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Monitoring large herbivore diversity at different scales: comparing direct and indirect methods

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Abstract Monitoring of large herbivores is central to research and management activities in many protected areas. Monitoring programs were originally developed to estimate (trends in) population sizes of individual species. However, emphasis is shifting increasingly towards conservation of diversity and communities instead of individual species, as a growing literature shows the importance of herbivore diversity for ecosystem functioning. We argue that the design of monitoring programs has not yet been adapted well to this new conservation paradigm. Using large herbivore census data from Hluhluwe-iMfolozi Park, South Africa, we studied how monitoring methodology (observational counts vs. dung counts) and spatial scale interact in influencing estimates of large herbivore species richness and diversity. Dung counts resulted in higher herbivore species richness and diversity estimates than direct observational counts, especially at finer monitoring resolutions (grid cells smaller than 25 km^2). At monitoring resolutions coarser than 25 km^2 both methods gave comparable diversity estimates. The methods also yielded different spatial diversity estimates, especially at finer resolutions. Grid cells with high diversity according to the dung count data did not necessarily have high diversity according to the observational counts, as shown by low correlation of grid cell values of both methods. We discuss these results in the light of estimates of the sampling effort of each method and, hence, suggest new monitoring designs that are more suitable for tracking temporal and spatial trends in large herbivore diversity and community composition.

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Introduction

Large herbivore species characterize ecosystems around the African continent and have important ecological (Bell 1971; McNaughton 1985; Owen-Smith 1988) as well as economic value (Prins et al. 2000; Gordon et al. 2004). Their populations, however, are increasingly threatened by human activities (Prins 1992; Cincotta et al. 2000; Olff et al. 2002). A unique aspect of African large herbivore groups is the high diversity of species (Olff et al. 2002), ranging from small forest-dwelling duikers to massive savanna elephants (Kingdon 2001). An increasing number of studies illustrate the importance of herbivore species diversity in structuring ecosystems because different-sized species have different effects (Du-Toit and Cumming 1999; Bakker et al. 2004, 2006; Cumming and Cumming 2003; Hobbs and Searle 2005). This growing acknowledgment of the ecological importance of herbivore diversity coincides with a shifting paradigm in the management of savanna systems from a focus on single target species towards conserving complete and diverse herbivore communities (Du-Toit and Cumming 1999; Stalmans et al. 2001; Du-Toit et al. 2003). As a result diversity targets are increasingly incorporated in reserve management plans (e.g., Conway et al. 2001).

Monitoring programs are essential for the evaluation of these targets. Large herbivore population management and monitoring programs have long focused on determining population numbers of certain target species (especially the largest species). These programmes are not necessarily well designed for monitoring species diversity. A wide range of methods has been used in the past to monitor African mammals, ranging from direct observational counts (aerial, drive, waterhole and foot counts) to indirect counts based on signs left behind by the animal (dung counts, track counts or a combination of indirect signs, such as dung, tracks, hairs and feeding signs) (see Wilson et al. 1996). Several studies have compared these methods based on species abundance estimates (Caughley et al. 1976; Norton-Griffiths 1978; Bothma et al. 1990; Peel and Bothma 1995; Reilly and Haskins 1999). However, few studies have looked at the effect of monitoring methodology on large herbivore diversity estimates. Gaidet et al. (2005) showed that methodology can influence estimates of mammal species richness, but they did not consider the impact on species diversity indicators that include relative abundances of species. Species richness estimates give little information on the structure and composition of species communities. Diversity indicators that include data on species proportional abundance give more insight in the response of communities to environmental change due to unwanted anthropogenic processes or changes in management regime (Magurran 1988, 2004). To our knowledge, no studies have evaluated the impact of monitoring methodology on large herbivore diversity indicators that include species abundance data.

Diversity can be monitored at the park level but this does not help management authorities to understand changes in diversity as a response to, e.g., environmental change. It is necessary to monitor at finer resolutions to get insight in the processes that determine herbivore diversity patterns, including the effect of management practices such as prescribed burning. The scale at which monitoring results should be evaluated depends on the scale of the processes that determine herbivore diversity. Spatial scale, however, can

influence monitoring results (Condit et al. 1996; Magurran 2004). Therefore, it is important to include spatial scale in evaluations of monitoring methodology. Monitoring methods might result in perfectly interchangeable diversity estimates but only above a certain spatial scale. It is unclear how scale interacts with the methodology of monitoring diversity of large herbivores.

