The distribution of dung and its nutrients by dung beetles

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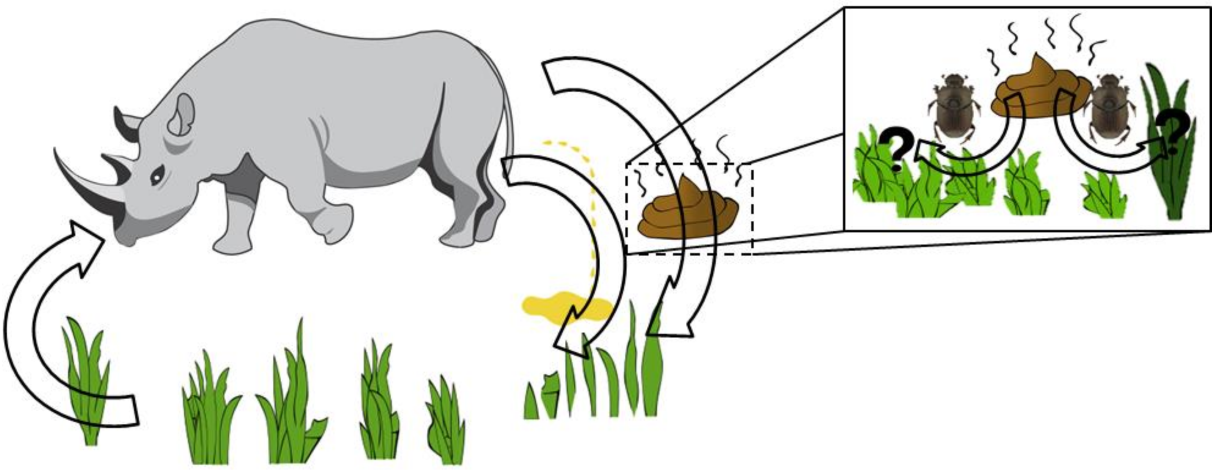
Master report



Abstract

Nutrient cycling is essential for ecosystem functioning and is a complex process influenced and determined by many different components. In African savannas, large grazers can accelerate nutrient cycling through creating readily available nutrients in their urine and dung, thereby enhancing the carrying capacity of their ecosystem. Despite theories involving the importance of dung fertilization, this has barely been researched, in contrast to fertilization through urine. The theory described above assumes that large herbivores fertilize the areas where they graze most, namely the highly nutritious lawn vegetation. In heterogeneous savannas this might not be the case, even when dung is originally deposited on the grazed lawn grasses. Dung beetles could move large amounts of dung to other vegetation patches, such as the low nutritious bunch grasses or shrubs.

Here we investigated how do dung beetles influence the nutrient cycling process of large herbivore dung through post-depositional dung translocation in a heterogeneous South-African savanna. In the Hluhluwe-iMfolozi Game Reserve in South-Africa, dung counts were performed to determine where and how much dung is deposited. Dung piles were placed to investigate what percentage of a dung pile is removed by rolling dung beetles, and dung beetles were followed to determine in what type of vegetation they bury their dung balls. Finally, vegetation surrounding a dung pile of 2.5 months old was sampled and the nitrogen concentration was measured to determine the influence of a dung pile on nutrient availability for plants.

Our results show that herbivores have no influence on the dung distribution between lawn and bunch vegetation. However, dung beetles seem to have a preference for bunch vegetation when burying their dung balls, eventually moving almost 17% of, in this case, a white rhino dung pile from lawn vegetation to bunch vegetation. Finally, the nitrogen concentration of vegetation surrounding a dung pile increases, indicating that there is indeed a fertilization process of large grazers on the lawn grasses and dung beetles are interrupting this process.

Concluding, dung beetles seem to have a preference for bunch grasses which means that they influence the distribution of dung and its nutrients, creating a nutrient flow from lawn grasses to bunch grasses. This effect has, so far, been overlooked and thus greatly underestimated, but should be taken into account when researching the nutrient cycle in ecosystems were dung beetles are present.

Introduction

Nutrient cycling is essential for ecosystem functioning and is a complex process influenced and determined by many different components (Bornemissza, 1976). A change or malfunction in one of these components might have serious repercussions, influencing the entire ecosystem (Jankielson, 2000). In African savannas, large grazers play a key role in nutrient cycling. They can accelerate nutrient cycling and thereby enhance the carrying capacity of their ecosystem (Ruess and McNaughton, 1987; McNaughton et al., 1997). One of the major pathways through which large grazers affect nutrient cycling is by increasing nutrient cycling rates by fertilizing vegetation through dung and urine (McNaughton, 1979). When plant litter is decomposed above ground, most of the nutrients are added to the soil organic matter compartment which has slow turnover rates. However, when large herbivores ingest plant material, their nutrients become available through dung and urine excretion, resulting in a fast turnover rate. Thus, large herbivores can change the slow nutrient cycles (particularly of nitrogen and phosphorus) into a much faster ones, creating an increased flow of nutrients (Ruess and McNaughton, 1987; McNaughton et al., 1988; Bakker et al., 2004).

Vegetation in grazed ecosystems has been found to be generally limited by nitrogen (Vitousek and Howarth, 1991) and large herbivores recycle most of the nitrogen through urine (Ruess & McNaughton, 1987). Phosphorus, next to nitrogen, has also been found to be a nutrient that is limiting for plant growth (Penning de Vries et al., 1980) and phosphorus is mostly recycled through dung (Ruess & McNaughton, 1987). Despite theories involving the importance of dung fertilization, this has barely been researched, in contrast to fertilization through urine (McNaughton, 1979; Hobbs, 1996). It has been suggested that the ratio of these two minerals can be used as an indicator to determine which nutrient is the limiting factor for plant growth. A N:P ratio of >16 indicates phosphorus limitation, while a N:P ratio of <14 indicates nitrogen limitation (Koerselman and Meuleman, 1996; Augustine et al., 2003). Grasses on the African savanna are often characterized by low N:P ratios and thus nitrogen limited (Ratnam et al., 2008).

