

Two dung beetle species that disperse mimetic seeds both feed on eland dung

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Scarabaeus spretus zur Strassen was observed to roll and bury *Ceratocaryum argenteum* (Restionaceae) seeds in the sandplain fynbos of the Potberg area of the De Hoop Nature Reserve, South Africa. This species is the second dung beetle species found to be deceived by the faecal mimicry of *C. argenteum* seeds – the first species being *Epirinus flagellatus*. An isotopic analysis suggests that both these dung beetle species most likely feed on eland (*Taurotragus oryx*), not bontebok (*Damaliscus pygargus pygargus*), dung. Thus the model in this mimicry is eland dung; this interaction suggests large herbivores are an integral part of this fynbos.

Introduction

The dung beetle *Epirinus flagellatus* was observed to roll and bury seeds of the Cape plant *Ceratocaryum argenteum* (Restionaceae) at a site in the Potberg part of the De Hoop Nature Reserve in South Africa.¹ This primary dispersal of seeds involves chemical and visual mimicry because neither the dung beetle nor its larvae can eat these hard seeds. Chemically the seeds have characteristics of the dung of both of the most common large herbivores in the reserve: the eland (*Taurotragus oryx*) and the bontebok (*Damaliscus pygargus pygargus*).¹ However, the seeds are more similar in shape and size to the smaller faeces of the bontebok, which is then the possible visual model that *C. argenteum* mimics. At the same Potberg site, during February 2016, we observed similar seed dispersal of *C. argenteum* seeds by another dung beetle, *Scarabaeus spretus* zur Strassen. The aim of this paper is to document this new burial behaviour and to investigate both dung beetle species to determine whether the faeces of the bontebok or the eland is the likely model of the mimic.

The bontebok is a short grass grazer whereas the eland is a mixed feeder.^{2,3} The two dominant grassland/renosterveld grass species at Potberg are *Cymbopogon popschilli* (Andropogoneae) and *Cynodon dactylon* (Chloridoideae),³ to which can be added the relatively widespread *Themeda triandra* (Andropogoneae). All three species utilise the C4 photosynthetic pathway rather than the C3 pathway.⁴ This pathway is common in tropical grasses whereas the C3 system is more common in woody plants and temperate grasses. The enzymes of these two different photosynthetic pathways produce different carbon $\delta^{13}\text{C}$ signatures in their photosynthetic products. The relatively rare stable isotope of carbon, ^{13}C , is slightly heavier than the more common ^{12}C , which affects the ratios of these isotopes in different plants depending, for example, on enzyme preferences for the lighter isotopes. Fractionation is the process which reflects changes in relative proportions of isotopes, such as $^{13}\text{C}:^{12}\text{C}$ during C3 photosynthesis. Fractionation can also occur in ^{15}N because, as it is heavier than ^{14}N , it may increase in tissues depending on factors such as levels of metabolism, catabolism and excretion. Thus animals are typically enriched by +3–5‰ in $\delta^{15}\text{N}$ compared to their diet, although typically they are less than +1‰ enriched in $\delta^{13}\text{C}$.⁵ During metamorphosis, larval tissue is broken down and then used to form new adult tissue and thus metamorphosis is also known to increase both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the adult tissue in much the same way as would happen in adult tissue with an increase in trophic level.⁶ Thus the hypothesis that bontebok dung is the likely model *C. argenteum* mimics can be tested using the isotopic method for diagnosing animal diets, including those of dung beetles.⁷

Methods

The study took place in the Potberg area of the De Hoop Nature Reserve (34.374420 S, 20.533060 E) in the sand plain vegetation type in which *C. argenteum* grows. During 3 days in early February 2016, we placed out 5 to 10 piles of *C. argenteum* seeds, with each pile comprising 10–20 seeds. Piles of seeds were 10 m apart on the edge of a 100-m stretch of a sand road through natural vegetation. We monitored the seed piles in the early morning for approximately 2 h (starting at about 08:00). This experiment took place after a 24-h rain event.