We used large herbivore census data from a protected savanna site in South Africa to analyze how monitoring methodology affects estimates of species diversity and how this depends on the spatial resolution at which the monitoring scheme is evaluated. We evaluated a direct versus an indirect method and determined sample effort and intensity for each method to be able to evaluate their effectiveness in measuring herbivore diversity.

Methods

The study was performed in the Hluhluwe-iMfolozi Park, an 89,665 ha reserve in Kwazulu-Natal, South Africa. This reserve is situated in the southern African savanna biome, with vegetation types ranging from open grasslands to closed *Acacia* and broad-leaved woodlands. It has a coastally modified climate with a strongly seasonal annual rainfall, most rainfall falling between October and March. The mean annual rainfall mostly depends on altitude, ranging from 985 mm in the high altitude regions to 650 mm in the lower areas. Annual daily maximum temperatures range from 13 to 35°C. The park is inhabited by a diverse set of indigenous large herbivores and carnivores (Brooks and MacDonald 1983). In 2004 we monitored large herbivore distribution (species richness and abundance) on line transects that were evenly distributed over the park (Fig. 1). We used a direct (observational counts) and an indirect (dung counts) method and compared the methods on the basis of commonly used species richness and diversity estimates.

Every 2 years since 1986 observation teams walked a total of 26 fixed line transects that vary between 3.9 and 10.4 km (7.9 km on average, Table 1) to monitor the abundance of all large herbivore species that are present in the park. We used the data from the 2004 census to compare with the results from a dung counting method. Transects were evenly distributed over the reserve, covering all vegetation types and topography. The most southern part of the park is managed according to a wilderness concept, which limits

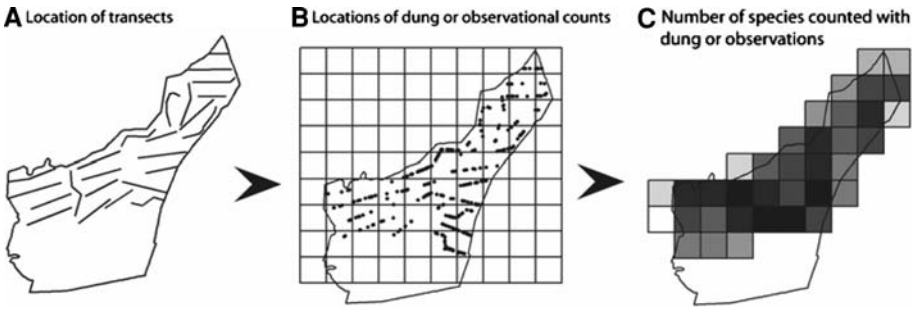

Fig. 1 Process of joining a 5 by 5 km grid with the dung and observational count data using ArcView 8.3 (ESRI 2003). **a** Outline of Hluhluwe-iMfolozi Park showing the position of the 24 transects. **b** Locations of dung or observational counts of a species, overlaid with a grid of 5 by 5 km cells. **c** Values of species diversity per grid cell, based on the join of the overlay grid with the dung or observational count data, for example the number of species counted per grid cell

