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# What do dung beetles eat?

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**[Figures and Tables at the bottom of the document]**

## Abstract

1. Most adult coprophagous beetles feed on fresh dung of mammalian herbivores, confining ingestion to small particles with measured maximum diameters from 2–5 to 130 µm, according to body size and kind of beetle. This study explores benefits and costs of selective feeding in a 'typical' dung beetle with a maximum diameter of ingested particles (MDIP) of 20 µm.

2. Examined dung types (from Danish domestic sheep, cattle and horse, and African wild buffalo, white rhino and elephant) contained 76–89% water. Costs of a 20 µm MDIP were often low, since 69–87% of the total nitrogen in bulk dung other than that of elephant and rhino (40–58%) was available to selective feeders.

3. Nitrogen concentrations were high – and C/N ratios low – in most types of bulk dung compared with the average food of terrestrial detritivores or herbivores. Exceptions were elephant and rhino dung with low nitrogen concentrations and high C/N ratios.

4. Estimated C/N ratios of 13–39 in bulk dung (sheep–elephant) were decreased by selective feeding to 7.3–12.6 in the ingested material. In assimilated food, ratios are

probably only 5–7, as most assimilable nitrogen and carbon may be of microbial origin. If so, the assimilable food contains a surplus of nitrogen relative to carbon.
5. The primary advantage of selective feeding, particularly in dung with a high C/N ratio, may be to concentrate assimilable carbon in the ingested food. Effects of changing the MDIP within 20–106 μm are modest, especially in dung with a low C/N ratio.

# Introduction

This study explores the quality and available quantity of the food ingested by adult beetles that feed on fresh dung. The vast majority of these coprophagous beetles belong to the Scarabaeidae, superfamily Scarabaeoidea, with roughly 5000 and 2000 dung-feeding species within the subfamilies Scarabaeinae and Aphodiinae respectively. In the considerably smaller scarabaeoid family Geotrupidae, many species also feed on fresh dung, and finally the subfamily Sphaeridiinae within the Hydrophilidae (superfamily Hydrophiloidea) contains some dung feeders. Many coprophagous beetles are large, conspicuous and relatively easy to sample and identify. They have a highly interesting biology with, for example, sophisticated brood care in scarabaeines and geotrupids. Moreover, they provide important ecological services (Losey & Vaughan, 2006) because of their prominent role in dung decay. For these and other reasons, the ecology of dung-feeding beetles has been studied by numerous workers over the last 100 years, and much of the extensive literature has been reviewed by, for example, Halffter and Matthews (1966), Halffter and Edmonds (1982) and Hanski and Cambefort (1991).

In spite of all this work, the food of the adult beetles, clearly one of their most vital resources, has been poorly known for many years – apart from the obvious fact that it is somehow extracted from fresh dung. But precisely which components of this complex substrate do the beetles actually eat? The early literature (e.g. Madle, 1934; Miller, 1961) has been briefly reviewed by Holter (2000), the main conclusion being that the beetles' guts contain a more or less fluid, paste-like suspension of tiny dung particles. More recent experimental evidence (Holter, 2000; Holter *et al.*, 2002) indicates that this is caused by some filtering mechanism in the mouthparts that rejects all larger particles prior to ingestion, rather than by a grinding of such particles by the mandibles as assumed earlier by Miller (1961) and Hata and Edmonds (1983).

The maximum diameter of ingested particles (MDIP) has now been measured for representatives of dung-feeding Scarabaeinae (26 species, 2–5 to 130 μm) (Holter *et al.*, 2002; Holter & Scholtz, 2005), Aphodiinae (six species, 2–5 to 25 μm) (Holter, 2000), Geotrupidae (two species, 50–80 μm) and Hydrophilidae (one species, about 17 μm) (Holter, 2004). Figure 1 illustrates the relationship between body size and MDIP in the largest group, the Scarabaeinae. Three functional groups are represented: (i) tunnellers (paracoprids), burying dung stores for feeding and breeding directly underneath the dung pat (filled circles); (ii) endocoprids that feed and breed in the dung pat itself (open circles); and (iii) the rollers (telecoprids) that form a food ball or brood ball, which is rolled away and buried at some distance from the pat (squares). The regression of $\log_{10}$ MDIP against $\log_{10}$ body weight has a higher slope and $r^2$-value in (iii) than in (i) + (ii), which is discussed by Holter and Scholtz (2005). Across functional groups, MDIPs are in the interval 10–30 μm in 17 (65%) of the 26 species. Thus, the MDIP for many common species (scarabaeines as well as coprophagous aphodiines and hydrophilids) of ‘normal’ size is around 20 μm.

In conclusion, although the MDIP shows some dependence of body size, all adult coprophagous beetles restrict their ingested food to very small particles, while large particles in the fresh dung are rejected by the mouthparts. Most of this coarse material is likely to consist of lignocellulosic plant fibres, too hard to digest for mammalian herbivores as well as for dung beetles, whereas the fine particles that are eaten may include easily digestible, high-quality food such as bacteria and dead epithelial cells from the herbivore’s gut. Hence, the quality of the food is probably maximised by rejection of the coarse material.

But which improvement, in quantitative terms, of ingested food compared with bulk dung is achieved by the choosiness about MDIP illustrated in Fig. 1? This paper attempts to provide an answer, particularly with regard to the nutritionally highly important nitrogen and carbon. Also, selective feeding implies a trade-off between a probable improvement in food quality and an inevitably decreased quantity of available food, since much of the material in the dung is rejected by the mouthparts. How much of a dung pat, in terms of both dry matter and nitrogen, is actually available to coprophagous beetles – and what is the effect of the MDIP and the kind of dung on that percentage? These questions are also addressed in the present study.

