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Estimating the abundances of large herbivores in the Kruger National Park using presence–absence data

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Abstract

Conservation planning and practice rely heavily on abundance information generated at local scales for decision-making. Unfortunately most distributional data are only provided as presence–absence records at regional or national scales and cannot be used for making local conservation decisions. To date, two methods have been proposed for estimating local abundances and area of occupancy from coarse-scale presence–absence data. Kunin (1998) proposed the use of the fractal method, which assumes that species distributions are self-similar across scales. He & Gaston (2000*a*), in turn, proposed the use of the negative binomial distribution (NBD) for estimating abundances from presence–absence data collected at different scales. Previously only plant data were used to test these models. In the present study, they were tested using distributional presence–absence, as well as abundance data for a selection of large herbivores that have a restricted distribution in the Kruger National Park, South Africa. The results illustrate that the fractal method tends to overestimate areas of occupancy, while the NBD method underestimates the areas of occupancy of all species. This means that there were significant differences between the predictions provided by the two methods. Both these methods rely on the relationship between the area of occupancy and the size of the area over which the survey is conducted, but describe this relationship in a different way. These techniques could prove useful in the field of conservation biology and this study illustrates that these methods can be used on large mammal species and deliver results that are consistent with previous studies on plants.

INTRODUCTION

Abundance information tells us how many individuals occur in a population of a certain species (Caughley & Gunn, 1996; Gaston & Blackburn, 2000). Modern conservation practice is highly dependent on data on the abundances of species within an area, since it provides a basis for making practical conservation decisions. Unfortunately species abundance information at local scales is difficult or expensive to obtain (Gaston *et al.*, 2000). Thus, the ability to predict fine-scale species abundances from coarse-scale presence–absence data, which are more readily available, has considerable application in conservation biology.

The positive relationship between the local abundances of organisms and the extent of species distribution ranges has become axiomatic (Hanski, 1982; Brown, 1984) and is the focus of much attention in the field of macroecology (Brown, 1984; Brown & Maurer, 1989; Lawton, 1993; Gaston, 1996; Gaston, Blackburn & Lawton, 1997). Kunin (1998), and He & Gaston (2000*a*) have tried to use this relationship to solve the problem of estimating intra-specific abundances from presence–absence data.

Kunin (1998) proposed the fractal method, which is based on the assumption that the distribution patterns of all species are self-similar across scales and consequently display similar space-filling properties across these scales. Presence–absence data from two maps of different resolutions are used to generate scale-area curves (area of occupancy against grid cell size). These scale-area curves are then used to estimate abundances through extrapolation to scales where fine-scale occupancy is considered to approximate abundance (Kunin, 1998). Abundance can, in theory, be predicted if the area occupied by an individual of a species can be determined and all the underlying assumptions are met (He & Gaston, 2000*a*). This assumption can be problematic, especially when considering the space-filling properties of large mammals, where grouping patterns may vary between sexes of the same species or seasonally within the same species.

He & Gaston (2000*a*) proposed the use of an alternative method, the negative binomial distribution method (NBD). The negative binomial distribution is characteristic of many species distributions and can be used to describe regular, random or aggregated distributions (He &

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Gaston 2000*b*). Area of occupancy and abundance of aggregated individuals can be calculated using the NBD function. This function uses the relationship between the distribution of a species across a landscape and the mean abundance of that species, to calculate the probability of the presence of a species in a sampling unit. The NBD method used by He & Gaston (2000*a*) turns this relationship around, assumes a common aggregation parameter across scales and uses the presence of a species in a sampling unit to calculate the number of individuals of that species. In order to solve for the unknowns of abundance and the aggregation parameter, the area of occupancy of a species at two different scales must be known.