Table 1 Transect characteristics of observational counts

Transect number	Transect frequency (year^{-1})	Transect length (km)	Transect duration (h)	Walk speed (km/h)	Visibility (m)
1	14	3.9	2.3 (0.24)	2.1 (0.38)	79 (77; 6.7)
2	13	8.2	4.8 (0.27)	1.8 (0.09)	61 (81; 3.4)
3	12	8.4	3.6 (0.16)	2.4 (0.11)	92 (82; 8.0)
4	13	5.4	2.2 (0.10)	2.6 (0.10)	64 (54; 6.3)
5	14	8.5	3.1 (0.11)	2.8 (0.09)	61 (83; 3.3)
6	14	8.5	4.4 (0.27)	2.1 (0.15)	54 (84; 1.6)
7	13	8.7	3.3 (0.15)	2.7 (0.12)	57 (87; 2.3)
8	12	9.6	4.1 (0.21)	2.4 (0.11)	78 (97; 4.9)
9	15	8.3	3.8 (0.17)	2.2 (0.09)	115 (82; 9.5)
10	15	6.2	2.3 (0.10)	2.8 (0.13)	54 (61; 2.7)
11	14	9.2	3.9 (0.15)	2.4 (0.10)	88 (92; 6.3)
12	16	6.1	2.8 (0.27)	2.4 (0.14)	102 (62; 7.9)
13	16	8.7	4.1 (0.22)	2.2 (0.12)	106 (89; 7.3)
14	16	7.7	3.8 (0.18)	2.1 (0.10)	82 (78; 5.2)
15	16	6.9	3.0 (0.17)	2.4 (0.17)	74 (70; 5.1)
16	13	8.7	3.6 (0.19)	2.5 (0.13)	77 (88; 5.3)
17	15	6.4	2.9 (0.09)	2.3 (0.08)	65 (65; 4.9)
18	16	6.9	3.3 (0.16)	2.1 (0.10)	94 (70; 7.2)
21	13	9.4	4.0 (0.12)	2.4 (0.07)	55 (95; 2.0)
22	17	10.4	4.3(0.14)	2.5 (0.09)	96 (104; 6.8)
23	13	9.6	3.3 (0.17)	3.0 (0.14)	53 (97; 1.3)
24	18	8.2	2.8 (0.11)	3.0 (0.13)	63 (84; 4.8)
25	15	9.1	3.3 (0.08)	2.7 (0.07)	61 (92; 3.2)
26	11	7.6	3.1 (0.20)	2.6 (0.16)	60 (77; 2.5)
Average	14.3 (24; 0.4)	7.9 (24; 0.3)	3.4 (24; 0.1)	2.4 (24; 0.06)	74.6 (24; 3.8)
Sum	344	190.6	835.5	–	–

Transect duration, walk speed and visibility are transect averages; *N* and *SE* given between *brackets*, for transect duration and walk speed *N* equals the transect frequency. The last two rows of the table give overall transect average and sum for the different characteristics. These overall values were used to determine method sampling intensity and effort

management and research practices, and was, therefore, not covered by any line transects. Different teams of two observers walked transects just after sunrise during a period of about 3 months in the dry season (end of July up to beginning of October). Teams walked each transect 14 times on average with a speed of 2–3 km per hour (Table 1). All herbivore observations (of species larger than hare) were recorded that were sighted within 500 m of both sides of the transect. For each observation the species and number of individuals was recorded. Furthermore, the position of each observation was recorded in decimal degrees using a handheld gps, as the position of the observer at the time of the observation. Because visibility was generally lower than 500 m, we estimated visibility every 100 m on both sides of each transect according to three classes: up to 50 m visibility, up to 250 m visibility and up to 500 m visibility.

During the 2004 observational census period we conducted dung counts on the same line transects as used for the observational counts. The transects were walked with a team

of two well-trained observers that continuously counted the number of dung pellet groups for all large herbivore species (larger than hare) on and within 1 m on each side of the transect. Instead of recording the spatial position of each pellet group, we summed the number of pellet groups per species for every 5 m on the transect and recorded the spatial position of these 5 m plots in decimal degrees.

Data analysis

Sampling effort and intensity

For the observational counts we averaged transect walk time, walk speed and visibility per transect and calculated an overall average over the 24 transects (Table 1). We compared both methods on the basis of their sampling effort and sampling intensity. We defined sampling effort as the number of man hours that it took to perform a complete census. For the observational counts we summed the total walk times of all transects (Table 1). For the dung counts we used an average walk time per transect of 5 h and multiplied this with 24 (number of transects).

We estimated sampling intensity as a measure for the number of hours that an area is sampled by each method. We defined sampling intensity, I as.

$$I = (t \times f)/A$$

where t is the sample period, f the sample frequency and A is the sample area. The sample area, A, was the actual area that was sampled by both methods. The dung counts were sampled 1 m on both sides of the transect, so the dung count sampling area was 2 m times the total length of transects (190.6 km, Table 1). For the observational counts we multiplied the total length of transects with twice the average transect visibility to estimate the sample area (74.6 m, Table 1). We defined the sample period, t, as the period (in h) that a certain point on the transect was observed. For the dung counts this period depends on the dung decay rate. In a study in Hluhluwe-iMfolozi GR, Jacobs (2002) showed that in the dry season dung from a range of herbivore species was still perfectly recognizable at the end of her 2 months study period. We used this period of 2 months (=1,464 h) as our minimum sample period for the dung counts. For the observational counts we divided average overall transect visibility by the average overall walk speed (Table 1) to estimate the sample period, assuming that the point is not visible as soon as the point is passed. The sample frequency, f, equaled the number of times a transect was sampled per year. For the observational counts we used the average number of times a transect was walked (Table 1). For the dung counts the transects were sampled once.

