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Comparison of aerial counts with ground counts for large African herbivores

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Summary

1. Over the past 50 years, aerial counts have been widely used in African wildlife management; however, the accuracy of the resulting estimates has rarely been questioned. The reliability of aerial counts of large African herbivores was examined by comparing the results of a series of systematic aerial sample counts with those from a series of line transect foot counts conducted in the Lupande Game Management Area in Zambia.

2. For most large herbivore species, the estimates from the aerial counts were considerably lower than those from the ground counts. The data pointed to undercounting as a major problem of aerial surveys. During the aerial counts, significant numbers of animals were missed on the transects, first due to the low probability of spotting single animals, small groups of animals and less conspicuous ones (sighting probability bias), and secondly because part of the population was concealed by obstructions and therefore not visible to the observers (visibility bias).

3. The main factors that influence visibility of large herbivores from the air are the animals' reactions to an over-flying aircraft, dispersion, body size and colour. Animals that move in response to an aircraft are more likely to be seen than static ones; dark-coloured animals are easier to spot than light-coloured ones against a light background; large herds are easier to detect than small ones; and large animals are more easily seen than small ones. Body size is important while trying to spot grazers and mixed feeders from the air, while colour is important for spotting browsers. This is mainly due to the differences in habitat use, with browsers being confined to the thicker habitat.

4. To minimize undercounting bias, both conventional aerial counts and aerial line transect counts should be restricted to large conspicuous grazers and mixed feeders in medium to large group sizes, such as elephant *Loxodonta africana africana*, buffalo *Sincerus caffer*, zebra *Equus burchell*, wildebeest *Connochaetes* and lechwe *Kobus leche*. Operational factors, such as height, speed and strip width, should be kept within reasonable limits for conventional aerial counts. Only one species should be counted at a time, always applying the double-count technique. For aerial line transect counts, the use of a helicopter is a prerequisite to obtaining accurate estimates. Other important considerations are observer experience and flight duration.

Key-words: aerial, Africa, bias, counts, line transect, population density, sampling, wildlife.

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Introduction

On the African continent, light aircraft have been used to assess the abundance of wildlife since the mid-1950s. The first attempts aimed at total counts of animals of all species in a particular area. It was not until the mid-1960s that these expensive total counts were gradually replaced by more efficient sampling techniques. Because of the vastness and remoteness of many wildlife areas in Africa, aerial counts continue to be an important tool for wildlife management. This is definitely the case in Zambia, where over the past 30 years most wildlife counts have used aerial techniques. The main problem with aerial counts is that their accuracy has always been overrated (Jachmann 2001).

There are many sources of bias in aerial counts, some of which can be avoided with a proper design, but

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others cannot be remedied, almost always leading to incomplete counts. One can argue that such counts can be used as an index of relative density if the bias is constant; however, this is unlikely to be true. Many factors affect visibility, and even with repeat counts of the same area during the same time of the year and day, some will be different from one count to the next. Generally, spotting and counting problems represent the most important source of bias in aerial techniques (Norton-Griffiths 1978). Spotting and counting bias may be influenced by the density of the vegetation, by the size and colouring of the animals, by group size, by their reaction to an over-flying aircraft, by light conditions (i.e. time of year, time of day and weather conditions) and by operational factors, such as height and searching rate. Sources of bias that can be avoided with a proper design are: (i) insufficient coverage of the census area, when parallel flight lines are set too far apart (total count); (ii) visual estimation of large herds, when photography should be used, and; (iii) double-counting of animals, as a result of poor navigation. The first two biases lead to undercounts, whereas the third one leads to high estimates. Sources of bias that usually lead to underestimates, and are difficult to avoid are the following. (iv) Observer bias, which is related to the quality of the observers in terms of eyesight, experience and ability to concentrate during long, and sometimes turbulent, flights (Jachmann 1995, 2001). This bias can be corrected by applying the double-count technique (see below). (v) Sighting probability bias, which relates to the low probability of sighting single animals and small groups of animals, and can be minimized by keeping operational factors, such as searching rate and height above ground level, within reasonable limits. (vi) Visibility bias, which is related to animals not available to the observers because they are concealed by other animals or by obstructions, such as tree canopies, or because their colour makes them blend imperceptibly with the background. For example, browsers that spend much of their time under or near trees are generally more difficult to see than grazers of the same size that spend much of their time in open habitat. Animals that feed mostly during the night and sleep in the shade during the day are also more difficult to spot than those mainly feeding during daylight hours. Thus, for most animal species, the combined observer, sighting probability and visibility biases lead to undercounts.

In the past, several techniques have been proposed to eliminate bias from aerial counts (Caughley & Goddard 1972; Caughley, Sinclair & Scott-Kemis 1976; Cook & Jacobson 1979; Grier *et al.* 1981; Caughley & Grice 1982). Most unfortunately, these proposed techniques are impractical and expensive (Barnes, Hill & Wilson 1986). The only application that is practically feasible and theoretically sound is the double-count technique. This method is based on the concept of the mark–recapture model (Caughley 1974), while most applications use an adaptation of the Petersen estimate (Seber 1982; Caughley & Sinclair 1994). Two observers sitting in line, independently and without collusion, make simultaneous counts of the target species. From numbers of animals seen by the front observer only (marked animals), those seen by the rear observer only (captured animals), and those seen by both observers (marked animals recaptured), a correction factor can be derived (Magnusson, Caughley & Crigg 1977; Cook & Jacobson 1979; Grier *et al.* 1981; Caughley & Grice 1982; Graham & Bell 1989; Caughley & Sinclair 1994; Jachmann 2001).

