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ORIGINAL PAPER

# Using simulations of past and present elephant (*Loxodonta africana*) population numbers in the Okavango Delta Panhandle, Botswana to improve future population estimates

**Anna Songhurst · Michael Chase · Tim Coulson**

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**Abstract** An ability to reliably estimate population numbers, trends and densities of wildlife has a prominent role in conservation and management of wetlands. We use aerial surveys and simulation techniques to explore the results of past and present elephant population surveys in the Okavango Delta Panhandle, Botswana, and use these to propose a technique of simulation to improve counts in the future. Population numbers and density estimates from past survey results show large fluctuations, which are unlikely to come from reproduction. Reasons for such variations could be attributed to imprecision in survey techniques or may be because only part of the elephant range is being surveyed. Simulated surveys of hypothetical elephant populations were used to explore the effect of different survey techniques, spatial distributions of animals and spatial scale on the precision of aerial survey population estimates and trends. Our study reveals the usefulness of using simulations to test the reliability of survey data and plan more efficient surveys. We also find that while there may be some uncertainty in individual population estimates, there is more certainty in the recorded trends. These findings reinforce the need to address elephant management in the Okavango and surrounding wetland systems and call for the urgent consideration of management strategies such as fence realignments to affect the objectives of the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA) initiative, which will help relieve elephant population pressure.

**Keywords** Elephant · Wetlands · Human–wildlife conflict · Okavango Delta · Population estimates · Simulation

## Introduction

The ability to reliably estimate population numbers and densities of animals is a fundamental component of many ecological studies (Elphick 2008) and has a prominent role in the conservation and management of wildlife. In general, it is not possible to count all the individuals in a population with certainty, especially when animals are free ranging over a vast area. It is, therefore, necessary to sample the population using methodology that allows robust inferences to be made about the entire population from the observed sample (Milner-Gulland and Rowcliffe 2007). Wildlife surveyors need to decide how much bias is acceptable and how precise the estimates of population abundance

A. Songhurst (✉)
Ecoexist Project, Maun, Botswana
e-mail: anna.songhurst@hotmail.com

A. Songhurst · T. Coulson
Department of Zoology, University of Oxford, Tinbergen Building, South Parks Road, Oxford OX1 3PS, UK

M. Chase
Elephants Without Borders, P.O. Box 682, Kasane, Botswana

and density need to be for the relevant wildlife management applications (Hone 2008). Simulations could provide a cost effective method to do this.

The Okavango Delta of northern Botswana is considered one of the most pristine wetlands in Africa (Gumbricht et al. 2004). Elephants (*Loxodonta africana*) form a major part of the wildlife resource in the Okavango Delta and contribute considerably to its ecological functioning (Mosepele et al. 2009) as well as its economic sustainability (i.e. attractiveness to tourists). An understanding of elephant population numbers and trends is needed by wildlife managers to monitor population changes over time and help understand important drivers of change in populations. For example, a decline in numbers could highlight impacts of illegal hunting (Booth and Dunham 2014) or increased numbers may indicate the need for management decisions that, for example, open up cross border movement and relieve pressure on the Delta resources from potential overpopulation and resulting ecological impacts. Wildlife population estimates from recent intensive aerial surveys of the Okavango Delta have identified considerable declines in the populations of many large herbivore species (Chase 2011). Loss of habitat connectivity as a result of anthropogenic barriers such as fences and land conversion to arable use and human settlements has been proposed as one of the main causes of these declines. Indeed, a Strategic Environmental Assessment (SEA) for the Okavango Delta Management Plan identified habitat connectivity as a critical factor contributing to the long term viability of wildlife populations in the Okavango, currently under serious threat (Anon 2012). Accordingly, the SEA calls for concerted efforts in appropriate, preferential monitoring and protection of habitat connectivity. Aerial surveys continue to play an important role in monitoring wildlife populations, their distribution, habitat use and key movement corridors in order to help guide effective management of wildlife populations and factors impacting their visibility like habitat connectivity. A key tool for monitoring this connectivity threshold and the wildlife populations of Delta's wildlife is aerial surveys. Recent developments in the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA) initiative also requires a greater understanding of population numbers and trends in the Kavango region.

