Measuring species diversity while counting large mammals: comparison of methods using species-accumulation curves

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Abstract

With a growing need for wildlife conservation and management in the communal lands of Africa, comprehensive ecological monitoring tools need to be developed and evaluated. While wildlife census methods are often compared in terms of precision and accuracy to estimate the population size of various target species, little attention has been paid to the measure of species diversity in mammal communities. A combined measure of abundance and community composition is, however, a crucial source of information in determining conservation priorities and to evaluate the ecosystem responses to management activities. In this study, we present five census methods of large to medium-sized mammals and compare their efficacy in measuring species diversity. A species accumulation curve analysis is used with a predictive model to estimate the local species richness, the level of completeness of our censuses as well as the effort required to carry out a census. Advantages and limits of each method are discussed through comparison of their respective measure of species richness and their species accumulation rate. Results illustrate a large difference between methods in the ability for species detection, with censuses completed by bicycle offering the best option within the context of a unprotected area.

Key words: census methods, inventory completeness, mammals diversity, nonprotected area, sampling effort, species accumulation curve

Résumé

Un besoin croissant de conservation et gestion de la vie sauvage dans les terres communs d'Afrique nécessite le développement et évaluation des outils de surveillance écologique. Tandis que les méthodes employées pour le recensement de la vie sauvage sont souvent comparées - en termes de précision et d'exactitude - afin d'estimer la taille de la population de diverse espèces, peu d'attention est donnée à l'évaluation de la diversité d'espèces dans les communautés de mammifères. Néanmoins, une mesure combinée de l'abondance et composition de la communauté s'avère une source d'information importante pour déterminer les priorités de conservation et évaluer les réponses de l'écosystème aux activitès gestionnaires. Au cours de cette étude, nous présentons cinq méthodes du recensement des mammifères de taille moyenne à grande, et comparons leur efficacité dans la mesure de la diversité d'espèces. Nous employons une courbe d'accumulation d'espèces avec un modèle de prévision afin d'estimer la profusion d'espèces locales, et le niveau de complétude de notre recensement ainsi que les efforts nécessaires pour exécuter un recensement. Les avantages et les limites de chaque méthode sont évalués à travers la comparaison de leur mesure respective de la profusion d'espèces et taux d'accumulation d'espèces. Les résultats montrent une grande différence entre les méthodes dans leur capacité de percevoir des espèces, avec les recensements par vélo fournissant la meilleure option dans le contexte d'un lieu non-protégé.

Introduction

Counting animals represents one of the first methods used for monitoring the consequences of action in wildlife

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management or conservation. Numerous techniques have been employed to census large to medium-sized African mammals (Norton-Griths, 1978), with counting options selected according to objectives and site specific conditions. With an exceptional mammal diversity characterizing African savannahs, censuses may potentially include a large number of species. Results from different techniques tested in a study area were often compared in terms of precision and accuracy to estimate the population size of some target species (Jachmann & Bell, 1984; Koster & Hart, 1988; Knott & Venter, 1990; Jachmann, 1991; Peel & Bothma, 1995; Reilly & Haskins, 1999; Walsh & White, 1999) but authors have generally paid little attention to the measure of species diversity in mammal communities. Whereas the combined measure of abundance and diversity is a widespread practice in bird surveys (Bibby, Burgess & Hill, 1992), to our knowledge no study has reported results on the comparative efficiency of census methods for estimating the diversity of large to medium-sized mammals.

A measure of the species diversity is a meaningful complementary result from a wildlife count survey. It allows managers to document the ecosystem health with reference to similar eco-geographical areas and to evaluate the biological potential of an area managed with objectives of natural resources exploitation. Under a monitoring scheme, regular information on community composition and species assemblage rather than target species (flagship or harvested species) provides greater sensitivity to evaluate ecosystem responses to development of anthropogenic activities or to changes in management strategies (Kremen, Merenlender & Murphy, 1994). Comprehensive ecological monitoring is therefore a crucial source of information to integrate both conservation and management objectives.

Several factors can affect the measure of biological diversity in an area, and reliability of censuses has been discussed for various taxa according to the impact of the community spatial structure and the sampling design (Smith, Solow & Chu, 2000), the sampling method used (Pomeroy & Dranzoa, 1997), the unit of sampling effort chosen (Moreno & Halter, 2001; Willott, 2001), the size of the study area (Soberón & Llorente, 1993), the habitat heterogeneity (Pomeroy & Dranzoa, 1997; Moreno & Halter, 2000), the local individual density (Moreno & Halter, 2001), the diversity of the study group and species natural history (Willott, 2001).

