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Application of distance sampling to estimate population densities of large herbivores in Kruger National Park

J. M. Kruger[A], *B. K. Reilly*[B,C] *and I. J. Whyte*[A]

[A]South African National Parks, Private Bag X402, Skukuza 1350, Republic of South Africa.
[B]Department of Nature Conservation, Tshwane University of Technology, Private Bag X680, Pretoria 0002, Republic of South Africa.
[C]Corresponding author. Email: reillybk@tut.ac.za

Abstract. Aerial surveys have been used in the Kruger National Park, South Africa, to count large ungulates since the late 1970s. After 1998, aerial line-transect sampling using fixed-wing aircraft and Distance analyses replaced the 'total' counting method. This paper investigates these methods and three sampling intensities for estimating the densities of nine large ungulate species in Kruger National Park. Estimates suitable for the detection of population trends and making management decisions were decided by examination of coefficients of variation (set <20%, *a priori*). Despite the likely violation of some key assumptions of Distance sampling methods, analyses gave population estimates with adequate coefficients of variation for monitoring trends in impala, giraffe, zebra, kudu, white rhinoceros, and elephant bull populations. Significant improvements in precision were obtained at higher sampling intensities for kudu, giraffe, bull elephants and white rhinoceros, but these species already had sufficiently precise population estimates for the detection of trends at the lowest sampling intensity (15%). The estimates for warthog, wildebeest and waterbuck populations were, however, insufficiently precise for assessing population trends. Increasing sampling intensity to 22% and higher did not significantly increase the precision of the Distance estimates for these species. Shortcomings in interpretation of the data caused by violations of critical assumptions of analyses are identified and discussed.

Introduction

In the last 10 years, the Kruger National Park (KNP) in north-eastern South Africa has undergone a paradigm shift in management. An adaptive management approach (Walters and Holling 1990) has been adopted and part of this process involves the identification of 'thresholds of potential concern' (TPCs: Keeney 1992) for ecological variables for which concerns are raised. Declines in population numbers of large herbivores that do not represent a natural flux are one such concern. The TPCs determine when actions from the KNP management plan (Braack *et al*. 1997) are deployed to reverse declines. Therefore, a technique to estimate population densities that will reliably detect these changes is required.

Aerial surveys, using fixed-wing aircraft, of the larger herbivores in KNP (excluding elephant, *Loxodonta africana*, buffalo, *Syncerus caffer*, and hippopotamus, *Hippopotamus amphibius*) were initiated in the early 1970s. Initial counts were conducted in areas of KNP where rare species, such as sable antelope (*Hippotragus niger*) occurred at high density, and were later expanded to all the ungulates throughout the total area of KNP. The first count attempting total coverage of the whole area of KNP was conducted in 1977 (Joubert and Viljoen 1988) and the methods used for these surveys were described by Joubert (1983). Because of the large size of KNP, these surveys took at least 3.5 months to complete each year and were undertaken between July and October.

In the interpretation of population responses to environmental change (particularly climatic fluctuations), these survey data proved invaluable in understanding the KNP ecosystems (e.g. Whyte and Joubert 1988). The implementation of the new management plan for the KNP (Braack *et al*. 1997), the setting of TPCs, shifts in priorities, declining budgets, and new research and monitoring priorities required a re-evaluation of survey methods. Alternative methods of population quantification, such as the use of presence–absence data and area of occupancy estimations (e.g. Tosh *et al*. 2004), do not provide estimates at the scale required for local management of ungulate species within the KNP management plan. On the basis of Eiselen's (1993, 1994) study, a more time-efficient and less costly aerial sampling strategy yielding acceptable population estimates and precision for management decisions was adopted in 1998. Since then, line-transect sampling (with DISTANCE analyses: Thomas *et al*. 2004) from fixed-wing aircraft has been used to estimate ungulate density.

Distance sampling entails counting the number of a species along a transect line as well as measuring the perpendicular distance to individuals or group of animals from the transect line (Buckland *et al*. 1993). A detection function is fitted to the data in DISTANCE, with model selection aided by Akaike's information criterion (AIC: Akaike 1973). The key assumptions of distance sampling and analysis are: (1) that all the animals on the transect line are detected, (2) animals are detected in their original locations and (3) perpendicular distances are measured accurately (Buckland *et al*. 1993; Buckland 2004). Furthermore, animals must be counted accurately (Fleming and Tracey 2008), and transects must be purely randomly placed or systematically placed with a random starting point (Buckland *et al*.