An array of sampling techniques have been used to estimate wildlife population density, abundance and distribution varying from transect (strip, point or line) surveys (e.g. Norton-Griffiths 1978; Buckland et al. 1993) to mark-recapture methods (e.g. Jolly 1965; Hargrove and Borland 1994; Southwell and Low 2009). Finite population sampling methods such as total counts and strip transects, are often used to survey wildlife populations (Caughley and Grigg 1981; Marsh et al. 1997; Redfern et al. 2002; Jackson et al. 2008). Aerial transect surveys are the most commonly used method for surveying large mammals where the terrain is difficult or inaccessible, or where large areas need to be surveyed. Such surveys are used over a range of habitat types, including African savannah (e.g. Redfern et al. 2002; Chase and Griffin 2009; Ferreira and van Aarde 2009), oceans (e.g. Baumgartener 1997; Marsh et al. 1997; Wright et al. 2002; Marsh et al. 2004; Pollock et al. 2006), the Australian pastoral zones (e.g. Caughley and Grigg 1981) and the arctic tundra (e.g. Rivest et al. 1995). All these types of surveys encompass a significant economic cost and, therefore, verification of sampling designs by repeat surveys is often not feasible.

Even when sound survey methodology is adhered to, it is generally accepted that most aerial surveys are subject to a number of potential sources of bias (Caughley 1974; Marsh and Sinclair 1989; Jachman 2002; Elphick 2008; Laake et al. 2008). Such sources of bias include: Survey method bias (controllable by correcting for height variation and transect width variation); observer effects (minimized by training observers and using photo-corrected observations); environmental variables i.e. rainfall (uncontrollable); species-specific characteristics i.e. habitat preference, herd cohesion, herd size, species colouration (uncontrollable), and; undercounting bias (Caughley 1974; Norton-Griffiths 1978; Samuel and Pollock 1981; Milner-Gulland and Rowcliffe 2007; Elphick 2008; McIntosh et al. 2009). For example, in transect survey methods, population variance is often used as a measure of precision of the density estimate in such surveys, (Norton-Griffiths 1978). Animal populations are, however, often aggregated due to environmental and behavioural factors, which contradict the fundamental assumption of this precision estimate that all individuals are independently and randomly distributed within the sampling plot (Milner-Gulland and Rowcliffe 2007).

An accurate estimate is one that is near to the true total but may have wide confidence limits. Alternatively, a precise estimate has narrow confidence limits but the population estimate itself may be biased (Norton-Griffiths 1978). Precise censuses are needed to follow population trends, but the repeatability must be high (i.e. the degree of bias remains constant from census to census). On the other hand, accurate estimates are required, for example, if a population is to be reduced or if biomass estimates are being calculated (Norton-Griffiths 1978; Ferreira and van Aarde 2009). Choosing an appropriate sampling strategy is, therefore, critical because it influences precision and bias of estimated parameters and, therefore, may determine whether objectives are attained (Pearse et al. 2009). Assessing the efficiency of sample designs can be difficult in field studies because the tests themselves are subject to similar biases and direct empirical comparisons can be costly (Khaemba et al. 2001; Jackson et al. 2008; Pearse et al. 2009). Simulation is, therefore, a viable alternative to compare and validate different survey techniques applicable to aerial surveys of animals and has proven useful for such survey (e.g. Khaemba et al. 2001; Ferreira and van Aarde 2009; Pearse et al. 2009).

The largest contiguous population of African elephants (*Loxodonta africana*) is estimated at 218,091 elephants (Blanc et al. 2007), occurring across five countries, Angola, Botswana, Namibia, Zambia and Zimbabwe (Chase and Griffin 2006), with a total range of approximately 187,220 km$^2$, (Blanc et al. 2007). This total estimate consists of results from twenty-one separate surveys, which were estimated from sampled sub populations living in separately defined geographic areas. Extrapolating survey results to larger areas is a useful tool in wildlife management and conservation initiatives, but it is important to understand the bias involved with such results.

This study took place in the eastern Okavango Panhandle, Botswana, an area that forms a central part of the contiguous elephant population range across the Kavango region and KAZA TFCA. The eastern Panhandle study site boundaries (i.e. Namibian border fence, northern buffalo fence and the permanent Okavango River) are, however, potential barriers to elephant movements (Chase 2007; Chase and Griffin 2009; Ferreira and van Aarde 2009), indicating that elephants could effectively be trapped in this area. Over 15,000 people are also living in the eastern Panhandle, sharing and competing for resources with this elephant population. Yet, it is unclear how many elephants occur here or how fast the population is growing. Previous aerial surveys have been conducted in the area by Department of Wildlife and National Parks (DWNP) during 1996–2004 and Jackson et al. (2008) in the dry season 2003 and wet season 2004. Population numbers and density estimates that have resulted from these surveys show large fluctuations, which are biologically unlikely. Reasons for such variations could be attributed to either survey/observer/sampling bias or because only part of the elephant range is being surveyed.