We present five ground-based methods we conducted in a nonprotected area of Zimbabwe to estimate abundance of wildlife populations under the framework of an integrated conservation and development project (Biodiversity Project, 2001). We compared the efficiency of these counting methods for the measure of species diversity in large to medium-sized mammals, as well as census completeness using species accumulation curve analysis. Such an approach provides both a predictive tool for conservation objectives, through estimates of the total number of resident species, and a planning tool for designing field work, by providing information on effort and the cost-effectiveness of carrying out a census (Soberón & Llorente, 1993).

Method

Study area

The study area is a nonprotected area of 2044 km^2, located in the Rural Guruve District in the middle Zambezi valley, Zimbabwe. The site is characterized by two contrasting habitats: a dense human settlement with crop lands (25% of the area), and a wooded savannah where wildlife coexist with people. A total of 42 large to medium-sized mammal species have been recorded in the area (Biodiversity Project, 2001). The natural land cover is a deciduous dry savannah, dominated by mopane trees (*Colophospermum mopane* Kirk ex Benth), which form a mosaic of woodland and shrubland.

Census methods

The census methods we employed consisted of four different transect counts (car day count, car night count, bicycle count and foot count) and a water point count. Observers involved in these censuses were local agents from Anti Poaching Units, the Natural Resources Monitors from the District Council and local technicians trained by the Biodiversity Project. All had previously conducted regular patrols in the study area and had good knowledge of local wildlife. All censuses were based on direct sightings. We recorded all the large to medium-size mammals we encountered (>200 g, Skinner & Smithers, 1983). Animals detected were identified either by the naked eye (bicycle and foot counts), with binoculars (water point and car day counts) or a spot light (car night counts). Censuses involved one (foot and bicycle counts), two (water point and car day counts) or three observers (car night count). Foot and bicycle counts were conducted in the early mornings, car day counts in both early mornings and late afternoons, while car night counts started around 21.30 hours. For water point counts, observations were made continuously during a 24 h period from a tree-blind, offering a complete and safe view of the water point. Water point surveys took place during 2–3 days over each full moon period to allow clear observations and identification by night. Daylight and night observations were analysed separately for car counts, but data recorded during the continuous water point counts were pooled.

Survey design

Details of the survey design are presented in Table 1. Sampling units (i.e. transects and water points) were spread over the same study area and were designed to cover all vegetation types. Transects were established on four-wheel drive roads opened up by the Regional Tsetse and Trypanosomis Control Program (some bush areas were cleared to create small paths for the foot transects). This network was established to cover the whole area for the maintenance and control of Tsetse fly targets, regardless of human activities or vegetation units. Although the network did not allow for a proportional coverage of vegetation units, we considered the roads provided a representative sample of the area for a reliable estimate of mammal diversity. The length of transects established was constant in foot counts (1.8 km), but varied in bicycle (3.7–23.0 km) and car counts (6.6–17.8 km). For the water point surveys, we selected only those water points within the study area that held permanent water and showed low human disturbance (27 selected out of 49 identified).

Each sample units was repeated several times over the dry season (see Table 1). Censuses were conducted in either 1997 or 1999. Rainfall recorded in the Zambezi Valley during the 1996–1997 and 1998–1999 rainy seasons (November to March) was high, 1140 and 1650 mm, respectively. These are two of the three highest rainy seasons of the last decade recorded at that station (mean of 770 mm over 20 years). The two dry seasons of both survey years were, therefore, considered to be very similar in terms of water resource availability. We assumed the species diversity of the study group remained identical during the 2 years separating these surveys.

Data analysis

In order to standardize the measure of sampling effort in a rigorous comparison of different censuses, we used a species accumulation curve analysis, based on the measure of the rate at which species accumulate with increased sampling effort. We fit a predictive asymptotic model to these curves (Soberón & Llorente, 1993) to estimate: (i) the total species richness potentially detected in the area; (ii) the level of completeness of our censuses for the sampling effort we invested; as well as (iii) the minimum effort required to reach an acceptable level of completeness (Moreno & Halter, 2000).