# Methods

### Collection of dung

Fresh, i.e. less than 1 day old, dung of several large herbivores, ruminants and non-ruminants was examined (see Table 1). Dung of wild African animals was collected in the wet season, when most dung beetles are active, in natural habitats near Skukuza (24°55'S, 31°40'E), Kruger National Park, South Africa. White rhinoceros is an exclusive (Owen-Smith, 1988) grazer, and African buffalo is primarily a grazer (e.g. Hofmann, 1989; Estes, 1991). Likewise, grass, if available, is the main food of the African elephant during the wet season, although some woody browse is also taken (Owen-Smith, 1988; Estes, 1991). Dung of domestic animals (cattle, sheep, and horse) was collected in spring/early summer (May) and in late summer (late July to early September) from pastures 30–40 km north-west of Copenhagen, Denmark, where the animals obtained all their food from grazing. The Danish grazing season is about 6 months (May–October). The dung was stored in a fridge (3–5°C) until further processing within a week after collection.

### Processing of dung – *sieving* and *filtering*

Initially, % dry matter of the dung to be *sieved* or *filtered* was determined by drying two 100–200 g (wet weight) samples to constant weight at 110°C. The dried dung was kept for analyses of nitrogen and ash content. The filtration carried out by the mouthparts of a feeding, ‘typical’ dung beetle with an MDIP of 20 μm was then imitated in two ways: *sieving* and *filtering*.

For *sieving*, a portion of 20–40 g wet dung (with a known dry weight of 3–8 g) was suspended in 1 litre of tap water, and the suspension was slowly poured through a 1-mm mesh sieve (8 cm dia., Endecotts, London) into a 1 litre container (no. 1). Gentle stirring in the sieve was necessary to prevent clogging of the meshes. With a suitably adjusted jet from the tap, the sieve was flushed with another litre of water collected in another container (no. 2). This was repeated until container no. 10 had been filled with almost clean water, indicating that practically all particles small enough to pass the sieve had done so. What remained on the sieve was defined as the fraction with a particle diameter (PD) > 1 mm. The contents of each of the 10 containers were then poured through a 250 μm sieve into another container, starting with no. 1 being poured into a new no. 1, then no. 2 into a new no. 2 etc., finishing with no. 10. Material remaining on the mesh was the fraction 250 μm < PD < 1 mm. Likewise, fractions 106 μm < PD < 250 μm, 53 μm < PD < 106 μm, and 20 μm < PD < 53 μm were successively collected.

In the last sieving, fluid passing through the mesh (20 μm) was not collected, and the material on the mesh could therefore be flushed with a gentle jet of tap water until pure water came through the sieve. It was usually necessary to divide the very particle-rich contents of container 1 into two or three portions and then sieve each portion separately (each time removing and collecting most of the material remaining on the sieve) to avoid clogging of the mesh. All size fractions were dried (110°C), weighed, and analysed for nitrogen and ash content (see below). To obtain the dry weight, ash or nitrogen content of the 0–20 μm fraction, the amounts in the other fractions were subtracted from that of the original dung sample. Pouring the initial dung suspension directly through 20 μm mesh was impossible due to immediate clogging of the sieve, whereas the use of a series of decreasing mesh sizes – gradually reducing the particle load to be finally handled in the 20 μm sieve – worked well in a reproducible way.

For *filtering*, a mixture of 50–60 g dung and 20–40 ml water (more water added to drier dung) was divided into four portions, each portion being wrapped tightly into 20 μm mesh nylon fabric. As much fluid as possible, applying the forces of the fingers, was then pressed out of the wet dung through the mesh. This fluid was dark and thick because of its very high content of small particles. It was collected in a small bowl and dried

(110°C). The dry material, i.e. the 0–20 μm fraction, was weighed and analysed for nitrogen and ash content.

Prior to analysis, dried samples were ground if necessary. *Sieving* fractions with PD > 250 μm were milled (in a Micro hammermill, Culatti, Zürich, Switzerland), and the *filtering* material was pulverised in a mortar. Total (organic) nitrogen was determined by a micro-Kjeldahl procedure as described in Hesse (1971). Ash contents were determined as residues after ignition in a muffle furnace at 500°C.

# Results

### Dung contents of water, ash, and nitrogen

As shown in Table 1, water contents varied from about 76 (horse, late summer) to 89% (cattle) of total wet weight. Ash contents ranged from 11 (elephant, January 2001) to 27% (horse, late summer) of total dry weight, and nitrogen concentrations varied from about 1.2 (elephant and rhino, January 2001) to 3.5% (horse, spring) of total dry weight.

Figure 2 shows the percentage of bulk dung dry matter and nitrogen present in the 0–20 μm and PD > 20 μm particle size fractions according to the *sieving* method. A total of 19.5% (elephant, January 2001) to 59.1% (sheep, spring) of the dry matter was in the 0–20 μm fraction. Values for domestic animals, spring, and buffalo were about 54–59%, with lower values (39–47%) for domestic animals, late summer. January 2001 percentages for the two large non-ruminants were only 20–25%. On average, across all species and times, the 0–20 μm fraction contained 42.9% of the dry matter in bulk dung. For nitrogen, all percentages were much higher, with an average of 71.3% and only one value (elephant, January 2001: 39.5%) below 50%.