The prevailing theory involving nutrient cycling by large herbivores is that they fertilize the areas where they graze most, namely the highly nutritious vegetation, through their dung and urine excretion. Through this fertilization they actually promote the growth of the highly nutritious plants which they then again can graze, often referred to as grazing lawn formation (McNaughton et al., 1997; Augustine et al., 2003). This theory assumes that large grazers release their urine and dung on the same location where they graze, namely the grazing lawn vegetation type. When in, for instance, the Serengeti, this is likely to be correct. There you find grazing lawn stretching for many kilometres, creating homogeneous plant vegetation where dung and urine will always end up on the same type of vegetation.

However, in heterogeneous savannas, like in South-Africa, the nutrients might end up on another vegetation type, even when originally deposited on the grazed lawn grasses. Certain organisms like dung beetles could move large amounts of dung to other vegetation patches (such as the low nutrient bunch grasses or shrubs). For instance, Ruess and McNaughton's (1987) personal observation is that dung beetles bury virtually all fresh dung beneath the soil surface within 24 hours, indicating their enormous impact on dung nutrient recycling. Furthermore, Gillard (1967) found that 80% of the nitrogen content of cattle dung was lost when it remained on the surface until it was dry, but when dung beetles were present this loss was reduced to 5-15%. Nichols (2008) also described the important ecosystem services the dung beetles provide, including nutrient cycling. Therefore it is expected, specifically in heterogeneous locations, that dung beetles could have an important impact on the nutrient distribution and recycling by dispersing dung. For instance, if dung beetles prefer to displace dung to low nutrient bunch grasses, which is a higher and more sheltering vegetation type, they are removing nutrients from the lawn grasses. However, it could also be that they prefer the lawn grasses, in which case they strengthen the increased nutrient cycling rate by large herbivores through preventing the loss of nutrients as Gillard (1967) found. This potential effect of dung beetles on the nutrient cycle in heterogeneous savannas has so far been overlooked and has not yet been investigated.

Research question

During this research we investigated how dung beetles influence the nutrient cycling process of large herbivore dung through post-depositional dung translocation in a heterogeneous South-African savanna. This question was divided into four sub questions; (1) Where do the herbivores deposit their dung? (2) How much of the deposited dung is distributed by dung beetles? (3) Where is this dung distributed to? And, (4) what is the effect of the dung pile nutrients on surrounding vegetation?

Hypothesis

I have incorporated these four sub questions into two hypotheses for the main research question: (i) When dung beetles show a preference for distributing large grazer dung to bunch grasses, they will interrupt the fertilization process of large grazers on high nutrient lawn grasses through distributing nutrients to the low nutrient bunch grasses. (ii) When dung beetles show a preference for distributing large grazer dung to lawn grasses, they will promote the fertilization process through distributing nutrients into the soil beneath the high nutrient lawn grasses.

By determining where dung beetles take the large grazer dung, what amount, and what the effect of the nutrients of the dung pile are, I hope to get a clear picture of how dung beetles influence and possibly interrupt the fertilization process of large grazers on high nutrient lawn grasses. When trying to preserve a habitat, you need to know the mechanisms that influence that habitat. In this case the fertilization process of dung, the nutrient cycle and the influence dung beetles have on these, are a piece of the puzzle.

Material and Methods

Study site.

This study was performed in the Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal, one of the oldest game reserves in South-Africa. Besides having shrub and tree vegetation, this park is characterized by heterogeneous grasslands consisting of lawn and bunch grasses with temporal and spatial variation between them (Cromsigt and Olff, 2008). Within this park five sites were selected with on each site both lawn and bunch vegetation present, where all sites were burned before the research started.

(1)Where is herbivore dung dropped?

To determine where herbivores deposit their dung, a grid was plotted on each of the five sites that were used during this research. These grids were a total of 50 by 25 meter, consisting of 50 squares of 5 by 5 meter. Subsequently, every two weeks a dung count was performed within these grids. The dung counts started during the beginning of the growing season, namely October, and were executed 9 times in total. The amount of dung, herbivore species and the vegetation type on which the dung was dropped were determined for each square. When a dung pile was counted, we destroyed this pile to avoid repetition two weeks later. Using literature, the number of dung piles was converted to dry weight in grams (see table 1, Appendix A).

(2)How much dung is distributed?

White rhinoceros dung was used for the experiments that required herbivore dung, since they are present in large numbers in the Hluhluwe-iMfolozi Park. Therefore their dung is abundantly available and moreover, easily collected. The average white rhino dung pile weighs around 8 to 10 kg and during this experiment these weights were used. Early in the morning, white rhino dung was collected from middens at the side of the road, making sure the dung was fresh from that day. Two dung piles between 8-10 kg were then placed on one of the five sites. This experiment was replicated 14 times, so a total of 28 dung piles were placed. A sample of the fresh rhino dung was taken and the fresh weight and dry weight were determined to establish the fresh to dry weight ratio. The dry weight was measured after the dung sample had been dried in an oven at 70°C for two days.

