

Biases in estimating population size from an aerial census: a case study in the Kruger National Park, South Africa

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In the Kruger National Park (KNP), South Africa, aerial census data for approximately 15 herbivore species were collected from 1981 to 1993 using a total area count, strip transect method. No estimates of bias or precision error were obtained for the census data. Visibility bias, however, has been shown to be a primary source of error in aerial census data collected using methods similar to the KNP's. Starfield¹ argues that a pragmatic modelling approach can be used to understand the importance of uncollected data and improve data collection strategies. Following this pragmatic approach, we develop a simple, deterministic model to estimate the potential range of bias in the KNP census data. Sources of visibility bias considered in our model include undercounting detected herds and failing to detect small herds. We apply the model to data collected for impala, zebra, wildebeest and waterbuck, because these species represent a range of potential censusing challenges. The model suggests that visibility bias represents a major source of error in the KNP census data. In particular, the model indicates that visibility bias may confound comparisons among species or comparisons of a particular species' abundance among years, under different environmental conditions, or in different habitat types.

Introduction

The Kruger National Park (KNP — see Fig. 1) is an officially designated long-term ecological research area and has one of the most sophisticated long-term ecological research programmes in Africa.² One component of this programme is an annual aerial census conducted in the dry season. The goal of this census is to provide insight into herbivore population trends and the relationship between these trends and environmental variables.^{3,4} From 1981 to 1993, the census used a total area count, strip transect method and surveys were conducted throughout most of the park.^{3,4} The census recorded the location and herd size of approximately 15 herbivore species as well as a range of environmental variables. Although it was acknowledged that the data contained bias and precision errors,⁴ no attempts were made to estimate the size of these errors (pers. obs.).

Visibility bias, resulting from the failure of observers to detect all individuals, may be a primary source of error in an aerial census conducted using a total area count, strip transect method.⁵ In particular, it has been estimated that a census of wild ungulates may miss 12–77% of populations (as summarized by Caughley⁵). Four primary sources of visibility bias have been identified: census method,^{5–7} observer effects,^{6,8,9} environmental variables,^{8,10–13} and species-specific characteristics.^{10,11,14}

Controllable sources of bias, such as census method and observer effects, were minimized in the KNP aerial censuses through the development of a consistent census method, including specific rules for environmental conditions under which surveys could be conducted, observer training, and the use of multiple observers.⁴ We expect, however, that the census data are also subject to uncontrollable sources of visibility bias resulting from environmental variables, such as rainfall, and species-specific characteristics, such as habitat preference, behaviour (specifically herd cohesion), colouration and herd size distribution. Specific problems arising from uncontrollable sources of bias that we expect in the KNP data include missing small groups, undercounting large groups, and missing portions of a group due to the species' habitat preference and/or herd cohesion. KNP censuses conducted from 1999 to 2002 using a distance sampling technique¹⁵ suggest that these sources of error may bias the census data collected from 1981 to 1993.

The 1999–2002 KNP censuses followed procedures similar to those used in the 1981–1993 censuses to minimize controllable sources of error. Hence evidence of uncontrollable sources of bias in the 1999–2002 census data suggests that these sources of bias are also present in the 1981–1993 census data. Specifically, the 1999–2002 censuses provide information about how herd size and distance from the observer influence detection probabilities. For many species, data from these recent censuses reveal that detection probabilities decrease for smaller herds and at the edges of the transect (which is the same size as that used in the censuses conducted from 1981 to 1993). In addition, the data reveal that these detection probabilities vary between years. Although the 1999–2002 census data suggest that visibility bias is present in the 1981–1993 data, estimates of bias obtained from the recent data cannot be used to estimate bias in the 1981–1993 census data because distance from the observer was not recorded.

The 1981–1993 KNP census data are assumed to represent

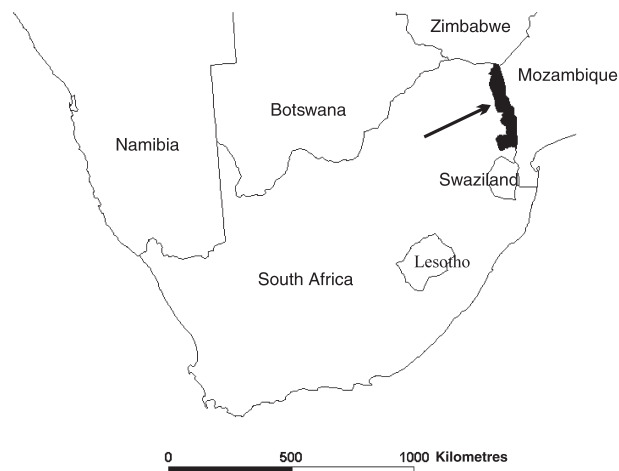


Fig. 1. A map of southern Africa showing the study site, the Kruger National Park (arrowed).