Figure 3 illustrates the higher nitrogen concentration in the 0–20 μm fraction ($Y$) compared with that in bulk dung ($X$). Values provided by sieving and filtering were fitted by two, approximately parallel (difference between slopes: $t = 0.276$; d.f. = 16; $P > 0.5$) lines, nitrogen percentages from filtering being about 1 higher than those based on sieving. The ratio $Y/X$ expresses the improvement of food quality, in terms of nitrogen concentration, obtained by eating the PD < 20 μm fraction instead of bulk dung. These *improvement factors* are shown as a function of bulk dung concentrations in Fig. 4. $X$-

and *Y*-values in this figure are not independent; hence statistical tests would not be strictly valid. But it seems clear that the points based on the two methods were reasonably well ($r^2$-values around 0.8) fitted by two, roughly parallel regression lines with negative slopes. In other words, the improvement of food quality in terms of nitrogen concentration, obtained by eating the PD < 20 µm fraction rather than bulk dung, increased with decreasing nitrogen concentration in the bulk dung. For the lowest concentration measured, the improvement factors based on regressions for sieving and filtering were about 2.0 and 2.4 respectively, with corresponding values for the highest concentration at 1.4 and 1.7.

### Effects of different MDIPs

Table 2 compares three situations in four dung types: feeding with an MDIP of 20 µm, or 106 µm, or ingesting bulk dung. The effects of the MDIP were expressed in five different ways. Column III shows the percentages of the dry matter in bulk dung available in the three fractions. The corresponding percentages for nitrogen are given in column IV. For each fraction and dung type, the amount that must be ingested to get 1 mg of nitrogen is shown in column V. Also, column VI presents the quantity of bulk dung containing the amount of the fraction given in column V. In other words, the quantity of bulk dung that must be processed/filtered by the mouthparts to provide an amount of the fraction to be ingested that contains 1 mg of nitrogen. Finally, column VII shows the carbon:nitrogen (C/N) ratios of the different fractions, calculated on the assumption that the organic matter in the fractions contained 50% carbon (e.g. Allen *et al.*, 1974). C/N ratios based on *filtering* are also shown in parentheses.

## Discussion

### Water and ash in bulk dung

All dung types in the hopefully representative selection shown in Table 1 had high water contents, 76–89% of total wet weight, with a clear tendency for sheep and horse towards higher moisture in spring (lush grass low in fibre) than in late summer (high fibre). Edwards (1991) found similar wet season values for zebra (*Equus burchelli*) (75–80%) and wildebeest (*Connochaetes taurinus*) (74–78%). Dung pellets produced by some herbivores, for example impala (*Aepyceros melampus*) and giraffe (*Giraffa camelopardalis*), are somewhat drier. Thus, wet season water contents of 67–71% (Edwards, 1991) (samples from a year with unusually high rainfall) and 52% (Paetel, 2002) have been found in impala pellets. Also, Paetel (2002) reported 54% water in giraffe dung. However, field tests in the Kruger Park (Paetel, 2002) showed that most dung beetles preferred moist dung of elephant or buffalo over drier impala or giraffe pellets, which agrees with observations made in the present study. Even the large roller *Kheper nigroaeneus* (Boheman), which sometimes does exploit impala and giraffe dung (Edwards & Aschenborn, 1988), showed the same preference in spite of higher nitrogen contents in impala and, particularly, giraffe pellets (Paetel, 2002). This agrees with Edwards' (1991) finding that breeding (brood balls per female) of the Afrotropical scarabaeine *Euoniticellus intermedius* (Reiche) in wildebeest dung was positively correlated with dung water content within the range 65–78%. Below 65%, no breeding, and hence probably not much feeding, took place. The explanation could be that filtering out coarse particles prior to ingestion – an essential part of the feeding process – is easier with moist dung.

Ash contents (Table 1), varied between 11% and 27% in a somewhat erratic way without clear trends with regard to season (spring/late summer), species, or digestive physiology (ruminant/non-ruminant). Ash contents are probably mainly determined by the amount of silica in the grass and of the mineral soil particles (mostly adhering to roots) that are swallowed during grazing and are easily detectable in most dung samples. Such particles with diameters below the MDIP are also ingested by dung beetles and can be observed in their guts (P. Holter, unpublished). However, apart from causing some dilution, these particles are hardly important determinants of the quality of dung as food.

### Nitrogen in bulk dung

Nitrogen concentrations were from 1.1 to 3.5% (Table 1), with both the lowest and the highest value in dung of non-ruminants (elephant and horse respectively). Likewise, Edwards (1991) found wet-season contents for zebra and wildebeest of 1.2–1.6% and 1.5–2.2%, while Paetel (2002) reported 1.2, 1.3, and 1.5% nitrogen in dung of zebra, buffalo, and elephant respectively. There is no obvious, consistent association between % nitrogen and digestive physiology (ruminant/non-ruminant), although values for the non-ruminant megaherbivores were in the lower end of the range. The relatively high nitrogen concentration in elephant dung from December 2002 was probably caused by very good grazing promoted by higher rainfall than in 2001. Also, domestic animal dung from spring had a higher nitrogen content than that from late summer, reflecting the generally declining quality of the grazing from May to July–August. Similar seasonal differences have been found by, for example, Greenham (1972). Dry-season dung from wild animals may have lower nitrogen contents than those reported here (Edwards, 1991), but few dung beetles are active during that part of the year.