Rivest *et al.* (1995) proposed a method to use several correction factors within a survey to correct for heterogeneity in sighting probabilities due to varying group size and alertness in a particular animal species. Briefly, a population is divided into subgroups or poststrata with a more or less constant sighting probability, and a correction factor is estimated for each of these. However, when the method was applied to a numerical example from the field, the use of several correction factors, as compared with a single correction factor, only added 3% to the estimate (Rivest *et al.* 1995).

The double-count technique probably corrects for most observer bias and possibly for a small proportion of sighting probability bias, but never for visibility bias. Furthermore, correction factors apply to a single animal species, for a particular count only. These correction factors are routinely used in aerial counts conducted throughout the continent, but the accuracy of resulting estimates is rarely questioned. Inaccuracies may be large, which is particularly relevant where results are used to determine management procedures that require estimates that are both precise and accurate. Therefore, it is important to know the accuracy of estimates obtained through aerial counts after correcting for observer bias.

The purpose of this study was to examine the reliability of aerial counts of a number of wildlife species that are commonly found in African woodland savannas. We began by comparing the results of line transect foot counts with those of systematic aerial sample counts, conducted in the Lupande Game Management Area in Zambia. During the aerial counts, sighting probability bias and observer bias were minimized by keeping operational factors within reasonable limits (Caughley 1974) and by applying the double-count procedure described in Jachmann (2001). Line transect counts were designed to limit potential sources of bias. The results of both types of counts were then related to body size, mean group size and various behavioural characteristics, to determine key factors that influence visibility of large herbivores from the air.

The resulting model was tested by applying it to the results of a systematic aerial sample count and two line transect foot counts, conducted in Kasanka National Park in October 1999 and 2000, respectively.

Study area

The Lupande Game Management Area (LGMA) covers 4840 km^2 on the east bank of the Luangwa

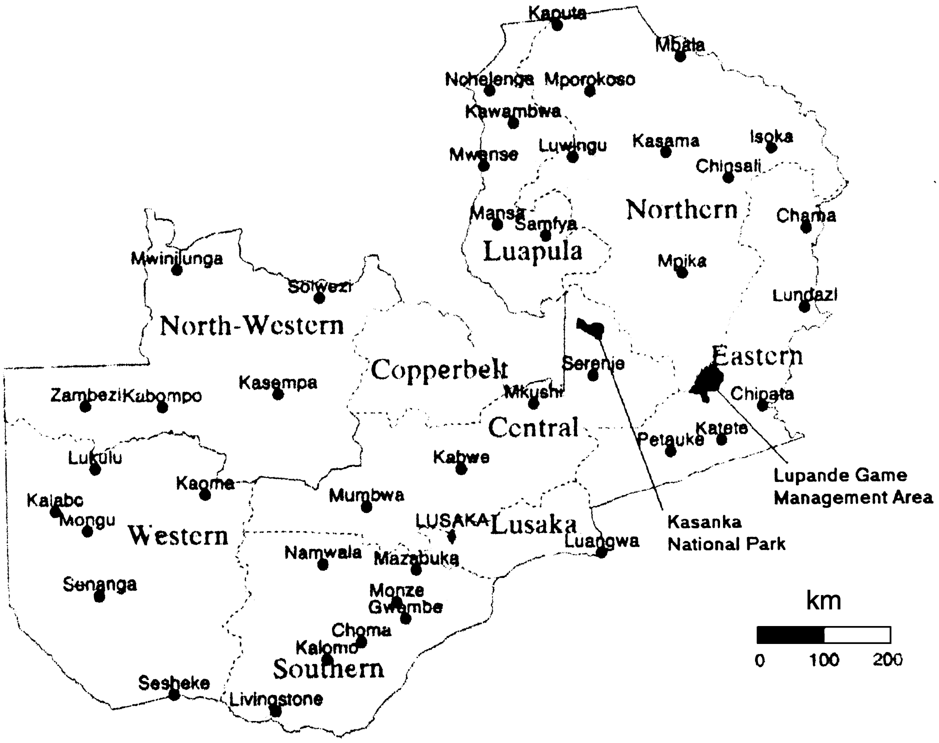

Fig. 1. Location of the Lupande Game Management Area and Kasanka National Park in Zambia.

River, in the Eastern Province of Zambia (Fig. 1). It borders on the Lumimba Game Management Area (GMA) in the north, Sandwe GMA in the south, and South Luangwa National Park in the west. The Luangwa River forms the boundary between the national park and the study area. The study area has several landscape units, starting with the alluvial valley floor at about 500 m above sea level, with a small strip of riverine woodland and mopane *Colophospermum mopane* woodland as the dominant vegetation type. In the northern part, the slightly undulating landscape slowly rises to the mid-level plateau at about 1100 m above sea level, with miombo woodland (*Brachystegia* and *Julbernardia* species) as the dominant vegetation type. In the southern part, the Chindeni Hills run north–south, between the valley floor and the Lupande River, a small tributary of the Luangwa River. The hills are covered by poor quality shrub vegetation, whereas thickets, ecotone mopane/miombo and miombo woodlands dominate the Lupande Valley. From the Lupande River, the landscape rapidly rises to the mid-level plateau, with miombo woodland as the main vegetation type. Annual rainfall varies between 700 mm on average in the valley, to 1000 mm on average on the plateau. Most rain falls between November and March, with April to August being the cool dry season, and September to October the hot dry season. The LGMA has fair numbers of most of the common wildlife species, mostly concentrated in a strip about 20 km away from the Luangwa River. Low wildlife densities are related to habitat type, water availability and the presence of settlement. Low densities of wildlife are found in the Lupande Valley, but in October wildlife is absent from the Chindeni Hills. Depending on the availability of food, elephant *Loxodonta africana africana*, Thornicroft's giraffe *Giraffa camelopardalis thornicrofti* and Cape buffalo *Sincerus caffer* move between the park, the southern part of Lumimba GMA and the study area throughout most of the year. There are no movements to the east, nor to the south. Burchell's zebra *Equus burchell*, greater kudu *Tragelaphus strepsiceros*, waterbuck *Kobus ellipsiprymnus* and impala *Aepyceros melampus* rarely cross the river, but move freely between LGMA and Lumimba GMA. The other species counted, Grimm's duiker *Sylvicapra grimmia*, puku *Kobus vardoni* and warthog *Phacochoerus aethiopicus*, are more or less sedentary. With the exception of elephant and giraffe, all species are hunted through a national, resident and safari licence system. As a result of seasonal movements, illegal off-take and legal hunting, numbers of most species may vary from one year to the next. Kasanka National Park is located just north of Serenje, in the Central Province (Fig. 1). Most of this small National Park (470 km^2) is covered by miombo woodland with large dambos (82%), with the remainder consisting of ecotone woodland (13%), permanent swamp (3%) and dry evergreen and riverine forest (Jachmann 2000).