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1993; Khaemba and Stein 2002). Uniform distribution of distances to individuals or groups is also assumed (first raised by Barry and Welsh 2001; and see Fewster *et al*. 2008; and Melville *et al*. 2008). For rarer species, sufficient sample size (60–80 observations per transect: Fewster *et al*. 2005) is also required for valid distance estimates.

In this paper we estimated the densities of nine species of ungulate in KNP, from 1998 to 2006. Densities were estimated from aerial surveys with distance-sampling methods and analysis. Coefficients of variation (CV) of less than 20% were suitable for monitoring significant changes in abundance (Eiselen 1993, 1994). Three sampling intensities were evaluated by con-

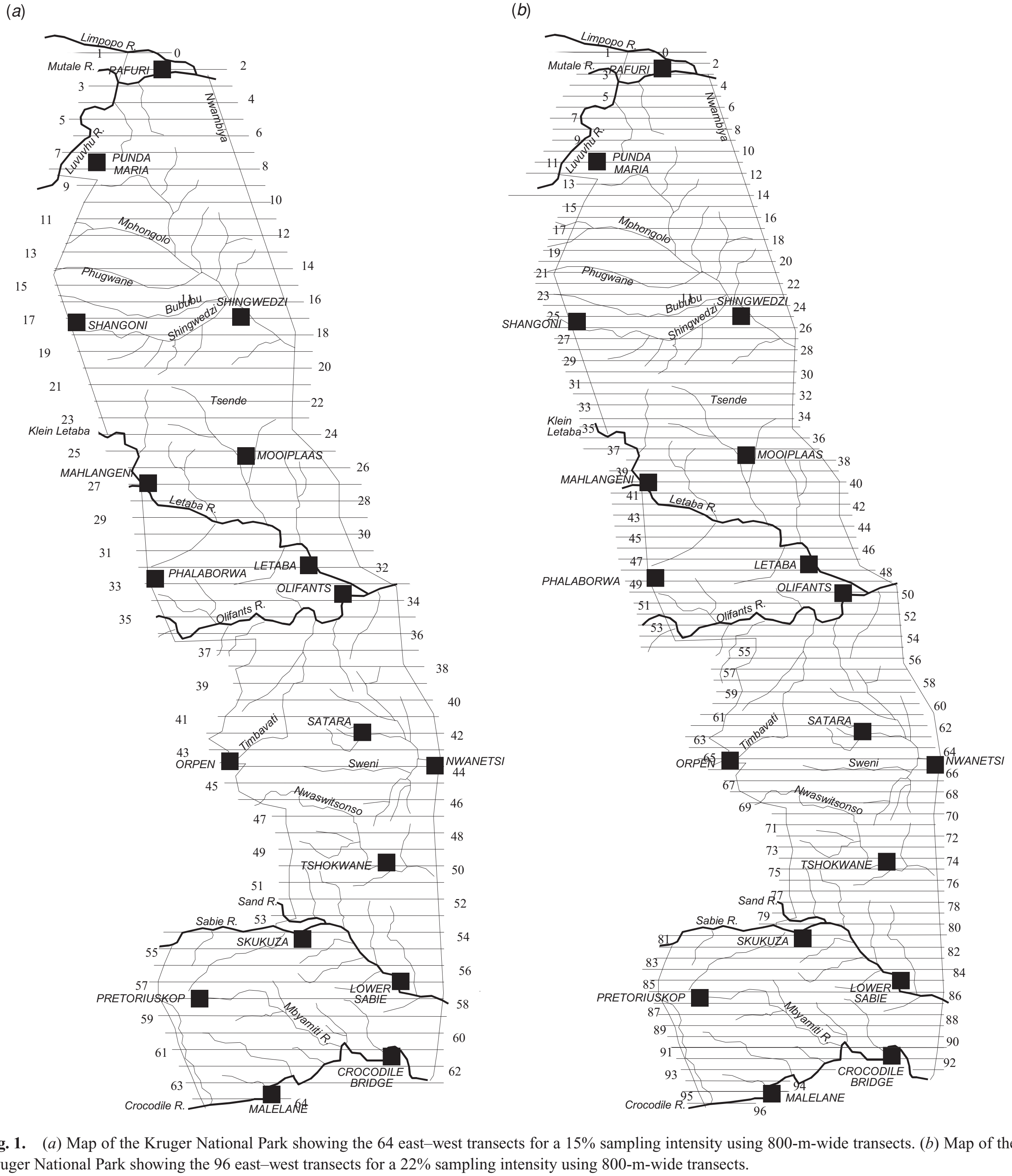

Fig. 1. (*a*) Map of the Kruger National Park showing the 64 east–west transects for a 15% sampling intensity using 800-m-wide transects. (*b*) Map of the Kruger National Park showing the 96 east–west transects for a 22% sampling intensity using 800-m-wide transects.

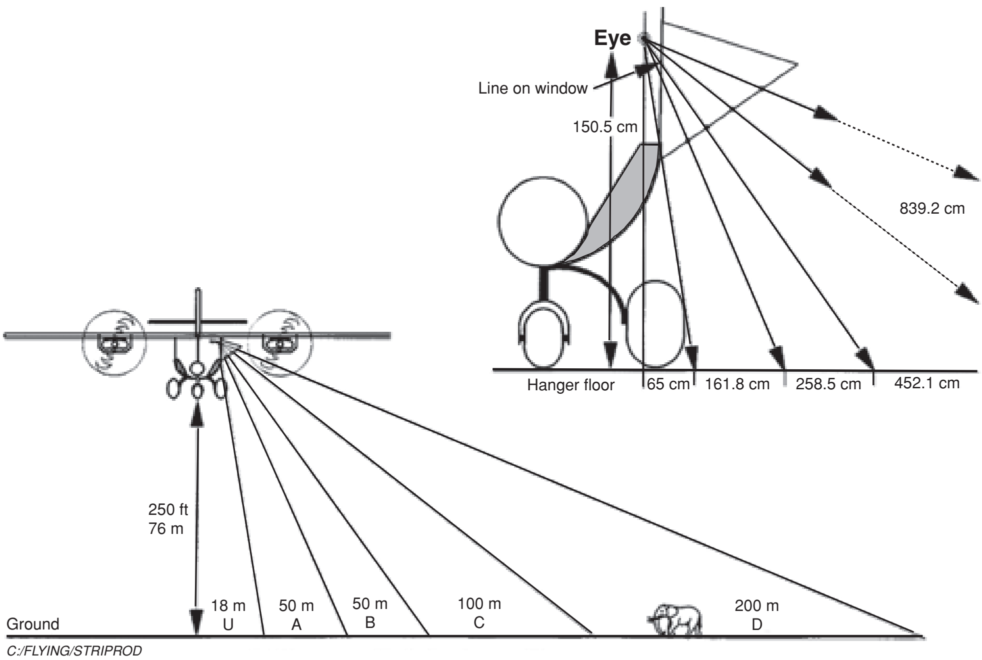

Fig. 2. Diagrammatic representation of Distance bins (A, B, C, D) used to estimate the densities of nine large herbivores at KNP. Inset shows the calibration distances along the external frame and the internal 65 cm resulting in the 18-m blind area (U) under the aircraft.

trasting CVs. We evaluated the usefulness for managers of the distance estimates by determining yearly and mean coefficients of variation of the density estimates for each surveyed species and by contrasting them with the suitable CVs.

Methods

KNP was divided into east–west transects (Fig. 1*a*,b) and a Partenavia Observer high-winged aircraft, flown at a height of 250 ft above ground level (a.g.l., ~76 m), was used in the surveys. A radar altimeter was used for guidance, and airspeed was maintained between 90–100 kn (~167–185 km h^{-1}). The aircraft, which lacks wing support struts, was fitted with a simple frame structure outside each window (Fig. 2*a*,b, 3), which was calibrated to give four distance classes: A = 0–50 m, B = 50–100 m, C = 100–200 m and D = 200–400 m. Two observers on each side of the aircraft recorded counts of animals