The carbon:nitrogen (C/N) ratio, which unlike nitrogen concentration is independent of the rather variable ash content, is a widely used index of the quality of organic material as food for heterotrophic organisms (e.g. Swift *et al.*, 1979; Fog, 1982; Elser *et al.*, 2000; Dorgelo & Leonards, 2001). Bulk dung ratios (weight/weight) in Table 1 are from 12–14 (domestic animals in spring) to 34–39 (rhino and elephant, January 2001), and Paetel's data (2002) lead to wet-season values of about 22, 25, 32, and 37 for impala, buffalo, elephant, and zebra respectively. Compared with the C/N ratios that many terrestrial decomposers must cope with, most of these dung values are low. For Danish beech litter, for example, the C/N ratio is about 45 (P. Holter, unpublished), and Christensen's (1987) data imply values of 40, 91, 109, and 184 for wheat, rye, barley, and oats straw respectively. Ratios for decomposing wood are even higher. Many dung types are also relatively rich in nitrogen compared with the average food of terrestrial herbivores. For the foliage of 406 plant species, Elser *et al.* (2000) found a mean C/N ratio of 31 (atomic ratio: 36). Values for most dung types in Table 1 are considerably lower, and only the ratios for rhino and elephant (January 2001) are higher. Beetles feeding on the latter substrates may need a mechanism that decreases the C/N ratio of the ingested food relative to that in bulk dung. This is further discussed in the section on *Costs and benefits of selective feeding*.

### *Sieving* and *filtering*

Prior to an analysis of what the selective feeding of dung beetles may achieve, a brief discussion of whether the action of dung beetle mouthparts was best simulated by *sieving* or by *filtering* seems necessary. The 0–20 µm fraction obtained by *sieving* contained everything with a diameter below 20 µm. During *filtering*, on the other hand, particles larger than 20 µm may soon have blocked, at least partly, the passage through the meshes of particles in the upper end of the 0–20 µm range. Even for particles with diameters below 20 µm, the chance of passing the filter may therefore have decreased with increasing particle size. This is confirmed by the higher nitrogen concentrations in the *filtering* than in the *sieving* fractions (Fig. 3). The latter probably contained a higher proportion of relatively large (within the 0–20 µm range) plant fragments with very low nitrogen content.

In dung beetles, a particle's chance of passing the mouthpart filter – even if that particle is below the MDIP – also declines gradually with increasing particle size as illustrated in Fig. 5. This means, for example, that although the MDIP in the very large roller *Circellium bacchus* Fabricius is 125–130 µm, a 60 µm particle's probability of passing the filter is only about 50%. Extrapolation of the curves (dotted lines in Fig. 5) suggests that only particles with diameters below about 5 µm in the tunneller *Heteronitis castelnaui* (Harold) (MDIP approximately 25 µm) and 25 µm in *Circellium* will never be filtered out. Hence, the action of the mouthparts was probably better mimicked by *filtering* than by *sieving*. On the other hand, sieving provided data (e.g. columns III–IV in Table 2) that could not be obtained by filtering. Fortunately, nitrogen concentrations resulting from the two methods were not highly different, and so at least qualitative conclusions based on sieving are likely to hold.

### Costs and benefits of selective feeding

Table 2 compares data for three particle size fractions in four contrasting dung types: fine ruminant dung with high (domestic sheep) or intermediate (buffalo) nitrogen content and coarse, non-ruminant dung (rhino, elephant) low in nitrogen. In bulk sheep dung, the C/N ratio (column VII) is already very low and the beetles may not need the additional reduction caused by selective feeding. A more important benefit could be the decrease by 37% (sieving) or, perhaps more realistically, 43% (filtering) in the amount of food to be processed by the gut per mg ingested nitrogen (column V), assuming a 20 µm MDIP. A potential cost could be that 44% or 35% (column III) of the total dry matter in bulk dung will be filtered out by beetles with MDIPs of 20 or 106 µm respectively. This, however, is hardly essential because about 90% of the total nitrogen (and probably of the assimilable carbon, see below) is still available for ingestion (column IV and Fig. 2). Similar arguments apply to buffalo dung, although there is a larger decrease in the C/N ratio due to selective feeding (20 µm MDIP). The reduction of ingestion per mg nitrogen (column V) is 35% (sieving) or 52% (filtering). No really important effect of increasing the MDIP from 20 to 106 µm is indicated in either type of ruminant dung.

The C/N ratios of 34–39 (column VII) in bulk dung of rhino and elephant are much higher, and the reduction to 13–15 (sieving) or 12–13 (filtering) in the ingested food is probably a very beneficial effect of selective feeding (20 µm MDIP). This could also be true of the large decrease – by 57–59% based on filtering values – in the amount of food to be processed by the gut per mg ingested nitrogen (column V). Regarding costs of selectivity, only 52% (rhino) or 40% (elephant) of total nitrogen (and available carbon, see below) in the bulk material is accessible (column IV and Fig. 2), but the absolute amount of nitrogen available to choosy dung beetles is still considerable because most dung piles of rhino or elephant are big. The amount of elephant bulk dung that must be processed by the mouthparts to yield ingested food with 1 mg nitrogen is increased by selectivity (MDIP 20 µm) to 222 mg dry weight (column VI), or about 1 g wet weight. This is 6.5 or 4.2 times the corresponding values in sheep or buffalo dung respectively. If this were an important parameter, elephant dung should be much less attractive to dung beetles than most other dung types. However, it is highly attractive to many species (e.g. Anderson & Coe, 1974; Heinrich & Bartholomew, 1979; Paetel, 2002; authors' observations). Hence, the large amount of bulk dung needed to obtain sufficient nitrogen (and carbon, see below) is probably of minor importance – if there is enough dung. There could, however, be a problem for rollers with considerably less dung available for feeding than is usually the case with tunnellers of similar size (Holter & Scholtz, 2005).