Methods

Multi-species systematic aerial sample counts and line transect foot counts were conducted in October 1994, 1996 and 1998. To limit bias as a result of movements of animals, we only used aerial and ground counts that were conducted within the same 2–3-week period.

AERIAL COUNTS

For the three aerial counts we used the same aircraft (Cessna 206), pilot (H. Jachmann), navigator (W. Grove) and two out of four observers (i.e. two observers were the same for three counts). A double-count was applied to correct for observer bias. Calibrated height above ground level was between 106 and 139 m, and calibrated strip width between 168 and 194 m (single strip). These small differences in height and strip width would result in minor differences in bias levels. These differences, however, were negligible compared with presumed levels of undercounting bias. Based on differences in topography, the western part of LGMA was divided into two strata, i.e. the Upper Lupande (about 730 km^2) and the Lower Lupande (about 930 km^2). In the Upper Lupande, five transects, about 37-km long on average, were flown east–west on a 2-min grid line. In the Lower Lupande, 12 transects, about 20-km long on average, were flown north–south on a 2-min grid line. Aerial survey data were analysed with Jolly's method II for unequal-sized sample units (Jolly 1969), using the program AERIAL (Jachmann 2001). With Jolly's method II, the ratio of animals counted to area sampled (ratio method) gives an estimate of density for the sample zone.

GROUND COUNTS

Line transect methodology has been described in detail by Burnham, Anderson & Laake (1980) and Buckland *et al.* (1993). In line transect sampling (distance sampling), a team of three observers follows a straight line of known length. Each group of animals is recorded, as well as the distance of the animals from the observer and the sighting angle. The sighting distances and sighting angles are then converted to perpendicular distances. A frequency diagram of grouped perpendicular distances will show the probability of detecting a group of animals of a particular species in a particular habitat at particular distances from the transect line (detection function). Depending on its shape, this detection function can be modelled with four different estimators (i.e. hazard, negative exponential, half normal and uniform) and three different adjustment terms (cosine, polynomial and hermite), using the program DISTANCE (Laake *et al.* 1994).

Survey design followed that described in Jachmann (2001), using the same strata as for aerial counts. Briefly, a total of 20 block transects was placed at more or less regular intervals. Block transects are used in areas that lack a proper road system. A team of observers first covers a transect away from the drop-off point (5–6 km), then walks at right angles (2–3 km), and then turns and walks back to the road (5–6 km). The section across is only valid when there is no density gradient for the target species. Transect length and sighting distances were measured by pacing (Jachmann 2001). Prior to each survey, recorders covered a distance of 100 m 10 times, to determine personal step length. After the survey, all measurements were converted to actual distances. The accuracy of this method, checked with a global positioning system (GPS), was greater than 98% (Jachmann 2001). Each year, the block transects were counted three times in October. Because it was assumed that animal density did not change over a 2–3-week period, the data of three repeat counts were pooled to increase precision of the estimates. Line transect data were analysed with program DISTANCE (Laake *et al.* 1994).

ANALYSES

To examine the influence of body size, colour, dispersion and several behavioural characteristics on visibility of large herbivores from the air, a multiple linear regression analysis was performed with the program STATISTICA (Statsoft Inc., Tulsa, OK), with the ratio of the aerial estimate to ground estimate as the independent variable. As an indication of size we used the combined weights of adult males and females (Weight$^{2/3}$), mostly from Zambia (Skinner & Smithers 1990; Jachmann 2001). As a measure of dispersion we used the mean group size from aerial counts. As an indication of colour, all species were arbitrarily grouped into 14 different colour classes, ranging from 1 for pale sandy to 14 for blackish. To differentiate between grazers and browsers we used (1) browser, (2) mixed feeder and (3) grazer. To differentiate between nocturnal and diurnal species, we used the average number of hours that animals are active during the day (Estes 1993; Skinner & Smithers 1990). As an indication of the reaction to an over-flying aircraft we used (1) animal never moves, (2) animal sometimes moves, (3) animal usually moves and (4) animal always moves (H. Jachmann, personal observation). We continued by performing a stepwise forward linear multiple regression analysis, with the objective of explaining the most variation with the least number of variables. The same analysis was performed for browsers, and for grazers and mixed feeders, omitting the variable that differentiates between grazers and browsers. Mallows' *Cp* statistic (Draper & Smith 1990) was calculated to determine whether the model was consistent with the data.

Multiple linear regression assumes linear relationships between the variables, a more or less constant variance of the independent variable, and a normal distribution of residuals. Violations of these assumptions were checked with normal probability plots of residuals, and data were transformed when required (program STATISTICA). Normal probability plots of residuals were also used to check for outliers. Pearson product–moment correlation coefficients were calculated amongst all variables.

