pellets or as amorphous lumps, recognised by its non-homogeneous texture often comprising a compacted mass of small fragments of grass leaf and stem. Such disarticulated dung may be found adhering to seeds, but more typically dung fragments are found in mixed deposits with seeds and other plant remains. As has previously been noted (Charles 1998), there is a paradox in the quantification of dung and dung-derived material: as the number of dung-derived items increases, the more the dung itself is broken up and becomes less identifiable and quantifiable. Criteria for identifying dung-derived material have previously been set out (Miller and Smart 1984; Charles 1998), but one aspect that has received relatively little attention is the impact of the digestive processes of livestock on the composition of plant remains surviving into dung. This is crucial to understanding the biases imposed by digestion and identification of plant material which may have been derived from livestock dung.

Fig. 1 outlines the key taphonomic steps involved in the creation of archaeologically preserved dung deposits. The route of plant material from its growing location to archaeological deposit is potentially long and complex, involving a series of animal and human interactions. In essence, the major elements for dung-derived material are plant selection, digestion, fuel preparation and use, and finally incorporation into the archaeological record. Each stage favours particular types of plant material over others, typically resulting in resilient plant parts being over-represented due to destructive processes such as digestion and charring.

Livestock Consumption and Digestion

The botanical content of dung, while a product of consumption, is by no means a simple reflection of diet. The digestive systems of animals are hostile environments designed to extract nutritive value from consumed materials, as such plant material losses during digestion are expected. Most animals that are likely to have been used as a source of dung for fuel at archaeological sites have ruminant digestive systems (e.g. sheep, goat and cow), although contributions from mono-gastric animals (e.g. horse, mule and donkey) are also plausible (Anderson and Ertug-Yaras 1998). Typically, dung would be collected from livestock (given their proximity to human settlements; Broderick and Wallace in press), and so preserved dung could contain plant remains from grazing and/or foddering. Dung could also be collected from wild animals such as deer (Miller 1996). Here, we focus on ruminant digestion of sheep, as ethnographic studies show that the dung of sheep is one of the most often used dung fuels (Vidyarthi 1984; Anderson and Ertug-Yaras 1998; Reddy 1998; Sillar 2000; Moreno-Garcia and Pimenta 2011). Moreover, in Western Asia and Southern Europe sheep and cattle, likely sources of dung fuel, are often prominent in faunal assemblages from early farming sites (Legge 1996; Halstead 2006).

Multiple studies have been conducted which show that a proportion of seeds survive the digestive environment to be found intact in excrement. A large corpus of data exists on the role of animals in the dispersal of seeds via their dung (endozoochory). Dung dispersed seeds are typically scarified by digestion, which increases germination rates, and hence they have major consequences for landscape ecology, range management and the spread of weed species (see Table 1). It has been proposed that there is a mutual benefit system between certain plant and animal taxa, in which animals receive nutritive benefit from foliage and a proportion of the seeds, and plants benefit from the dispersal of the remainder of seeds over the area roamed by the consumer (Janzen 1984). The consumption of seeds by animals and their subsequent excretion in dung is one of the most important dispersal routes, and for medium-sized and heavy seeds it is often the predominant means of dispersal (Ridley 1930; Janzen 1982; 1984; Manzano et al. 2005). The results of such endozoochory studies, particularly those that involve feeding (including mastication, i.e. by mouth) of plant material to farm animals (see Table 1 for summaries and references), have shown that:

1. Seeds of a wide variety of plant taxa can survive passage through the gut of livestock and be found in an intact and often viable (i.e. capable of germination) state in the consumer's dung.

2. Most seeds emerge around 1.5 to 3 days after their ingestion, although seeds have been reported in dung as little as half a day after consumption and as late as 6–10 days later.

3. Seed size and the hardness or permeability of seed coats are key determiners of survival rates.

4. Digestion by animals increases germination rates by breaking dormancy, scarification of seed surface (reducing resistance against embryo emergence) and by providing moist conditions in dung for germination.

Clearly dung-derived plant remains could be a major component of the archaeobotanical record in dung fuel burning regions. Yet digestion will impose biases on the plant remains deposited by this route, with larger and thinly coated seeds predicted to be underrepresented. To date, there has been no concise attempt to quantify the features of seed and cereal chaff which influence the chances of survival through digestion with an emphasis on the morphological condition of surviving material and their likeliness to be preserved archaeologically. This study aims to evaluate the potential of dung as a source of plant remains in the archaeobotanical record and to identify the biases that consumption and digestion are likely to have imposed. The focus is on the taphonomic stage of digestion, specifically that of the ruminant sheep, and whether material survives into dung in an archaeobotanically recognisable state.

Methods Used in This Study

Eight healthy, yearling ewes kept in individual pens were selected on two farms, one in the UK and the other in Spain. The eight sheep were of three breeds: in the UK, a commercial crossbreed and Soay, a 'primitive' hardy breed and, in Spain, hill sheep locally known as Alcarras-type. In addition to their main diet, comprising cut grass hay and condensed vegetative matter, the animals were fed a known quantity of specific plant material (Tables 2 and 3).

Included in the diet of the animals were taxa commonly found on archaeological sites, particularly in deposits associated with dung remnants. Wheat was fed largely in the form of loose grains (with or without glumes attached) or spikelet forks. All of the barley was hulled but devoid of chaff. Some of the wheat (of diet B, see Table 3) was given as ears, in which case the entire above-ground part of the plants including the stems and any leaves were fed. Small tubers of Cyperus esculentus (tiger nuts) were added to the diet of the commercial breed sheep (Table 3). Diet B also included whole, seeding (seeds matured) plants of five wild species. The numbers of seeds present in the feed of each day were approximately the same (Table 3).

The feeds listed in Table 3 were given to the sheep each morning for five consecutive days. The animals were fed normally, by mouth. While the animals were free to eat at will, observation of the animals indicated that in all cases the majority of the plant material was consumed. An essential feature of this method of feeding is that the effects of the initial stage of mastication are included in the study.

The dung pellets produced by the sheep were collected twice a day for 5 or 6 days, from plastic meshes. A similar method was employed by Manzano et al. (2005). Collected pellets were typically round, or were slightly elongated with or without a pointed apex, and between 0.5 and 1 cm in diameter. Pellets were dried at 30°C for 2 days before being carefully disintegrated by hand. Testing of the disintegration process showed that it did not damage the plant material contained within the dung. The disintegrated dung was sieved into 4, 1 and 0.3 mm fractions and scanned under ×8–40 optical microscopy for identifiable plant remains (seeds, chaff and tubers). Seed identifications were made with reference to unconsumed fodder as well as to the seed reference collection of the Department of Archaeology at the University of Sheffield.

Results

Production of Pellets

Approximately 23 600 dung pellets were collected from the eight sheep, which equates to an average of ca. 500 pellets per sheep per day (Table 4 and Fig. 2). The number of pellets produced during a day by a single sheep ranged from 400 to 1100. While the breed of sheep had no clear impact on the quantity of dung produced, the amount produced per animal varied considerably. Given the short period of collection and the small number of sheep, the quantity of dung produced is impressive. Extrapolating these results to a flock of 50 sheep stalled over winter (e.g. for a 5-month period), gives figures of between 3 and 8 million dung pellets; assuming an average pellet is round with a diameter of 1 cm, this equates roughly to filling between 100 and 400 ten litre buckets.