Before placing the dung piles, the vegetation underneath them was estimated in a square of 50x50 cm and their locations were saved on GPS. One of the dung piles was placed straight on the underlying vegetation, the other was placed on a round mesh (Ø=1.6 mm) that was secured to the ground to exclude the influence of tunnelling dung beetles. Finally, a mesh (Ø=1.6 mm) with 10 grams of the same white rhino dung was placed inside each of the two dung piles to eventually determine the microbial activity. After four days, the two dung piles and the two meshes with dung inside were collected and the presence of dung beetle holes beneath the dung pile and the mesh were checked. The collected dung piles and the two meshes were dried in the oven at 70°C for at least four days and the dry weight of the dung piles was determined, after trying to remove any soil left on the dung of the normal dung piles. The dry weight from the dung inside the meshes was also weighed. With the fresh/dry weight ratio, the dry weights of the placed dung piles at day zero and of the dung inside the meshes at day zero were calculated. From the difference in dry weight of the meshes that were placed in the dung piles, the microbial activity could be determined. This way, the effect of the microbial community and of dung beetles could be separated from each other and the effect of both can be determined. So, separating and accounting for the effect of the microbial activity over four days, the dry weights from day zero and day four could then be compared and the amount of dung removed by dung beetles could be calculated.

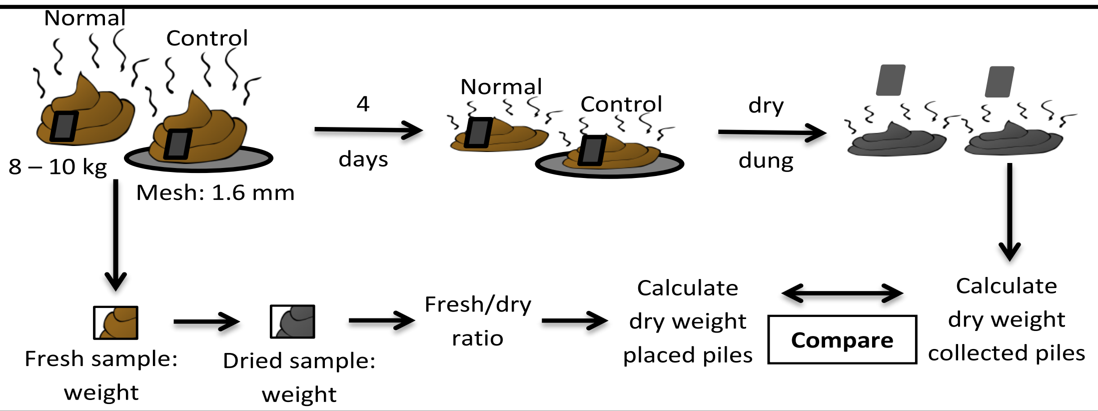


Figure 1: The dung pile experiment designed to determine what percentage of a dung pile is removed by rolling dung beetles. Fresh dung piles are placed, taking a sample and determining the fresh/dry weight ratio from it and calculating the dry weight of the placed dung piles with this ratio. Within the dung piles a mesh is placed with 10 grams of dung, since other organisms are excluded by the mesh, this will be used to eventually determine the microbial activity. After four days, the dung piles and meshes are collected and the dry weights are determined. Correcting the dry weight of the four days old dung piles for the microbial activity, the dry weight at day zero and day four can now be compared.

(3)Where is the dung taken to and by whom?

After placing the two fresh dung piles on a site, as many rolling dung beetles as possible were followed. The dung beetles were followed by placing coloured wooden sticks on their location every minute, creating the path they rolled. The dung beetle species was identified and the diameter of their dung ball was measured. When the dung beetle had buried its ball, which was determined to be when the dung ball was buried beneath ground level, their path was measured. The distance between consecutive sticks was measured, as well as the increasing distance from the dung pile itself; measuring between the first stick, which was placed at the dung pile, and every other stick. Then the direction of the sticks was determined. This way, the path of the dung beetles could be recreated. Besides distances and direction, the vegetation type was determined for every individual stick. From this, the percentage abundance of each vegetation type was calculated, determining what percentage of sticks was placed in lawn, bunch or shrub vegetation types. This percentage was then used as the expected percentage in which the dung beetles would bury their dung ball if this would be a random decision. The observed values were taken as percentage of lawn, bunch or shrub the dung beetles eventually buried their dung balls in. The type and vegetation cover was determined for a 50 by 50 cm square with the end point at the centre, the same way the vegetation cover was determined before placing the dung piles.

(4)What effects do the nutrients of a dung pile have on surrounding vegetation?

To examine the effect of dung on plant nutrient concentration, the experiment of another student was used, who also placed dung piles. Dung piles of around 20 kg were placed on put on chicken mesh and on fine mesh. The fine mesh was used to exclude tunnelling dung beetles and the chicken mesh was used to mimic the use of mesh. Finally a control plot was determined where no dung was placed. When sampling surrounding vegetation, the dung piles had been there for 11 weeks. So the surrounding vegetation was sampled, selecting two grass species on each site with a high abundance. From these grasses, leaves were gathered till around 5 grams in dry weight was collected. For the two dung piles, the grasses were taken from right next to the piles and the control was taken with no dung nearby. The samples were dried for two days at 70°C and then grinded. Once back in the Netherlands, the samples were analysed using the NIR (Near-infrared spectroscopy). For each sample, the nitrogen concentration was determined three times from which an average could be taken.

Statistical analysis

All statistical analyses were performed with R 2.15.3 (R Core Team, 2013). For sub question 1 (to determine where herbivore dung is dropped), a mixed-effects model was used (nlme package: Pinheiro et al., 2014) with dung in dry weight, combined for all herbivore species, as response variable, vegetation type, either lawn or bunch, as predictor and site as the random factor. A linear model was conducted to determine whether the amount of dung dropped differs between sites. For sub question 2 (how much dung is distributed), an ANOVA was performed comparing percentage of dung removed against site. Then a t-test was performed to determine whether the percentage of dung removed differed between the normal and the control dung piles, all used weights were of course corrected for the microbial activity. To test whether the microbial activity differed between the two treatments, another t-test was performed. To answer sub question 3 (where is the dung taken to), a mixed-effects model was used with percentage as response variable, the observed and expected models as predictor and site as the random factor. After the model proved to be significant, a post-hoc test was performed to determine the significant factors. The Tukey test was applied using the glht function from the multcomp package (Hothorn et al., 2008). For sub question 4 (the effect of nutrients), again a mixed-effects model was used. Here the nitrogen concentration was taken as the response variable, while treatment and species were the predictor variables and finally site was modelled as random factor. If the model proved to be significant, a post-hoc test was performed, again applying a Tukey test using the glht function from the multcomp package. Finally, for all models the assumptions of the models were checked.