These models have been applied mostly to plant species data (e.g. Kunin, 1998; He & Gaston, 2000*a*) at various scales. The present study investigates the value of these methods for estimating the abundances of large herbivores from the Kruger National Park, South Africa. Large herbivores differ from plants in that they are not stationary and their space-filling properties are different within and between species. This can result in multiple occurrence records for the same individual, which can complicate the relationship between abundance and range size. Furthermore, the study area is a conservation area which effectively constrains the distribution of these species. Thus using large ungulate presence–absence data from the Kruger National Park to test these methods presents a major challenge. The practical value of the success of these methods is very important when it comes to modern conservation practice and management. Survey costs can be alleviated, especially in difficult landscapes where large herbivores occur and when species that are difficult to monitor or count are under consideration.

This study aims to determine if the two proposed methods can be applied to a set of large mammal species with limited ranges at very coarse scales. The study aims to evaluate the relationship between area of occupancy and scale, the ability of the methods to predict fine-scale area of occupancy from coarse-scale presence–absence data, the species specificity of these occupancy-scale relationships and the consistency of the estimated area of occupancy figures derived. In addition, the ability of the NBD method to predict abundances is also investigated. If these methods can be successfully applied within the Kruger National Park, their applicability within conservation practice will be strengthened.

METHODS

The study area and data sets

The two techniques were compared using distributional data for six herbivore species from the Kruger National Park ($\sim 13\,912$ km^2), South Africa (Fig. 1). The following species were used in the analysis: *Diceros bicornis* (black rhinoceros), *Taurotragus oryx* (eland), *Hippotragus niger* (sable), *Damaliscus lunatus* (tsessebe), *Kobus ellipsiprymnus* (waterbuck), *Ceratotherium simum* (white rhinoceros) and *Hippotragus equines* (roan antelope).

Presence–absence distributional data were available at 4 km^2 and 625 km^2 resolutions. The 4 km^2 occupancy data originate from ecological aerial surveys (EAS) conducted annually in the Kruger National Park from 1977 onwards (Eiselen, 1994). A high degree of standardization is maintained in these aerial surveys, and conditions are kept constant in order to obtain a high degree of precision (Eiselen, 1994). The 625 km^2 data set is equivalent to the quarter degree squares (QDS) data for the whole of South Africa, and was obtained from museum records of mammal distribution for South Africa collected between 1900 and 1980 (Freitag & van Jaarsveld, 1995). The nature of the species being studied and the fact that the Kruger National Park is one of the best managed parks in South Africa, renders data at this scale very accurate. These two data sets are independent of each other and therefore comparisons can be made between predictions obtained from the 625 km^2 data set and the observed areas of occupancy at the 4 km^2 resolution.

Species abundance data from the Kruger National Park collected from 1980 to 1988 during the aerial surveys were used in this analysis and could be compared with estimates of abundance generated. Abundances are obtained annually during the aerial surveys by means of a multispecies, total area count of large herbivores, conducted in the dry season for maximum visibility (Nicholls *et al.*, 1996). Roan antelope *Hippotragus equines* was added to the analysis due to its rarity and it was omitted from the area of occupancy analysis, because the NBD function failed to provide a coarse-scale abundance or aggregation parameter estimate for this species at the 2500 km^2 scale. Presence–absence, as well as abundance, data were available for 16 herbivore species. However, nine of these species occurred throughout the study area and thus achieved grid saturation at the 625 km^2 level and were not useful for testing the models. The observed areas of occupancy, percentage area covered in the Kruger National Park and observed abundances are listed in Table 1.

These data, thus, provided a means of testing the models and for comparing the generated abundance and occupancy results. At such coarse scales (625 km^2) and in an area of limited size (13 912 km^2) the accuracy of presence–absence data cannot be contested. The abundance data were also collected using methods that result in a high degree of accuracy for large mammal counts (Eiselen, 1994). Thus, both the presence–absence data and the abundance data were considered to be suitable for testing the fractal and NBD methods.

Area of occupancy

Both techniques were assessed using the 625 km^2 resolution maps, from which 2500 km^2 resolution maps were generated by superimposing a 50 km by 50 km grid (Fig. 1).