Botanical Finds

A sub-sample of pellets, usually 10, was randomly selected from the pellets recovered from each collection point (sheep–day–time). This produced a total of 808 pellets (3.4% of the total collected) that were disintegrated and had their contents studied individually for identifiable botanical remains. Material from certain collection points was not studied as the quantified plant material (Table 4) was unlikely to have passed through the sheep quickly enough to be found or only a small amount of dung was collected.

The total number of recognisable botanical items identified in the scanned pellets was 412 (Table 5), an average of 5.1 finds for every 10 pellets examined (5.1/10 pellets). The finds rate for individual sheep ranged between 2.7 and 13.0/10 pellets. Seed survival rates were fairly similar across breeds. The Soay and Alcarras-type breeds had slightly higher find rates than those of sheep fed diet A, but this is presumably because of the inclusion of greater number of seeds in diet B (Table 3). One sheep, #7, of the Alcarras-type, produced dung containing an atypically large amount of seeds (Table 5).

Diet A Results

Very little cereal material (four glume bases and one grain) was found in the dung of animals fed diet A, and none of the tuber material fed to the animals was identified. The single cereal grain (Einkorn) was the only cereal grain found in the entire study to have survived in a recognisable state (Fig. 3). Glume bases were recognisable as such but were heavily damaged. These cereal items represent just

7% of the total cereal and tuber items provided to the animals. Moreover, these cereal items were only 4% of the total number of identified plant remains found in the studied dung. The remainder of the botanical finds (124 of the 129 items) were seeds of various wild species (Table 5 and Fig. 4). As wild seeds were not deliberately included in diet A, they were not routinely identified to species level, but it was observed that there was a high proportion of small grass seeds and occasional Chenopodium album seeds. These seeds were probably introduced to the diet of the animals via hay.

Diet B Results

Nine cereal items (glume bases and barley internodes) were recovered from the five sheep fed diet B (Table 5). No recognisable cereal grains were recovered. This result is comparable with that for diet A despite the considerable increase in the amount of cereal material included. The glume bases were, again, poorly preserved. Also as before, the majority of finds (270 of 279) were seeds of wild species, most (215 of 270) of which were of one of the five species listed in Table 3 (Fig. 5).
By far, the most common species of seed found in the dung was Chenopodium album (mean = 3.0/10 pellets), though this value may have been slightly boosted if present in the hay, as was the case for diet A. The five species of seed fed as part of diet B differed markedly in size (Table 3). Chenopodium album, Suaeda maritima and Bolboschoenus maritimus (previously Scirpus maritimus) all have longest length of 1–2 mm. The latter two species (both found in the dung of animals fed diet B at approximately 0.3/10 pellets) were not found in as great quantity as Chenopodium album, but their ability to survive digestion is markedly superior to that of cereal grains.

The survival of the smaller seeds, Juncus effusus (0.4/10 pellets) and Trifolium pratense (0.2/10 pellets), was at similar rates to those of the larger wild seeds. This indicates that for all seeds of 2 mm and below, seed size did not impose a clear bias on survival. Juncus effusus was fed to the sheep in greater quantity than the other wild species (Table 3), potentially explaining its slightly greater representation in dung. Nevertheless, the very similar rates at which the four wild species, excluding Chenopodium album due to its occurrence in hay, were found in dung indicates that the number of seeds in dung could be used to infer the number of seeds in the original diet.

The rates at which these wild species seeds were found in dung can be extrapolated to approximate the total number of seeds that might be expected if all 23 600 pellets had been studied. For the wild species found least often in dung, Trifolium pratense (0.2/10 pellets), around 450 of the 1000 seeds may have survived intact, whereas around 700 of the 1000 each of Suaeda maritima and Bolboschoenus maritimus each could have survived, as well as 950 of the 1500 Juncus effusus seeds. These extrapolations must be treated with caution as they are based on small sample sizes and estimated seed intake. However, they represent survival rates of between 45 and 70%, which are in keeping with those reported in endozoochory studies (Table 1), and provide clear indication that high proportions of consumed wild plant seeds can survive digestion.

Finds of plant material that were fed to the sheep in quantified amounts first appeared within 2 days of feeding, and the number of these finds increased around the fifth day, after which find rates reduced quickly (black bars in Fig. 4). This observation is consistent with the expected rate of passage through the digestive system (see above), in that most seeds take around 2–3 days to pass through sheep. For example, the peak in finds around day 4 can be explained by the dung from that day containing much of the material from days 2 and 3 as well as a small amount of material from day 1. Find rates decrease somewhat more sharply than expected (e.g. few finds were found in the dung from day 6, despite material fed on days 3, 4 and 5 potentially being present). Currently, this decline cannot be fully explained, but one possible explanation is that changes in the gut flora of the animals resulted in more complete digestion of the plant material over the course of the feeding (Annison and Lewis 1959). Overall, though, the results indicate that consumed material passes fairly quickly, being excreted only 2 or 3 days after ingestion. A similar study by Valamoti and Charles (2005), in which goats were fed test material on a single occasion, found plant material passed through the animals within 4 days.

Comparison of Diets

Overall, the two diets resulted in broadly similar proportions of macroscopic plant remains in dung that were identifiable with archaeobotanical criteria. The average find rate of diet B (6.5/10 pellets) was higher than that for diet A (3.5/10 pellets), which can be explained by the greater number of seeds consumed by the animals consuming diet B. The rarity of cereal finds in the dung of all the observed sheep suggests that cereals survive ruminant digestion very poorly. The seeds of wild plants are prevalent in both the dung of animals deliberately fed weed seeds (sheep fed diet B) and in the dung of animals for which hay was the only possible source of wild seeds (sheep fed diet A). This indicates that some seeds have a natural capacity for enduring digestive environments.

Discussion

Crop Remains

This investigation shows that the crop material fed to sheep, such as tiger nut tubers, glume wheat grain and chaff and hulled barley grain rarely survived digestion. Similar results were found in an earlier study by Valamoti and Charles (2005) of goat, another ruminant, which found that no intact cereal grains and only a few, damaged chaff fragments survived. The few cereal chaff fragments recovered from sheep dung are recognisable as such, and could be identified in an archaeological context. These findings are, however, in contrast to the situation reported for cattle, another ruminant, where cereal grains are recorded as passing through undigested. This is problematic as the animal derives no nutritional benefit from this undigested grain, which is why in modern agriculture grain is usually rolled or flaked before feeding (e.g. Kaiser 1999).

Wild Species

Unlike the crop remains, a wide range of wild seeds, of various types and sizes, were found intact in the dung of the studied sheep. Most of these seeds were less than 2 mm in their greatest dimension, and so should pass through the ruminant digestive system relatively unhindered. The estimated survival rates were high and, given the vast amount of dung that can be produced by even a few sheep, many seeds could potentially be retrieved from fuel derived from sheep dung.

The prevalence of Chenopodium album in small ruminant dung highlights its tenacity to survive digestion even if consumed in modest amounts. The impermeable coat of Chenopodium album seeds also would have improved their chances of survival. However, it appears that the seeds of four other wild species (Bolboschoenus maritimus, Suaeda maritima, Juncus effusus and Trifolium pratense) were also able to survive in fairly similar proportions to each other regardless of their size or the resilience of their seed coats.