Results

(1)Where is herbivore dung dropped?

When looking at the amount of dung (g/m^2/week), corrected for the percentage of lawn or bunch present on each site, there is no significant difference between the total amount of dung deposited on lawn (24.16 g/m^2/week, SD=10.60 g/m^2/week) and on bunch vegetation (19.53 g/m^2/week, SD=6.72 g/m^2/week) ($t= -1.5201$, $p=0.2031$, see graph 1). There was no significant difference in dung deposition between sites ($F=5.7843$, $p=0.0588$).There are some differences between herbivore species when it comes to dung deposition per vegetation type (see graph 7, Appendix C).

(2)How much dung is distributed?

The average percentage of dry weight dung removed is 22.6% (see graph 2). Distinguishing between dung piles, the average for the normal dung pile is around 24% and for the control dung pile around 20%, calculated from dry weights and corrected for microbial activity. There is no significant difference in the amount of dry weight dung removed between the normal and the control dung pile ($t=0.7466$, $p=0.4623$) or between sites ($F=1.264$, $p=0.316$). This indicates that there is no significant effect of tunnelling dung beetles or location. Although we always corrected for the microbial activity, the overall effect of the microbial community was negligible (average=0.14% removed), but extremely variable (SD= 7.33%) (see graph 6, Appendix B). Finally, when checking for holes made by dung beetles underneath the dung piles, no holes were found underneath the control dung pile, confirming the mesh placed underneath did indeed exclude tunnelling dung beetle.

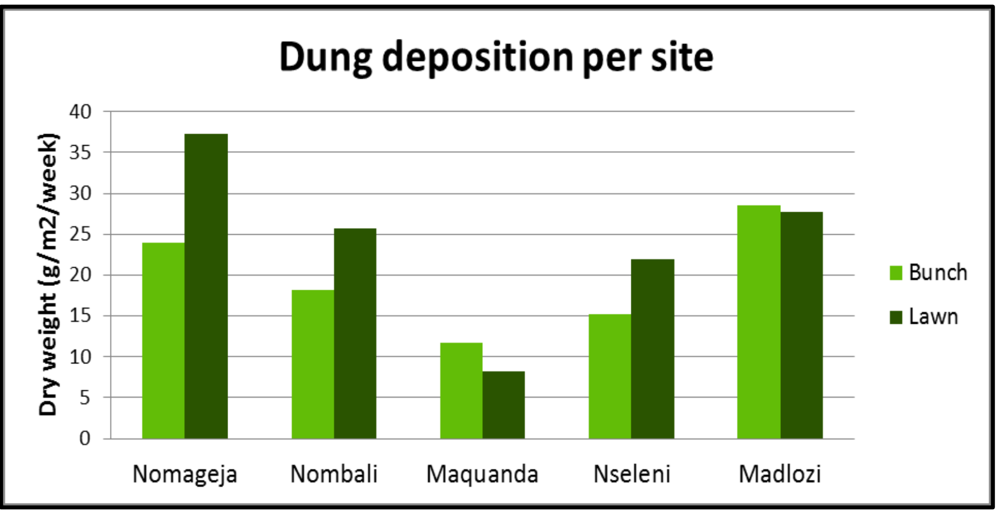
(3)Where is the dung taken to and by whom?

Dung beetles prefer to bury their dung balls in bunch vegetation (N=34), rather than in lawn vegetation (N=7). Comparing the percentages of dung balls buried in lawn or bunch vegetation with the percentages of lawn and bunch vegetation (calculated with the vegetation steps), shows that dung beetles indeed bury more dung balls in bunch vegetation than expected ($t= -3.1069$, $p=0.0064$) and less in lawn vegetation than expected ($t=2.922$, $p=0.0112$, see graph 3). The most common dung beetles found were the Gymnopleurus humanus (code name: green roller), Kheper nigroaenues (code name: purple roller) and Kheper *cf* nigroaenues (code name: black roller). Less present was the *cf* Allogymnopleurus chloris (code name: little black roller). Dung beetles walked an average of 45.17 meter (SD=33.78m) and bury their ball at an average of 35.40 m (SD=26.50m) from the dung pile. The distance between the placed dung pile and the burial point of a dung ball differed significantly between dung beetle species ($F=3.529$, $p=0.0218$). The larger species (purple and black rollers) took their dung balls further when compared to the much smaller green roller (see graph 8, Appendix D).

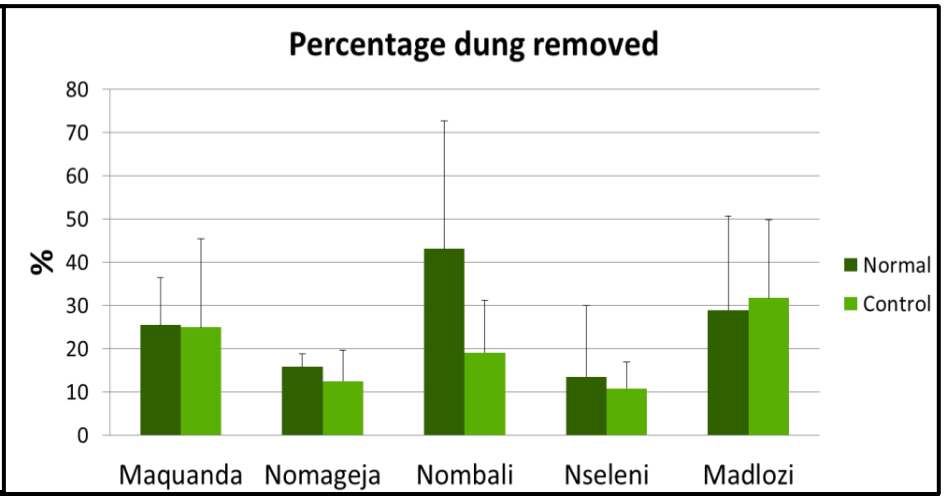
(4)What effects do the nutrients of a dung pile have on surrounding vegetation?