With limited supplies, a relatively large MDIP might be an advantage because an increase of the MDIP from 20 to 106 μm leads to a 14% decrease in the amount of elephant bulk dung that must be processed by the mouthparts. This could be a reason why large rollers have higher MDIPs than do tunnellers of the same size (Fig. 1) (Holter & Scholtz, 2005). Otherwise, like in the ruminants, effects of changing the MDIP from 20 to 106 μm are modest. Hence, a strong selective pressure towards a sharply defined relation between MDIP and body size seems unlikely in tunnellers, given their relatively large dung supplies. This is in accordance with the rather low $r^2$-value (0.50) for these beetles in Fig. 1.

To summarise, beneficial effects, related to nitrogen, of selective feeding are much more obvious in nitrogen-poor (e.g. elephant) than in nitrogen-rich (e.g. domestic sheep) dung. This agrees with the point already made in Fig. 4, based on all examined dung types: the *improvement factor* owing to selective feeding is higher in poor than in rich dung. However, the carbon economy of the beetles, alluded to several times above, must also be briefly considered.

The optimum C/N ratio in the assimilated food of a heterotrophic organism is supposed to be roughly twice the ratio of the organism itself (or slightly higher), because extra carbon, in addition to that used for tissue production, is needed to cover energy expenses (Russell-Hunter, 1970; Fog, 1982). As the C/N ratio of a ‘typical’ insect body is about 5–7 (Allen *et al.*, 1974; Elser *et al.*, 2000), the optimum ratio in the assimilated food of a dung beetle should be approximately 10–20. The ratio of ingested food (based on filtering) is about 7–13 – already in the low end of, or below, the optimum range – but that of assimilated food must be even lower. The reason is that whereas most dung nitrogen, located in easily digestible microbial biomass (dead or alive) and gut secretions/waste products such as dead epithelial cells, is assimilable, a substantial part of the ingested carbon is not. Although without larger plant fragments, the ingested food may still contain high numbers of lignocellulose particles smaller than the MDIP. This is confirmed by microscopic inspection as well as the chemical analyses reported by Paetel (2002). Most carbon in these particles is probably inaccessible as the beetles do not have any known specialisation, such as a gut fermentation chamber, for the digestion of structural plant carbohydrates or lignin. If so, the main source of carbon must be the same as that of nitrogen. The C/N ratio of the assimilated food should therefore be close to that of microbial biomass dominated by bacteria, i.e. 5–7 (e.g. Merckx & Van der Linden, 1988), no matter what the ratios in ingested food and bulk dung are. As ratios of 5–7 are only half the supposed optimum, the assimilable food contains a surplus of nitrogen relative to the carbon. For sufficient carbon assimilation, mouthparts and gut must actually process roughly twice the amounts of bulk dung and ingested food needed for adequate nitrogen, amounts that are already large in, for example, elephant dung.

Thus, the main advantage of selective feeding may be to maximise the concentration of assimilable carbon in the ingested food. This is achieved partly by removal of intractable lignocellulose by the mouthpart filter, and partly [at least according to a hypothesis put forward by Holter (2000)] through elimination of superfluous water by the mandibular molars. If assimilable carbon and nitrogen are both mainly of microbial origin, their concentrations in the dung should be closely linked. Hence, it is particularly in substrates with a low nitrogen content, for example elephant dung, that selective feeding is needed. This agrees with the earlier finding that, contrary to intuitive expectations, tunnellers specialising in coarse dung of rhino or elephant do not have larger MDIPs relative to body size than do species feeding on much finer ruminant dung (Holter *et al.*, 2002).

## Concluding remarks

This study deals mainly with nitrogen and carbon, whereas analyses of other nutrients had to be omitted. With this limitation, the evidence suggests that the primary problem for animals feeding on fresh dung, particularly if the nitrogen concentration is low, is to get enough assimilable carbon without ingestion of enormous quantities of dung. The problem is solved by selective feeding, concentrating both assimilable carbon and nitrogen in the ingested food. The main sources of these nutrients are probably microbial biomass and intestinal waste products (mucus, dead epithelium), because the herbivore has already used easily accessible carbon and nitrogen in the original plant material. This means that dung beetles are rather far from being phytophagous as assumed by Gäde and

Auerswald (2002). The low C/N ratio, probably 5–7, of the likely sources of assimilable carbon and nitrogen also means that if sufficient carbon is acquired, it will automatically be accompanied by more than adequate supplies of nitrogen.

Selective feeding seems to have evolved independently in the three families with coprophagous beetles: Geotrupidae, Scarabaeidae, and Hydrophilidae (Holter, 2004). This evolution, of course, did not take place in a modern world dominated by domestic, mainly ruminant herbivores grazing in agriculturally managed, high-quality pastures. In the resulting dung with high availability of nutrients, advantages of selective feeding can be rather modest. In fact, simple bulk feeding might be feasible in, for example, the *spring dung* of domestic Danish sheep. In the evolutionary past, on the other hand, that kind of dung was probably uncommon, whereas dung piles of the once very prominent (Owen-Smith, 1988) non-ruminant megaherbivores – and of ruminants subsisting on relatively poor grazing – may have been the predominant resources that coprophagous beetles had to adapt to. Under such circumstances, evolution of selective feeding appears to have been essential for efficient exploitation of the patchy and ephemeral, but locally abundant, form of detritus made up by fresh dung.