Mechanisms of Survival

Endozoochory studies have indicated that key factors determining survival through the gut relate to seed size and seed coat thickness (Table 1). Both of these elements may explain the poor survival rate of cereal remains, as the grain and chaff are relatively large (shortest dimension ≥2 mm), and the grains have thin seed coats. The resilience of a seed's coat determines the protection given to the easily digestible, carbohydrate-rich seed interior. Seeds with a broken seed coat are unlikely to survive the microbial stages of digestion (Beauchemin et al. 1994). In fact, seed endosperm is so readily digested that a grain-rich diet can lead to malnutrition, as carbohydrate-digesting microbes dominate the gut fauna at the expense of microbes capable of digesting other nutrients (Annison and Lewis 1959, 82–83; Doyle 1987, 435; Kaiser 1999, 737). A permeable seed coat may also allow moisture to penetrate into the inner seed and initiate germination in the gut or the excreted dung

(Janzen et al. 1985), making survival and preservation unlikely. It might be anticipated that the protective chaff layers (glumes, lemma and palea) surrounding or fused to the grain surface would provide some protection to the grain. However, this study has shown that this was not the case, with neither Einkorn (with or without glumes attached) nor hulled barley regularly surviving digestion. The only grain to have been found in the analysed dung was devoid of chaff (Fig. 3), and while it is conceivable that the chaff was removed during digestion, there is no evidence to indicate that this was the case.

The importance of seed size to digestion survival is partly due to the reticulo-omasal orifice, which separates the upper and lower portions of the ruminant digestive system (Poppi et al. 1985; Dehority 1996). Consumed plant items unable to pass through this orifice are retained in the upper portion of the ruminant digestive system, thus delaying excretion, prolonging exposure to the digestive environment and resulting in further rounds of mastication. The reticulo-omasal orifice is small and can impose major resistance to the passage of digested objects. Poppi et al. (1985) reported that particles <1.18 mm in size meet little resistance as they pass through sheep and cattle, whereas particles in the size range 1.18–4.75 mm experience considerable resistance to passage. As an example of the level of resistance imposed, Poppi et al. (1985, 10) reported that only 3.4% of objects in the size range 1.18–2.36 mm were passed by cattle, and only 1.1% by sheep. Objects can pass through the reticulo-omasal orifice in any direction and, so, consumed plant material with one dimension greater than 2 mm (e.g. length), have an increased chance of being retained in the gut for a prolonged period, whereas objects with all dimensions (length, breadth and thickness) over 2 mm, such as cereal grains, are especially likely to be retained.

Poppi et al.'s (1985) study indicated that objects greater than 4.75 mm in size do not survive intact through the digestive system of sheep. This conclusion is supported by the paucity of cereal grain in the dung of sheep studied here. However, neither the leaf and stem of the Poppi et al. (1985) study, nor the cereal grain of this study, are highly resilient plant parts. In contrast, Prosopis seeds are often dispersed via consumption by animals despite being large-seeded (e.g. P. farcta seeds are typically 7 × 4 × 2 mm in size). The ability of Prosopis seeds to survive digestion lies in their toughened endocarp, which offers protection against the harsh conditions of digestion despite extended retention in the gut due to their size (Peinetti et al. 1993; Campos and Ojeda 1997). The classic case of Prosopis seed dispersal via dung, thus, serves as an indication that the failure of cereal grains to survive digestion is partly due to their size and partly due to their thin testa.

Archaeological Implications

At the rates at which seeds and other plant remains are found in the dung of the eight studied sheep, it is clear that burning of livestock dung from animals eating wild seeds would potentially result in the preservation and deposition of a substantial suite of plant remains. The composition and quantity of seeds in an animal's diet will obviously influence the contents of dung, but the digestive process will impose biases against large seeds and those with weak outer coats. Regardless of the impact of such biases though, it is clear that the remnants of burnt dung provide an opportunity for the inference of animal diet. Consequently, spent-fuel deposits and other dung-containing samples should be examined for such potential.

There are a number of other taphonomic processes (Fig. 1) involved in determining the final quantity of seeds retrieved by archaeologists. The results presented here indicate that many seeds could be dung-derived, and for seeds of less than 2 mm in length digestion may have imposed very little compositional bias. However, interpretations of dung-derived assemblages must take account of the probable under-representation of species with large and thinly coated seeds. Archaeobotanical samples rich in species that are resistant to the digestive environment, particularly if they are derived from fuel burning contexts, could be considered likely candidates of having been purely dung-derived even if dung fragments are absent.

The results presented here support the notion proposed by Miller (2010, 51), that the ratio of seeds to charcoal in domestic burning contexts could be used to differentiate wood-fuelled and dung-fuelled fires. However, in the application of this ratio at Gordion (Turkey) only seeds, including cereal grain, from the 2 mm fraction are included in the ratio, meaning the ratio in essence 'is effectively a cereal:charcoal ratio' (Miller 2010, 53). Given the rarity of cereal grains in the dung of animals studied here, such a ratio would underestimate the presence of dung-derived deposits. Study of the <2 mm fraction, particularly with a view to identify species typical of grazed habitats or selected as fodder, would be a more effective approach to the identification of a dung source.

The susceptibility of cereal remains to destruction during digestion is clear, and so the co-occurrence of dung remnants and cereal remains in archaeobotanical samples are more likely a product of the mixing, intentional or unintentional, of dung-derived and non-dung material. However, the dung component of such deposits should not be ignored, to do so would risk misleading interpretations of human consumption choices. The interpretation of archaeobotanical samples remains complex, but this study has proven the potential of dung-derived plant remains as a major contributor to the archaeobotanical record.

Within the studied group of healthy, 1 to 2-year-old sheep, of three different breeds, there are relatively consistent and predictable patterns for the survival of plant material tested. It should, however, be considered that sheep of different ages, and accustomed to different diets, may differ in their ability to digest plant material. There may also be differences between different livestock genera; for example, Valamoti (2013) presents results from her study of dung from a goat in which cereal chaff survives, albeit in a highly damaged state.

Future Directions

There are several important variables that could be included in the design of future follow-up studies. Among these are a greater variety of breeds and ages of animals. A crucial aspect to be tested would be survival rates of the types of plant material that are fed to animals over the long-term, such that the animals are well-accustomed to their diet, and are the primary component of diet. These conditions will ensure the quantities of plant material found in dung are representative of normal consumption behaviour.

Several other animal species could have contributed to dung fuel stocks, and so should be included in further research. Of particular importance are cattle, which produce substantial amounts of dung and where grain is known to pass through digestion intact to a greater extent than through sheep (Poppi et al. 1985; Kaiser 1999). It is predicted that the shared features of the digestive system of ruminants will mean that survival rates of plant material in the <2 mm range are comparable between most ruminants. However, plant material in the size range of ca. 2–4 mm, such as cereal grain, may experience somewhat different degrees of resistance between animal genera. Differences in the consumption habits of browsing goat compared with grazing sheep could be another source of such differences. Other species could be investigated in future trials, although the focus should remain on the most likely contributors to dung fuel in the past: sheep, goat and cattle.

A further area of investigation is surface detail analysis of digested plant parts by means of scanning electron microscopy or (see Marinova et al. 2011) reflected light microscope. Valamoti (2013) reports that glume bases digested by goat exhibit a 'shredded' surface pattern, which may serve as a diagnostic indicator of digestion. It is thought that digested seeds may also exhibit pitted or otherwise damaged surfaces due to their exposure to acidic and microbial attack during digestion.