For the fractal method, area of occupancy for each species was calculated so that the total area occupied by a species (A_a) was equal to:

$$A_a = \sum ax \tag{1}$$

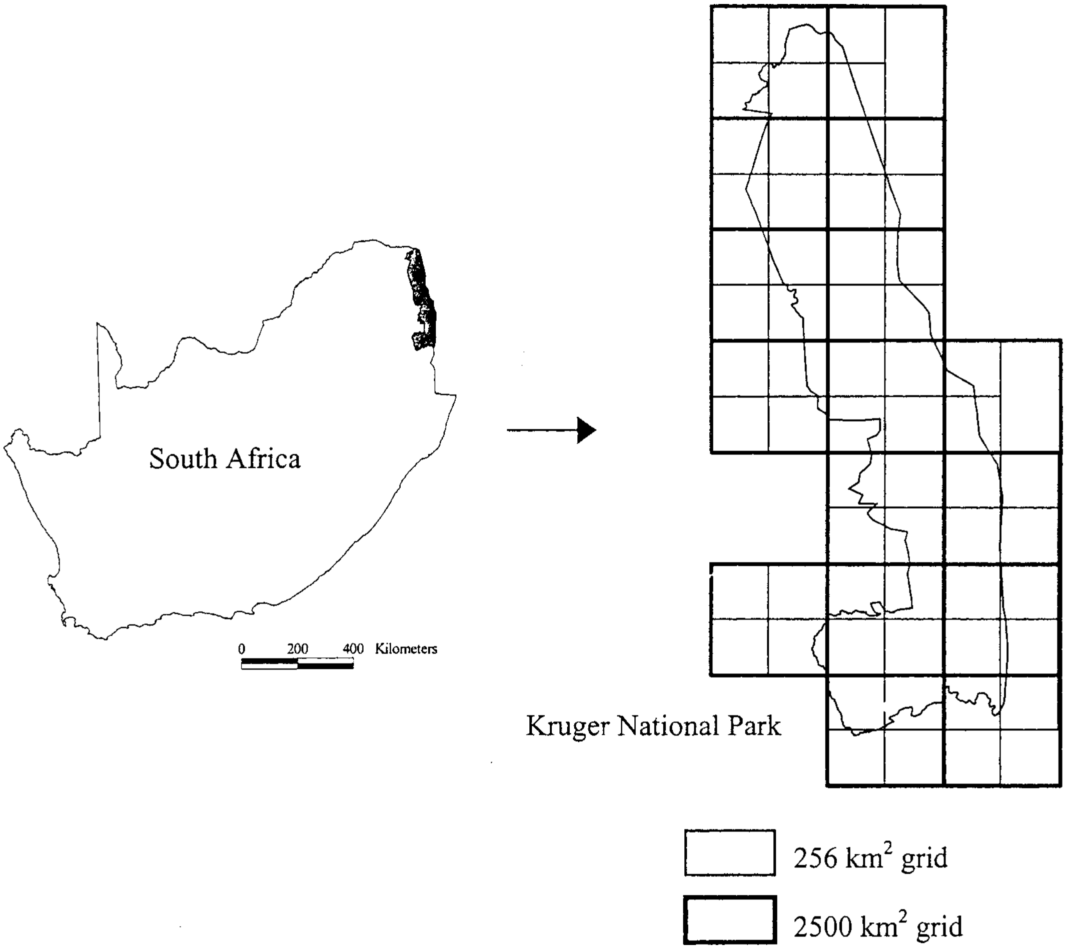

Fig. 1. Map of South Africa showing the location of the Kruger National Park and the placement of the 256 km^2 and 2500 km^2 grids over the Park.

where a is the scale, or area of each grid square and x is the number of grid squares occupied by each species. Total area occupied by each species, A_a, at 625 km^2 and 2500 km^2 resolutions were then plotted against scale (625 km^2 and 2500 km^2) on logarithmic axes and the resultant scale-area curve was used for linear regression. The scale-area curve was extrapolated to predict area occupied for each species at a 4 km^2 scale (fine-scale). Although the calculation of scale-area curves may seem inappropriate in this situation the main objective of using this approach was to see whether or not the predicted values coincide with the observed values. The scale-area curves allowed for the use of minimal data to arrive at a prediction, which could be compared to the observed areas of occupancy collected from the Kruger National Park. For the NBD method, the area of occupancy on the coarse-scale grid maps was calculated using the following equation (He & Gaston, 2000*a*):

$$A_a = A[1 - (1 + Na/Ak)^{-k}] \qquad (2)$$

where A_a is the area of occupancy, A is the total area covered by the 4 km^2 grid map, a is the scale, N is the