Diversity measures

We overlaid our dung and observational count data with grids of different spatial resolutions using ArcView 8.3 (ESRI 2003). The spatial resolution increased from 0.01, 0.25, 1, 6.25, 25, 56.25 to 100 km^2. We joined the dung and observation count data with each of these grids, summing the number (n) of dung pellet groups and individuals per species per grid cell (Fig. 1). We also summed the total number (N) of dung pellet groups and individuals over all species per grid cell for all resolutions, giving a sample size for both methods per grid cell.

For both methods and for all seven resolutions we determined three commonly used indices of species richness and diversity: species richness (S), the Shannon–Wiener diversity index (H') and Fisher's α. We calculated S as the number of species that we counted per grid cell. The Shannon–Wiener diversity index is defined as:

$$H' = -\sum p_i x \ln(p_i)$$

where p_i is the relative abundance (n_i/N) of species i (Pielou 1975). We determined Fisher's α from:

$$S = \alpha \ln\left(1 + \frac{N}{\alpha}\right)$$

where α is the sole parameter (Fisher et al. 1943; Condit et al. 1996).

We used the Wilcoxon signed rank method to test if the effect of monitoring methodology on the diversity indices was significant. This method accounts for the fact that diversity indices from the same grid cell, but resulting from different monitoring methods, were paired samples. For each diversity index and all monitoring resolutions we calculated Pearson correlation coefficients (r) between the estimates of the two monitoring methods per grid cell. A high Pearson r would indicate that both methods measure the same relative differences in herbivore diversity between grid cells, regardless of the absolute estimate of each method (which could be significantly different as shown with the Wilcoxon test).

Results

Sampling effort and intensity

Sampling effort was 7 times higher for the observational method than for the dung counts (Table 2). While the average walk time was lower for the observational counts than for the dung counts (3.5 h instead of 5 h), the sampling frequency for the observational counts was much higher. Sampling intensity was 45 times higher for the dung count methodology compared with the observational counts. This means that on average each point on the transects was sampled 45 times longer using dung counts than using observational counts (Table 2). This difference was caused by the large difference in observation period. The high sampling frequency of the observational counts only partly made up for the low observation period.

Diversity measures

Average species richness per grid cell was higher using the dung count method than with the observational counts, except for the 56.25 and 100 km^2 resolutions (Fig. 2a). For the

Table 2 Table shows estimated sampling intensity and effort of the two monitoring methods

Method	A (km^2)	t (h)	f (year^{-1})	I (h km^{-2} year^{-1})	Sample effort (h year^{-1})
Dung counts	0.3812	1464	1	3840.5	120
Observational counts	28.44	0.031	14.3	0.016	835.5

Sampling intensity, I, is calculated as $(t \times f)/A$, where t is the sample period, f the sample frequency and A is the sample area