The number of species was used as a classical estimate of diversity (Magurran, 1988). Sampling time was used in our analysis as a measure of the sampling effort (see details in Table 1). The average speed to cover the transects (including observation stops) varied according to the method used: 11.6, 5.5 and 1.3 km h^{-1} for car, bicycle, and foot counts respectively. A mean sampling time was calculated for each transect from the time recorded in the field. For each method, time to complete a transect varied according to transect length and habitat heterogeneity: 0.6–1.5 h in car counts = 40h to 1h30 m in car counts, 1.1–3.4 h in bicycle counts = 1h to 3h30 m in bicycle counts and 1.2–2.0 h in foot counts = 1h15 to 2h in foot counts. A 24 h period was used for each water point count.

Table 1 Details of survey design and total sampling effort for each method. The number of replicates from all sampling units, namely transects and water points, as well as their respective sampling times, were pooled for the analysis of total sampling effort

	Survey design					Sampling effort	
Method	Year	Month	Day/night	No. of sample units	Total transect length (km)	Total no. of replicates	Total sampling time (h)
Car day count	1997	June to October	day	12	137.7	96	95.1
Car night count	1997	June to October	night	12	137.7	24	23.8
Bicycle count	1999	September to December	day	10	121.3	304	669.0
Foot count	1999	June to November	day	18	32.4	108	153.8
Water point count	1997	May to October	day-night	27	–	46	1104.0

We used replicates of all samples (i.e. transects or water points) as the units of analysis. For all count methods, we produced the total sampling effort by pooling sampling time from all replicates. Final estimates could be biased as replicates of transects pooled in the analysis differed in sampling effort and were not independent but drawn from a pool of common sampling units. In order to eliminate influence of the selection order in which these replicates are added to the total sampling effort, we performed a sample order randomization. We repeated random reordering 30 times and calculated the average number of species added to the inventory list on increased period class of 2 h to generate a smooth species accumulation curve (Moreno & Halter, 2000).

We fitted an asymptotic model to our smoothed species accumulation curves of observed data, using nonlinear regression procedures. We applied the exponential equation of the linear dependence model recommended by Soberón & Llorente (1993) for a low diversity study group, with a relatively well-known natural history, over a relatively small area where all species could theoretically be detected over a finite sampling effort. In this model, the predicted number of species $S(t)$ added to the list decreases linearly as sampling time (t) increases:

$$S(t) = a/b[1 - \exp(-bt)]$$

The parameter a represents the increase rate at the beginning of the collection and a/b the asymptote. The minimum sampling time t_q required to reach an arbitrary level of census completeness q is given by:

$$t_q = -1/b \ln(1 - q)$$

Following Moreno & Halter (2000), we selected 90% as an acceptable level of census completeness ($q = 0.9$) to compare within inventory sampling effort.

Results

A total of 27 different species were observed and identified during the survey, half of them being ungulates (Table 2). It should be noted that all the different censuses share only seven species of 27. Apart from the species excluded from protocols, nocturnal species were effectively recorded during night surveys (car and water point counts), as well as during daylight bicycle counts. For ungulates, only the bicycle method allowed recording of all the local species (except roan *Hippotragus equinus* Desmarest, see discussion). Finally, large predators were only detected during bicycle and water point counts, but frequencies of observation were very low (1.05, 0.15 and 0.30 sightings per 100 h for lion, leopard and painted hunting dog respectively on bicycle counts; 0.18 and 0.09 sightings per 100 h for leopard and painted hunting dog respectively during water point counts).

The total number of species recorded varies greatly between census methods, ranging from 12 to 26 species (Table 2). Bicycle counts provide the most complete census, including all those species (except one) also recorded by the other methods. Census completeness then decreases from water point, car night, foot and car day counts. Different effort was, however, invested in observation time, from as little as 24 h on a car night count to more than 1100 h on a water point count. Predictive models that were fitted to species accumulation curves allow more rigorous comparisons through a standardized measure of sampling effort. Models provided a good fit to the species accumulation data ($r^2 \geq 0.98$; Table 3) for reliable prediction on census completeness. However, bicycle census data did not fit as well, but we considered the accumulated data was acceptable in order to make reliable predictions.