Early work on archaeobotanical assemblages thought to be dung-derived suggests that these kinds of damage may also be found on charred plant remains. Further research is required to investigate the formation and preservation of these surface patterns, but they offer the potential to independently identify the passage of individual plant remains through animal digestive systems.

Conclusion

The results of this study indicate that sheep digestion can impose significant biases on the composition of plant remains surviving in dung. Plant material larger than 2 mm is exposed to considerable damage during digestion and is unlikely to survive unless it has a highly resistant coat. Though digestion is only one stage in a series of processes between the consumption of plant material and recovery on archaeological sites, it can have a major and, as shown here, potentially predictable impact on the composition of plant remains in an archaeobotanical assemblage.

The susceptibility of cereal grain to digestion, even when fed to sheep with its enclosing chaff, means that the archaeological occurrence of grain with dung is likely to be a consequence of either deliberate mixing during dung cake preparation or accidental mixing. In contrast, small and/or hard-coated seeds found in similar settings may well have survived animal digestion and offer scope for investigating animal diets, grazing environments and foddering practices. Consequently, dung-derived plant material presents archaeobotanists with an opportunity, as yet little-exploited, to explore the relationship between plants and grazing or fodder-fed animals.

The results presented here, and those of future studies, will prove important in the interpretation of complex archaeobotanical assemblages where plant material is derived from multiple sources. While research into the taphonomy of dung-derived plant remains, and their significance to archaeological interpretations, is still at an early stage, this study has gone some way to develop a framework for assessing the probability of plant remains having been dung-derived. It is hoped in the future that archaeobotanists working in dung fuel burning regions will, as a matter of routine, consider the potential of dung-derived plant remains. Doing so provides new avenues by which we can explore the intertwined economies of plant and animal resources in the past.

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References

Akeret O., Haas J., Leuzinger U., Jacomet S. 1999. Plant macrofossils and pollen in goat/sheep faeces from the Neolithic lake-shoe settlement Arbon Bleiche 3, Switzerland. The Holocene 9, 175–82.

Anderson S., Ertug-Yaras F. 1998. Fuel fodder and faeces: an ethnographic and botanical study of dung fuel use in central Anatolia. Environmental Archaeology 1, 99–109.

Annison E., Lewis D. 1959. Metabolism in the Rumen. London: Methuen and Co.

Beauchemin K., McAllister T., Dong Y., Farr B., Cheng K. J. 1994. Effects of mastication on digestion of whole cereal grains by cattle. Journal of Animal Science 72, 236–46.

Bottema S. 1984. The composition of modern charred seed assemblages, pp. 207–12 in , van Zeist W., Casparie W. (eds.), Plants and Ancient Man. Studies in Palaeoethnobotany. Rotterdam: A. A. Balkema.

Broderick L. G., Wallace M. in press. Manure: Valued by Farmers, Undervalued by Zooarchaeologists. In , Broderick L.G. (ed.), People with Animals: Perspectives and Studies in Ethnozooarchaeology. Oxford: Oxbow Books.

Burton G., Andrews J. 1948. Recovery and viability of seeds of certain southern grasses and Lespedeza passed through the bovine digestive tract. Journal of Agricultural Research 76, 95–103.

Campos C., Ojeda R. 1997. Dispersal and germination of Prosopis flexuosa (Fabaceae) seeds by desert mammals in Argentina. Journal of Arid Environments 35, 707–14.

Charles M. 1998. Fodder from dung: the recognition and interpretation of dung-derived plant material from archaeological sites. Environmental Archaeology 1, 111–22.

Charles M., Bogaard A. 2005. Identifying livestock diet from charred plant remains: a Neolithic case study from Southern Turkmenistan, pp. 93–103 in , Davies J., Fabis M., Mainland I., Richards M., Thomas R. (eds.), Diet and Health in Past Animal Populations. Current Research and Future Directions. Oxford: Oxbow Books.

Charles M., Pessin H., Hald M. M. 2010. Tolerating change at Late Chalcolithic Tell Brak: responses of an early urban society to an uncertain climate. Environmental Archaeology 15, 183–98.

Cosyns E., Hoffmann M. 2005. Horse dung germinable seed content in relation to plant species abundance, diet composition and seed characteristics. Basic and Applied Ecology 6, 11–24.

Dehority B. 1996. Foregut fermentation, pp. 39–83 in , Mackie R., White B. (eds.), Gastrointestinal Microbiology: Gastrointestinal Ecosystems and Fermentations. London: Chapman and Hall.

Derreumaux M. 2005. How to detect fodder and litter? A case study from the Roman site ‘Le Marais de Dourges’, France. Vegetation History and Archaeobotany 14, 373–85.

Doyle P. 1987. Supplements other than forage, pp. 429–64 in , Hacker J., Termouth J. (eds.), The Nutrition of Herbivores. London: Academic Press.

Gardener C., McIvor J., Jansen A. 1993. Passage of legume and grass seeds through the digestive tract of cattle and tehir survival in faeces. Journal of Applied Ecology 30, 63–74.

Halstead P. 2006. Sheep in the garden: the integration of crop and livestock husbandry in early farming regimes of Greece and Southern Europe, pp. 42–55 in , Serjeantson D., Field D. (eds.), Animals in the Neolithic of Britain and Europe. Oxford: Oxbow Books.

Helbaek H. 1969. Plant-collecting, dry-farming, and irrigation agriculture in prehistoric, Deh Luran, pp. 383–426 in , Hole F., Flannery K., Neely J. (eds.), Prehistory and Human Ecology of the Deh Luran Plain. Ann Arbor: University of Michigan Museum of Anthropology.

Janzen D. H. 1982. Differential seed survival and passage rates in cows and horses, surrogate Pleistocene dispersal agents. Oikos 38, 150–6.

Janzen D. H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. American Naturalist 123, 338–53.

Janzen D., Demment M., Robertson J. 1985. How fast and why do germinating Guanacaste seeds (Enterolobium cyclocarpum) die inside cows and horses? Biotropica 17, 322–5.

Kaiser A. 1999. Increasing the utilisation of grain when fed whole to ruminants. Australian Journal of Agricultural Research 50, 737–56.

Karg S. 1998. Winter- and spring-foddering of sheep/goat in the Bronze Age site of Fiavè-Carera, northern Italy. Environmental Archaeology 1, 87–94.

Legge T. 1996. The beginning of caprine domestication in southwest Asia, pp. 238–62 in , Harris D. (ed.), The Origins and Spread of Agriculture and Pastoralism in Eurasia. London: UCL Press.

Linseele V., Marinova E., Van Neer W., Vermeersch P. 2010. Sites with Holocene dung deposits in the Eastern Desert of Egypt: visited by herders? Journal of Arid Environments 74, 818–28.

Malo J., Suárez F. 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. Oecologia 104, 246–55.

Manzano P., Malo J., Peco B. 2005. Sheep gut passage and survival of Mediterranean shrub seeds. Seed Science Research 15, 21–8.

Marinova E., van der Valk, J., Valamoti, S., Bretschneider J. 2011. An experimental approach for tracing olive processing residues in the archaeobotanical record, with preliminary examples from Tell Tweini, Syria. Vegetation History and Archaeobotany 20, 471–8.

Michael P., Steadman K., Plummer J., Vercoe P. 2006. Sheep rumen digestion and transmission of weedy Malva parviflora seeds. Australian Journal of Experimental Agriculture 46, 1251–6.