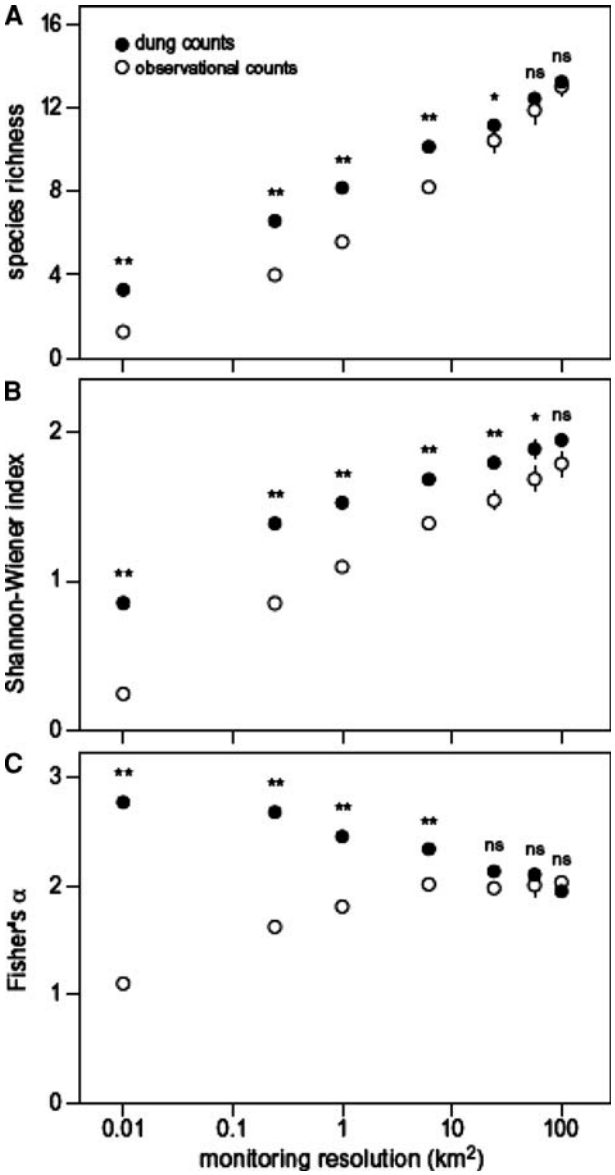

Fig. 2 Graph showing the estimates of three species richness and diversity indices versus monitoring resolution (km^2) for two different counting methods, dung counts (*solid circles*) and observational counts (*open circles*); **a** Species richness (*S*), **b** Shannon–Wiender index (H'), **c** Fisher's α. The *asterisks* indicate that diversity estimates were significantly different between counting methods for that monitoring resolution (Wilcoxon signed rank test, ** $P < 0.01$, * $P < 0.05$). *ns* indicates that diversity estimates did not differ significantly between methods ($P > 0.05$)

25 km^2 resolution the difference was significant, but smaller than one species (0.8). At the finer resolutions species richness was substantially higher using the dung counts, ranging from 20 to 166% higher going towards higher resolution. The Shannon–Wiener index also increased with decreasing resolution (Fig. 2b). H' dung count based estimates were higher

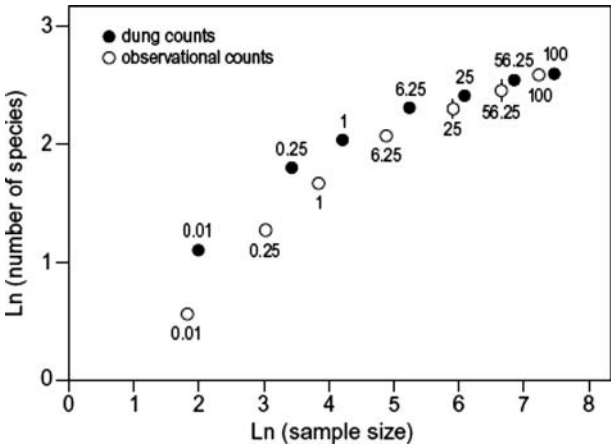

Fig. 3 Graph showing the relation between the natural log of the average number of species and the natural log of the average sample size per grid cell for two different counting methods, dung counts (*solid circles*) and observational counts (*open circles*). *Error bars* show the standard error of the mean of the number of species. Samples sizes and number of species were averaged over all grid cells per monitoring resolution. This monitoring resolution is illustrated as a foot note next to each circle in the graph

than using observational counts even at the coarser resolutions, though at 100 km^2 this difference was just short of significant ($Z = -1.9$, $P = 0.06$). The proportional difference in value of H' between methods increased with increasing resolution to as large as 240% for the 0.01 km^2 grid cells. Fisher's α showed a different trend than the other two indices (Fig. 2c). Again the proportional difference between dung counts and observational counts increased with increasing monitoring resolution, where diversity was higher when we used dung counts. Fisher's α, however, decreased towards coarser resolution for the dung counts, while it increased for the observational counts. Fisher's α directly reflects the nature of the relation between S and sample size N. To illustrate this behavior we calculated average sample size per grid cell for each monitoring resolution and compared this with the number of species present in that sample size (Fig. 3). As indicated by the behavior of α, more species were found with dung counts than with observational counts, especially in smaller sample sizes. Furthermore, on average, sample size was larger for the dung counts than for the observational counts, especially at the higher resolutions (Figs. 3, 4).