Table 1. Mean (± SD) observed areas of occupancy (number of 4 km^2 squares occupied), relative area of occupancy within the entire Kruger National Park (13 912 km^2) and observed abundance (for the entire park) values for the seven species used in this analysis

Species	Method	Observed area of occupancy	Area of occupancy (%)	Observed abundance
Black rhinoceros (*Diceros bicornis*)	Fractal & NBD	59.5 ± 20.4	0.43	23.88 ± 8.9
Eland (*Taurotragus oryx*)	Fractal & NBD	463.5 ± 112.5	3.33	730.88 ± 198.9
Sable (*Hippotragus niger*)	Fractal & NBD	1189.5 ± 146.1	8.55	2019.50 ± 211.6
Tsessebe (*Damaliscus lunatus*)	Fractal & NBD	731 ± 103.1	5.25	965.75 ± 131.1
Waterbuck (*Kobus ellipsiprymnus*)	Fractal & NBD	1668.5 ± 347	11.99	3581.75 ± 647.3
White rhinoceros (*Ceratotherium simum*)	Fractal & NBD	1046.1 ± 209.1	7.52	812.88 ± 182.2
Roan antelope (*Hippotragus equinus*)	NBD	–	–	333.38 ± 59.6

abundance and k is the aggregation parameter. The aggregation parameter, k, was taken to be the same aggregation parameter as that calculated from equation (3). In order to test the coarse-scale applicability of this equation, estimates of N and k generated at the 625 km^2 and 2500 km^2 scales were used to calculate the area of occupancy at the 4 km^2 scale. Area of occupancy predictions were compared with observed values and across methods, using the Wilcoxon Matched Pairs Test for small sample sizes (Siegel, 1956) and Spearman's Rank Order Correlation assessments.

Estimating abundance

By manipulating equation (2), He & Gaston (2000*a*) derived a direct estimate of species abundance, such that abundance equals:

$$\tilde{N} = A_k/a\left[(1 - A_a/A)^{-1/k} - 1\right] \qquad (3)$$

Grid maps of 4 km^2, 16 km^2, 256 km^2, 625 km^2 and 2 500 km^2 resolution were used for the analysis. In each instance, the coarser scale distributional maps were generated from their finer scale counterpart (e.g. 2 500 km^2 from 625 km^2). Any two maps at different scales can be used to solve for abundance and the aggregation parameter, k, simultaneously. The performance of the model and the limitations of the equation were investigated by performing the analysis over a variety of scales. The predicted abundances for the seven species (i.e. the six species used in the area of occupancy analysis plus the Roan antelope) were then compared to observed abundance data collected from the Kruger National Park. The difference between the observed and predicted abundance estimates generated by different scale combinations was also explored.

RESULTS

Estimating fine-scale area of occupancy from coarse-scale data

Roan antelope data were excluded from the area of occupancy analysis due to the fact that a coarse-scale abundance and k-value could not be extracted using the NBD method.

Across the remaining six species, the NBD and fractal methods delivered fine-scale area of occupancy estimates that were strongly positively correlated with the observed areas of occupancy at a 4 km^2 scale (Spearman's $r = 0.83$, $P = 0.04$ (fractal); Spearman's $r = 0.83$, $P = 0.04$ (NBD): Fig. 2(a)). The areas of occupancy delivered by the fractal method were significantly different from the observed values (Wilcoxon, $T = 0$, $P = 0.05$) and the values predicted by the NBD method ($T = 0$, $P = 0.05$). There was no significant difference between the areas of occupancy predicted by the NBD method and the observed areas of occupancy (Wilcoxon, $T = 8$, $P > 0.05$). The percentage difference between the observed and predicted values showed that the fractal method consistently overestimated the area of occupancy for all species, whereas the NBD method underestimated the area of occupancy (Fig. 2(b)).