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# Figures and Tables

**Fig. 1.** Maximum diameter of ingested particles (MDIP) in relation to mean fresh body weight for tunnellers + three endocoprids (filled circles, solid regression line) and rollers (open squares, dashed regression line). $\text{Log}_{10}$ scales on both axes. The regression for rollers [$\log \text{MDIP} = 1.69 + 0.48 \log W$ ($r^2 = 0.92$; $P < 0.0001$)] includes one, two, four, and four species in the tribes Canthonini, Sisyphini, Gymnopleurini, and Scarabaeini respectively. To obtain a better picture of the relationship for all the other rollers, the highly deviant sisyphine *Neosisyphus rubrus* (black square) is not included in the regression (cf. Holter & Scholtz, 2005). The regression for tunnellers and endocoprids [$\log \text{MDIP} = 1.43 + 0.25 \log W$ ($r^2 = 0.50$; $P < 0.01$)] includes three, three, four, and five species in the tribes Coprini, Onitini, Oniticellini, and Onthophagini respectively. Data from Holter *et al.* (2002) (tunnellers + endocoprids) and Holter and Scholtz (2005) (rollers), supplemented by one point (grey square) for the large canthonine roller *Circellium bacchus* (P. Holter & L. Stenseng, unpublished).

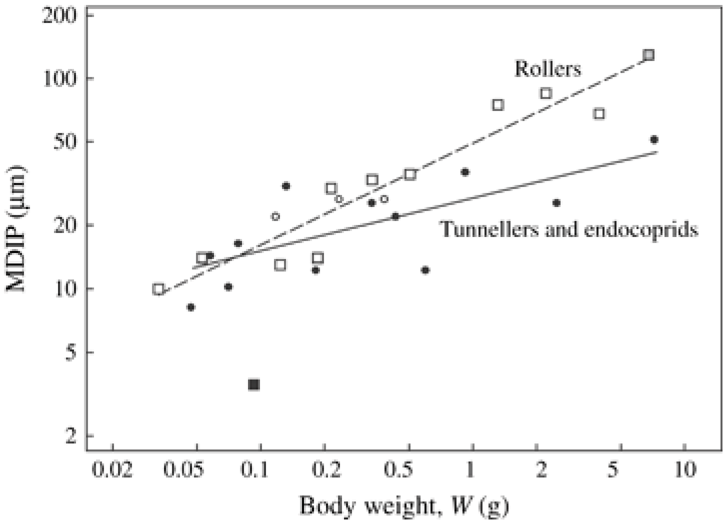

**Fig. 2.** Percentages of the total dry matter and nitrogen in bulk dung located in the particle size fraction 0–20 µm and in the remaining dung with particle diameters (PD) larger than 20 µm. Data based on *sieving* (see main text).