This paper aims to (a) estimate current population numbers and densities of elephant in the Panhandle region; (b) determine the elephant population growth rate in the area; (c) use simulation to explore the reliability of past and present survey results; and (d) explore the effect of spatial scale in the precision of aerial surveys.

## Materials and methods

### Study area

The study was conducted within the Kavango region of southern Africa, on the eastern side of the Okavango Panhandle, where the Okavango River reaches the Okavango Delta in Botswana. The area encompasses three controlled hunting areas (CHAs), namely NG11, NG12 and NG13. The Namibian border marked the northern boundary, while the northern buffalo fence marked the southern and eastern boundary, and the Okavango River the western boundary (UTM Zone 34 7910000–7990000 South and 580000–710000 East) (Fig. 1).

Average annual rainfall was 360–500 mm and generally fell between mid October and March. The mean monthly maximum temperatures in the ODP ranged from 26.1–35.1 °C. Deep Kalahari sands dominate throughout NG11 and NG13, and main vegetation types include shrub land towards dune crests with Burkea (*Burkea Africana*) and shrubbed woodland with mixed mopane (*Colophospermum mopane*), (Mendelsohn and El Obeid 2004). NG12 comprises predominantly seasonal floodplain. Fertile soils that support subsistence agriculture are confined to lower depressions on land near the Okavango River and floodplains (Tawana Land Board 2005). Protected areas occur north of the Namibian border fence, namely Babwata National Park and Mahango Game