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trends in population dynamics⁴ and have been useful in exploring landscape-scale relationships between herbivore distributions, forage condition and surface water availability.¹⁶ Census data containing unmeasured biases, however, cannot be used to estimate absolute animal abundance. In theory, this unmeasured bias limits the applicability of the census data. For example, any questions regarding the specific number of individuals to harvest or cull cannot be directly addressed because absolute population sizes are unknown. Starfield¹ argues that a pragmatic modelling approach can be used to understand the importance of uncollected data and improve data collection strategies. In addition, Starfield and colleagues have demonstrated the value of using a pragmatic modelling approach, particularly when data are relatively crude or even unavailable, to address critical wildlife management issues.¹⁷⁻¹⁹

Following Starfield's pragmatic approach,¹ we develop a simple, deterministic model to understand how uncontrollable sources of visibility bias affect the applicability of the KNP aerial census data to management and research questions. Our model specifically explores two sources of bias: undercounting detected herds and failure to detect small herds. We apply our model to census data for impala (*Aepyceros melampus*), zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*) and waterbuck (*Kobus ellipsiprymnus*). These species were selected to represent a range of potential censusing challenges. The model is used to understand the potential range of bias contained in the census data and how this bias range is affected by factors such as a species' habitat preference, herd cohesion, colouration and herd size distribution.

Methods

Species characteristics

We expect sources of bias to affect species differently, depending on their habitat preference, behaviour (specifically herd cohesion), colouration and herd size distribution. Previous research on the habitat preferences and behaviour of impala, zebra, wildebeest and waterbuck suggests that populations of these species may represent a range of censusing challenges. Impala populations may be composed of large herds and typically occur on the boundary between woodlands and grasslands.²⁰ Zebra and wildebeest both occur chiefly in open grasslands,²⁰ where the wildebeest's dark colouring should increase detection probabilities. Waterbuck typically occur in riparian habitat, where canopy cover may be dense; they also occur in loosely aggregated groups.²⁰

Differences in relative herd sizes among species were verified for the KNP populations by organizing the census data for impala, zebra, wildebeest and waterbuck into a histogram portraying the distribution of herd sizes observed over the study period (1981–1993). Although this histogram is derived from the biased census data, one may assume that the herd size patterns are characteristic of the differences between species. A 5×2 contingency test²¹ conducted by summing the number of herds detected during the 1981–1993 censuses in size categories 1, 2, 3–5, 6–10, >10 was used to determine whether these herd size distributions were significantly different among species having the same mode herd size, specifically impala, wildebeest and waterbuck. We also used the census data to calculate the mean herd size over the study period for each species.

Statistical models

The KNP census data were collected as a series of herd size measurements. Analysis of these data, to answer management questions of interest, relies on some form of aggregation of the

herd size variable y , including by species, by year, by groups of years organized according to rainfall, etc. Two kinds of bias exist in generating such aggregations: bias in the actual measurements x_i of the size of the i -th herd, $i = 1, \dots, n$, and omission of herds of various sizes (that is, we count n herds but in reality $n + m$ herds exist, so that implicitly we have to correct the values $x_i = 0$, $i = n + 1, \dots, n + m$).

We reconstruct an estimate y_i of the unbiased herd size using an appropriate transform $y_i = f(x_i)$, which accounts for sources of bias that lead to incorrect observations of a herd's size. Several systematic biases may arise in the measurement of x_i , $i = 1, \dots, n$. When species reside in areas of high vegetation biomass or cover, it is likely that observers will fail to detect some members of a herd. The same may be true for species that occur in loosely aggregated groups. For these species a simple count of the individuals seen is not adequate to estimate the herd's size accurately; the nearby area must be scanned to ensure detection of the entire herd. Because of the difficulty of detecting single individuals, some members of a diffuse herd may be missed. Additional difficulties may arise in counting large herds. In particular, a stronger than linear increase in the number of individuals missed may occur for larger herd sizes due to factors such as the increased time necessary to ensure an accurate count and the confusion of trying to count a large number of moving individuals.