Table 1. Summary of results of line transect foot counts and aerial sample counts (estimates of total population size), conducted in the Lupande Game Management Area in October 1994, 1996 and 1998. CV, coefficient of variation; CF, correction factor

Species	Year	Line transect estimate	CV (%)	Aerial survey estimate	CV (%)	Double-count CF	Ratio aerial to line transect
Duiker	1994	3709	22·40	230	70·43	3·00	0·062
Duiker	1996	3072	21·60	29	79·31	3·00	0·009
Impala	1994	7678	21·89	1231	46·55	1·26	0·160
Impala	1998	15405	23·00	3136	36·10	2·33	0·204
Warthog	1994	1465	20·89	142	44·37	2·47	0·097
Warthog	1996	2437	23·72	274	66·79	2·40	0·112
Warthog	1998	2922	20·89	181	50·28	3·83	0·062
Puku	1994	1232	53·73	328	59·76	2·14	0·266
Puku	1998	2075	30·99	315	60·32	1·47	0·152
Waterbuck	1994	512	43·36	689	54·57	2·00	1·346
Waterbuck	1998	747	48·06	35	111·43	2·10	0·047
Kudu	1994	1383	29·57	30	93·33	1·57	0·022
Kudu	1996	715	40·56	19	84·21	2·00	0·027
Kudu	1998	996	36·04	17	100·00	2·16	0·017
Zebra	1994	1488	41·53	689	54·57	1·41	0·463
Zebra	1996	495	44·85	1654	53·32	1·74	3·341
Zebra	1998	830	46·02	244	60·24	2·54	0·294
Buffalo	1996	385	76·88	146	84·25	2·30	0·379
Giraffe	1994	783	36·40	275	42·91	2·33	0·351
Giraffe	1998	930	33·01	99	74·75	1·60	0·106
Elephant	1994	829	37·27	1863	82·66	1·39	2·247
Elephant	1996	286	59·79	840	63·45	1·30	2·937
Elephant	1998	1129	33·04	920	36·41	1·88	0·815

Prior to analyses, a one-way ANOVA was performed to examine how much of the variation in the transformed aerial to ground ratio reflects variation between species, as opposed to variation within species, i.e. repeat observations on the same species.

The regression model was tested by applying it to the results of a systematic aerial sample count, conducted in Kasanka National Park in October 1999. For the aerial count we used the same aircraft, crew and design as for surveys flown in LGMA. These results were compared with the population estimates from two line transect foot counts conducted in October 2000. The estimate for puku was compared with the results of a total ground count carried out during the same period.

Results

Comparison of the results of the line transect counts with those of the aerial counts done in 1994, 1996 and 1998 involved 10 animal species. Unfortunately, we were unable to collect three pairs of estimates for each species. There were no waterbuck, giraffe and puku sightings during the line transect count in 1996, no duiker sightings during the aerial count in 1998, and only one aerial count returned buffalo sightings (Table 1). Furthermore, normal probability plots of residuals showed that both impala estimates for 1996 had to be omitted as extreme outliers. In nearly all cases the hazard or negative exponential estimators with cosine or polynomial adjustment terms provided the best fit for the line transect data. A few cases with small sample sizes were analysed with the uniform estimator (Jachmann 2001).

During the aerial surveys, the double-count technique was applied to correct for observer bias. The variability in observer bias correction factors for repeat observations on the same species showed that a number of factors affecting visibility differed from one count to the next (Table 1). Thus, bias was never constant, and therefore one should always be cautious when using results of aerial counts as an index of relative density.

The ratios of the estimates from the aerial survey to those from the ground survey are shown in Table 1. With the exception of the 1994 estimates for waterbuck and elephant, and the 1996 estimates for elephant and zebra, the estimates from aerial counts conducted in LGMA were considerably lower than those from the ground counts (Table 1). High estimates from aerial counts usually concern large animals with large group sizes and low densities and therefore an uneven distribution. During aerial counts, observations of one or two large groups will inflate the estimate and reduce the precision (Table 1).

For the first multiple linear regression analysis, six different variables (variables 2–7; Table 2) were related to the ratio of the aerial and ground count estimates (variable 1; Table 1). Next, a stepwise forward linear multiple regression analysis was performed with the same variables. A second stepwise forward regression analysis was performed, excluding duiker, kudu and giraffe cases (browsers), and variable 5 (diet) (Table 2). The description of the 14 colour classes (variable 4; Table 2) with examples is provided in Table 3. To linearize trends, and to stabilize variance, the independent variable (variable 1), mean species weight

Table 2. Description of 14 colour classes with examples, running from light coloured animals, such as addax, to dark coloured animals, such as buffalo

Description of colour class	Rank	Examples
Sandy: pale	1	Addax *Addax nasomaculatus*
		Beisa oryx *Oryx beisa*
Sandy: fawn	2	Dorcas' gazelle *Gazella dorcas*
		Coke's hartebeest *Alcelaphus buselaphus cokii*
Sandy: brownish	3	Western hartebeest *Alcelaphus buselaphus major*
Fawn*: bluish	4	Greater kudu *Tragelaphus strepsiceros*
		Cape eland *Taurotragus oryx*
Fawn: greyish	5	Southern reedbuck *Redunca arundinum*
		Grimm's duiker *Sylvicapra grimmia*
Fawn: reddish to light brown	6	Roan antelope *Hippotragus equinus*
		Lichtenstein's hartebeest *Sigmoceros lichtensteinii*
Rufous†: glossy to tawny	7	Impala *Aepyceros melampus*
Rufous: patchy light to dark tawny	8	Thornicroft's giraffe *Giraffa camelopardalis thornicroftii*
Rufous: light to medium brown	9	Puku *Kobus vardoni*
		Cape Grysbok *Raphicerus melanotis*
Chestnut‡: light to dark	10	Tsessebe *Damaliscus lunatus*
Grey: black and white stripes	11	Burchell's zebra *Equus burchell*
Grey: light to medium	12	Elephant *Loxodonta africana africana*
		Common waterbuck *Kobus ellipsiprymnus*
Grey: medium to dark	13	Warthog *Phacocoerus aethiopicus*
Black: blackish to glossy black	14	Cape buffalo *Sincerus caffer*
		Sable antelope *Hippotragus niger*

*Light greyish brown.
†Reddish brown.
‡Golden reddish brown.