The models indicate that species accumulation curves of all our censuses reached an asymptote, except for the car night count (Fig. 1). Our censuses registered 100% or more of the predicted asymptote (Table 3), hence the probability of counts to add new species with increased sampling effort is low. We can assume the capacity of these methods, to measure species diversity, will have reached a saturation point during our survey and this level may be restricted by technical constraints. The level of species richness registered by each method over the same area is very different, illustrating the different ability of census methods for species detection. Models hence predict the same hierarchy of efficiency between methods in the measure of species diversity as our field inventories.

When we consider the effort-effectiveness, we observe another hierarchy of efficiency between methods (Table 3): the effort required to reach an acceptable level of census completeness (90% of the predicted asymptote) ranges from 36 h in foot counts to 812 h in water point counts (Table 3). However, this measure of effort is related to different estimates of species richness between methods. Figure 2 illustrates simultaneous species accumulation curves of methods we employed. The rate at which species accumulate is highest in car night counts then decreases for other methods from bicycle, foot, car day to water point counts. The noticeable lower efficiency of water point

Table 2 Species inventories recorded with various census methods. Species were ranked according to body height (Skinner & Smithers, 1983). Among the species we observed, we excluded from the analysis all the species that were not rigorously recorded during counts (bushbabies *Galago senegalensis* A. Smith and *G. crassicaudatus* E. Geoffroy, rock dassie *Heterohyrax brucei* Gray, greater canerat *Thryonomys swinderianus* Temminck and scrub hare *Lepus saxatilis* F. Cuvier) or not precisely identified in the field by observers (slender mongoose *Galerella sanguinea* Rüppell, *Helogale parvula* Sundevall, white-tailed mongoose *Ichneumia albicauda* G. Cuvier and *Mungos mungo* Gmelin)

Species	Scientific name	Car (day)	Car (night)	Bicycle	Foot	Water point
Elephant	*Loxondota africana*	*	*	*	*	*
Eland	*Taurotragus oryx*			*		
Buffalo	*Syncerus caffer*	*	*	*	*	*
Kudu	*Tragelaphus strepsiceros*	*	*	*	*	*
Waterbuck	*Kobus ellipsiprymnus*			*		
Sable	*Hippotragus niger*	*	*	*	*	*
Zebra	*Equus burchelli*			*	*	*
Impala	*Aepyceros melampus*	*	*	*	*	*
Lion	*Panthera leo*			*		
Bushbuck	*Tragelaphus scriptus*	*		*		*
Hyaena	*Crocuta crocuta*		*	*		*
Leopard	*Panthera pardus*			*		*
Painted hunting dog	*Lycaon pictus*			*		*
Bushpig	*Potamochoerus porcus*		*	*	*	*
Warthog	*Phacochoerus aethiopicus*	*		*	*	*
Aardvark	*Orycteropus afer*		*	*		*
Baboon	*Papio cynocephalus*	*	*	*	*	*
Klipspringer	*Oreotragus oreotragus*			*		
Duiker	*Sylvicapra grimmia*	*	*	*	*	*
Grysbok	*Raphicerus sharpei*	*	*	*	*	
Side-striped jackal	*Canis adustus*			*		*
Porcupine	*Hystrix africaeaustralis*		*	*		*
Vervet	*Cercopithecus aethiops*			*	*	*
Civet	*Civettictis civetta*		*	*		*
African wild cat	*Felis libyca*		*	*		
Honey badger	*Mellivora capensis*	*	*			*
Genet	*Genetta tigrina*	*	*	*		*
Total = 27 species		12	16	26	12	21

counts would be related to the continuous 24 h survey, where some hours were associated with low sighting probabilities (Fig. 3).

Discussion

Several mammal species of both conservation and exploitation concern in Africa remain undetected by aerial surveys (Caro, 1999; Hulme & Taylor, 2000), classically used in savannahs for their high ground-covering capacity (Norton-Griths, 1978). Such inability of aerial surveys has been emphasized by authors who promote the development and the evaluation of alternative ground-based methods, in order to respond to the growing need for conservation and management monitoring tools in communal lands of Africa (Caro, 1999; Hulme & Taylor, 2000). The ability to collect information over a large part of the resident species community must therefore be a crucial criterion to take into account when selecting conservation or management monitoring methods (Kremen *et al.*, 1994).

The species accumulation curves approach that we transposed in our study for large to medium-sized mammal censuses is a valuable tool for selecting the optimal sampling technique for an acceptable minimum level of diversity representation for a particular area. Models indicate if increasing the level of census completeness is a matter of increased sampling effort or if the implementation of a complementary or alternative census method will be more judicious.