In general, sources of visibility bias result in an undercount of populations.^{5,13} For example, Caughley⁵ found that undercounting was a major problem in aerial surveys compared to sources of bias that would tend to inflate the population size estimate, and Cogan and Diefenbach¹³ found no instances of overcounting in their study. Our model, therefore, addresses only undercounting bias. In particular, we propose that bias in the size of detected herds can be modelled using the transformation:

$$f(x) = x^{1/a}, \quad (1)$$

where $0 < a \leq 1$. This transformation was chosen to model a stronger than linear increase in the number of individuals missed at larger herd sizes. Smaller values of a indicate that higher undercounting bias is expected, particularly at larger herd sizes, for a species.

As mentioned, omission of herds can also bias aggregations of aerial census data and a method must be derived to estimate the number and size of undetected herds. This source of bias is herd size dependent, with small herds having a higher probability of omission. Samuel and Pollock²² developed a negative exponential detection function (i.e. the relationship between probability of omission and herd size). More recent studies used a detection function of the form $D(y) = 1/[1 + \exp(-U(y))]$ where $U(y)$ is some function of the herd size y .^{11,13,14} This model generalizes the shape of the detection function by incorporating a shoulder in the omission probabilities for small herds (Fig. 2). This shoulder may be important for species where single individuals and small groups have a similar probability of omission.

The detection function used in this paper also incorporates a shoulder in the omission probabilities for small herds but has the advantage of providing increased control of the extent and shape of the shoulder. Specifically, we used the following detection function to calculate the probability of missing a herd of size y :

$$D(y) = \frac{s}{(1 + (y/h)^a)}, \quad (2)$$

where s determines the y -intercept, h sets the point at which $[1 -$

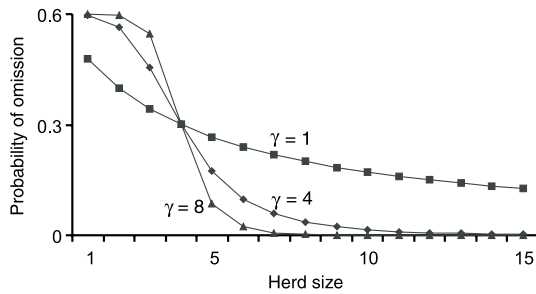


Fig. 2. An example of the detection function [Equation (2)] used in this paper is plotted for $s = 0.6$, $h = 4$, and three values of γ . The assumption that single individuals and small groups have similar omission probabilities while large groups have negligible omission probabilities can be modelled using larger values of γ , which produce a reverse logistic-like curve.

($s/2$) individuals are missed (i.e. the midpoint of the curve), and γ governs the steepness of the curve around this midpoint.

We used equations (1) and (2) to explore the effects of different values of the parameters — a , s , h and γ — on population size estimates for impala, zebra, wildebeest and waterbuck. First, for selected values of a , we used Equation (1) to obtain y_i , representing corrected size estimates for all detected herds. The corrected herd sizes were aggregated to form a population histogram. We then applied the detection function, Equation (2), to estimate the number of herds missed in each size category. This number was rounded to the nearest integer and added to the population histogram of corrected herd sizes. Population size estimates for each species were then calculated from the corrected histograms for each year.

Parameter estimates

Species-specific estimates of the model parameters, a , s , h and γ , were derived from discussions with KNP scientists having at least ten years of census experience. Because no measurements of bias were collected during the censuses, this expert knowledge currently provides the only information available to estimate the potential range of bias contained in the census data. For each species, the scientists were asked to evaluate how size estimates of detected herds are effected by two sources of visibility bias: 1) bias arising from a species’ habitat preference and behaviour (specifically herd cohesion); and 2) bias arising from the difficulty of counting large herds. KNP scientists expect visibility bias arising from species’ habitat preference and behaviour to have little effect on herd size estimates for species occurring in open habitats, such as zebra and wildebeest. The effect is expected to increase as species, such as impala, occur more frequently in dense cover and reach its greatest impact for species, such as waterbuck, which occur in dense cover and loosely aggregated groups.

The KNP scientists expect that visibility bias arising from the difficulty in counting large herds will increase for species in which individuals are small and/or of a light colour. Hence, they

expect that this source of bias will have the greatest effect on impala population size estimates, the least impact on wildebeest estimates, with waterbuck and zebra falling in between. The expectations of the scientists, regarding the relative influence of these two sources of visibility bias on size estimates for detected herds, were combined to estimate low and high a values [see Equation (1)] for each species (Table 1).