There is a significant effect of treatment on nitrogen concentration of grass species ($F=5.3879$, $p=0.0065$). The post-hoc test revealed that the dung treatments (Fine and Chicken) have a positive effect on the nitrogen levels of plants surrounding the dung, when compared to the treatment where no dung was nearby the grass species (Control) (see graph 4). The nitrogen concentration also differs between grass species ($F=23.2448$, $p<0.001$). The species that differed the most from other grass species is the *Urochloa mosambicensis* (Uro_mos). Its nitrogen levels are much higher than other species. The species *Sporobolus nitens* (Spo_nit) also differed from other grass species. This is most likely because of the increased nitrogen concentration of the treatment with chicken mesh (see graph 4).

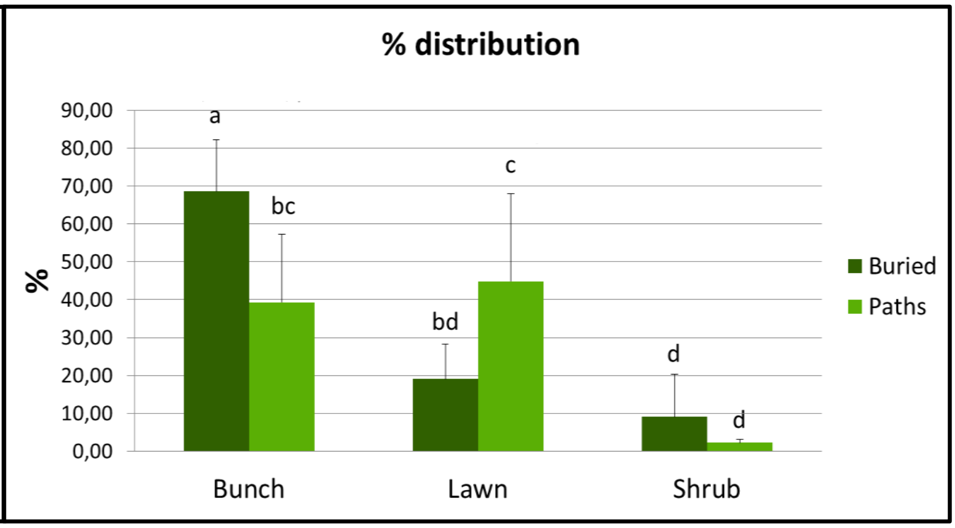
Graph 1: The dung deposition of large grazers per site per week. The dry weight was corrected for the present vegetation percentages.