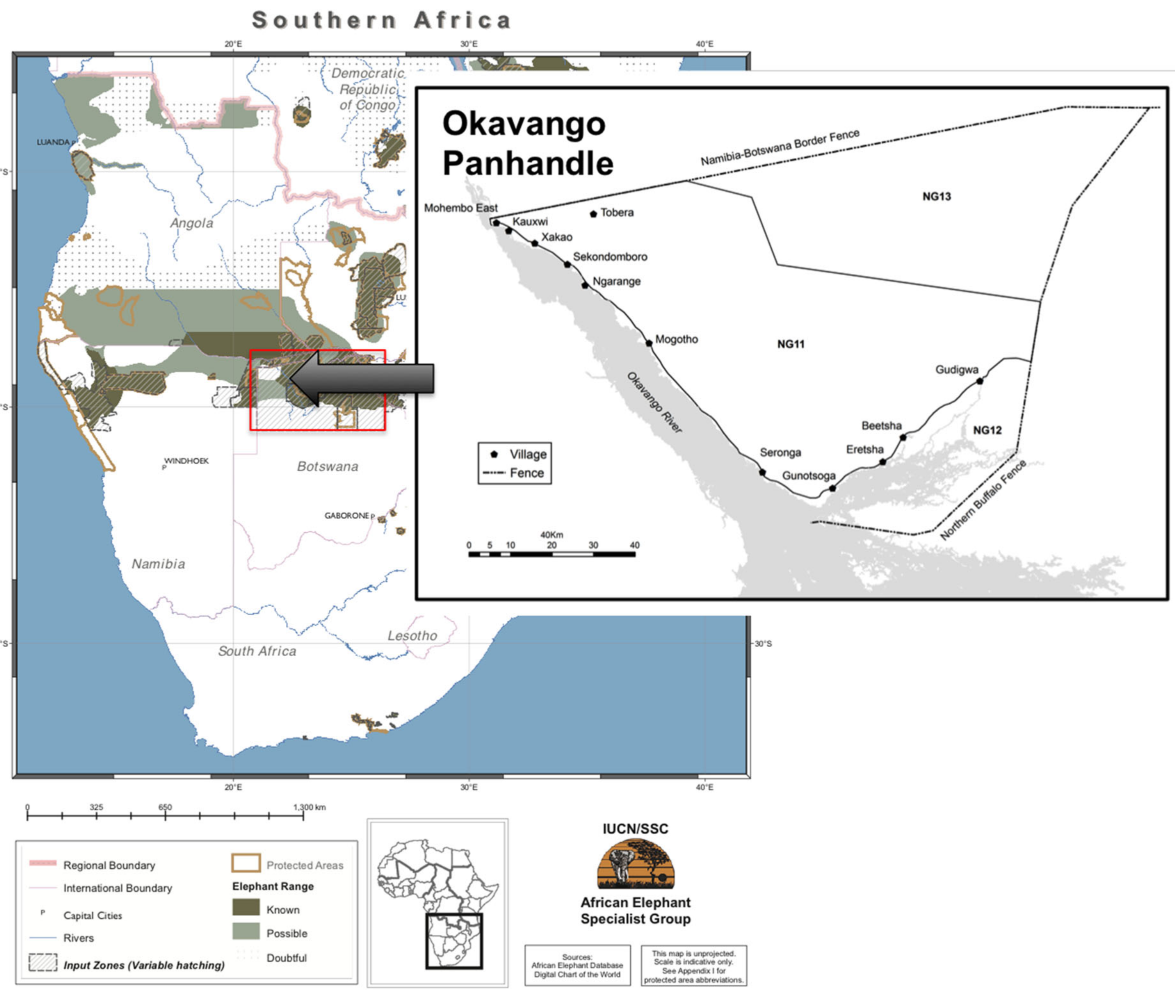


**Fig. 1** Elephant range in southern Africa with the Kavango region highlighted in *red box*. The Okavango Panhandle survey areas (NG11, NG12 and NG13) are *enlarged* and fences potentially restricting elephant movement are marked with *dotted line*

Reserve. South and east of the northern buffalo fence are wildlife management areas (WMAs), which are utilized by photographic and hunting tourism operations.

The estimated elephant population in the eastern Panhandle was 3782 in 1996 (DWNP 1996) and 15,429 in 2010 (this study), with elephants ranging throughout the study area. Telemetry studies by Jackson et al. (2008) in the Okavango Panhandle region indicated that the north–south buffalo fence blocks elephant movements from the Okavango River east to the Kwando River and it is reported that the Namibian border fence (see Fig. 1), poses a significant barrier to elephant movements between Namibia and Botswana, (Chase and Griffin 2009). This information suggests that elephant movement is restricted out of the eastern Panhandle.

## Aerial surveys

We conducted two aerial surveys over NG11, NG12 and NG13. The first took place in August 2008 over 6 days (22–25 and 27–28 August 2008) and the second in June/July 2010 over 6 days (30 June–5 July 2010). We conducted surveys during morning hours (0730–1130 h) and during the dry season when vegetation cover is sparse and therefore visibility of herds is increased. We used transect rather than block or quadrat sampling, to minimise sampling error from the effect of animals not being distributed evenly.

We conducted aerial surveys along flight transects using a Cessna 206 in 2008 and a Cessna 182 in 2010. We flew all transects at 100 kn and used a radar altimeter to maintain an altitude between 90 and 92 m (300–308 ft.). Prior to flying, we incorporated all transects into a digital map of the study area, using ArcView 3.3 (ESRI), with their beginning and end point coordinates. We systematically flew all flight transects along generally north/south axes (Fig. 2) so that transects traversed the shorter dimension of the study area making the transect lengths shorter and hence the sample unit smaller. We also aligned transects perpendicular to the Okavango River, to reduce sampling error (Norton-Griffiths 1978). We used GPS receivers (Garmin 12 xl, Garmin 176c) and DNR Garmin software (Minnesota Department of Natural Resources, MIS Bureau, GIS Section) to navigate along transects.

We used the standard methodology for strip transect sampling developed by Norton-Griffiths (1978). We attached two wands to the wing struts of the plane to delineate a 250 m interval for recording elephant observations at an altitude of 90 m (300 ft.). Additionally, we placed a mark on the plane window to help observers keep their eyes at a consistent height to maintain the same sighting angle for each observation. This helped keep consistent interval widths for each observation. We calibrated and confirmed each interval width on each side of the plane prior to initiating the first survey by placing markers at measured distances on the ground and conducting flyover tests (Norton-Griffiths 1978). Where necessary we adjusted the wands to provide a 250 m wide strip at 90 m (300 ft.) altitude and attached struts for the duration of each survey.

We divided the census zone into three strata (see Table 1), delineated according to wildlife management areas, and expected distribution and abundance of elephants from prior surveys (DWNP 1996, 1999, 2001, 2002, 2003, 2004, 2005, 2006; Jackson et al. 2008). We used three levels of sampling intensity. In areas designated for high intensity sampling, NG11, we spaced transects 2 km apart, providing a ~25 % sampling coverage. For moderate sampling intensity in NG12, we spaced transects 2.5 km apart, providing a sampling coverage of ~20 %. We spaced transects 5 km apart for low intensity sampling in NG13, providing ~10 % sampling coverage (Fig. 2).