The parameters s , h and γ determine the shape of the detection function [Equation (2)] and hence govern the probability of omission for herds of various sizes. The range of values associated with the parameters s and h were based on each species’ habitat preference and colouration. Higher values were assigned to waterbuck and impala because these species typically occur in dense cover (Table 1). Although zebra and wildebeest both occur in more open habitat, zebra were associated with a slightly higher range of values for the parameter s (Table 1) because of their lighter colouring. The parameter γ cannot be automatically described in terms of low and high bias values. A value of $\gamma = 1$ results in a negative exponential-like detection function, while a value of $\gamma = 4$ results in a reverse logistic-like detection function (Fig. 2). Whether a particular curve shape results in low or high bias depends in part on the species’ herd size distribution.

Model simulations used four combinations of the species-specific parameter sets to determine the potential range of bias in the KNP census data for impala, zebra, wildebeest and waterbuck. Setting all parameters equal to their low bias value (Table 1) simulated a best-case censusing scenario, and provided an estimate of the lower limit of bias contained in the census data for each species. Setting all parameters equal to their high bias value (Table 1) simulated a worst-case censusing scenario and provided an estimate of the upper limit of bias. In both scenarios, values of $\gamma = 1$ and $\gamma = 4$ were tested to determine the effect of the shape of the detection function on these bias limits.

Model simulations also used four additional parameter sets in which parameter estimates were the same for all species (Table 1). This application of the model assumes that the sources of bias have the same effect on all species. This assumption allowed us to derive and compare a non-specific estimate of bias for all species. The lower limit of bias, or best-case censusing scenario, for this non-specific bias range was determined by setting each parameter equal to the parameter estimate yielding the lowest bias for any one of the four species (i.e. values of a range from 0.82–0.98 for the four species, therefore we used $a = 0.98$ as the non-specific, low bias value) (Table 1). Likewise, the upper limit of bias, or worst-case censusing scenario, for this non-specific bias range was determined by setting each parameter equal to the parameter estimate yielding the highest bias for any one of the four species (Table 1). In both scenarios, values of $\gamma = 1$ and $\gamma = 4$ were implemented.

For each parameter set, we applied the model (as explained above) to obtain an estimate of unbiased population sizes for impala, zebra, wildebeest and waterbuck. Using the model esti-

Table 1. Species-specific and non-specific parameter values for worst-case (W) and best-case (B) censusing scenarios. Species-specific parameter values were derived through discussions with KNP scientists. Parameter values reflect the scientists’ understanding of differences in expected census bias resulting from a species’ habitat preference, herd size distribution, colouration and herd cohesion. The non-specific parameters were used in simulations for all four species to derive and compare a non-specific bias estimate. Non-specific low and high bias values for a , s and h were defined as the maximum or minimum values of the species-specific parameter values assigned to any one of the four species.

Parameters	Impala		Zebra		Wildebeest		Waterbuck		Non-specific	
	W	B	W	B	W	B	W	B	W	B
s	0.75	0.4	0.5	0.3	0.45	0.25	0.75	0.4	0.75	0.25
h	4	3	3	2	3	2	4	3	4	2
a	0.85	0.93	0.92	0.97	0.94	0.98	0.82	0.92	0.82	0.98

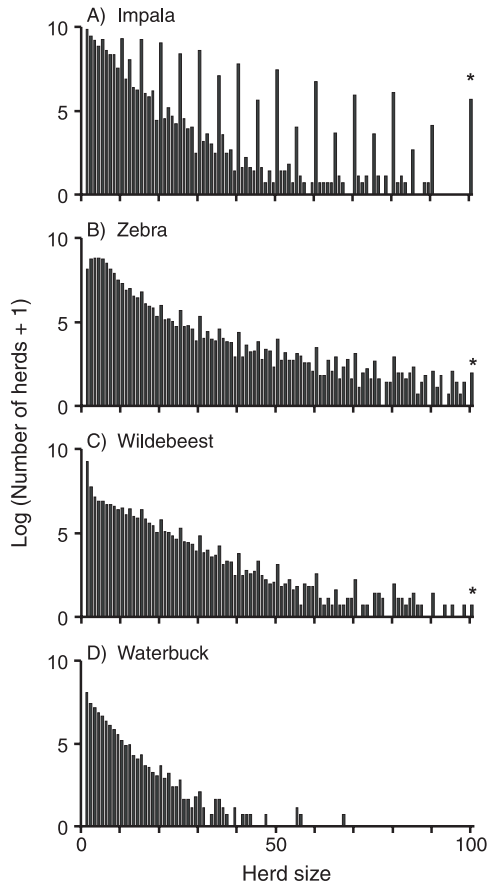


Fig. 3. Herd size distributions are plotted as histograms for each species by aggregating the KNP aerial census data collected from 1981 to 1993. The last category in the histogram (denoted by *) represents the number of herds containing 100 or more individuals.