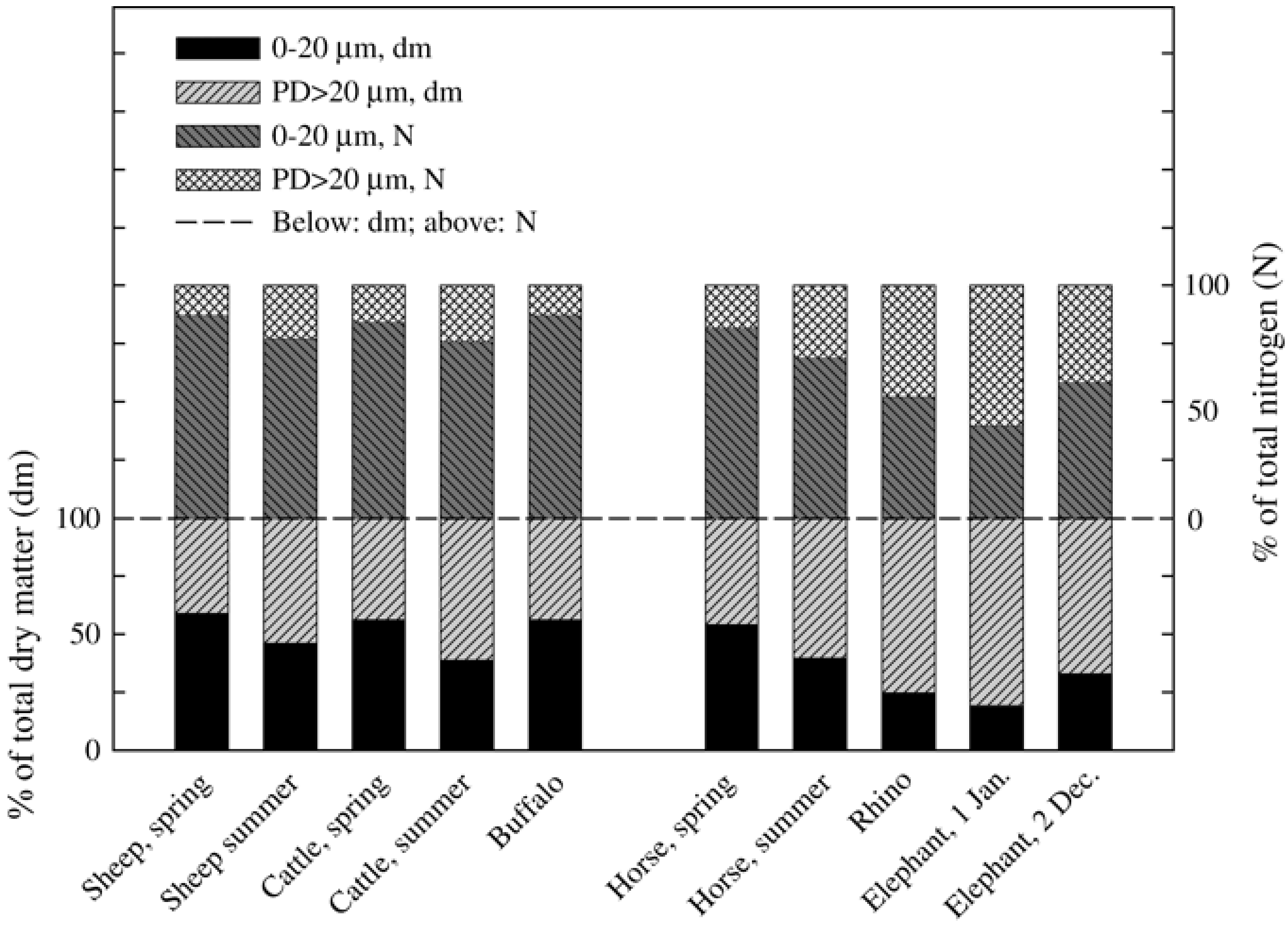

**Fig. 3.** Nitrogen concentrations (% of dry weight) in the 0–20 µm particle fraction based on *sieving* (filled symbols, solid regression line) and *filtering* (empty symbols, dashed regression line) against concentrations in bulk dung. Symbols used for the different kinds of dung are as given in Table 1. Regression for sieving: $Y = 1.12 + 1.16X$ ($r^2 = 0.96$; $P = 0.0004$). Filtering: $Y = 1.55 + 1.32X$ ($r^2 = 0.90$; $P = 0.003$).

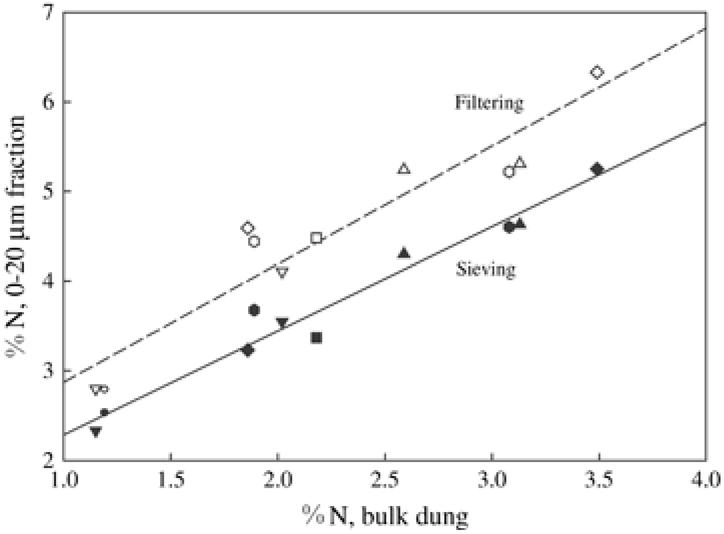

**Fig. 4.** Nitrogen *improvement factors*, i.e. % nitrogen in the 0–20 µm fractions divided by concentrations in the corresponding bulk dung, in relation to % nitrogen in bulk dung. Symbols as in Fig. 3. Regression for sieving: $Y = 2.31 - 0.26X$ ($r^2 = 0.82$). Filtering: $Y = 2.82 - 0.32X$ ($r^2 = 0.79$).

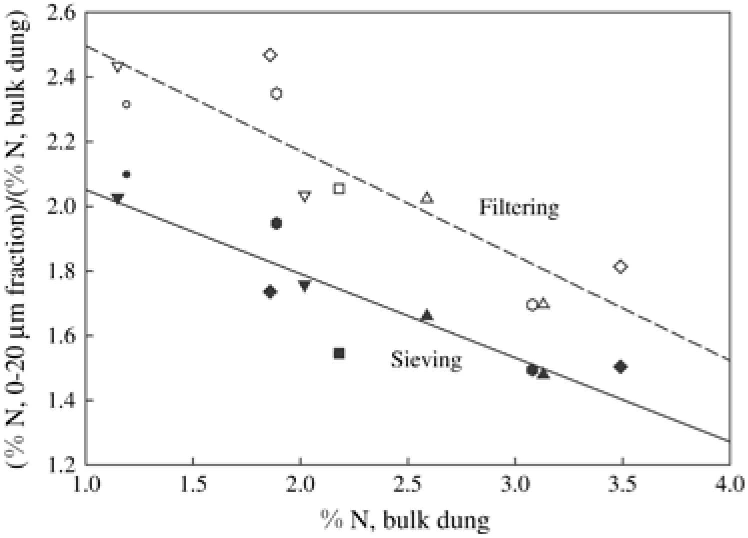

**Fig. 5.** Mean probabilities of passage through the mouthpart filters of the tunneller *Heteronitis castelnaui* [data from Holter *et al.* (2002)] and of the roller *Circellium bacchus* (P. Holter & L. Stenseng, unpublished) for ball-shaped particles of different diameters. The maximum diameter of ingested particles (MDIP) is defined as the diameter with a 5% probability of passage (dashed line). Dotted lines are explained in the text.