Miller N. 1993. Preliminary archaeobotanical results from the 1989 excavation at the Central Asian site of Gonur Depe, Turkmenistan. International Association for the Study of Cultures of Central Asia [IASCCA] Information Bulletin 19, 149–63.

Miller N. 1996. Seed eaters of the ancient Near East: human or herbivore? Current Anthropology 37, 521–8.

Miller N. 1997. Farming and herding along the Euphrates: environmental constrait and cultural choice (fourth to second millennia B.C.), pp. 123–32 in , Zettler R. (ed.), Subsistence and Settlement in a Marginal Environment: Tell es Sweyhat, 1989, 1995 preliminary report. (MASCA Research papers in Science and Archaeology 14), Philadelphia: University of Pennsylvania Museum of Archaeology and Anthropology.

Miller N. 2009. From food and fuel to farms and flocks: the integration of plant and animal remains in the study of the agropastoral economy at Gordion, Turkey. Current Anthropology 50, 915–24.

Miller N. 2010. Botanical Aspects of Environment and Economy at Gordion, Turkey. Philadelphia: University of Pennsylvania Museum of Archaeology and Anthropology.

Miller N., Gleason K. 1994. Fertilizer in the identification and analysis of cultivated soils, pp. 25–43 in , Miller N., Gleason K. (eds.), The Archaeology of Garden and Field. Philadelphia: University of Pennsylvania Press.

Miller N., Smart T. 1984. Intentional burning of dung as fuel: a mechanism for the incorporation of charred seeds into the archaeological record. Journal of Ethnobiology 4, 15–28.

Moens M. F., Wetterstrom W. 1988. The agricultural economy of an old kingdom town in Egypt's west Delta: insights from plant remains. Journal of Near Eastern Studies 3, 159–73.

Moreno-Garcia M., Pimenta C. 2011. Animal dung: rich ethnographic records, poor archaeozoological evidence, pp. 20–8 in , Albarella U., Trentacoste A. (eds.), Ethnozooarchaeology: The Present and Past of Human–Animal Relationships. Oxford: Oxbow Books.

Neef R. 1989. Plants, pp. 30–7 in , van der Kooij G., Ibrahim M. (eds.), Picking up the Threads a Continuing Review of Excavations at Deir Alla, Jordan. Leiden: University of Leiden Archaeological Centre.

Oeggl K., Schmidl A., Kofler W. 2009. Origin and seasonality of subfossil caprine dung from the discovery site of the Iceman (Eastern Alps). Vegetation History and Archaeobotany 18, 37–46.

Pakeman R., Digneffe G., Small J. 2002. Ecological correlates of endozoochory by herbivores. Functional Ecology 16, 296–304.

Peinetti R., Pereyra M., Kin A., Sosa A. 1993. Effects of cattle ingestion on viability and germination rate of Caldén (Prosopis caldenia) seeds. Journal of Range Management 6, 484–6.

Poppi D. P., Hendricksen R. E., Minson D. J. 1985. The relative resistance to escape of leaf and stem particles from the rumen of cattle and sheep. Journal of Agricultural Science 105, 9–14.

Razanamandranto S., Tigabu M., Neya S., Odén P. 2004. Effects of gut treatment on recovery and germinability of bovine and ovine ingested seeds of four woody species from the Sudanian savanna in West Africa. Flora 199, 389–97.

Reddy S. 1998. Fueling the hearths in India: the role of dung in paleoethnobotanical interpretation. Paléorient 24, 61–9.

Ridley H. N. 1930. The Dispersal of Plants Throughout the World. Ashford: Reeve and Co.

Riehl S. 1999. Bronze Age environment and economy in the Troad: the archaeobotany of Kumtepe and Troy. BioArchaeologica 2, 1–192.

Russi L., Cocks P., Roberts E. 1992. The fate of legume seeds eaten by sheep from a Mediterranean grassland. Journal of Applied Ecology 29, 772–8.

Sillar B. 2000. Dung by preference: the choice of fuel as an example of how Andean pottery production is embedded within wider technical, social, and economic practices. Archaeometry 42, 43–60.

Tjelele J., Dziba L., Pule H. 2012. Recovery and germination of Dichrostachys cinerea seeds fed to goats (Capra hircus). Rangeland Ecology and Management 65, 105–8.

Valamoti S. 2013. Towards a distinction between digested and undigested glume bases in the archaeobotanical record from Neolithic northern Greece: A preliminary experimental investigation. Environmental Archaeology 18(1), 31–42.

Valamoti S., Charles M. 2005. Distinguishing food from fodder through the study of charred plant remains: an experimental approach to dung-derived chaff. Vegetation History and Archaeobotany 14, 528–33.

van Zeist W., Bakker-Heeres J. 1985. Archaeobotanical studies in the Levant 1. Neolithic sites in the Damascus basin: Aswad, Ghoraifé, Ramad. Palaeohistoria 24, 165–256

van Zeist W., Bakker-Heeres J. 1988. Archaeobotanical studies in the Levant 4. Bronze Age sites on the north Syrian Euphrates. Palaeohistoria 27, 247–316.

Vidyarthi V. 1984. Energy and the poor in an Indian village. World Development 12, 821–36.

Wallander R., Olson B., Lacey J. 1995. Spotted knapweed seed viability after passing through sheep and mule deer. Journal of Range Management 48, 145–9.

Wetterstrom W. 2003. Ninevite 5 period agriculture at Tell Leilan: preliminary results, pp. 387–400 in , Weiss H. (ed.), The Origins of North Mesopotamian Civilization: Ninevite 5 Chronology, Economy, Society. New Haven: Yale University Press.

Figure 1
Taphonomic flow-chart for archaeological dung-derived plant remains.