Using the standard methodology for strip transect sampling developed by Norton-Griffiths (1978), we counted and recorded only elephants that were observed within the interval. For each elephant seen

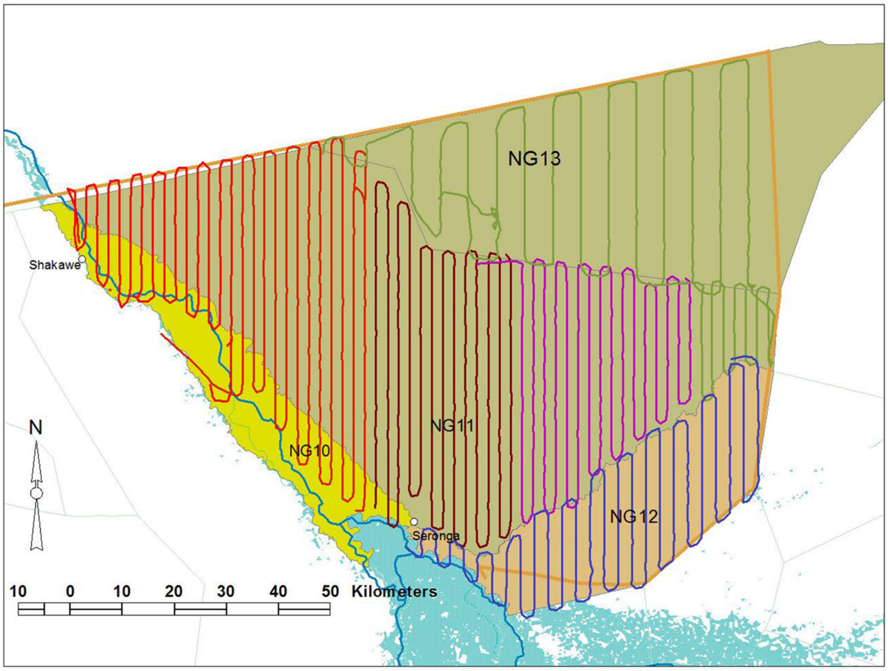


**Fig. 2** Map of transects flown over the survey area

**Table 1** Aerial survey transects flown in the eastern Okavango Panhandle by block/strata

| Strata name | Area ($km^2$) | Year | Actual strip width (km) | Area covered ($km^2$) | Total time (Min) | Transect spacing (km) | Sampling intensity (%) | Search rate ($km^2$/min) |
|---|---|---|---|---|---|---|---|---|
| NG11 | 5140 | 2008 | 0.513 | 1252.7 | 766 | 2.0 | 23.7 | 1.64 |
| | | 2010 | 0.499 | 1220.4 | 819 | 2.0 | 23.1 | 1.49 |
| NG12 | 1092 | 2008 | 0.513 | 226.3 | 144 | 2.5 | 18.6 | 1.57 |
| | | 2010 | 0.499 | 220.5 | 170 | 2.5 | 18.1 | 1.30 |
| NG13 | 2500 | 2008 | 0.513 | 211.3 | 132 | 5.0 | 10.3 | 1.60 |
| | | 2010 | 0.499 | 205.8 | 137 | 5.0 | 10 | 1.50 |
| Total | 8732 | 2008 | 0.513 | 1690.3 | 1042 | – | 19.7 | 1.62 |
| | | 2010 | 0.499 | 1646.8 | 1126 | – | 19.2 | 1.46 |

within the transect interval, the observer called out the numbers of elephants and herd type (bull or breeding herd). We used the same two observers [A. Songhurst (R) and K. Landen (L)] throughout the survey, one on each side of the plane and the front seat recorder (M. Chase) logged all elephant observations made by the observers whilst assisting the pilot with navigation along the pre-determined transect lines and recording the start and end times for each transect. With each herd observation, we recorded the GPS waypoint, waypoint number, time of observation, altitude, and number of elephants observed.

We used two Canon EOS 10D digital cameras with 20 mm wide-angle lenses, camera backs with time code generators and window camera mounts to verify herd size and the sighting of herds within the interval defined by the wands. A camera was mounted on each side of the plane. The cameras provided high-resolution images to verify counts in subsequent analyses. Observers took a photo with each elephant observation of $> 10$ animals and we recorded a GPS time code to the minute for every frame exposed. We interpreted the digital images of each herd and compared these to the observers' counts. This enabled us to correct for counting bias following methods outlined in Norton-Griffiths (1978) and determine whether elephants recorded actually occurred within the strip interval.

## Population growth

We collated data from past aerial surveys undertaken in the eastern Okavango Panhandle. All past surveys used the standard methodology for strip transect sampling developed by Norton-Griffiths (1978) and calculated population estimates using Jolly's method II (Jolly 1969). Surveys were conducted by the Department of Wildlife and National Parks (DWNP) in eight dry seasons (1996, 1999, 2001, 2002, 2003, 2004, 2005, 2006) over a survey area incorporating NG11, NG12 and NG13. Areas varied slightly between years (see Appendix 1) ranging from 9835 to 9919 $km^2$. Strip widths of 400 m (200 m each side of the plane) were used in DWNP surveys and 6 nm (12 km) were left between transects, giving a mean sampling intensity of 3.46 % (DWNP 1996, 1999, 2001, 2002, 2003, 2004, 2005, 2006). In the dry season of 2003, Jackson et al. (2008) conducted a survey in NG11 covering an area of 5952 $km^2$, using strip width of 800 m (400 m each side of plane) and one nautical mile (2 km) between transects, giving a sampling intensity of 40 %.