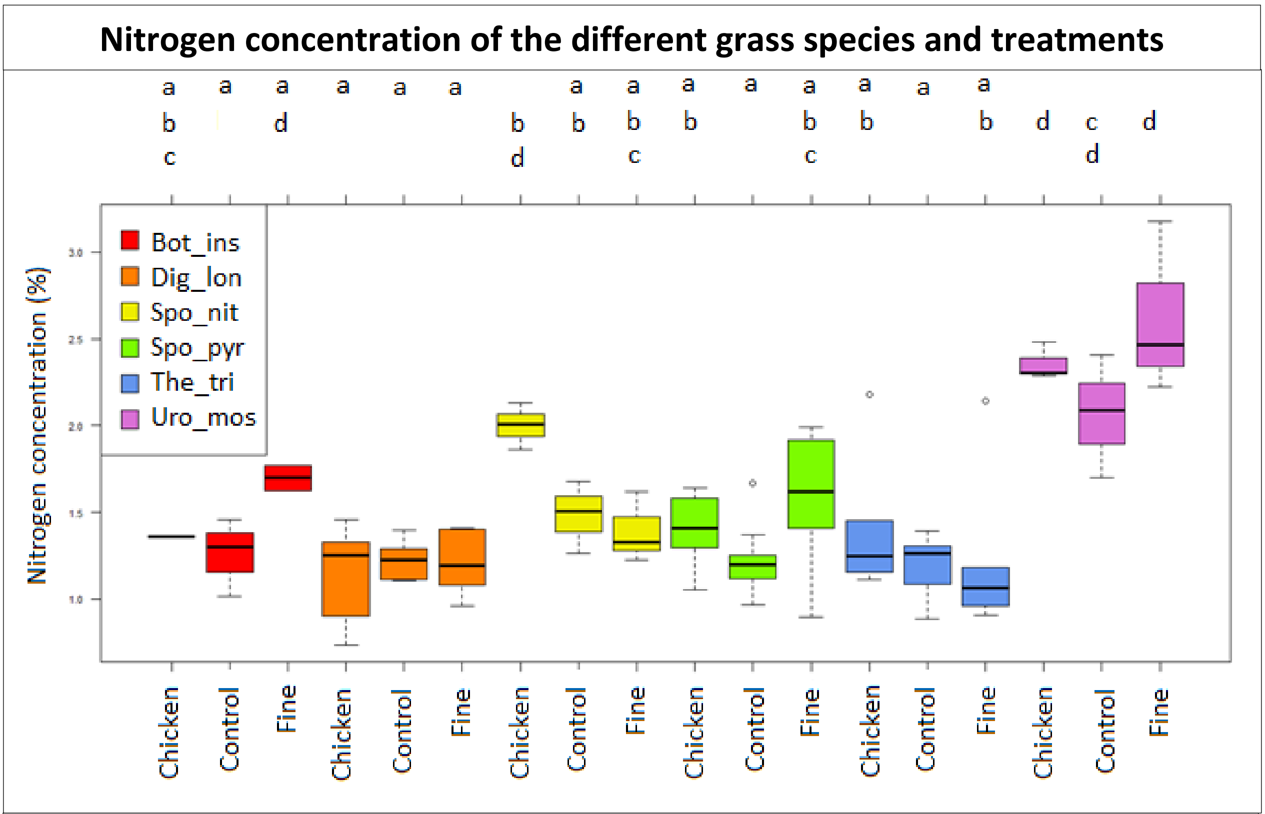


Graph 2: The percentage of dung removed per site, differentiating between the two treatments. Normal dung piles were placed on the ground, while the control dung piles were placed on a mesh to exclude the activity of tunnelling dung beetles.



Graph 3: The percentage per type of vegetation where dung beetles buried their dung balls (Buried). The expected percentages were calculated using the vegetation steps from the paths of the dung beetles (Paths) (see method section 3).





Graph 4: Nitrogen concentration of the different plant species with different treatments. The letters on top of the graph show significant differences. The Fine and Chicken treatment differ from the Control treatment and the Uro_mos and Spo_nit species differ from other grass species.

Discussion

It seems that, at least in the Hluhluwe-iMfolozi Park, there is no difference in herbivore dung deposition between lawn or bunch vegetation. This contradicts present literature, which states that since herbivores spend more time on lawn vegetation, this is where most of their dung will be deposited. This is what McNaughton et al. (1997) found, concluding that nitrogen and sodium concentrations were higher in soils of highly grazed sites than in soils where animal density was sparse due to the presence of dung. Augustine (2003) states that large herbivores play a role in maintaining the nitrogen enriched status of highly productive and intensively grazed sites through dung addition on these sites. Then why wasn't there a higher deposition on lawn vegetation recorded during this research?

First of all, this research was performed during the growing season. Before the experiments started, all sites were burned down. Therefore, all vegetation types start with practically no biomass. When first starting to grow all types of vegetation are nutrient rich, but bunch grows fastest and thus has the highest biomass (Fakkert, 2014). It seems logical that herbivores graze more of the bunch grasses during this stage and therefore spend a lot of time on bunch vegetation. This was confirmed by another experiment done during the same period this research was performed (Fakkert, 2014), concluding that during the growing season, there was a higher consumption of bunch grasses rather than lawn grasses.

Secondly, when looking at metabolic biomass of the large grazers in the Hluhluwe-iMfolozi Park, it shows that around 40% is comprised of white rhinos, 37% of buffalos, only 10% of impalas, 6% of zebras and 3% of wildebeests (EKZN Wildlife, 2012). Though white rhinos heavily graze the short lawn grasses (Estes, 1991; Waldram et al., 2008), their dung ends up on middens, therefore having no effect on the nutrient enrichment of the vegetation they graze. Furthermore, the buffalos, who also represent a large percentage of herbivore biomass, mostly eat bunch grasses (Estes, 1991). So it is logical to find more buffalo dung on bunch grasses than on lawn grasses. It seems that the lawn grass grazers that might influence the dung deposition on lawn grasses, namely the impala and wildebeest, are currently highly underrepresented in this park.

We found that about 22.6% of the white rhinoceros dung pile was removed by dung beetles, though this percentage differed greatly between dung piles. Holter (1979) found that around 20-25% of the dung disappeared during the first part of his experiment (11 days), though this percentage included a lot of different organisms and he concluded that the effect of dung beetles was very small. The effect of dung beetles is found to be much higher during this research, which corresponds with what other studies, such as Gillard (1967) and Nichols (2008), described, namely a large effect on the nutrient cycle of dung beetles when present. When it comes to the microbial activity, the average percentage removal from a dung pile over four days is extremely small. This concurs with Holter (1979), who concluded that microbial decomposition of an isolated dung patch is a very slow process.

During this research, only white rhino dung was used for convenience which means the results presented here might only relate to white rhino dung. For instance, the percentage of dung that is removed could differ between herbivore species. However, it might be that the percentage dung removed is even higher for smaller herbivore species. White rhino dung piles are quite large and it takes large numbers of dung beetles to remove a substantial amount. But when one dung beetle finds one impala dung pile, it might use almost all the available dung.

Around 75% of the removed dung is displaced to bunch vegetation (see graph 2). As a result almost 17% of an entire white rhino dung pile is moved from lawn vegetation to bunch vegetation, interrupting the possible fertilization of herbivore dung on lawn grasses. Also, the smaller dung beetle (green roller) is responsible for 4 of the 7 dung balls buried in lawn. They bury their dung ball closer to the dung pile (see graph 8, Appendix D). This might explain why they seem to bury them more often in lawn vegetation than larger dung beetles (purple roller and black roller) since during the experiments, bunch was farther away from the dung pile than lawn. The larger dung beetles also make larger dung balls (see table 2, Appendix E), so when looking at dung weight, the amount of dung that is displaced to bunch vegetation is even higher.

It is important to realize that dung beetles are only active part of the year. This research was performed during the growth season, the period in which dung beetles are most active (Stronkhorst and Stronkhorst, 1997). Their effect on dung and especially displacing dung will be less during other parts of the year. However, when dung beetles are less active, they make way for other organisms to feed on the dung. For instance, though it has not yet been thoroughly researched, termites seem to have a very large impact on dung distribution (Freymann et al., 2008), only they arrive much later at a dung pile than dung beetles. Since they take their food from its original place and bury it elsewhere underground, they essentially have the same effect as dung beetles on dung distribution, namely the interruption of the fertilization process of large grazers.