mate of population size, we also calculated the percentage of the population detected in censuses. Specifically, the model assumes constant bias between years, hence the mean and standard deviation of the percentage of the population detected during the censuses was found using the results from the 13 years of census data. We use the mean percentage of the population detected during the censuses as a diagnostic tool for understanding the magnitude of potential bias error resulting from the different parameter sets.

Results

Species characteristics

Each species' herd size distribution, calculated by aggregating the census data over the study period (1981–1993), is illustrated in Fig. 3. Immediately distinguishable is a marked tendency in the case of impala to estimate herd size to the nearest five indi-

Table 2. Species-specific herd size mean and standard deviation (s.d.) for the 1981–1993 KNP census data.

Species	Mean herd size ± s.d.
Impala	12 ± 16.4
Zebra	8 ± 10.4
Wildebeest	7 ± 9.6
Waterbuck	4 ± 4.4

viduals (Fig. 3A). Other evidence of this pattern in the herd size distributions, although not as pronounced, occurs at larger herd sizes in the zebra and wildebeest census data (Fig. 3, B and C). Comparison of the herd size distribution curves (Fig. 3) and mean herd sizes (Table 2) indicates that impala are the only species for which a substantial number of herds are larger than 30. While the mode herd size for impala, wildebeest and waterbuck is one (Fig. 3, A, C and D), the 5 × 2 contingency test²¹ conducted by summing the number of herds detected during the 1981–1993 censuses in size categories 1, 2, 3–5, 6–10, >10 reveals that the herd size distributions of these three species are significantly different ($P < 0.01$). Mode herd size for zebra clusters around 2–4 individuals (Fig. 3B), although the mean herd size is not much larger than that for wildebeest (Table 2).

Statistical models

The results of the model simulations using the non-specific parameter values (Table 1) suggest that during the censuses 45–95% of impala, zebra, wildebeest and waterbuck populations in the KNP may have been counted (Table 3). This estimate of the potential range of bias in the census data falls within the range of bias observed for censuses conducted using total area count, strip transect methods.⁵ In general, the estimates of the percentage of the population counted were similar between the four species (Table 3). Within the best-case and worst-case censusing scenarios, the shape of the detection function had a small effect on the corrected population size estimates and hence the percentages of populations detected during the censuses (Table 3). In particular, the shape of the detection function had a slightly greater influence on zebra and impala population size estimates compared with estimates of wildebeest and waterbuck population size.

Species-specific parameter estimates (Table 1), which take into account species habitat preference, herd cohesion, colouration, and expected herd size distribution, were also used in the model to understand differences in the potential range of bias in the KNP census data for impala, zebra, wildebeest and waterbuck. Overall, the results of the model simulations using the species-specific parameters suggest that during the censuses 49–93% of KNP populations may have been counted (Table 3). The results reveal that population size estimates for waterbuck may be the

Table 3. Estimates of the percentage of the population detected under best-case and worst-case censusing scenarios for $\gamma = 4$ and $\gamma = 1$ are shown for simulations using the species-specific and non-specific parameter values. The model was used to estimate the unbiased population size for each year of census data. We then calculated the percentage of the population that was detected in the census. The model assumes constant bias between years, hence the mean and standard deviation of the percentage of the population detected were found using the results from the 13 years of census data.

Scenario	γ	Mean (s.d.) per cent of population detected in the census							
		Species-specific parameters*				Non-specific parameters*			
		Impala	Zebra	Wildebeest	Waterbuck	Impala	Zebra	Wildebeest	Waterbuck
Worst-case	4	54 (1.1)	76 (0.6)	79 (0.5)	49 (1.2)	48 (1.3)	51 (1.1)	48 (0.8)	49 (1.2)
	1	51 (0.7)	72 (0.2)	77 (0.1)	49 (0.3)	45 (1.0)	48 (0.8)	47 (0.4)	49 (0.3)
Best-case	4	78 (0.7)	92 (0.3)	93 (0.4)	77 (0.4)	94 (0.3)	95 (0.2)	93 (0.4)	94 (0.3)
	1	75 (0.5)	89 (0.1)	92 (0.1)	74 (0.3)	92 (0.1)	92 (0.1)	92 (0.1)	92 (0.3)

*Worst-case (W) and best-case (B) values of the parameters (s, h, a) are given in Table 1.