We plotted population estimates from past and current surveys to investigate the population growth rate in the study area. Generalised linear models with normal error structure were conducted for (a) the total study area survey population estimates and (b) for the management area NG11 survey population estimates, with year of survey fitted as the explanatory variable and significance tested at $p < 0.05$. We calculated the maximum growth rate for an elephant population at 7 % by Calef (1988), using a minimum inter-calving period of 3 years (ranges between 3 and 4.7 years) and a mean age of first birth of a calf at 11 years (ranges between 8 and 14 years). We compared the estimated population growth rate to this predicted maximum rate of increase. The death rate of natural elephant populations vary between different populations but appear to range between 1.43 and 7.4 %, while population growth rates average 2.17 % (ranging between 3.75 and 11.28 %).

### Carcass ratio

We estimated the number of dead elephants (carcasses and skeletons) in 2008 and 2010 surveys, using the Jolly method II (Jolly 1969). We calculated carcass ratios (Number dead/(Number dead + Number alive) for both years and estimated population change following methods in Douglas-Hamilton and Burrill (1991).

### Simulation surveys

We used simulations to compare precision of population estimates and estimated population growth rates with different sample designs, varying spatial distributions of elephants and a range of spatial scales. Distribution of elephants were simulated as spatial point patterns following a clustered distribution, using similar approaches to other studies, such as Khaemba et al. (2001) and Stein and Georgiadis (2006). We used the Matérn Cluster process to generate spatial patterns of elephants (Matérn 1986; Baddeley and Turner 2010). The Matérn's cluster process is constructed by first generating a Poisson point process of "parent" points with intensity (kappa). Then each parent point is replaced by a random cluster of points, the number of points in each cluster being random with a Poisson (μ) distribution, and the points being placed independently and uniformly inside a disc of radius (r) centred on the parent point (Baddeley and Turner 2010).

Simulations used the total census zone (8732 $km^2$) and 1000 simulated survey samples were taken at varying sampling intensities (3, 5, 10, 20, 40, 50 and 80 %). We repeated the simulations using five different spatial distributions of elephants by varying the value of r in the Matérn Cluster process, ranging from very clumped ($r = 0.006$) to very dispersed ($r = 1$). These simulations represented the radius of an elephant herd being 6 m (approximate length of one adult elephant) up to 1000 m. We used the root mean square error (RMSE), defined as $\sum(\hat{Y} - Y)^2$ to measure the precision of simulated surveys and compare sampling intensities and elephant distribution (Khaemba et al. 2001).

The average family unit size of African elephants is between eight and nine animals (ranging from 2 to 25), (Moss and Poole 1983; Wittemyer 2001) and bulls generally tend to be solitary or associate in all male herds (range 1–30) (Moss 1988; Eltringham 1991; Moss 1996). Our survey results showed that the average herd size in the Okavango Panhandle (combining family group and bull herd results) was eight animals, therefore we used eight as the mean cluster (herd) size (μ) in our simulations.

To decipher how real our calculated population growth rates were (with respect to them occurring by chance alone), we simulated 10 (number of actual surveys conducted in total study area) surveys and explored the probability of observing the change in elephant population numbers (slope) actually observed in the data. First, we generated 10 random population estimates with a normal distribution using the simulated mean and standard deviation of population estimates derived from methods above and regressed these against a vector (1:10) representing time. This was repeated 1000 times for each combination of elephant distributions and sampling intensities. We then looked to see where the slope actually observed in the data lay in the frequency distributions of these simulated slopes.

To investigate the effect of spatial scale on the precision of aerial surveys, we repeated the whole simulation process, using a census zone covering the whole of the estimated elephant range in the Kavango region (187,220 $km^2$).

### Population growth in relation to HEC incidents

We collated the yearly totals of elephant crop-raiding incidents from Department of Wildlife and National Parks (DWNP) Problem Animal Control (PAC) records from 1998 to 2010, as well as past population survey estimates of elephant numbers and densities in the Panhandle over the past 12 years.

To determine whether the number of elephants or elephant density affects the number of elephant crop-raiding incidents in the area, we plotted estimated elephant population numbers and densities against the total number of crop-raiding incidents recorded per year over the past 12 years. We conducted a linear regression for the yearly number of crop-raiding incidents, with the estimated elephant population per year or elephant density per year fitted as continuous variables.