Table 3. Animal species, year of survey and the six dependent variables used for analyses, i.e. mean weight for adult males and females combined ($W^{2/3}$), mean group size for aerial counts, colour rank, diet, average number of hours of activity during the day, and reaction to an over-flying aircraft

Species	Year	$W^{2/3}$ (kg) (variable 2)	Mean group size (variable 3)	Colour rank (variable 4)	Diet (variable 5)	Daytime activity (h) (variable 6)	Reaction to aircraft (variable 7)
Duiker	1994	5·285	1·25	5	1	7	2
Duiker	1996	5·285	1·00	5	1	7	2
Impala	1994	13·379	12·75	7	2	12	2
Impala	1998	13·379	10·70	7	2	12	2
Warthog	1994	16·561	1·75	13	3	11	3
Warthog	1996	16·561	3·00	13	3	11	3
Warthog	1998	16·561	4·00	13	3	11	3
Puku	1994	19·310	2·00	9	3	8	2
Puku	1998	19·310	4·00	9	3	8	2
Waterbuck	1994	33·037	8·00	12	3	12	2
Waterbuck	1998	33·037	4·00	12	3	12	2
Kudu	1994	34·809	1·00	4	1	2	1
Kudu	1996	34·809	1·00	4	1	2	1
Kudu	1998	34·809	3·00	4	1	2	1
Zebra	1994	46·386	4·70	11	3	12	4
Zebra	1996	46·386	6·10	11	3	12	4
Zebra	1998	46·386	3·67	11	3	12	4
Buffalo	1996	61·791	4·50	14	3	8	4
Giraffe	1994	103·014	1·67	8	1	12	2
Giraffe	1998	103·014	1·00	8	1	12	2
Elephant	1994	176·182	8·44	12	2	8	4
Elephant	1996	176·182	4·86	12	2	8	4
Elephant	1998	176·182	3·75	12	2	8	4

(variable 2) and mean group size (variable 3) required a ln-transformation. For the remaining dependent variables, no transformation appeared to be required.

The results of the one-way ANOVA were significant ($F = 5{\cdot}15$, $P < 0{\cdot}004$), with variation between species accounting for 78% of the total.

All of the dependent variables were significantly correlated with the independent variable (Table 4).

Table 4. Pearson correlations and *P*-values between different variables (A/L, ratio of aerial to ground estimates)

Variable	ln A/L	ln $W^{2/3}$	ln MGS	Colour rank	Diet	Daytime activity
ln $W^{2/3}$	0·608					
	0·002					
ln MGS	0·638	0.196				
	0·001	0·370				
Colour rank	0·619	0·368	0·439			
	0·002	0·084	0·036			
Diet	0·440	−0·018	0·509	0·808		
	0·036	0·935	0·013	0·000		
Activity	0·460	0·026	0·452	0·596	0·553	
	0·027	0·907	0·030	0·003	0·006	
Reaction to aircraft	0·720	0·456	0·428	0·781	0·551	0·445
	0·000	0·029	0·042	0·000	0·006	0·033

Table 5. Pearson correlations and *P*-values between different variables, excluding browsers

Variable	ln A/L	ln $W^{2/3}$	ln MGS	Colour rank	Diet	Daytime activity
ln $W^{2/3}$	0·231					
	0·389					
ln MGS	0·678	0·417				
	0·004	0·108				
Colour rank	−0·499	0·085	0·414			
	0·049	0·754	0·111			
Diet	−0·667	−0·361	−0·407	−0·584		
	0·005	0·170	0·118	0·018		
Activity	−0·022	−0·288	−0·514	0·230	−0·179	
	0·937	0·279	0·042	0·392	0·507	
Reaction to aircraft	0·158	0·551	0·739	−0·096	0·544	−0·103
	0·558	0·027	0·001	0·724	0·029	0·704

When browsers were excluded, only mean group size, colour and diet were significantly correlated (Table 5).

MULTIPLE REGRESSION ANALYSES

The results of the multiple linear regression analyses, relating the ratio of the aerial to ground estimates with the six dependent variables, were significant ($F = 8{\cdot}86$, $P < 0{\cdot}001$). The model accounted for 77% (R^2) of the total variation, but only two out of six variables were significant. The regression equation is:

$$\ln y = -6{\cdot}890 + 0{\cdot}719 \ln W^{2/3} + 0{\cdot}682 \ln \mathrm{MGS} - 0{\cdot}097\ \mathrm{Colour} + 0{\cdot}246\ \mathrm{Diet} + 0{\cdot}084\ \mathrm{A} + 0{\cdot}580\ \mathrm{RA}$$

where y = prediction of ratio of aerial estimate to ground estimate; $W^{2/3}$ = weight of adult males and females combined (to the power of 2/3); MGS = mean group size observed during aerial counts; colour = colour rank; diet = browser (1), mixed feeder (2) or grazer (3); A = daytime activity (h); and RA = reaction to an over-flying aircraft.

This model showed good evidence for the effects of body size (weight) and mean group size, even after allowing for possible confounding effects of the other variables. There may have been an effect of reaction to an over-flying aircraft ($P = 0{\cdot}081$) but the statistical significance in the full model was diluted by including diet, colour and activity (Table 4).