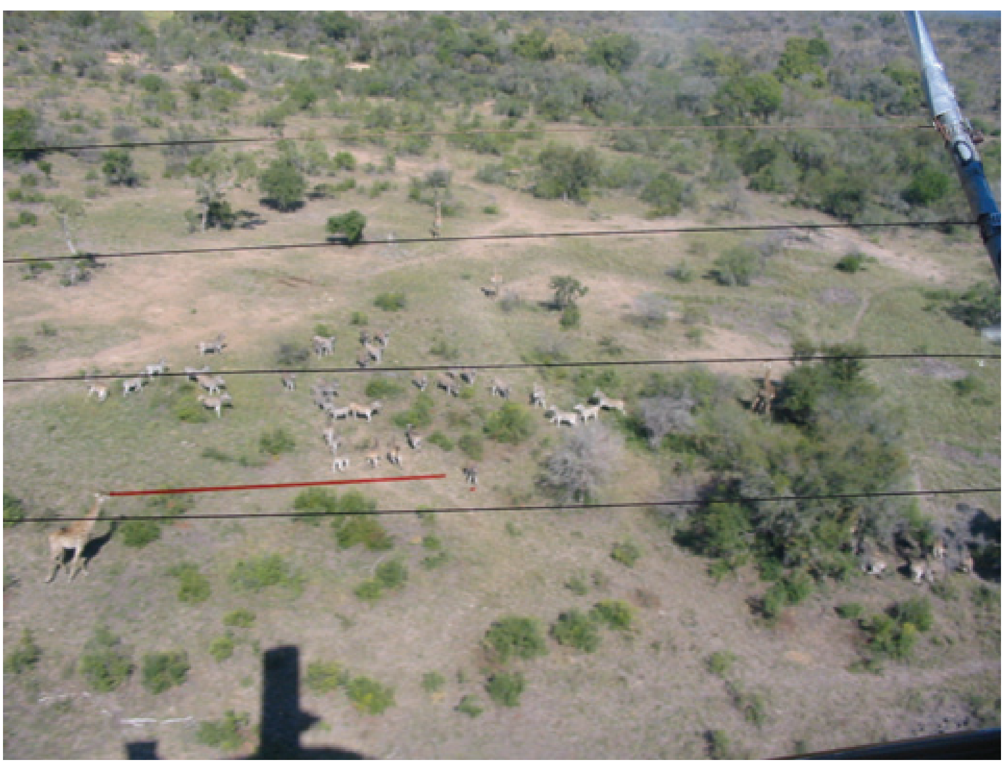

Fig. 3. View of giraffe and zebra from a Partenavia Observer aircraft showing the 'strip wires' attached to an external frame, and the calibration line drawn on the window that, when aligned with the bottom wire, allows correct strip allocations. Flight direction is from left to right.

or groups of animals for each of nine species and the distance class in which the animals were first seen. All observations beyond 400 m were ignored (Fig. 2*a*,b).

Impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes gnou*), waterbuck (*Kobus ellipsiprymnus*), white rhinoceros (*Ceratotherium simum*), Burchell's zebra (*Equus burchelli*), steenbok (*Rhaphicerus campestris*), warthog (*Phacocoerus aethiopicus*) and bull elephants (*Loxodonta africana*) were included in the surveys and analyses were undertaken using DISTANCE ver. 4.0 (Thomas *et al*. 2004). Conventional distance sampling, with binned (interval) data, was used to estimate the annual densities of these species. Average cluster sizes on the line, for species that occurred in groups (Buckland *et al*. 2004), were estimated in the DISTANCE engine.

Distance sampling with 15% coverage of KNP (Fig. 1*a*) was deemed adequate for sufficiently precise (<20%CVs) population estimates of all the larger ungulates (Eiselen 1993) in initial surveys from 1998 to 2000. For ease of surveying (see Caughley and Goddard 1975), the east–west transect lines were placed systematically on every 3′ of latitude (~5.6 km apart). From 2001 to 2003, inclusive, the sampling intensity was increased to 22% (Fig. 1*b*) by placing transects on every 2′ of latitude (~3.7 km apart). The intensity was increased again in 2004 to 27% by flying higher and increasing transect width. Because these changes precluded direct comparison with other years, the 2004 data were not included in this paper. In 2005 and 2006, the original height and transect width were used, and coverage north of Olifants River was increased to 28% (one transect every 1′36″ of latitude) by adding 13 transects. South of Olifants River (53rd transect on Fig. 1*b*), about half the area of KNP, transects remained on every 2′00″ (22% coverage).