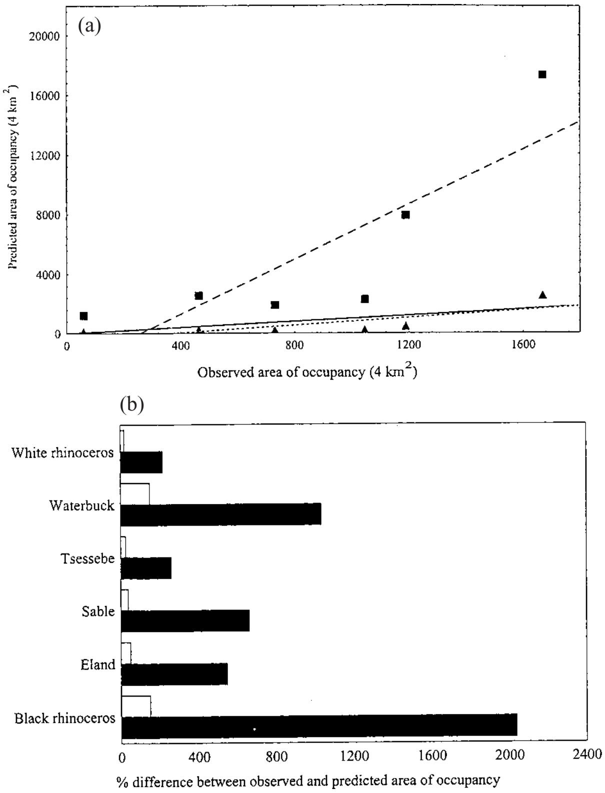

Fig. 2. The differences between the fractal and the negative binomial distribution (NBD) methods. (a) Graph of the relationships between the observed and predicted areas of occupancy. ——, 1:1 line; - -■- -, fractal results; · · ·▲· · ·, NBD results. (b) Graph showing the proportional differences for the fractal (solid bars) and the NBD (open bars) methods.

Estimating abundance

Abundance and aggregation parameters were calculated for seven species (including Roan antelope: Table 2). The abundance estimates for these species showed a significant positive correlation with observed abundances, except for the 625 km^2 and 2500 km^2 scale combinations (Table 3). However, the predictions generated at fine scales were significantly different from observed abundances. Only predictions produced at the coarser 625 km^2 and 2500 km^2 scale combinations did not differ significantly from the observed abundances (Table 3, Fig. 3). There were no significant differences between the abundances predicted by the different scale combinations for the respective species.

The relative differences between the observed and predicted abundances across scales were consistent for five out of the seven species, with black rhinoceros *Diceros bicornis* ($Z = -3.58$, $P < 0.0005$) and white rhinoceros *Ceratotherium simum* ($Z = -2.55$, $P < 0.05$) being significantly different from other species and from one another (Fig. 4).

Table 2. The different scale combinations used for estimating abundances (NBD method)

	Black rhinoceros		Eland		Sable		Tsessebe		Waterbuck		White rhinoceros		Roan antelope	
Scale combination	N	k	N	k	N	k	N	k	N	k	N	k	N	k
4 km^2 & 16 km^2	15.43	0.06	129.54	0.18	353.52	0.38	239.69	0.11	517.25	0.43	356.43	0.14	81.84	0.15
4 km^2 & 256 km^2	15.15	0.13	127.75	0.21	349.14	0.42	228.61	0.14	488.63	0.68	324.01	0.20	81.30	0.16
4 km^2 & 625 km^2	15.07	0.20	124.27	0.32	342.13	0.19	211.30	0.23	480.49	0.83	321.88	0.21	79.54	0.24
4 km^2 & 2500 km^2	15.36	0.14	121.97	0.5	330.29	0.86	197.77	0.52	484.84	0.74	290.33	0.45	76.87	0.91
16 km^2 & 256 km^2	14.48	0.15	123.61	0.22	339.03	0.43	207.31	0.15	432.28	0.75	270.30	0.22	79.98	0.16
16 km^2 & 625 km^2	14.25	0.23	113.50	0.35	318.53	0.54	168.49	0.26	414.08	0.91	267.87	0.23	74.54	0.25
16 km^2 & 2500 km^2	14.50	0.15	108.01	0.53	289.05	0.91	145.96	0.60	428.22	0.78	212.41	0.51	67.61	1.02
256 km^2 & 625 km^2	10.12	2.35	41.79	3.87	138.36	1.2	–	–	213.33	1.77	227.26	0.24	30.26	1.81
256 km^2 & 2500 km^2	14.70	0.14	49.88	0.96	125.12	1.53	42.29	1.96	396.02	0.80	75.47	0.93	28.04	18.40
625 km^2 & 2500 km^2	23.20	0.11	58.97	0.81	117.22	1.62	47.4	1.59	814.81	0.63	52.86	1.36	–	–