We continued by performing a forward stepwise linear multiple regression analysis with the ratio of the aerial to ground estimates as the dependent variable (variable 1; Table 1). We used default values of 1·0 and 0 for F to enter and F to remove, respectively. Overall, the multiple regression equation was highly significant ($F = 18{\cdot}88$, $P < 0{\cdot}001$), explaining about 76% (R^2) of the original variability with three out of six variables kept in the model (Table 6). The most important factor influencing visibility from the air was whether the animal moved in response to an over-flying aircraft, followed by mean group size (dispersal) and body size (Table 6). The regression equation was:

$$\ln y = -6{\cdot}268 + 0{\cdot}620\ \mathrm{RA} + 0{\cdot}828 \ln \mathrm{MGS} + 0{\cdot}581 \ln W^{2/3}$$

The above model accounted for almost as much of the total variation as the full model with six variables ($R^2 = 77\%$). Mallows' *Cp* statistic was 2·3, which was close to the expected value of 4 for a 'true' model. The analysis indicated that there was no statistical argument for increasing the complexity of the model beyond three variables.

Table 6. Summary of results of the forward stepwise linear multiple regression analysis. SE, standard error; B, slope

Variable	Beta	SE	B	SE	*t*	*P*
Intercept			−6·268	0·698	−8·974	0·000
Reaction to aircraft	0·407	0·134	0·620	0·203	3·053	0·007
Mean group size	0·397	0·125	0·828	0·260	3.184	0·005
$W^{2/3}$	0·358	0·123	0·581	0·199	2·918	0·009

Table 7. Results of an aerial survey carried out in October 1999, and two line transect foot surveys done in October 2000 in Kasanka National Park, showing the ratio of the two estimates, the mean weight for adult males and females combined, the mean group size, and the reaction to an over-flying aircraft

Species	Line transect estimate	Aerial survey estimate	Ratio A/L	$W^{2/3}$ (kg)	MGS	Reaction to aircraft
Warthog	2160	123	0·057	16·561	4·80	3
Duiker	1597	105	0·066	5·285	1·11	2
Hartebeest	967	104	0·108	26·350	6·40	1
Waterbuck	195	25	0·128	33·037	1·50	2
Reedbuck	206	32	0·155	16·223	5·00	2
Roan	173	54	0·312	40·422	7·67	2

Table 8. The ratios of the estimates from an aerial sample survey to those from two line transect foot surveys, and predicted ratios using the multiple regression model developed at LGMA

Species	Ratio aerial to ground Kasanka National Park	Predicted ratio	Difference (%)
Warthog	0·057	0·228	+17·1
Duiker	0·066	0·019	−4·7
Hartebeest	0·108	0·110	+0·2
Waterbuck	0·128	0·070	−5·8
Reedbuck	0·155	0·125	−3·0
Roan	0·312	0·304	−0·8
Mean	0·138	0·143	5·3

Our data set was too small to split into two categories, one for grazers and mixed feeders ($n = 16$), and one for browsers ($n = 7$), to yield a meaningful regression model for browsers. However, merely as an indication, the regression equation was significant ($P < 0{\cdot}02$) and explained about 67% (R^2) of the original variability, with only colour influencing visibility of browsers from the air.

The multiple regression equation for grazers and mixed feeders was significant ($F = 7{\cdot}64$, $P < 0{\cdot}004$), explaining about 66% (R^2) of the original variability. The factors influencing visibility of grazers and mixed feeders from the air were body size, dispersal and the response to an over-flying aircraft. These results were similar to those from the multiple linear regression analysis of browsers, grazers and mixed feeders combined. The regression equation is:

$$\ln y = -6{\cdot}030 + 0{\cdot}723 \ln W^{2/3} + 0{\cdot}842 \ln \mathrm{MGS} + 0{\cdot}376\ \mathrm{RA}$$

TESTING THE MODEL

The multiple regression equation for browsers, grazers and mixed feeders combined was used to predict the ratio of aerial estimate to ground estimate for six animal species counted from the air in Kasanka National Park, in October 1999. The results of the aerial sample count were compared with the combined results of two line transect foot counts conducted in October 2000 (Table 7). Although the line transect counts were done exactly 1 year later than the aerial count, it was assumed that animal densities were more or less the same for both years. Illegal hunting is common outside the park, and during the peak dry season (October), when most of the grass has been burned, animals seek safety in the park. Thus, in October most animals are concentrated in Kasanka. It was assumed that between 1999 and 2000 the rate of increase through natural recruitment was more or less the same as the rate of illegal off-take (E. Farmer, unpublished observation).

The estimates from the aerial count were considerably lower than the estimates from the line transect counts (Table 7). With the exception of the results for warthog, the predicted ratios were only slightly different from those observed (mean difference 5·3%), which confirmed the validity of the model developed at LGMA (Table 8).

The robustness of the model for a large part depended on the accuracy of the ground count estimates. Although we will never know how much these estimates deviated from the true numbers of animals, ample evidence exists that line transect foot counts give accurate estimates (Burnham, Anderson & Laake 1980; Buckland *et al.* 1993).

We tested the model further by applying the data of an aerial sample count of puku to the multiple regression equation, and then comparing the predicted ratio with the ratio of the aerial estimate to that of a total ground count. Both counts were conducted in the same week of October 1999. The results of the total ground count were assumed to be more or less accurate. The aerial count gave an estimate of 1392 ± 393 puku (MGS 11·07, $n = 28$), whereas the total ground count resulted in 3660 ± 366 puku (Jachmann 2001). The ratio was 0·380, with a predicted ratio of 0·268. The observed ratio of the aerial sample count (ASC) to total ground count (TGC) was higher than the predicted ratio of ASC to line transect count (LTC). If ASC/TGC = 0·380, and ASC/LTC = 0·268, then TGC = 0·70 LTC.