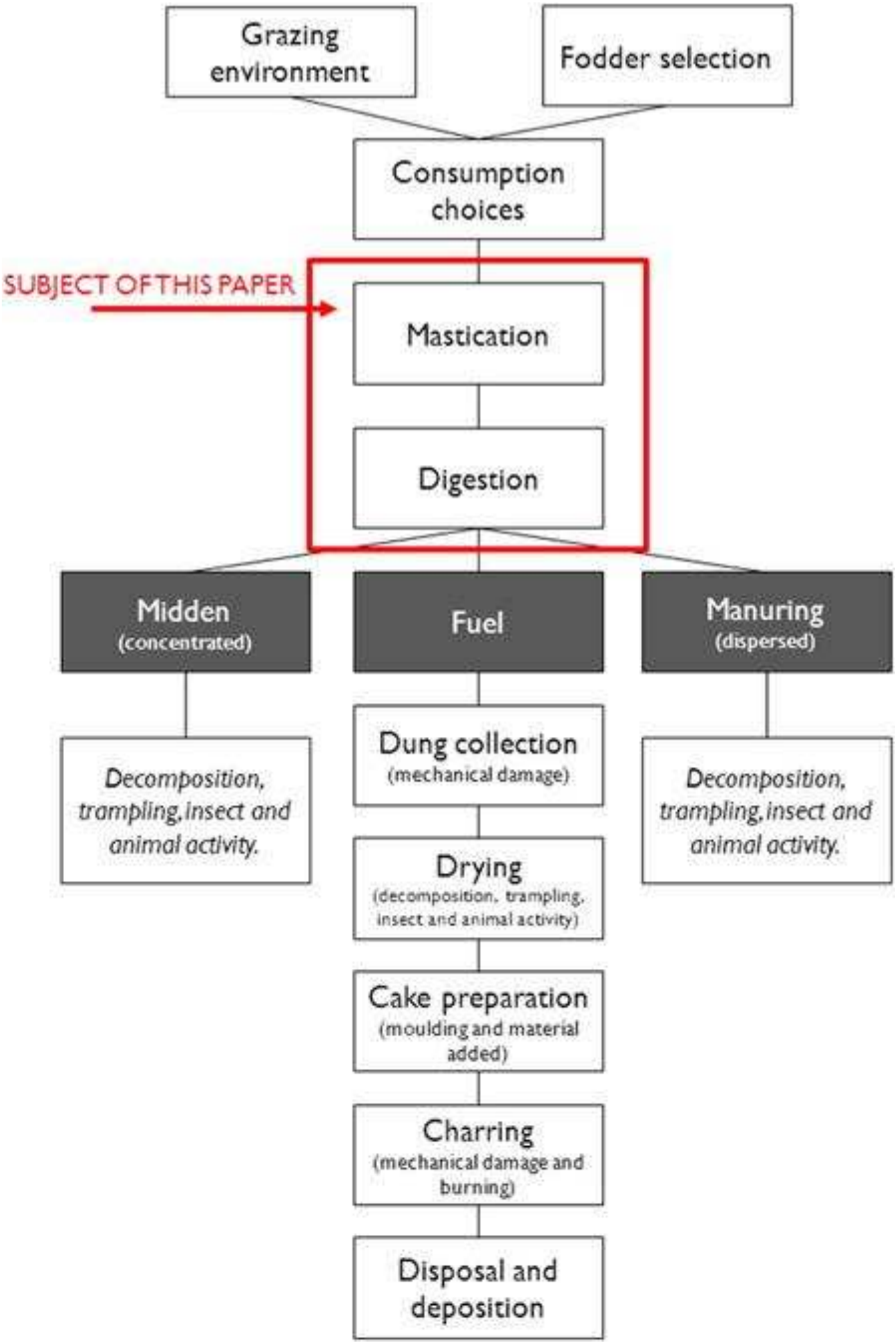

Figure 2

Cumulative count of pellets collected from each sheep. Left: sheep fed diet A, #1 (□), #2 (◇), #3 (○). Right: sheep fed diet B #4 (□), #5 (◇), #6 (○), #7 (△) and #8 (▽).

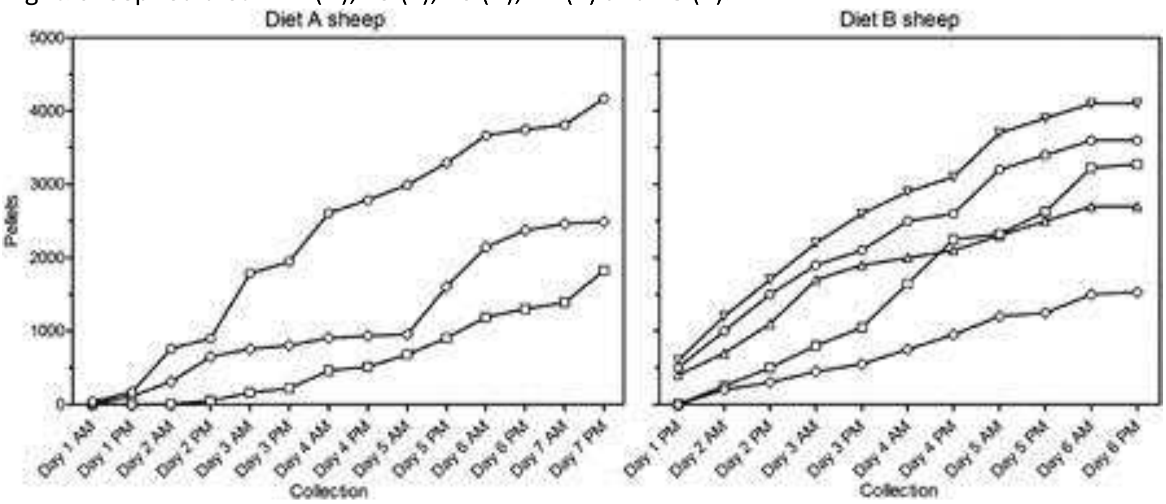

Figure 3
Photograph of a typical undigested Einkorn grain (left) and of the single Einkorn grain found in dung (right), which has a 'crumpled' appearance to its outer coat and is broader than the undigested grain.

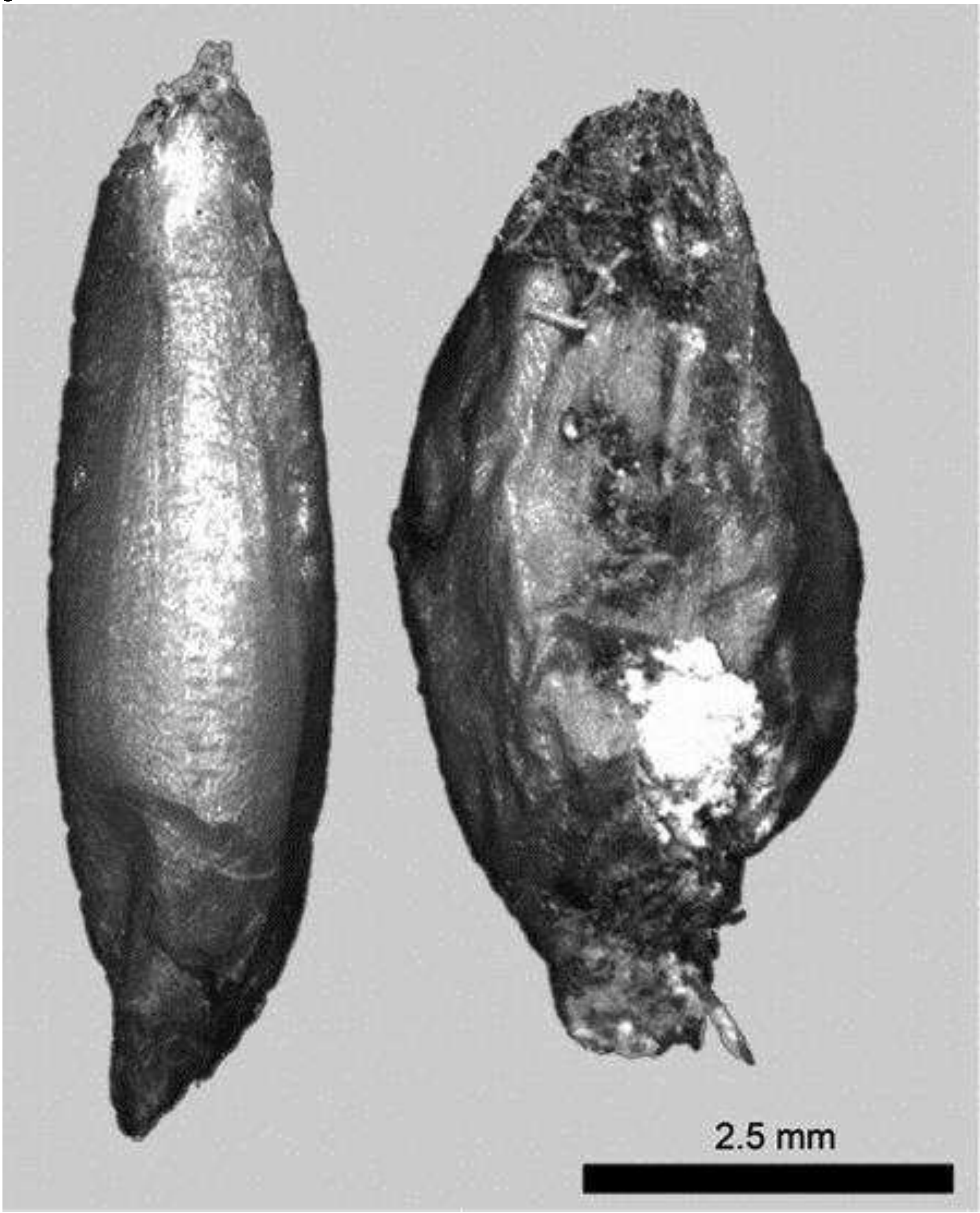

Figure 4
Botanical finds (seed, grain and chaff) of a species for which intake was monitored (see Table 3) presented as average per 10 pellets (▪). Also, seeds of other species (not monitored) presented as average per 10 pellets (●). Top: sheep #1–3 (diet A). Bottom: sheep #4–8 (diet B).