Detection functions, *g*(y), fitted to the data in DISTANCE were the uniform, the half-normal and the hazard function, with modifiers to these key functions being provided by cosine, simple polynomial and hermite polynomial functions. These functions were fitted for each species for each year using maximum-likelihood estimation methods. Akaike's information criterion (Akaike 1973) was used to select the best model (lowest AIC).

Coefficients of variation (%) were calculated in DISTANCE and precision of sampling intensities were contrasted with ANOVA.

Results

Population estimates with adequate precision for monitoring trends were found in all years for impala, giraffe, zebra, kudu, white rhinoceros and bull elephant populations (Fig. 4, Table 1). For warthog, wildebeest and waterbuck populations only three estimates was sufficiently precise (wildebeest in 1999, CV = 18.2, and in 2006, CV = 18.5; and warthog in 2006, CV = 18.0).

Significant improvements in precision were obtained at higher sampling intensities for kudu, giraffe, bull elephants and white rhinoceros (Table 1), but estimates for these species were already sufficiently precise for the detection of trends at the lowest sampling intensity (15%). No change in precision of zebra or impala estimates was achieved by increasing sampling intensity (Table 1). These two species were the most abundant in KNP (Fig. 4), and estimates for the most abundant ungulate species in all years, impala, were also the most precise in all years (Table 1).

In most years, warthog, wildebeest and waterbuck populations were insufficiently precise for assessing population trends. Increasing sampling intensity to 22% and higher did not significantly increase the precision of the Distance estimates for these species (Table 1).

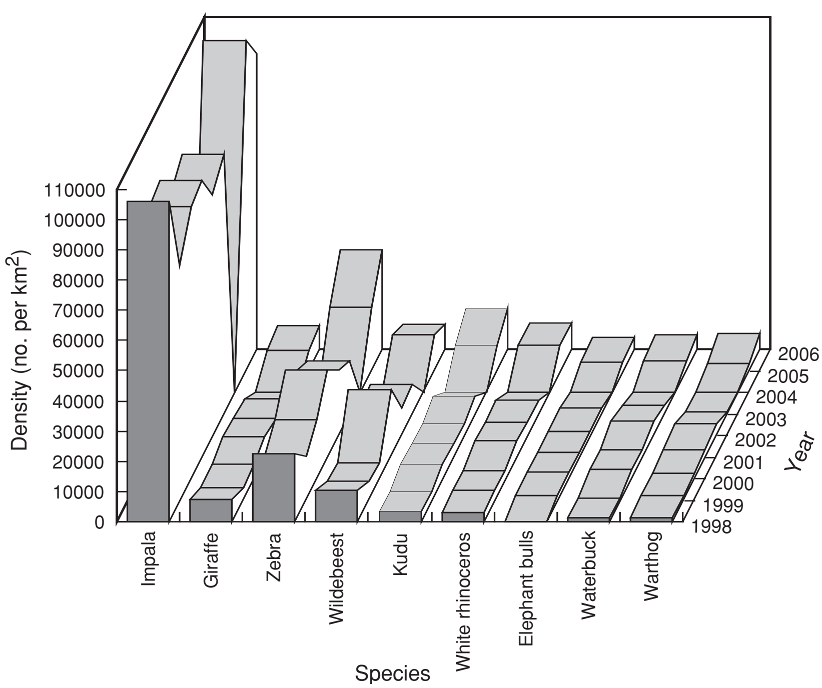

Fig. 4. Distance estimates of the density (number km^{-2}) of nine species of large herbivores in Kruger National Park, 1998–2006 (excluding 2004). Sampling intensities were 15% in 1998–2000, 22% in 2001–03, and 27% in northern KNP and 22% in southern KNP in 2005–06.