The predicted abundances (N) and the respective aggregation parameters (k) for each species are included.

Table 3. Spearman's rank order correlations (R) and Mann-Whitney U-test values (Z) between the observed and predicted abundances for all scale combinations

Scale combination	R-value	Z-value
4 km^2 & 16 km^2	0.96**	−1.98*
4 km^2 & 256 km^2	0.96**	−2.11*
4 km^2 & 625 km^2	0.96**	−2.11*
4 km^2 & 2500 km^2	0.96**	−2.24*
16 km^2 & 256 km^2	0.96**	−2.11*
16 km^2 & 625 km^2	0.96**	−2.24*
16 km^2 & 2500 km^2	0.96**	−2.24*
256 km^2 & 625 km^2	0.83*	−2.29*
256 km^2 & 2500 km^2	0.89**	−2.24*
625 km^2 & 2500 km^2	0.77	−1.86

*, significant at the $P < 0.05$ level; **, significant at the $P < 0.001$ level.

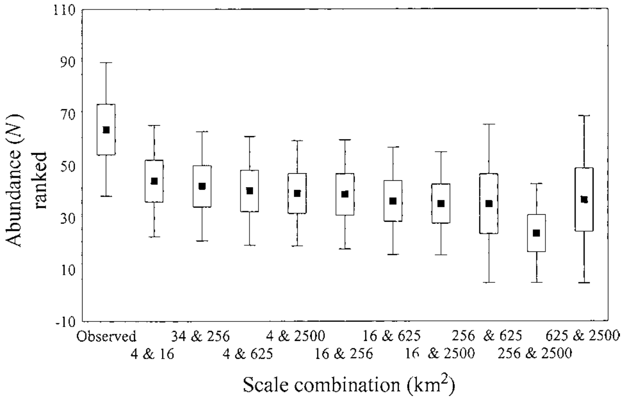

Fig. 3. The abundances predicted by the negative binomial distribution (NBD) method, for all scale combinations (km^2). Data are expressed as box whisker plots, showing means, standard deviations and standard errors.

DISCUSSION

The novelty of the fractal and NBD methods is that they rely solely on presence–absence data to predict fine-scale areas of occupancy and abundances. Presence–absence data are the most common form of information collected in a census, since they are less expensive and require less effort to collect (Gaston *et al.*, 2000). Therefore, the fractal and NBD methods, which incorporate the use of coarse-scale distributional data for estimating local distributions and abundances, have considerable potential.

These methods, however, have their restrictions when it comes to the scalar extent of the study as well as the nature of the species distributions and the techniques employed.

Scale employed

The scales employed in this study allow for rigorous testing of these methods, especially when assessing the practical application of these models. The ability of these two methods to predict areas of occupancy that correlate closely with the observed areas of occupancy is in accordance with the findings of Kunin, Hartley & Lennon (2000) as well as He & Gaston (2000*a*). When predicting area of occupancy, the NBD method tended to underestimate areas of occupancy that were similar to the observed areas of occupancy, but very different from those predicted using the fractal method.