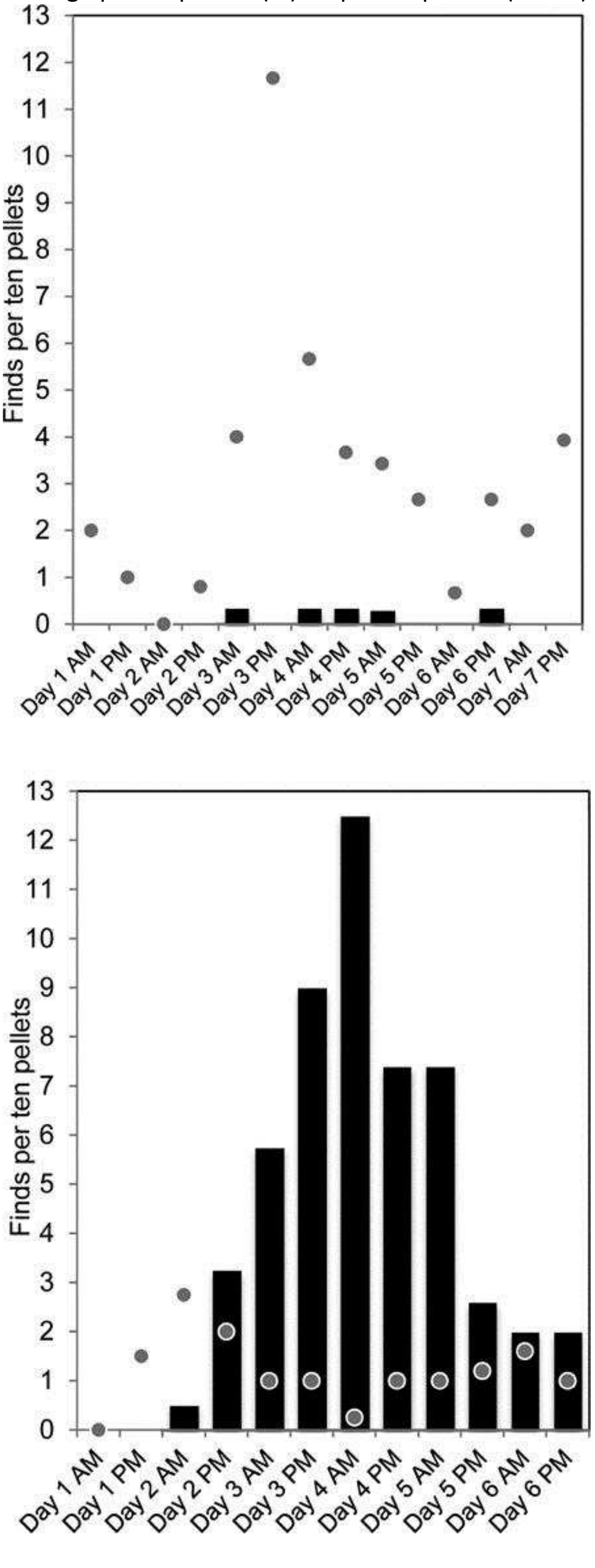

Figure 5

Mean number of seeds of monitored species (see Table 3) found per 10 pellets for sheep that consumed diet B. Sheep: #4 (black), #5 (grey), #6 (diagonal stripes), #7 (horizontal lines) and #8 (white).

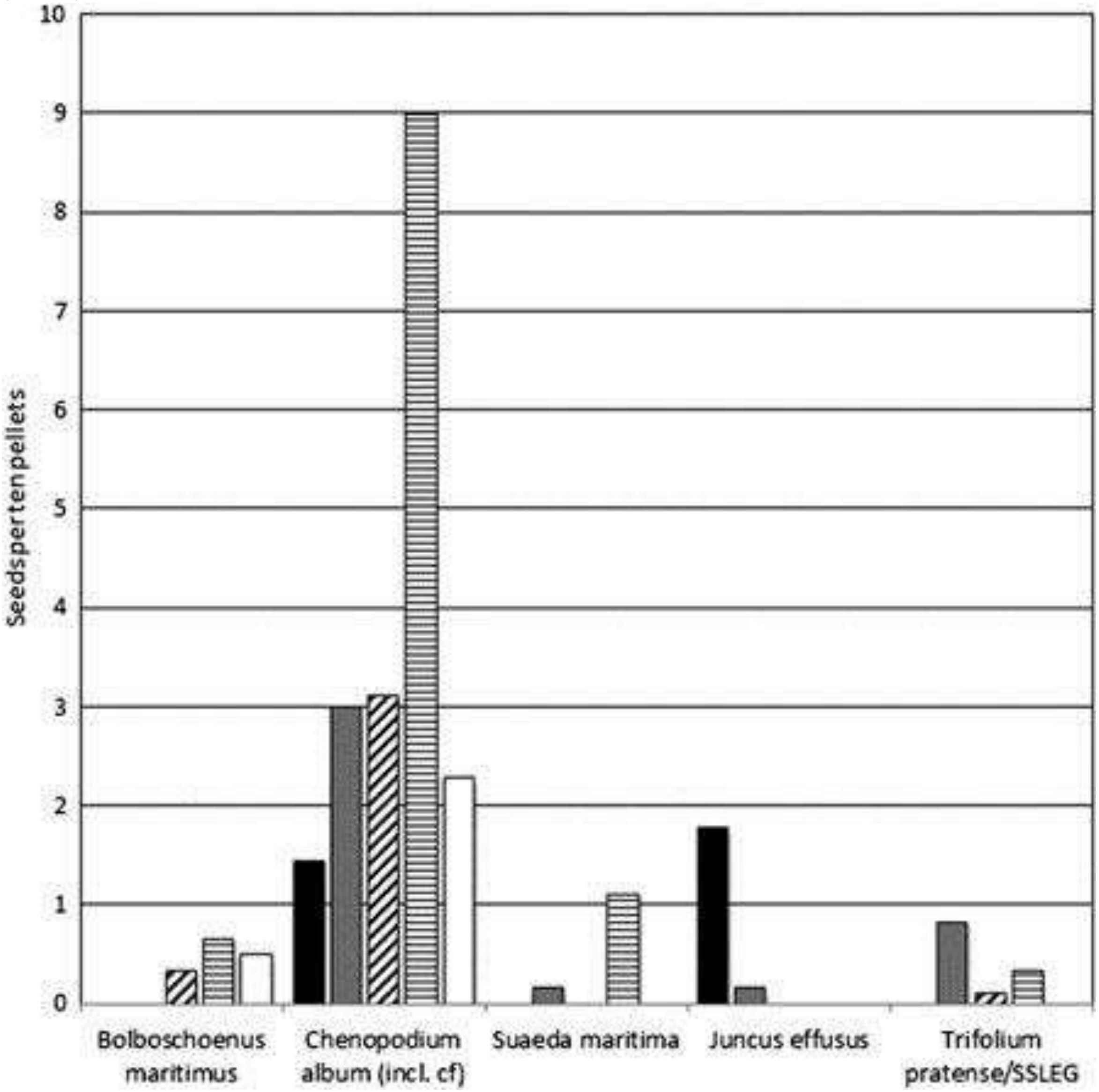

Table 1
Summary of selected experiments investigating the survival of seeds through the digestion tract of sheep, cattle, horse and deer.