Table 1. The effects of three sampling intensities on coefficients of variation (CoV, %) for Distance estimates of density of nine large herbivores in Kruger National Park, 1998–2006
Sampling intensity was 15% in 1998, 1999 and 2000; 22% in 2001, 2002 and 2003; and combined 28% and 22% in 2005 and 2006

Species	Sampling intensity			d.f.	F	*P*
	15%	22%	28% and 22%			
Impala	12.06	11.17	8.19	2,5	3.97	0.093
Giraffe	14.15	12.26	10.12	2,5	9.16	0.021
Zebra	13.15	13.48	9.82	2,5	3.73	0.102
Wildebeest	21.87	23.94	19.25	2,5	1.94	0.238
Kudu	17.04	13.28	10.68	2,5	46.57	0.001
White rhinoceros	17.96	12.68	10.21	2,5	10.13	0.017
Elephant bulls	16.69[A]	14.91	11.23	2,4	17.42	0.011
Waterbuck	31.84	29.70	23.63	2,5	2.73	0.158
Warthog	40.70	39.97[B]	20.58	2,3	1.30	0.393

[A]Only two replicates (1999 and 2000) of 15% sampling intensity for elephant bulls.
[B]Only one replicate (2001) of 22% sampling intensity for warthogs.

Discussion

Aerial surveys and Distance estimates were sufficiently precise in all years for populations of impala, giraffe, zebra, kudu, white rhino and elephant bulls. Therefore, management decisions for these species could be made with confidence, assuming that estimates are unbiased. However, non-adherence to assumptions of the Distance method poses questions about the accuracy of the estimates. Estimates for wildebeest, waterbuck and warthog were insufficiently precise and changes in density of these species are unlikely to be detected, limiting the usefulness of these estimates to managers. Increased sampling intensity did not consistently improve the estimates for these species either.

The accuracy of the density estimates depends on adherence to the assumptions of the Distance method (Buckland *et al*. 1993, 2001, Fewster *et al*. 2008; Melville *et al*. 2008). Depending on the starting point, the use of a systematic rather than random design may have biased all estimates, but for more common (e.g. impala and zebra) and more homogenously dispersed species the expectation is that the probability of inclusion in a detected sample is approximately equal (Fewster *et al*. 2005). If other assumptions are met then these estimates could be assumed to be accurate. However, detection on the line is known to be less than 1.0, even for large and conspicuous animals (Caughley and Goddard 1975), and so, without correction for non-detection on the line, the estimates are probably biased. Failure to detect all animals on the line could be corrected by using multiple observers on each side of the aircraft and mark–recapture distance sampling (Buckland *et al*. 2001; Borchers *et al*. 2006;).

In the case of wildebeest, their highly gregarious and flighty nature (Estes 1995) potentially violates Assumption 3 above (perpendicular distances are measured accurately: see Introduction) and the assumption of uniform distribution of distances from the line. A further problem is that wildebeest are difficult to count when in large groups, and multiple herd and sub-herd aggregations within large groups increases subjectivity by observers, causing further violation of Assumption 3. The association of waterbuck with drainages and watercourses leads to similar violations. The group sizes are also highly variable for these species. In these cases the recalculation of densities of animal groups, as opposed to numbers, may partly alleviate the problem as in these analyses group size was not used as a covariate.

The sampling intensity for warthog was too low to be used for unbiased estimates. Low precision was not overcome by increasing sampling intensity (Table 1), indicating that warthog were either too rare to enable minimum sample size (Fewster *et al*. 2005) or critical assumptions of the Distance method were violated for them. For example, the assumption of total counting on the line may not have been possible because of the usually small group size and cryptic colouration of warthogs (Estes 1995).

The distribution of waterbuck may not have been uniform as they are usually found close to water bodies (Estes 1995). While this, on its own, may not always bias the Distance estimates in the same direction, it introduces potential errors (Melville *et al*. 2008), especially at lower sample sizes.

Conclusion

Some critical assumptions of Distance estimators were violated in these aerial surveys of KNP ungulates: that all the animals on the transect line are detected and that animals are detected in their original locations. These were the first and second assumptions of Buckland *et al*. (1993) and the uniformity assumption of Barry and Welsh (2001) and Melville and Welsh (2001). Additionally, for rarer and highly clustered species, sample size was unlikely to be 60–80 observations per transect (Fewster *et al*. 2005). This raises the possibility that strip counts may be a less complicated and equally valuable way of obtaining indices of density in KNP.

It appears that the Distance technique and coverage of 15% provides adequate precision for certain species, particularly the more common ones, such as impala. However, more research is needed to determine the suitability of Distance estimators for other species, including highly clustered wildebeest, which also have highly variable group size, and the rarer and highly clustered warthog and waterbuck.

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