Both methods resulted in potentially very different spatial estimates of species richness and diversity, especially at finer resolutions (Fig. 5). This was especially true for the diversity estimates, Fisher's α and H'. Pearson r for these indicators did not exceed 0.5 and for α it even remained below 0.1 at all but one resolution. Species richness estimates from both methods were better comparable spatially, especially at resolutions coarser than 1 km^2. At these resolutions correlation between grid cells was 0.8 or higher, indicating that both methods resulted in the same relative differences in number of species between grid cells.

Discussion

We showed that monitoring methodology can strongly influence estimates of large herbivore species richness (S) and diversity (H' and Fisher's α) and that this effect interacts

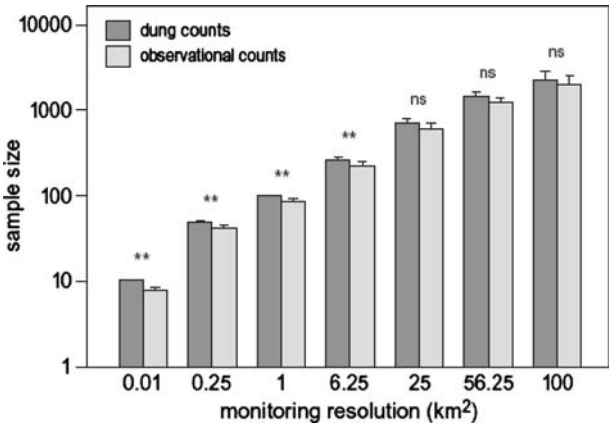

Fig. 4 Bar diagram showing the average sample size per grid cell per monitoring resolution for two different counting methods, dung counts (*solid bars*) and observational counts (*open bars*). *Error bars* show the standard error of the mean of the sample sizes. The *asterisks* indicate that sample sizes were significantly different between counting methods for that monitoring resolution (Wilcoxon signed rank test, ** $P < 0.01$, * $P < 0.05$). *ns* indicates that sampling sizes did not differ significantly between methods ($P > 0.05$)

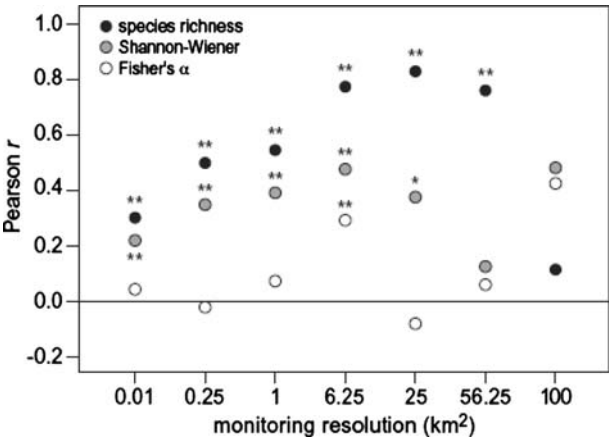

Fig. 5 *Graph showing* the Pearson correlation coefficients for the estimates of three species richness and diversity indices, Fisher's α (*open circles*), Shannon–Wiener index H' (*shaded circles*) and species richness S (*solid circles*), between two different counting methods (dung counts and observational counts), over a range of monitoring resolutions (km^2). High correlation illustrates that the two counting methods estimate the same changes of herbivore diversity in space. The *asterisks* indicate that the correlation was significant for that monitoring resolution (** $P < 0.01$, * $P < 0.05$), *no asterisk* shows that the correlation was not significant ($P > 0.05$)

with the scale of monitoring. Dung counts resulted in higher herbivore species richness and diversity estimates than direct observational counts, especially at finer monitoring resolutions (grid cells smaller than 25 km^2). This effect was the same for all three, commonly used, indicators; species richness, Fisher's α, and the Shannon–Wiener index. At monitoring resolutions coarser than 25 km^2 observational diversity estimates were comparable with dung count estimates. Methodology did not only affect absolute values of diversity

estimates but estimates of herbivore diversity also differed spatially. Especially at finer resolutions, correlation between grid cell values for richness and diversity estimates from both methods was very low (Fig. 5). This effect was stronger for the diversity estimates than for the richness estimate, indicating that methods especially differed spatially in their estimates of relative abundance.