### Data analysis

We used R 2.11.1 for all statistical analyses (R Development Core Team 2010) and R language verified using Crawley (2007).

We used generalised linear models (GLM) with normal error structures to explore elephant population growth. For each GLM used, the maximum model was fitted and simplified by stepwise deletion of non-significant interactions, quadratic terms, and main effects. Model-checking plots were drawn to check for constancy of variance and normality of errors. Model fit was then checked using F-test for normal errors and significance determined for all analyses at $p < 0.05$ (Crawley 2007).

Following the guidelines developed by Norton-Griffiths (1978) we calculated abundance and variance estimates for strip transect counts from observation data. We calculated actual strip width observed and adjusted for altitude following Norton-Griffiths (1978) and used the traditional Jolly's method II for unequal sized sampling units (Jolly 1969). The Jolly's method II 'ratio method' is based on the calculation of the ratio between animals counted and area searched. The population estimate is based on the density of animals per sample unit (transect) rather than number of animals per sample unit. We calculated population estimates for each block and summed these estimates to obtain an estimate for the entire survey area.

We used confidence intervals (CIs) as non-parametric measures of precision $\mathrm{CI(x)} = \mathrm{x} \pm \mathrm{t}_{2,\alpha} \times \mathrm{SE(x)}$, (Milner-Gulland and Rowcliffe 2007). The 95 % confidence intervals (CIs) were calculated and the CI expressed as a percentage of the population estimate as a measure of precision.

We used two sample *t* tests to compare mean bull and family group sizes per observer and between surveys, and Chi square $\chi^2$ goodness-of-fit tests to compare density estimates between years, and numbers of total herds, bull herds, and family groups seen per observer.

## Results

### Transect data

For the entire 8732 km$^2$ survey area, a total of 101 transects were flown in both 2008 and 2010: 63 in NG11, 25 in NG12; and 13 in NG13, totalling a distance of 3294.9 km. Sampling intensity and search rate were calculated for the total survey and per strata (see Table 1). The average transect length was 38.7 km (range 4–67 km), and the average time to fly one transect was 13.63 min (range 2–24 min).

### Elephant population size and density

A significantly larger number of elephants were observed in 2010 (n = 2834) than in 2008 (n = 1927), ($\chi^2 = 172.8$, df = 1, $p < 0.001$) for the whole study area (see Appendix 1). There were also significantly large differences in the number of elephants sighted in each survey block between 2008 than 2010: NG11 ($\chi^2 = 6.258$, df = 1, $p = 0.01$); NG12 ($\chi^2 = 106.4$, df = 1, $p < 0.01$); and NG13 ($\chi^2 = 160.19$, df = 1, $p < 0.01$).

Combining herd observations for both observers and accounting for average flight altitudes, strip transect sampling from the August 2008 survey provided an estimated total of 8905 elephants for the 8732 km$^2$ area (1.05 elephants/km$^2$) compared to 15,429 elephants in the same area (1.77 elephants/km$^2$) in 2010 (see Table 2), indicating a finite rate of population change of 1.3 over the past 2 years or a population increase of 30 % per year. The density estimates for the total study area were not significantly different between years ($\chi^2 = 0.18$, df = 1, $p =$ 0.67).

Population estimates and elephant densities for NG11, NG12 and NG13 showed increases between 2008 and 2010 (see Table 1), however these were not significantly different between years for each survey block ($p > 0.05$).

### Carcass ratio

A larger number of dead elephants were observed in the total study area in 2010 (n = 44) than in 2008 (n = 41), and estimated number of dead elephants were consequently higher in 2010 than 2008. In NG11, a larger number of dead elephants were estimated for 2010, but for NG12 and NG13 estimated numbers of dead elephants decreased in 2010 (see Table 2).

Carcass ratios were calculated for the total study area and per survey block (see Table 2) and percentage of population change per year estimated based on these carcass ratios (Douglas-Hamilton and Burrill 1991). Our carcass ratios for the whole study area ranged from 1 to 2 %, indicating a population increasing fast.