Finally, vegetation surrounding dung has an increased nitrogen concentration, so dung indeed has an effect on the nutrient cycle. Although the nutrient mostly recycled through dung is phosphor, it was unfortunately not possible to measure this, which should be conducted during future experiments. However, nitrogen is also present in dung piles. The finding that nitrogen concentration of surrounding vegetation increases when dung is placed nearby, corresponds with other studies (McNaughton et al., 1997; Weeda, 1967) and confirms that if dung beetles displace herbivore dung from lawn vegetation to bunch vegetation, they do interrupt the fertilization of the lawn grasses.

Conclusion

Concluding, dung beetles seem to have a preference for bunch grasses which means that they influence the distribution of dung and its nutrients. Moreover, there does not seem to be an effect of herbivores on dung distribution, while dung beetles do actually have an effect. The effect dung beetles have on the distribution of herbivore dung has, so far, been greatly underestimated and should be taken into account by future studies.

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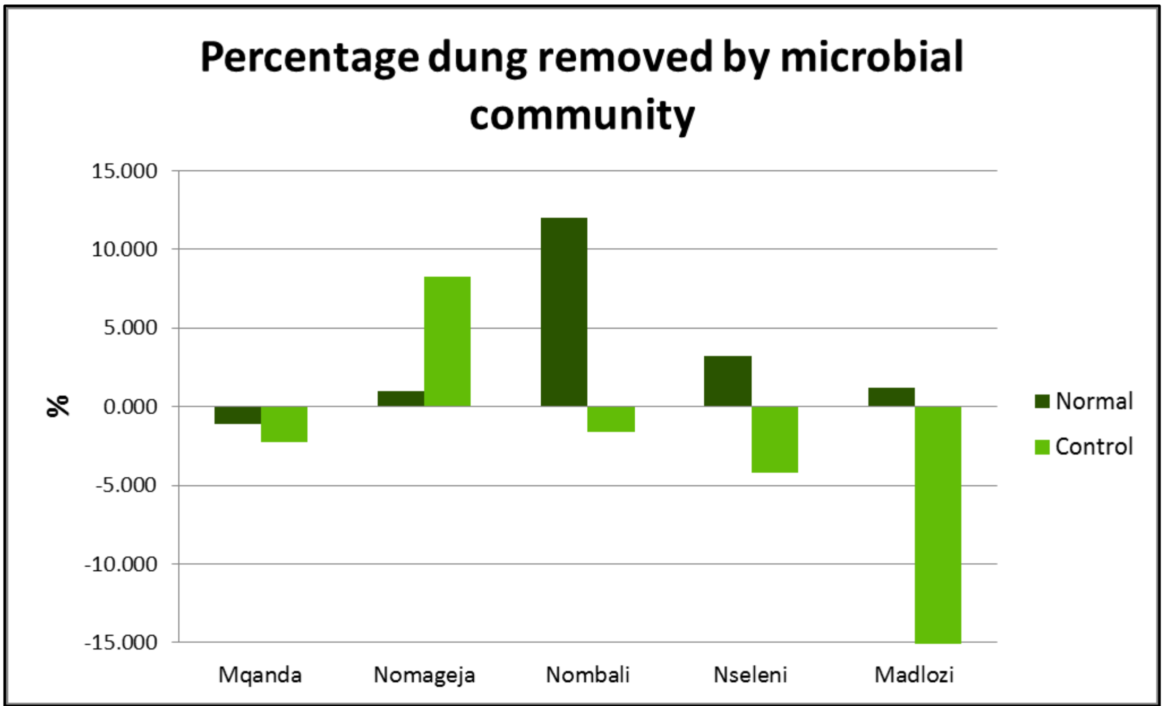
Appendix A

Herbivore	Dry weight/pile	Article
Buffalo	221.2	Waal, van der C. et al., 2011
Elephant	1920	Waal, van der C. et al., 2011
Grey Duiker	9.6	Waal, van der C. et al., 2011
Giraffe	289.5	Waal, van der C. et al., 2011
Impala	28.8	Waal, van der C. et al., 2011
Kudu	172.9	Waal, van der C. et al., 2011
Nyala	28.8	Edwards, 1991
Red Duiker	9.6	Waal, van der C. et al., 2011
Warthog	116.3	Waal, van der C. et al., 2011
Wildebeest	186	Waal, van der C. et al., 2011
White Rhino	1800	Waal, van der C. et al., 2011
Zebra	663	Edwards, 1991