Plants	Survival rates summary	Feeding method	Factor(s) deemed important for survival	Reference
Sheep and goat				
Various grazed legumes and grasses, plus controlled amounts of				
Trifolium stellatum, T. campestre, T. tomentosum	Between 20 and 60% of seeds survived digestion	By mouth	Small seed size	Russi et al. (1992)
Retama sphaerocarpa, Cytisus scoparius, Halimium umbellatum, Cistus ladanifer, Lavandula stoechas	Between 7 and 20% of seeds survived digestion	By mouth	Unclear, slight tendency for medium-sized seeds to survive well	Manzano et al. (2005)
Acacia dudgeoni, Acacia seyal, Burkea africana, Prosopis africana	Between 2.3 and 74% of seeds survived digestion	Oesophagus insertion	Animal size and behaviour	Razanamandranto et al. (2004)
Malva parviflora	20% of seeds survived digestion	Gut insertion	Hard seed coat	Michael et al. (2006)
Centaurea maculosa	4% of seeds survived digestion	By mouth	Duration of rumination	Wallander et al. (1995)
Various grazed species	0.1–0.6 germination-viable seeds per gram of dung	By mouth	Small and rounded seed size	Pakeman et al. (2002)
Dichrostachys cinerea	10–33% survived digestion depending on feeding method	By mouth		Tjelele et al. (2012)
Cattle				
10 wild legumes and eight wild grasses	6–80% of seeds survived digestion	Gut insertion	Dormancy and hard seed coat	Gardener et al. (1993)
Paspalum notatum, P. dilatatum, Sorghum halepense, Axonopus affinis, Cynodon	12–48% of seeds survived digestion	By mouth		Burton and Andrews 1948

dactylon, Lespedeza striata				
Acacia dudgeoni, Acacia seyal, Burkea africana, Prosopis africana	Between 46–87% of seeds survived digestion	Oesophagus insertion	Animal size and behaviour	Razanamandranto et al. (2004)
Enterolobium cyclocarpum	79–86% of seeds survived digestion	By mouth	Mastication habits	Janzen (1982)
Various grazed species	15–30 seeds per gram of dung during peak seed availability	By mouth	Small seed size and dormancy	Malo and Suárez (1995)
Deer				
Centaurea maculosa	11% of seeds survived digestion	By mouth	Duration of rumination	Wallander et al. (1995)
Horse				
Enterolobium cyclocarpum	17–56% of seeds survived digestion	By mouth	Mastication habits	Janzen (1982)
Various grazed species	382 seedlings (from viable seeds) per litre of dung	By mouth	Seed mass and density	Cosyns and Hoffmann (2005)

Table 2
Details of animals and diet used in the three trials.

	Commercial Suffolk-Texel			Soay		Alcarras-type		
Sheep	#1	#2	#3	#4	#5	#6	#7	#8
Archaeologically relevant diet type	Diet A			Diet B		Diet B		
Other components of diet	Hay, fodder beet (*Beta vulgare*), sheep cake (ground and condensed vegetable matter)			Hay, sheep cake (ground and condensed vegetable matter)		Hay, sheep cake (ground and condensed vegetable matter)		

Table 3
Details of dietary supplement packages (quantities are amount per day).

Species	Plant part	Approximate seed dimensions (mm)	Approximate seed coat thickness (mm)	Quantity included in diet A	Quantity included in diet B
Triticum monococcum L.	Grain	8 × 3 × 2	0.05	100 dehulled, 100 in spikelet	250 in ears
T. monococcum L.	Spikelet fork	10 × 5 × 2	–	100	–
Hordeum vulgare L.	Grain	9 × 4 × 3	0.05 + 0.04 hull	–	200
Cyperus esculentus L.	Tuber (tiger nuts)	3 × 3 × 3	–	20	–
Bolboschoenus maritimus (L.) Palla	Seed	3 × 2.5 × 1.5	0.01–0.02	–	ca. 200
Chenopodium album L.	Seed	1 × 1 × 1	0.04–0.06	–	ca. 200
Suaeda maritima (L.) Dumort	Seed	1 × 1 × 1	0.03–0.05	–	ca. 200
Juncus effusus L.	Seed	0.5 × 0.3 × 0.3	<0.01	–	ca. 300
Trifolium pratense L.	Seed	1.5 × 0.5 × 0.5	0.04–0.05	–	ca. 200

Table 4
Number of dung pellets produced.

	Diet A			Diet B				
Sheep	**#1**	**#2**	**#3**	**#4**	**#5**	**#6**	**#7**	**#8**
Day 1 AM	3	0	39					
Day 1 PM	0	112	130			500	400	600
Day 2 AM	0	200	591	250	200	500	300	600
Day 2 PM	50	340	140	250	100	500	400	500
Day 3 AM	107	105	885	300	150	400	600	500
Day 3 PM	62	50	164	250	100	200	200	400
Day 4 AM	240	100	662	600	200	400	100	300
Day 4 PM	54	26	177	600	200	100	100	200
Day 5 AM	163	24	205	75	250	600	200	600
Day 5 PM	228	650	300	300	50	200	200	200
Day 6 AM	285	540	375	600	250	200	200	200
Day 6 PM	112	230	80	50	30			
Day 7 AM	88	87	65					
Day 7 PM	437	29	360					
Average number of pellets per day	261	356	596	655	360	720	540	820

Note: Blank, no collection due to resource or time limitations. Pellets from animals fed diet A individually counted, pellets from animals fed diet B were counted to the nearest 25 pellets.

Table 5

Find counts and survival rates of plant remains recovered from dung.

	Diet A			Diet B				
Sheep	**#1**	**#2**	**#3**	**#4**	**#5**	**#6**	**#7**	**#8**
Pellets scanned	105	130	143	90	60	90	90	100
Cereal grains			1					
Glume bases	1	2	1		1		2	1
Barley internodes						1	4	
Bolboschoenus maritimus						3	6	5
Chenopodiaceae				1		25	2	7
Chenopodium album				12	18	3	79	16
Suaeda maritima					1		10	
Juncus effusus				16	1			
Trifolium pratense/SSLEG					5	1	3	
Unidentified weed seeds	42	49	37	12	10	14	11	9
Total	43	51	39	41	36	47	117	38
Average per 10 pellets	4.1	3.9	2.7	4.6	6.0	5.2	13.0	3.8

Note: *Chenopodium album* may be over-represented due to its presence in hay (see text).