Although these results coincide closely with previous studies, it should be borne in mind that these methods were tested on six large mammal species that have a small ($< 12\%$) percentage area of occupancy within the study area. The main reason for this was the inability of both methods to perform at coarse-scales with species that had high areas of occupancy. Under these broad-scale conditions, area of occupancy estimates were consistently 100% of the total area and, consequently, a weak fractal relationship was obtained between scale and area of occupancy. Moreover, at these scales the NBD method was not provided with sufficient resolution to extract aggregation parameters. Identifying the most appropriate resolutions for performing these studies appears problematic, especially when species with different spatial patterns are included in the analysis. Thus, the variable nature of large mammal species distributions

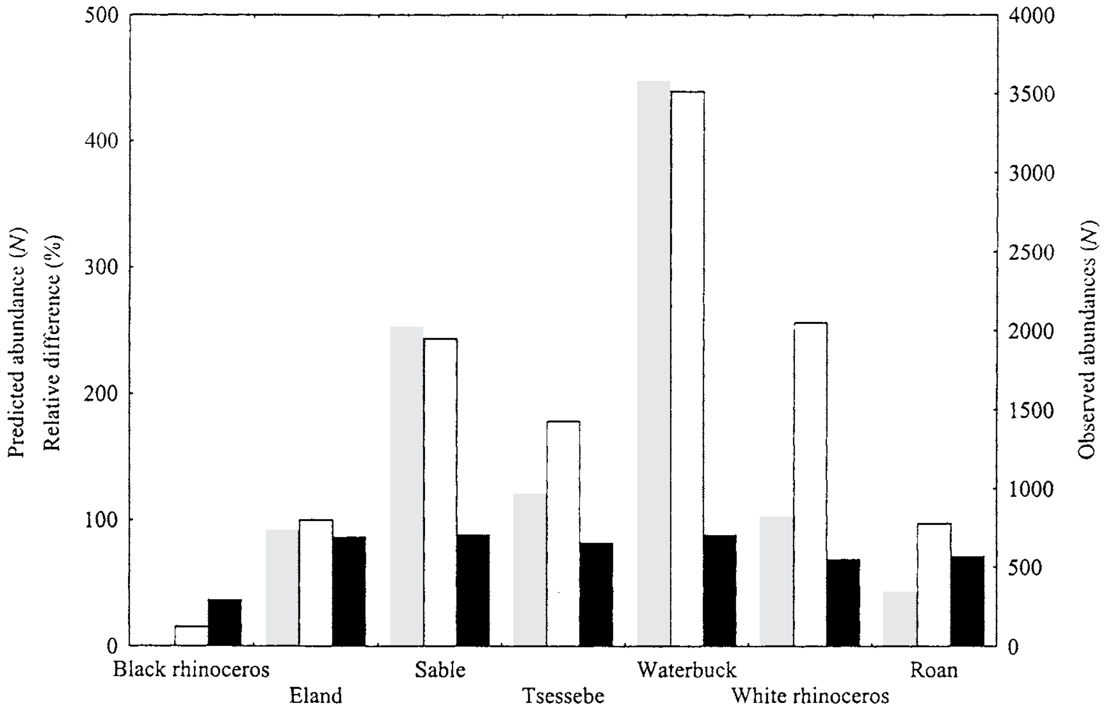

Fig. 4. Graphical representation of the observed abundance (grey bars), predicted abundance (white bars) and relative difference between observed and predicted abundance (black bars).

comes into play as well as the cost implications of collecting presence–absence data at finer resolutions. However, the way forward seems to lie in matching the distribution patterns of species with appropriate scale combinations for distilling accurate abundance data from presence–absence data.

The NBD method predicts areas of occupancy with greater accuracy than the fractal method (Fig 2(a)). The reason for this may be that the use of scale area curves to estimate the fine-scale area of occupancy has its limitations. Moreover, regressions from two points, especially when there are large steps between the points, contain significant variance around them and perhaps this method needs refinement in order to make the fractal method more accurate. The use of coarse-scale estimates of N and k in the NBD method succeeded extremely well in estimating the area of occupancy of species that occupy less than 12% of the Kruger National Park. Thus, there seems to be enough resolution at these scales (625 km^2 and 2500 km^2) to extract realistic N and k values.