Dung samples were taken in various vegetation types in the Potberg reserve. These types were renosterveld (dominated by the shrub *Elytopappus rhinocerotis* (Asteraceae)), grassland (dominated by *Cynodon dactylon*), salt marshes (dominated by Chenopodiaceae), valley bottom fynbos (dominated by the Proteaceae shrubs *Leucadendron linifolium*/ *L. coniferum*), sand plain fynbos (dominated by *Leucadendron laureolum*, where *C. argenteum* occurs) and limestone fynbos (dominated by *Leucadendron meridianum*). Eland dung was found at all six sites whereas bontebok dung was found at all but the last two fynbos sites (sand plain fynbos and limestone fynbos). Previously, Radloff et al.³ noted that bontebok avoid fynbos whereas eland are found throughout fynbos, including limestone fynbos. To reduce chances of pseudoreplication, we sampled only a single pellet of bontebok or eland dung from a dung pile; only dung piles greater than 5 m apart were sampled and, as judged by colour, only relatively fresh samples were collected until a total of 10 pellets had been sampled from within each vegetation type. Dung pellets and dung beetle exoskeletons were dried and analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, in ‰, using standard techniques at the Archaeometry Lab at the University of Cape Town. Dung beetle larvae have chewing teeth and are vigorous detritivores that depend on the plant remains that constitute the dung ball, rather than being dependent on microbiota associated with the ball.⁸ Although female beetles do select small fragments of plant remains from dung to constitute brood balls,⁸ this is not likely to significantly affect the isotopic signature of these balls nor the signature of the exoskeletons of adults that emerge from these balls.



Figure 1: (a) *Epirinus flagellatus* rolling a *Ceratocaryum argenteum* seed; (b) *Scarabaeus spretus* rolling a seed (the arrow indicates a sphaerocerid lesser dung fly); (c) the large hole made by *S. spretus* for burying several seeds (the arrow indicates the location of the dung beetle); and (d) a female sarcophagid fly on a seed.

Results

Dung beetles arrived at seed stations within a few minutes of placing seeds out; thus within 2 h each day, more than 10 beetles had arrived at seed piles along our short 100-m transect and had started burying seeds (Table 1 and Figure 1a–c). *E. flagellatus* crawled out of the vegetation towards seed piles, with only an occasional individual flying in, whereas all *S. spretus* individuals flew towards the seed piles. It was clear, based on the direct flight or crawling paths of both species to the seeds, that the attraction is strongly chemical. A *S. spretus* beetle even flew into a paper bag containing seeds. All cases of *S. spretus* burial involved limited movement of seeds (<0.25 m) from seed piles, whereas *E. flagellatus* moved seeds up to 2 m. *S. spretus* beetles were observed to frantically bury up to three seeds ($n=2$) and often five or more seeds ($n=4$) per excavated hole (see the video in the supplementary material online). *E. flagellatus* was observed to only bury seeds individually, similarly to observations by Midgley et al.¹ Flies of the Sarcophagidae were frequently observed to settle on *C. argenteum* seeds (Figure 1d), indicating that they too are deceived by the scent of the seeds. These ‘flesh flies’ are typically attracted to dung, carrion or rotting vegetation.⁹ Lesser dung flies (Sphaeroceridae) were observed on *S. spretus* (Figure 1b).

Samples of the grasses *Cynodon dactylon* and *Themeda triandra* from Potberg have a typical C4 isotopic signal ($n=2$ for each species, mean $\delta^{13}\text{C}$ of -13.61‰ and -14.29‰ , respectively).

Table 1: Observations of dung beetles at *Ceratocaryum argenteum* seed stations at Potberg

Date	Duration (min)	Number of <i>Epirinus flagellatus</i> individuals	Number of <i>Scarabaeus spretus</i> individuals
4 February 2016	120	10	3
5 February 2016	135	8	7
6 February 2016	90	7	3
Total	345	25	13

Dung of eland and bontebok are significantly different in both $\delta^{13}\text{C}$ ($U=52$, $p<0.001$, Mann-Whitney test) and $\delta^{15}\text{N}$ ($U=309$, $p<0.0001$, Mann-Whitney test) (Table 2). Bontebok graze a fairly equal mixture of C4 and C3 plants to create a mean $\delta^{13}\text{C}$ value of -20.10‰ , whereas eland are mostly eating C3 plants (Figure 2 and Table 2).

Table 2: Isotope analyses of dung beetles and dung from Potberg

	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Epirinus flagellatus</i>	8	-25.76 (0.54)	4.48 (1.24)
<i>Scarabaeus spretus</i>	9	-26.45 (0.37)	6.92 (0.97)
Bontebok dung	40	-20.1 (2.44)	2.6 (0.89)
Eland dung	60	-26.71 (1.33)	1.23 (0.78)

Values shown are mean (s.d.) in ‰.