Table 3 Results of fitting the linear dependence model to our species accumulation data. Number of species observed during censuses (*N*), parameters of the model (r^2 the coefficient of determination, *a* species × hours^{-1}, *b* hours $^{-1}$) and predictions of the total species richness (asymptote *a*/*b*), the level of completeness of our censuses (%, percentage of the predicted asymptote recorded) and the minimum effort required to register 90% of the total species diversity (time t_q, h)

Method	n	r^2	*a*	*b*	Asymptote	%	t_q
Car day count	12	0.99	0.48	0.04	11.85	101.26	57
Car night count	16	0.99	1.24	0.06	19.91	80.34	37
Bicycle count	26	0.86	0.45	0.02	24.40	106.54	124
Foot count	12	0.98	0.75	0.06	11.72	102.37	36
Water point count	21	0.99	0.06	0.00	21.14	99.35	812

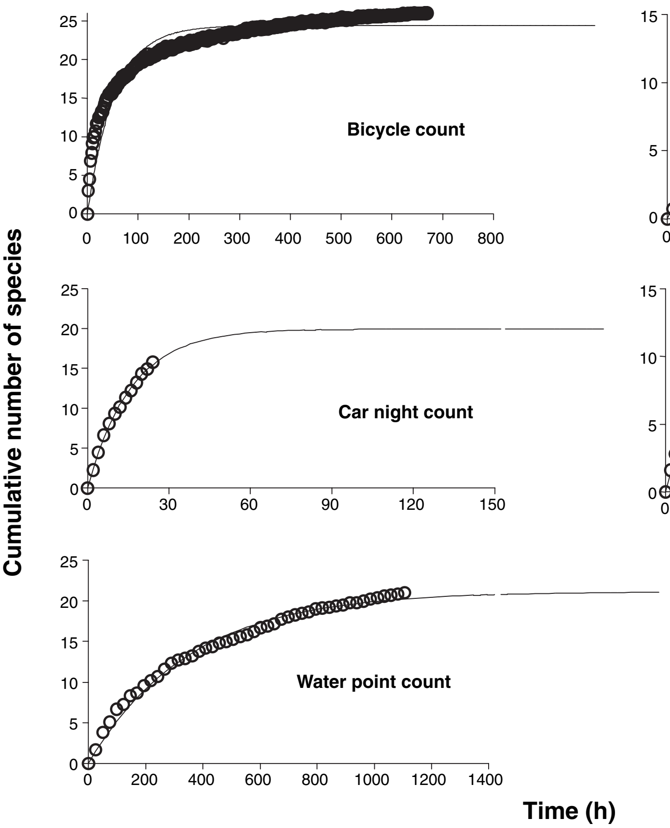

Fig 1 Species accumulation curves and linear dependence model for the five census methods. Scales of axes differ between methods. 'o', observed data; '-', prediction of the species accumulation model

The constant presence in our study area of experienced observers working in the field in association with local people since 1996 gave us a high level of confidence in our knowledge of the local species diversity of large to medium-sized mammals (Biodiversity Project, 2001). Apart from the nine species we excluded from the survey, most of the resident species were sighted during our survey (27 of 33 species). The species, which were not detected were two aquatic species whose habitat was not sampled (hippopotamus *Hippopotamus amphibius* L. and otter *Aonyx capensis* Schinz), three elusive species (pangolin *Manis temminckii* Smyts, serval *Felis servalina* Schreber and caracal *Felis caracal*), and the locally uncommon roan antelope.

The relatively low diversity and well known natural history of our study group, allowed us to select a suitable accumulation curve model (Soberón & Llorente, 1993).