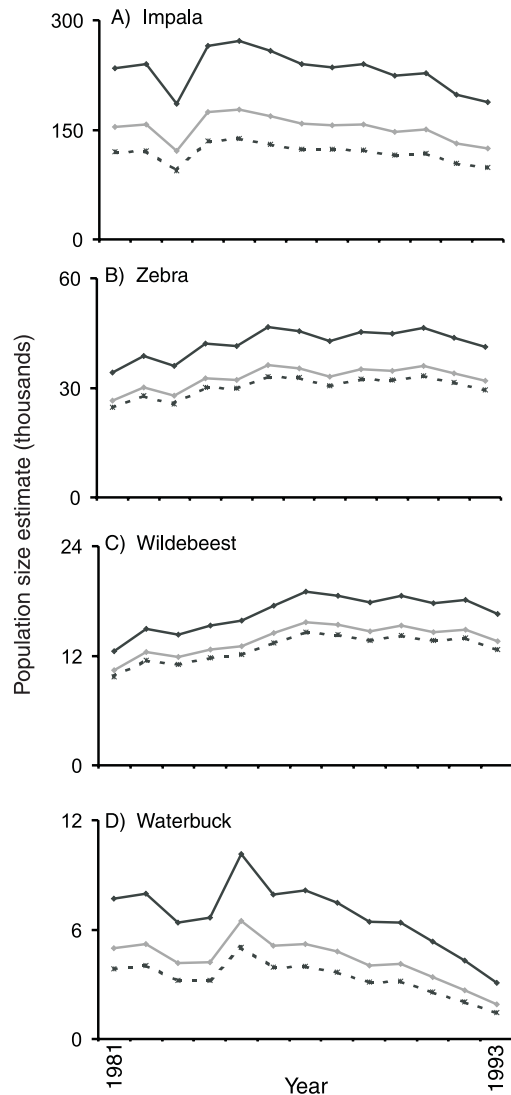


Fig. 4. Population size estimates, derived from the aerial census data (dashed black line) and from the results of the model simulations using the species-specific parameter values for best-case (solid grey line) and worst-case (solid black line) censusing scenarios (Table 1), are plotted annually during the study period. For all species, best-case censusing scenarios occur when $\gamma = 4$. Worst-case scenarios, however, for impala, zebra and wildebeest occur when $\gamma = 1$, whereas worst-case scenarios for waterbuck occur when $\gamma = 4$.

most biased, followed by impala, zebra and wildebeest (Table 3). The effect of the shape of the detection function was similar to that observed for the model simulations using the non-specific parameter estimates — in general, slightly greater differences were observed for zebra and impala compared to wildebeest and waterbuck.

Corrected population size estimates, derived using the species-specific parameters, are shown for impala, zebra, wildebeest and waterbuck in Fig. 4. For all species the population size distribution each year is skewed, with the lower bound of the distribution determined by the observed census data. The model results generally follow the trends in the census data (Fig. 4) as a direct consequence of the assumption that bias is constant between years.

Discussion

Our results suggest that visibility bias represents a major source of error in the KNP census data. For example, observers may detect between 51 and 78% of impala populations (Table 3). These percentages translate into large differences in the actual

size of the impala population. Specifically, the average population size derived from the 1981–1993 census data is 119 000, while the average model population size varies between 152 000 and 232 000, depending on whether low or high bias estimates of the parameters are used. Similar differences between the population sizes estimated during the census and the unbiased population sizes predicted by the model occur for all species (Fig. 4).

The potential range of bias in the KNP aerial census data affects the applicability of the data to management and research questions. Model simulations using the species-specific parameter estimates suggest that caution must be used when relying on census data containing unmeasured bias to make comparisons among species. In particular, the differences in bias among species indicated by our model suggest that comparisons of species' densities, population growth characteristics, and viability may be confounded.