During the total ground count, only puku in wide open dambos were counted, and groups that were concealed by trees on the fringe of the woodlands may have been missed, resulting in an undercounting bias. The predicted ratio was based on line transect foot counts, where movement of animals between two adjacent legs of a block transect may have slightly biased results upwards.

Using the regression equation, and given conditions found in the LGMA, the minimum mean group size for elephants should be 2·58, for buffalo 5·38 and for zebra 6·58, to obtain a ratio that approaches unity.

Discussion

In LGMA, the results of aerial counts of 10 large herbivore species, including elephant, buffalo and zebra, returned about 59% on average of the results of line transect foot counts. In Kasanka National Park, the results of an aerial count of six herbivore species, not including conspicuous species such as elephant, buffalo and zebra, returned about 14% on average of the results of line transect foot counts. In view of these results, we can make three alternative hypotheses: (i) line transect foot counts give overestimates, and aerial sample counts produce accurate estimates; (ii) aerial sample counts underestimate most animal populations, and line transect foot counts produce accurate results; (iii) both types of counts produce inaccurate results.

Only a few cases have been documented where the estimate of an aerial count was compared with a control estimate obtained by an assumedly more accurate method. In nearly all cases, aerial counts produced underestimates. For example, only 29% of a black rhino *Diceros bicornis* population, of which numbers were known exactly, was counted from the air (Goddard 1967). An aerial count of eight African large herbivore species returned only 23% of known numbers (Spinage *et al*. 1972). Aerial counts of non-African game returned similar results, such as 47% for brown bear *Ursus arctos* (Erickson & Siniff 1963), 57% for red kangaroo *Megaleia rufa* (Bailey 1971) and 56% for Indian rhino *Rhinoceros unicornis* (Caughley 1969). Only one case documents aerial total counts of elephants exceeding ground counts in four out of six occasions (Eltringham 1972).

These data point to undercounting as a major problem of aerial counts. Thus, for most animal species, aerial counts produce inaccurate results. Because our counts were conducted in open woodland savanna, and because bias varies by habitat type, aerial counts done in wide open terrain may generate estimates that are more accurate.

The accuracy of line transect foot counts depends on the design of the survey and on sample size. Sample size may determine the shape of the detection function, and consequently the estimator used for analysis. Because we used the combined results of a series of line transect surveys, most of our sample sizes were sufficiently large to avoid this type of bias. Moreover, line transect counts were designed to limit other potential sources of bias (Jachmann 2001). However, when using block transects, there is a possibility of some overcounting bias when animals move between the leg away from the road and that running back to the road.

In view of the above, and the many examples provided by Burnham, Anderson & Laake (1980) and Buckland *et al.* (1993), we conclude that our line transect results were probably relatively accurate, possibly with a slight overcounting bias. However, we believe that these bias levels are negligible compared with the presumed undercounting biases in our aerial counts. Thus, for most species, aerial counts are inaccurate and underestimate population size, whereas line transect ground counts may generate estimates that are more accurate. We should note, however, that our aerial data relate to multispecies counts. Bias may be reduced when only one species is counted (Norton-Griffiths 1978). If we assume that application of a double-count corrected for most of the observer bias in our aerial counts, then undercounting biases were mainly due to animals missed that were not visible (visibility bias) and animals missed that were visible but had a low sighting probability (sighting probability bias). When an animal moves in response to an over-flying aircraft, it may have been concealed, or it may have been in the open. Thus movement of animals will influence both visibility and sighting probability biases. The same applies to colour and body size. A light coloured animal may not be visible because it blends with the background (dry grass for instance). Also, it is often more difficult to spot a small animal concealed by an obstruction such as a tree than a large one. Dispersion, however, mainly influences sighting probability bias.

For example, for a given height and speed, the probability of sighting a single stationary donkey *Equus asinus* in wide open terrain is 0·66, increasing to 0·91 for a stationary group of eight (Graham & Bell 1989). However, when the donkey moves in response to the over-flying aircraft, sighting probability may increase to that of a stationary large group. Sighting probability of a group of eight donkeys that respond to disturbance from the aircraft will probably increase to one. These sighting probabilities apply when the donkeys are observed against a background of dry grass. If, however, the area was recently burned, sighting probabilities may drop considerably. Sighting probabilities may be further modified by varying height and speed of the aircraft, weather conditions, observer capabilities and other minor factors.

Although the predicted undercounts for the aerial count in Kasanka National Park were not significantly different from those observed, the regression equation cannot be used to generate undercounting bias correction factors under all circumstances. The analyses are based on conditions that prevail in the LGMA in Zambia, such as animal density, distribution, topography and vegetation density, which may be different elsewhere. Also, the weight of adult males and females combined, as well as the response of animals to an over-flying aircraft, may vary from one situation to the next.

Thus, unless the problem of variable undercounting bias is solved, aerial techniques are of limited use for most animal species. A minority of scientists attempt to tackle this problem by applying line transect methodology from the air, such as the most recent surveys flown in northern Botswana (Burm & Griffin 2000). Briefly, by attaching four to five wands to the wing struts of a fixed-wing aircraft, five to six distance intervals are created, with the last interval having an infinite distance.