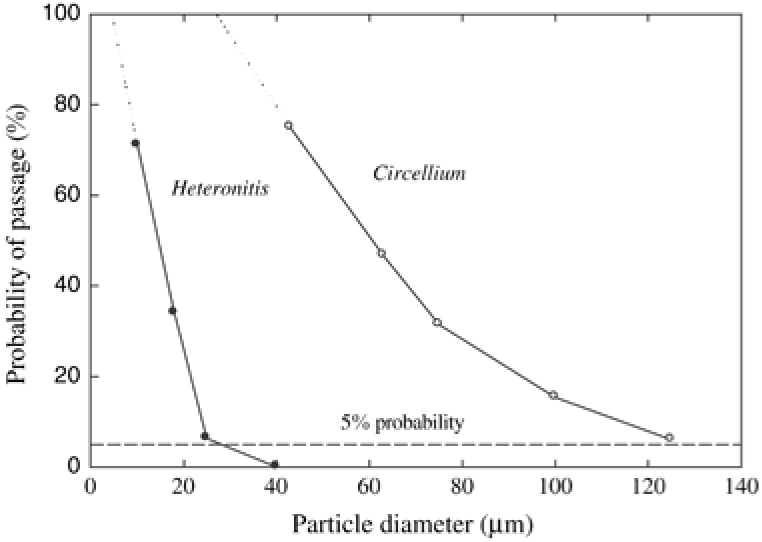

**Table 1.** Some basic characteristics of fresh bulk dung from three ruminants (sheep, cattle, buffalo) and three non-ruminants (horse, rhino, elephant). If *n* (number of independent dung samples) >1, percentages are means ± SE. The species symbols are used (filled or empty) in Figs 3 and 4. C/N (carbon/nitrogen) ratios were calculated assuming 50% carbon in the organic matter.

| **Dung from** | ***N*** | **Time of collection (month; year)** | **% water (of total wet weight)** | **% ash (of dry weight)** | **% nitrogen (of dry weight)** | **C/N ratio** |
|---|---|---|---|---|---|---|
| Sheep, ▲ | 3 | May; 2000, 2002 | 83.3 ± 1.20 | 20.0 ± 3.58 | 3.13 ± 0.102 | 12.8 |
| Sheep, ▲ | 2 | August, September; 2000, 2001 | 78.4 ± 4.01 | 12.3 ± 0.14 | 2.59 ± 0.077 | 16.9 |
| Cattle, ⬢ | 2 | May; 2000, 2001 | 88.7 ± 0.03 | 14.0 ± 0.23 | 3.08 ± 0.042 | 14.0 |
| Cattle, ⬢ | 2 | July, August; 2001, 2000 | 89.2 ± 0.45 | 15.8 ± 0.18 | 1.89 ± 0.002 | 22.3 |
| African buffalo (*Syncerus caffer*), ■ | 3 | January; 2003 | 84.3 ± 0.95 | 20.9 ± 1.50 | 2.18 ± 0.051 | 18.1 |
| Horse, ♦ | 1 | May; 2001 | 85.0 | 18.1 | 3.49 | 11.7 |
| Horse, ♦ | 2 | July, August; 2001, 2000 | 75.9 ± 4.82 | 27.0 ± 4.72 | 1.86 ± 0.243 | 19.6 |
| White rhino (*Ceratotherium simum*), • | 4 | January; 2001 | 79.3 ± 0.97 | 17.9 ± 1.18 | 1.20 ± 0.038 | 34.2 |
| African elephant (*Loxodonta africana*), ▼ | 4 | January; 2001 | 77.7 ± 1.08 | 11.2 ± 1.11 | 1.14 ± 0.029 | 38.9 |
| African elephant, ▼ | 1 | December; 2002 | 80.3 | 15.7 | 2.02 | 20.9 |

**Table 2.** Properties (mean values) of different particle size fractions in four types of fresh dung. Non-bracketed data for the small-particle fractions are based on *sieving*, bracketed values on *filtering*. Column V gives the amount of the size fraction that must be ingested to obtain 1 mg of nitrogen. VII is the carbon:nitrogen (C/N) ratio, assuming 50% carbon in the organic matter. Weights, percentages, and C/N ratios are based on dry weight. Further explanations in the text.

| **Dung** | **Dung fraction** | **% nitrogen** | **% of bulk dung dry matter in fraction** | **% of bulk dung N in fraction** | **mg ingested fraction per mg ingested N** | **mg bulk dung with the amount of the fraction given in V** | **C/N ratio** |
|---|---|---|---|---|---|---|---|
| | **I** | **II** | **III** | **IV** | **V** | **VI** | **VII** |
| Sheep, May 2005 | 0–20 µm | 5.17 (5.95) | 56 | 87 | 19 (17) | 34 | 9.9 (7.3) |
| | 0–106 µm | 4.64 | 65 | 91 | 22 | 33 | 11 |
| | Bulk | 3.33 | 100 | 100 | 30 | 30 | 12.8 |
| Buffalo, January 2003 | 0–20 µm | 3.37 (4.48) | 56 | 87 | 30 (22) | 53 | 11.2 (8.6) |
| | 0–106 µm | 3.00 | 66 | 91 | 33 | 51 | 12.3 |
| | Bulk | 2.18 | 100 | 100 | 46 | 46 | 18.1 |
| Rhino, January 2001 | 0–20 µm | 2.51 (2.77) | 25 | 52 | 40 (36) | 159 | 12.7 (12.0) |
| | 0–106 µm | 2.28 | 31 | 58 | 44 | 143 | 14.0 |
| | Bulk | 1.20 | 100 | 100 | 83 | 83 | 34.2 |
| Elephant, January 2001 | 0–20 µm | 2.33 (2.80) | 20 | 40 | 43 (36) | 222 | 15.2 (12.6) |
| | 0–106 µm | 2.20 | 24 | 46 | 46 | 192 | 16.3 |
| | Bulk | 1.14 | 100 | 100 | 87 | 87 | 38.9 |