Furthermore, comparisons of a particular species' abundance under different environmental conditions or in different habitat types may also be confounded by unmeasured sources of visibility bias. While it is possible that observed differences in a species' abundance are caused by ecological factors, these differences may also be the result of non-constant bias in the data. For example, visibility bias may vary if certain environmental conditions are correlated with the aggregation of individuals of a particular species or of multiple species around important resources (such as water sources). Large congregations may increase detection probabilities but decrease counting accuracy. In addition, increased vegetation coverage during years with above-average rainfall or in particular habitat types may correspond to a worst-case censusing scenario, whereas decreased vegetation coverage corresponds to a best-case censusing scenario. Our models suggest large differences in the percentage of the impala, zebra, wildebeest and waterbuck populations detected during best-case and worst-case censusing scenarios. Specifically, a minimum difference of 13% is predicted for the four species using the species-specific parameter estimates (Table 3) and 41% is predicted using the non-specific parameter estimates (Table 3). Hence, unmeasured differences in visibility bias may mask large changes in population sizes from year to year, or large differences in population sizes among habitat types.

The applicability of aerial census data to research and management questions will be limited until we are able objectively to estimate the amount of bias contained in the data, and hence derive more accurate population size estimates for the species counted. Considerable progress in dealing with sources of visibility bias has been made using line transect methods. Line transect methods do not assume that all individuals or groups are detected and statistical models for understanding the detection function and its relation to herd size have been proposed.^{15,23,24} A key assumption in line transect analyses, however, is that all individuals are detected on the line. While it can be expected that biases are minimized on the line, uncontrollable sources of bias may cause deviations from this key assumption. For example, the KNP censuses conducted from 1999 to 2002 using a distance sampling technique¹⁵ reveal that the highest detection probabilities for certain species are not achieved on the line (i.e. 0–50 m), but rather 50–100 m from the line. While the data can be truncated so that estimation of the detection function does not include the lower detection probabilities observed on the line, it is important to determine whether the truncated data are biased if management actions rely on census data.

Regardless of whether line or strip transect methods are used in an aerial census, a further investment of resources is needed to collect additional data that can be used to obtain objective

estimates of bias error. Several studies have used the detection of herds containing individuals fitted with radio transmitters to develop bias corrections for undercounting detected herds and failing to detect small herds.^{10,11,13,14} In general, a second set of observers locates these herds aerially or from the ground and obtains an accurate count of the herd sizes just prior to the start of the aerial census. Statistical analyses can then be used to determine the relationship between the aerial census estimates of the size of detected herds containing individuals fitted with radio transmitters and the actual size of each herd. These analyses could be used to parameterize the transformation proposed in this paper [Equation (1)] for modelling bias in the size of detected herds.

Likewise, statistical analyses that compare the actual number and size of herds containing individuals fitted with radio transmitters to detection of these herds in the aerial census can be used to determine the relationship between herd size and the probability of omission. For example, Samuel *et al.*¹¹ used logistic regression to assess the relationship between the detection of elk herds and visibility factors including herd size and vegetation cover. Statistical analyses could also be used to parameterize the detection function proposed in this paper [Equation (2)]. Unbiased estimates of population size can then be obtained from Monte Carlo simulations that correct for undercounting detected herds and failing to detect small herds using the observed statistical relationships.

Obtaining objective estimates of bias error may require a significant investment of additional resources. Eberhardt *et al.*¹⁴ note that a sizeable sample of herds containing individuals with radio transmitters is needed to estimate potential biases. In addition, objective estimates of bias error must be collected for the total range of habitat types and environmental conditions that potentially influence the population size estimates derived from the census data to account for possible variations in visibility bias. However, investment in this data collection will be justified by the increased utility of current and historical census data. Specifically, census data in which bias has been estimated can be used to address questions concerning absolute animal abundance, such as the number of individuals to harvest or cull. Estimates of bias error obtained under conditions similar to those encountered during past censuses may be used to derive unbiased population size estimates and hence extend the data sets available to address management and research questions.

The best investment of resources can be obtained by understanding the relationship between visibility bias and species' characteristics such as habitat preference, herd cohesion, colouration and herd size distribution. Results from our models, derived from the species-specific parameter ranges suggested by KNP scientists with at least ten years of census experience, suggest that the greatest return on an investment in additional data collection will be achieved by obtaining estimates of bias error for species that prefer dense vegetation cover, occur in loosely aggregated herds, and/or have light colouration. In addition, our results illustrate the importance of designing data collection methods to determine bias in undercounting detected herds for species that typically occur in large herds. For species in which the expected mode herd size is 1–2 individuals, data collection should be designed to determine omission probabilities for small herds. Finally, our results demonstrate the increasing importance of estimating the shape of the detection function for species whose expected herd size distribution is characterized by a larger mean herd size and a flatter distribution. In particular, determining the shape of the detection function is important because a negative exponential curve implies a higher

probability of missing larger herds than a reverse logistic-like curve.