The differences between the monitoring methods were caused by a sample size effect and, when sample size was constant, by differences in sighting probabilities. The dung counts resulted in a larger sample size than the observational counts per grid cell, especially at the finer resolutions (Fig. 4). Several studies have shown that an increase in sample size results in increasing species richness (see Magurran 2004 for a recent overview). The larger average sample size that we found per grid cell with dung counts can be directly related to the higher sampling intensity of dung counts, which is mostly caused by the much longer sample period of dung counts (Table 2). Further, even with an equal sample size for both methods we found more species with dung counts than with observational counts, especially in small samples (Fig. 3, samples smaller than 500 pellet groups or individuals). The much higher Fisher's α for dung counts, especially at finer resolution (Fig. 2c) also indicates that the dung counts resulted in relatively many rare species, while the small samples of observational counts consisted of fewer, but more abundant, species. This difference is probably due to the fact that the sample sizes of the observational counts were influenced by observations of herds of common species, while the dung counts have a higher sighting probability for rare species (low-density species and species that are difficult to observe directly, e.g., night-active species and species that are sensitive to disturbance). According to Gaidet et al. (2005) a high sampling effort is required to observe species that occur at low densities. Though this is true for direct observational methods, we showed that indirect dung counts have a relatively low sampling effort and high probability of observing rare species.

The sampling effort of our indirect dung counting method was much lower than of the observational counts, while it resulted in a much higher sampling intensity (observation h per km^2) due to the much longer sample period. Most studies that compare monitoring methods do not mention sampling effort (Magurran 2004). The few studies that we found that did estimate sampling effort of large mammal monitoring methods confirmed our finding. Jachmann (1991) also showed that his dung count method was much less labor-intensive than foot counts, though he compared methods in terms of costs. Gaidet et al. (2005) recently presented sampling effort data for a range of observational methods for a wooded savanna (comparable to our study site) and their sampling effort of the observational foot counts was very comparable to our study. They, however, did not evaluate indirect methods.

In many large African reserves, like the Kruger NP and Serengeti NP, aerial observational counts are the preferred monitoring method, because ground-counts are too labor-intensive when covering such a large sample extent. Aerial counts have indeed been shown to have an equally low sampling effort as dung counts (Jachmann 1991). Several studies, however, pointed out that aerial censuses hugely underestimate abundance and are strongly biased towards the largest species especially in forest or woodland habitat (Caughley 1974; Caro 1999; Barnes 2001; Jachmann 2002; Gaidet et al. 2005). Since the major part of African reserves is covered by these habitats we argue that aerial censuses are unsuitable to monitor mammal species diversity. Therefore, we suggest that even in these very large reserves the use of indirect dung counts should be considered. Instead of monitoring the whole reserve, one should consider setting up a monitoring network of fixed sampling units (line transects or blocks) that reflects a representative part of the reserve (such as the line

transect network discussed in this study). Using a method with a relatively low sampling effort, like dung counts, this network could be sampled on a regular basis (e.g., yearly or even seasonally) and equally as important, especially in large reserves, one could create a spatially more comprehensive sampling scheme (Brashares and Sam 2005). To illustrate this; in our study we could have carried out seven dung count programs with the same effort as one program based on observational counts (Table 2). More replication of monitoring in time and space would offer more insight in mammal diversity response to environmental change and management practices, making it much more suitable for adaptive management schemes. Moreover, because of its simplicity and low sampling effort, dung counts can be relatively easily incorporated in community-based conservation initiatives and management programs (such as patrols) in general (Danielsen et al. 2005).

We realize the potential conflict between the monitoring of diversity and the monitoring of abundance of certain target species. For certain species it might be important to get very accurate population abundance estimates (e.g., when estimating off take for translocation programs of endangered species). Direct observational counts might be better suitable to estimate accurate abundance of these species (using distance sampling techniques, Buckland et al. 1993). However, especially in systems with low visibility like tropical rain forests, this is contested and Barnes (2001) concluded that dung counts result in equal or even better estimates of population abundance in these systems. Since visibility in many savanna systems is often equally low (as shown in this study) dung counts might provide an underestimated alternative in these systems as well.

Concluding, monitoring methodology can strongly influence species diversity estimates. While conservation is more and more orientated at managing diverse herbivore communities, our results suggest that current monitoring programs that are based on direct observational counts are not the optimal method to monitor diversity. Dung counts seem to better represent diversity (including rare species) and are less labor-intensive.

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