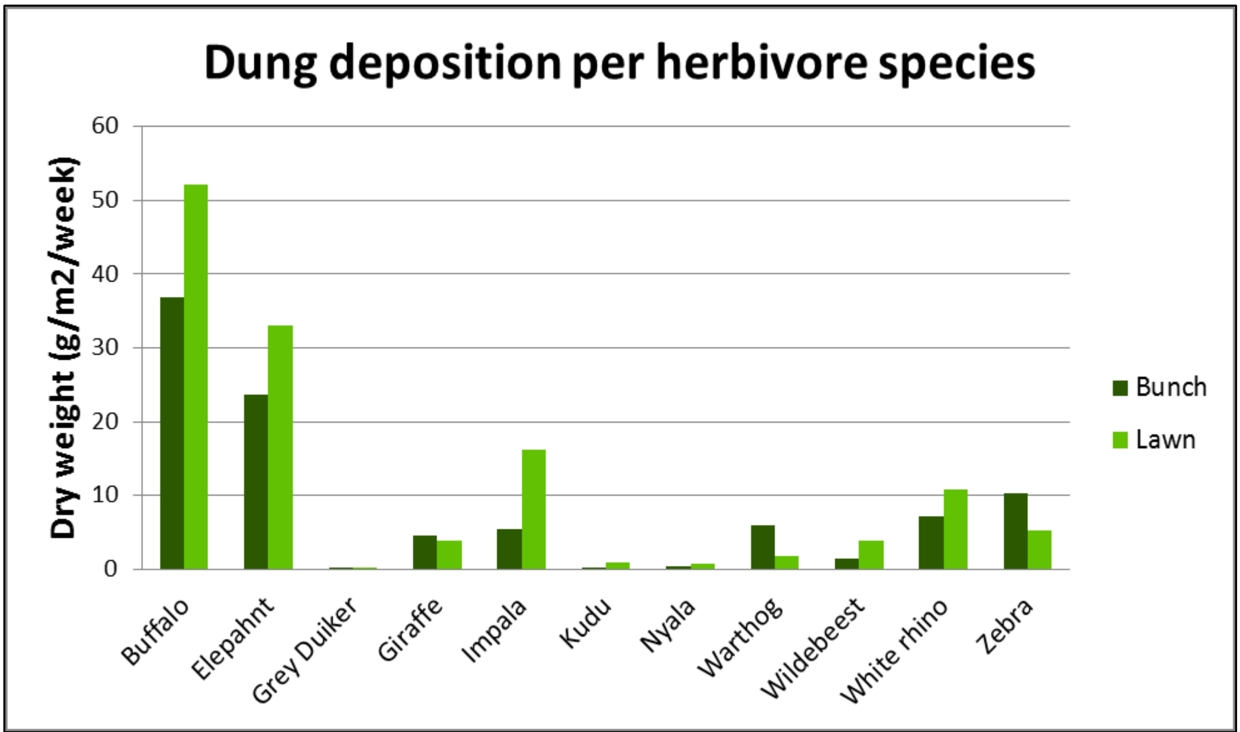
Table 1: Dry weights per dung pile for different herbivore types used in this study, extracted from literature shown in the last column.

Appendix B



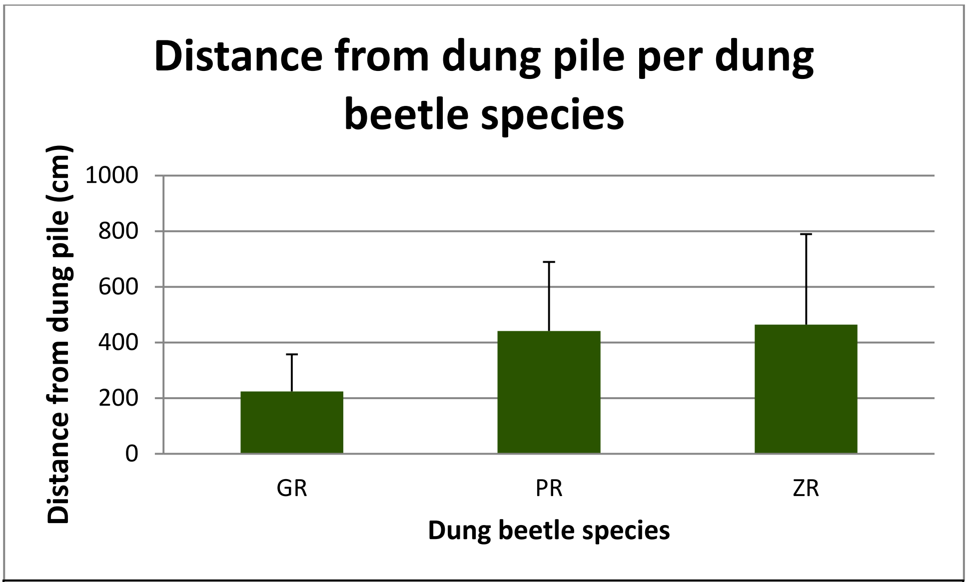
Graph 6: The percentage that was degraded by the microbial community of the dung piles that were placed, shown per site and per dung treatment.

Appendix C



Graph 7: The dry weight of dung deposited on lawn or bunch as a total of the 5 sites, shown per herbivore species and per week. The dry weights are also corrected for the average percentage of lawn or bunch vegetation of the five sites, resulting in the g/m2/week.

Appendix D



Graph 8: The distance of buried dung balls from the original dung pile, shown per different dung beetle species. GR=Green roller, PR=Purple roller and ZR= Black roller (F=3.5292, p=0.0218).

Appendix E

	Scientific name	**Kheper nigroaenues**	**Kheper *cf* nigroaenues**	**Gymnopleurus humanus**	***cf* Allogymnopleurus chloris**
	Code Name	Purple roller	Black roller	Green roller	Little black roller
	Functioning group	Roller	Roller	Roller	Roller
Dung beetle	Sample size	28	15	19	6
	Pronotum(mm)	20.95	16.86	11.92	11.48
	Fresh weight(g)	3.29	2.00	0.69	0.67
	Dry weight(g)	1.42	0.72	0.29	0.27
	Fresh/Dry ratio	0.43	0.36	0.41	0.41
Dung ball	Sample size	19	5	10	4
	Diameter(mm)	60.42	33.73	18.91	21.55
	Fresh weight(g)	169.62	19.55	3.42	4.69
	Dry weight(g)	47.20	6.20	1.02	1.35
	Fresh/Dry ratio	0.28	0.32	0.30	0.29

Table 2: The four rolling dung beetle species most often encountered during this study, showing their code name, the sample size, the averaged pronotum width, average fresh weight, average dry weight and the calculated fresh to dry weight ratio. Per species the average diameter of their dung ball is shown, as well as the average fresh and dry weight, fresh to dry weight ratio and the sample size of dung balls.