Conclusion

McNaughton and Campbell² identify three important uses of long-term ecological research. They suggest that this research documents subtle, chronic ecosystem changes, signals the onset of acute changes, and can be of use in designing management strategies. In African savanna ecosystems, large investments have been made in long-term ecological monitoring. As early as the 1950s, programmes were designed to collect baseline ecosystem data and to determine geographical distributions and population sizes of large mammal species.² Monitoring programmes conducted in national parks are financed in part by African governments and usually provide a foundation for management programmes.²

The Kruger National Park has one of the most sophisticated long-term ecological research programmes in Africa.² Our model, however, suggests that the unmeasured, systematic error contained in the aerial census data for KNP herbivores limits the applicability of the data to research and management questions. To obtain the data necessary to correct historical and current population size estimates, further investments in calibration censuses are required. Wise investment in calibration censuses can be achieved by understanding the important sources of bias to measure for the species of interest. The pragmatic modelling approach¹ applied in this paper illustrates a relationship between the relative importance of different sources of bias error and a species' characteristics, such as habitat preference, behaviour (specifically herd cohesion), colouration, and expected herd size distribution. Incorporating an understanding of this relationship in the survey design can help researchers balance study objectives with the resources allocated for data collection. In the long term, current investments in calibration censuses will be justified by the increased utility of census data. In particular, the development of calibration censuses that allow us to estimate the bias error contained in historical census data will significantly extend the time series of data available for ecological research.

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Using decision analysis to evaluate candidate OMPs for the South African west coast rock lobster fishery

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Simulation models frequently are used to provide information to assist in decision-making in natural resource management. The sheer volume of information to process can be overwhelming, however, and there is a danger that some management objectives are not adequately considered, because of the difficulties of making decisions when there are multiple, conflicting objectives. Formal decision-analysis methods have been used in conservation biology to choose among simulation model results. This paper suggests that they can also be used in South African fisheries management, where simulation models are used extensively in developing operational management procedures.

Decision analysis is a structured way of helping to make wise decisions.¹ It is a useful technology when complex, confusing and/or stressful decisions need to be made. Sometimes, such decisions are linked to the outputs of models of varying complexity, and when faced by an abundance of data, it can be difficult to choose among different options and to use consistent criteria in making choices. These difficulties are compounded when there are conflicting objectives that need to be considered, as is the case in many resource management situations. Rall and Starfield² showed how two structured decision-making methods could be applied in conservation biology where management decisions were based on the output of simulation models. They used these methods to help choose a management strategy to address the problem of 'mobbing' in the endangered Hawaiian monk seal, by evaluating the implications of different courses of action.

In South African fisheries management, operational manage-

ment procedures (OMP) are used as the basis for management of fisheries involving sardine (*Sardinops ocellatus*) and anchovy (*Engraulis capensis*), hakes (*Merluccius* spp.), and west coast rock lobsters (*Jasus lalandii*).³ The essence of the OMP approach is to use an algorithm (which can be a set of rules or an equation) to derive a management outcome. Importantly, the algorithm is tested by simulation in advance of its adoption. The testing procedures attempt to account for all reasonable sources of uncertainty, and this results in a large number of candidate OMPs with many simulations, the outputs of which need to be evaluated. Typically, this evaluation is carried out by one of the resource working groups of the Branch: Marine and Coastal Management Coordination of the South African Department of Environmental Affairs and Tourism. The final choice of an OMP lies with the minister, who is advised by the Consultative Advisory Forum.

In fisheries management, there are usually conflicting management objectives,⁴ and different people have different ideas about what constitutes a good management strategy. In this paper we suggest that the process of choosing among candidate OMPs can be made more rigorous by using decision analysis methods, as described for conservation biology applications by Rall and Starfield.²

Choosing an OMP for the west coast rock lobster fishery

To illustrate the decision analysis approach, a hindsight example is used, based on the development of the OMP for the South African west coast rock lobster fishery. Full descriptions can be found elsewhere of the history of this fishery and the development of the OMP,⁵ which was applied for the first time in 1997. The west coast rock lobster fishery is managed on the basis of a total allowable catch (TAC), based on the outputs of the OMP. The management of this fishery has multiple objectives, involving trade-offs between, for example, biomass recovery of the resource (which is believed to be below acceptable levels) and catch levels that will provide livelihoods for as many stakeholders as possible. The OMP was developed over a period of approximately two years, during which time many alternative

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