The NBD method: estimation of abundance

Although the NBD method seems to predict areas of occupancy accurately the same cannot be said of its ability to predict abundance. By testing the applicability on species with small areas of occupancy ($<$ 12%), the single most confounding factor, namely, grid saturation is excluded from the analysis. Nevertheless, the NBD method consistently underestimates abundances, with the same relative differences across species (excluding the black and white rhinoceros) and across scale combinations (Fig. 4). Although there seems to be no difference between the predictions generated at the 625 and 2500 km^2 scale and the observed abundances there is also no relationship between the observed abundances and the predicted abundances. The influence of small sample size ($n = 6$) and the ranking of the variables seems to have played a role and obscured the variation that exists between the predicted and observed abundance values.

The use of coarse-scale data may lead to unrealistically low estimates of abundance (Fig. 3; Kunin *et al.*, 2000). The degree of auto-correlation in the occupancy of a species across maps at different resolutions affects changes in k-values between scales (Kunin *et al.*, 2000) and even though this may not be a problem at fine scales (He & Gaston 2000*b*), it presents a problem in the present study. At coarse scales shifts in k values can result in large underestimates of abundance.

The recorded lack of a significant difference between the values of N and k for each species predicted using different scale combinations (Fig. 4) is a result of the large degree of auto-correlation between the grid maps generated during the analysis; essentially the same dataset is simply being viewed at different resolutions. Unfortunately, these data are not always collected independently at different resolutions, especially large mammal data in places like the Kruger National Park. These results therefore confirm that dependant data sets can influence one another to a significant degree.

The relative differences between observed and predicted abundances for each of the species gives an indication of the consistency of the method across species. Results of the NBD method seem to be consistent for all the ungulate species in the analysis (*Taurotragus* *oryx*, *Hippotragus niger*, *Damaliscus lunatus*, *Kobus ellisiprymnus* and *Hippotragus equinus*), but not for *Diceros bicornis* and *Ceratotherium simum*. The relative differences are smaller for *Diceros bicornis* and *Ceratotherium simum* (Fig. 4) and indicate that the predictions for these species were more accurate, especially so for black rhinoceros. A probable explanation is that the distribution of this species differs markedly from that of the other ungulate species. Black rhinoceros individuals are widespread, with few individuals occurring in a large area. Thus, there exists enough resolution to be able to extract realistic abundance and *k*-values. The distribution of the black rhinoceros, at this resolution in an area of this size, seems to come closest to displaying a negative binomial distribution.

CONCLUSION

The relevance of techniques used for estimating abundance from presence–absence data in conservation is considerable, even if they cannot be used for species that occur in all areas (Gaston *et al*., 2000). If these techniques are easy to implement and deliver consistent results, they can become all the more valuable. In the light of the importance of the economic costs associated with conservation (Balmford & Gaston, 1999; Drechsler & Wätzold, 2001), cost effective techniques for estimating species abundance warrant special attention. The fractal and the NBD methods, in principle, both require information that is easy to obtain and analyses that are reasonably easy to implement. The results obtained in this study support previous findings and describe similar patterns for large herbivores to those previously recorded for plant species. The NBD method consistently predicts similar areas of occupancy at finer scales than the original scales of data collection. The fractal method does the same but at a lower level of accuracy. Thus, it is clear that these methods could, in principle, be applied to plant and large mammal species. The potential exists to implement these methods using data collected at very coarse-scales, provided that species that occupy the complete area are not included in the analysis. The value of these methods in predicting fine-scale area of occupancy is thus supported by this study. However, fine-scale area of occupancy and abundance data are not the same and are not of equal value in conservation efforts. In species conservation, abundance data from presence–absence data can be considered to be the Holy Grail. Estimating abundances from fine-scale areas of occupancy, as recommended in the fractal method, may prove difficult to implement since the area of individual occupancy needs to be known. The NBD method has some role to play in calculating these abundance estimates, especially if more information can be incorporated into the model, but some caution is advised not to place too much reliance on these estimates since they can differ significantly from observed data.

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