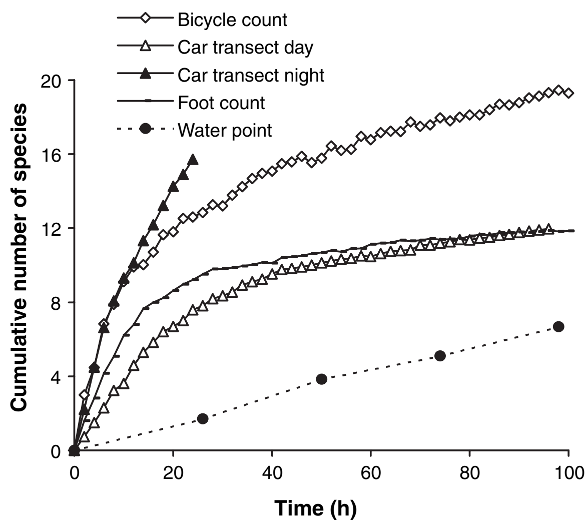

Fig 2 Species accumulation curves for the five census methods during the first 100 h of observation

However, spatial and temporal heterogeneity in community structure are two factors, which are known to affect measures of diversity (Soberón & Llorente, 1993; Smith *et al.*, 2000). The sample units that we used had a nonrandom spatial distribution, hence a risk exists of having the observed patterns generated by our sampling design. Our targeted sampling was designed so that observers passed through the majority of the local vegetation types, in order to detect the maximum number of resident species (Caro, 1999), and although nonrandom, it was considered representative of the area. Temporally, our sampling period was restricted to the dry season, which provides the period of best visibility in deciduous savannah, hence the highest detection probability. Although the species in our study area may show some local migration and seasonal abundance fluctuations (Jarman, 1972), they are all be encountered throughout the year in our study area, as indicated by a monthly track survey we performed for 1 year (N. Gaidet, unpubl. data).

When comparing the inventory efficiency of various counting methods, their respective advantages and limits should be considered according to the characteristics of the species under concern. Conspicuous and relatively common species are quickly detected by all censuses, but for a species dispersed at low densities, observation will require a high sampling effort. If we consider a species with restricted habitat or particular daily/seasonal distribution, protocol should cover the appropriate time or place for the species to be encountered, and thus maximize observation opportunities. Advantages will hence be given to methods, which are easily applicable to various environmental conditions with respect to principles of standardization. Finally, because some species are secretive and elusive, to be efficient a silent approach is crucial for wildlife census methods based on direct sightings. Indirect techniques based on sign detection may be a valuable tool in some instances, and track surveys reported reliable results for difficult-monitoring species such as large carnivores (Beier & Cunningham, 1996; Stander, 1998).

All methods implemented in our study have some advantages. Car counts offer the benefit of covering larger areas than other ground-based methods thanks to high cruising speed and allows effective night counts thanks to the use of spotlights (Monadjem, Monadjem & Putnam, 1998). However, in the context of a communal land where animals showed fear of the human approach, disturbance from motor vehicles limits the efficiency of car day counts.

In the specific conditions of a nonprotected area, low disturbances associated with bicycle, foot and water point counts are, therefore, considered to be a major advantage. Water point counts provided a good measure of species richness, but effort required for a census to be completed would be unaffordable for most monitoring programmes.

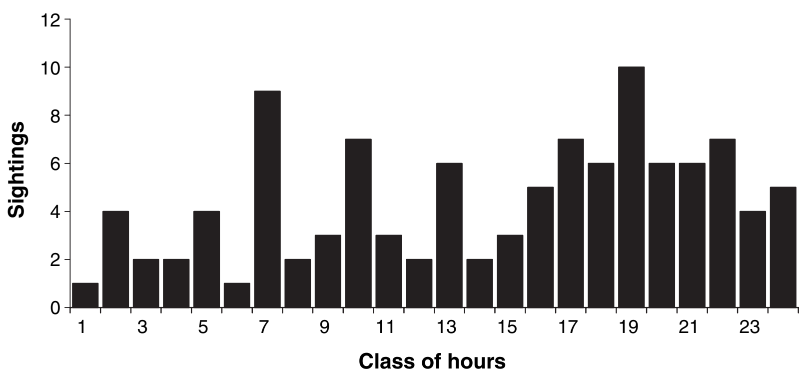

Fig 3 Water point count census: distribution of sightings per hour frequency during 24 h continuous count. We averaged the number of sightings of all species recorded during the 46 counts we conducted (total of 1104 h)

Nevertheless, water point surveys give meaningful results on utilization of water points as a key resource during the dry season, and it could be a valuable complementary source of information to specific conservation and management activities. Simple ground-based methods such as bicycle and foot counts benefit from low labour and cost requirements, hence potentially providing more replicates under logistical and budgetary constraints. Bicycle counts offer the advantage of covering a wider area and a more silent approach than foot counts, and therefore offer the optimal compromise under the context of a nonprotected area for a census method of measuring species diversity.

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