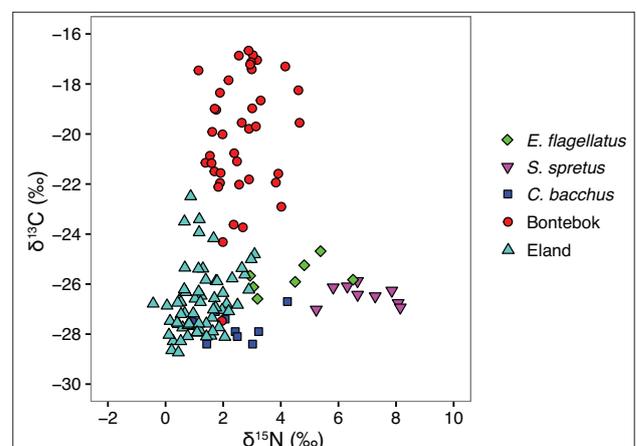


Figure 2: The distribution of isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the dung of bontebok and eland as well as of three dung beetle species.

Discussion

The increase in $\delta^{15}\text{N}$ as a result of metamorphosis is in the range of +3‰ and +5‰ for a selection of insects ranging from Diptera to Coleoptera to Lepidoptera⁶ and the increase in $\delta^{13}\text{C}$ is about +1‰⁵. Dung beetle adults whose larvae fed on bontebok dung should thus have values of slightly more than -20‰ $\delta^{13}\text{C}$ but up to 7.6‰ $\delta^{15}\text{N}$. The mean $\delta^{13}\text{C}$ values of both *E. flagellatus* and *S. spretus* clearly indicate a C3 dung diet and are thus much closer to that of the eland dung (Table 2 and Figure 2). The $\delta^{15}\text{N}$ values are 3.25‰ and 5.7‰ above eland dung but only 1.9‰ and 4.32‰ above bontebok dung. The evidence from $\delta^{15}\text{N}$ of the beetles is less equivocal about the larval food source because of the small 1‰ difference in dung between the two herbivore species. Overall the isotope results are compatible with eland being the main larval source of dung. Also bontebok dung is rare in the lowland fynbos habitat of *C. argenteum*. As these two dung beetle species are from different genera and are both attracted to *C. argenteum* seeds, these results indicate that the seed chemistry and deception by *C. argenteum* is not dung beetle species-specific. The deception appears most likely to be modelled on the chemistry of eland, rather than bontebok, dung.

Not much is known of the feeding biology of *Scarabaeus* or *Epirinus* beetles.¹⁰ For both species, we observed diurnal activity and no pair formation at seed burial sites. *C. argenteum* seeds are about the same size as bontebok droppings and about half the size of eland droppings. That many seeds were buried per site for *S. spretus* suggests that several pellets of eland dung are typically used for feeding or egg laying, whereas *E. flagellatus* only buried a single seed per burial event. This distinctive burial behaviour of the two species likely results in differential recruitment patterns for *C. argenteum* seedlings. Single *E. flagellatus* burials would lead to lower intraspecific competition between seedlings compared with the multiple burials by *S. spretus*.

Many other dung beetles occur at Potberg, for example, the millipede-eating *Sceliages adamastor*.¹⁰ The $\delta^{15}\text{N}$ dung beetle values presented in Table 1 provide a framework to interpret those of *S. adamastor* to determine whether this beetle is an obligate insectivore. For example, $\delta^{15}\text{N}$ values of an obligate millipede-eater should be a trophic level above herbivorous dung beetles such as *S. spretus* and *E. flagellatus* (i.e. they should have $\delta^{15}\text{N}$ values greater than 7‰). The very large Addo flightless dung beetle (*Circellium bacchus*) also occurs at Potberg¹⁰; elsewhere it feeds on elephant dung¹⁰ but as there are no elephants at Potberg, its diet there is unknown and could too be clarified using the isotopic method. Being flightless, *C. bacchus* is often killed on roads and our analysis of nine roadkill individuals (mean $\delta^{13}\text{C}$ of -27.70‰ and $\delta^{15}\text{N}$ of 2.39‰) indicates eland dung is also its major larval food source.

The fact that *Ceratocaryum argenteum* is an element of deep sand fynbos,¹¹ implies that sufficient quantities of large herbivore dung, such as that of eland, occurred in this vegetation. This would maintain the associated dung beetle species and the deceptive relationship between *C. argenteum* and these species. There is some debate as to whether large herbivores were once more common in fynbos and in this area of the Cape.³ Our observation that *C. bacchus*, *E. flagellatus* and *S. spretus* utilise eland dung suggests that the eland is, and has been, a key species

in this system and should be carefully managed as such. Finally, we suggest that there are now sufficient examples of seed dispersal by beetles for use of the term coleopterochory. This term would include primary dispersal such as that described above, as well as examples of beetle endozoochory¹² in which small seeds are swallowed, as well as incidental or secondary dispersal in dung or with fruit¹.

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Authors' contributions

Both authors participated in field work, analysis and writing.

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