The major advantage of using distance sampling is the variable strip width, which may potentially provide estimates free of biases to which conventional aerial sample counts are prone. However, the design violates an assumption critical to obtaining reliable estimates, that is, the probability of detection on and near the transect line is usually less than one, first because many animals move away in response to an over-flying aircraft, and secondly because the technique does not allow for correction of observer and sighting probability biases near the transect line. This violation results in a lower than expected detection for the first distance interval, leading to undercounts. The data in the first two intervals may have to be pooled. The distance classes remaining will be too few (< 5) to provide an unbiased estimate of population size. Lesser considerations are inaccuracies when assigning animals to a distance interval when the aircraft oscillates in the rolling plane, which leads to errors that are considerably larger than for a single strip. With speeds of > 100 knots it is not always easy to determine when animals are perpendicular to the aircraft, which also results in errors when assigning groups of animals to different distance intervals.

To our knowledge, the accuracy of distance sampling from the air has been tested twice (Hone 1988; Adcock 1995). In the first test, carcasses of feral pigs *Sus scrofa* were counted in an area of treeless floodplain and Eucalyptus woodland, using a helicopter (Hone 1988). The number of carcasses in the study area and their location were known exactly. Most of the distance estimators gave accurate and precise results. However, counting inanimate objects from a slow and low flying helicopter that is easy to manoeuvre in a mainly treeless floodplain cannot be compared with counting animals that are always on the move, from an aircraft that flies at > 100 knots and cannot be manoeuvred to search the strip beneath. Furthermore, prior knowledge of numbers and locations of study objects may give a higher than expected probability of sighting.

In the second test, aerial line transect sampling was used in the Madikwe Game Reserve, South Africa, to estimate abundance of a range of large herbivore species of which numbers were known through modelling from introductions and growth rates (Adcock 1995). One of the aims of these experimental counts was to test the relative efficiency of sampling with fixed-wing aircraft (Cessna 182 with four seats, and Partenavia with six seats), compared to helicopters (Hughes 500 and Jet Ranger). Line transect sampling with the Cessna 182 returned 36·3% on average of known numbers. The survey with the Partenavia returned 45·3% on average of known numbers (two additional observers). Although the Partenavia had the same number of observers on board as the Cessna 206 used in LGMA, application of a double-count in LGMA returned higher estimates. The Hughes 500 returned 77·1% and the Jet Ranger 89·7% on average of known numbers. Species underestimated by helicopter survey were browsers with small group sizes (kudu and giraffe), mixed feeders with small body size (impala) and waterbuck.

Thus, aerial line transect sampling has similar problems to conventional aerial strip counts. The technique should not be applied to estimate abundance of browsers or small and cryptic species, while the use of a helicopter is a prerequisite for obtaining accurate estimates. Most unfortunately, for a given level of effort, a helicopter survey is roughly five to six times more expensive than a survey with a small fixed-wing aircraft because it is slower and it costs more per hour. For a given level of effort, a line transect foot count is about four times more expensive than a conventional aerial sample count (Jachmann 2001). Thus, line transect foot counts are cheaper than helicopter surveys, and probably the preferred choice for small- to medium-sized study areas (< 5000 km^2).

Unfortunately, there are few alternatives to remedy the problem of variable undercounting biases in conventional aerial techniques. However, as long as the major problem of distance sampling from the air has not been solved (that is a lower than 1 probability of detection on and near the line of travel) results obtained with a fixed-wing aircraft should be treated in the same way as those from conventional methods. The alternative is to use the more expensive line transect sampling by helicopter for selected species, or the cheaper but slower ultra-light aircraft, which is not suitable for large areas and often lacks room for additional observers and equipment.

For animal species with very large group sizes and mainly found in wide open terrain, such as lechwe antelope *Kobus leche*, aerial sample counts, using a digital video camera calibrated on a fixed-width strip, may give accurate estimates of abundance (H. Jachmann, unpublished data).

Finally, the precision of estimates from conventional aerial sample counts can be improved by as much as 35% by using Markov Chain Monte Carlo (MCMC) modelling (Khaemba 2000). Development of this method stems from a criticism of Jolly's method II (ratio method), which gives large standard errors due to differences in the size of sample units and observed counts in species with large group sizes and therefore an uneven distribution. These differences invalidate a necessary assumption for ratio estimators, which is a through-the-origin regression and proportional variances (Khaemba 2000). However, mathematics are complicated and require highly specialized software, while the accuracy is the same as that of Jolly's method II. Therefore, it is not foreseen that the MCMC method will be widely applied in conservation science.

In conclusion, conventional aerial counts should be restricted to large conspicuous grazers and mixed feeders with medium to large group sizes, such as elephant, buffalo, zebra, wildebeest and lechwe, using photography for herds with more than 20 animals. Preferably, only one species should be counted at a time. Operational factors, such as height above ground level, strip width and speed, should be kept within reasonable limits. Height above ground level should be about 100 m, but never more than 200 m, strip width (one side) should be about 100 m, but it should never exceed 200 m, and speed should be between 180 and 250 km h^{-1}. Special aerial surveys, using low and slow flying microlight aircraft or helicopters, may be used for hippo *Hippopotamus amphibius*, crocodiles *Crocodylus niloticus* and sitatunga *Tragelaphus spekei* (Jachmann 2001). Attempts to count other animal species from the air will lead to estimates with large and variable undercounting biases. Therefore, the abundance of other species should be estimated with line transect techniques or alternative ground-count methodology. Observers should have at least 80 h of experience in counting the same animals in the same habitat (Jachmann 1995, 2001). Also, the duration of a single flight session should be limited to about 2 h, while observers need a short session prior to any survey or census, to form searching patterns for the animal species that require counting (Jachmann 1995, 2001). To correct for any remaining observer bias, the double-count technique should be applied.

Distance sampling from the air should be done with a helicopter or a slow and low flying microlight plane. We conclude that, in order to produce useable results, the following should be avoided: turbulent weather conditions; counting browsers or small and cryptic animal species; and counting animals that move in response to an over-flying aircraft.

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