**Table 2** Estimates of elephant numbers for the August 2008 and July 2010 dry season aerial surveys, Okavango Panhandle, Botswana

| Area | Dry season August 2008 | | | | | | | | Dry season July 2010 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Size ($km^2$) | N (alive) | SE | 95 % CI | CI as % of N | Density (ele/$km^2$) | N (Dead) | Carcass ratio (%) | N (alive) | SE | 95 % CI | CI as % of N | Density (ele/$km^2$) | N (dead) | Carcass ratio (%) |
| NG11 | 5140 | 6383 | 846 | 4692–8074 | 26.5 | 1.32 | 127 | 2 | 7816 | 1222 | 5373–10259 | 29.5 | 1.52 | 160 | 2 |
| NG12 | 1092 | 1303 | 292 | 700–1906 | 46.3 | 1.27 | 29 | 2 | 2937 | 1054 | 762–5112 | 74.1 | 2.69 | 15 | 1 |
| NG13 | 2500 | 1219 | 425 | 293–2145 | 76 | 0.48 | 47 | 4 | 4676 | 1288 | 1869–7483 | 59.5 | 1.87 | 36 | 1 |
| Cumulative total | 8732 | 8905 | – | – | | 1.02 | 203 | 2 | 15429 | – | – | | 1.77 | 211 | 1 |
| Calculated total | 8732 | 9963 | 1170 | 7642–12284 | 23.3 | 1.14 | 212 | 2 | 15027 | 2008 | 11043–19011 | 25.7 | 1.72 | 233 | 2 |

### Herd observations and abundance

In August 2008, 127 bull herds, and 131 family groups were observed, while seven herds were un-classified. Bull herd size averaged 2.8 elephants (range 1–18), while family group size averaged 11.8 (range 2–41).

For the July 2010 survey, 152 bull herds and 179 family groups were observed. Average bull herd size was 2.2 elephants (range 1–16), while family group size averaged 13.6 elephants (range 2–70) (see Appendix 3).

In 2008 and 2010 surveys, most herds were seen in NG11 (n = 208 and n = 213 respectively) with more family groups than bull herds observed. Bull herd size averaged 2.7 elephants (range 1–19) in 2008 and 1.95 elephants (range 1–9) in 2010, while family group size averaged 11.9 elephants (range 2–50) in 2008 and 13.3 elephants (range 2–70) in 2010. In NG12, 44 herds were observed in 2008 and 72 in 2010. Average bull herd size was larger in 2010 [3.02 elephants (range 1–16)] than 2008 [2.4 elephants (range 1–7)] as well as average family group size [18.04 elephants (range 2–70) rather than 11.6 elephants (range 3–32)]. The fewest number of herds were observed in NG13 in 2008 (n = 13) and 2010 (n = 46). Average bull herd size was larger in 2008 [5.7 elephants (range 1–10)] than in 2010 [1.43 elephants (range 1–4)], while family group size averaged 8.6 elephants (range 2–22).

### Observer and count bias

There were no differences between the number of herds observed by each observer in 2008 ($\chi^2 = 3.24$, df $= 1$, $p = 0.07$) or 2010 ($\chi^2 = 0.87$, df $= 1$, $p = 0.35$). Likewise, there was no significant difference between the number of bull herds observed by each observer in 2008 ($\chi^2 = 0.07$, df $= 1$, $p = 0.79$) or 2010 ($\chi^2 = 0.95$, df $= 1$, $p = 0.33$), or the number of family groups observed in 2010 ($\chi^2 = 0.05$, df $= 1$, $p = 0.82$). However, the number of family groups observed by each observer differed in 2008 ($\chi^2 = 5.2$, df $= 1$, $p = 0.02$), with observer L reporting more herds (n = 78) than observer R (n = 52).

There were no significant differences between the two observers for average bull herd size in 2008 ($t = 0.27$, df $= 95$, $p = 0.79$) or 2010 ($t = 0.32$, df $= 143$, $p = 0.75$), or family group size in 2008 ($t = 0.95$, df $= 100$, $p = 0.34$) or 2010 ($t = 1.22$, df = 177, $p = 0.23$), (see Appendix 3). There was no significant difference between the elephant numbers seen by observers compared to numbers in photographs in 2008 ($t = 0.26$, df = 195, $p = 0.79$) or 2010 ($t = 0.1$, df = 199, $p = 0.91$). The overall count bias calculated from photo-corrections was 1.02 in 2008 and 0.98 in 2010, this ranged from 0.94 in NG13 in 2008 to 1.1 in NG12 in 2008.

## Population growth

Survey estimates from the past 14 years in the whole study area and for the past 7 years in NG11, indicate that the elephant population is increasing faster than the calculated theoretical maximum rate of increase (see Fig. 3; Appendix 1). The finite rate of change over 14 years in the total study area using past and recent raw data is 1.1, (increase of 9.5 % per year) and the regression line indicates a growth rate of 8.6 % a year. Severe drought occurred in the mid 1990s, which could explain low population estimates in 1996–1999 and may therefore bias the finite rate of change. However, when these data were removed from analysis the finite rate of change remained the same (1.1). In NG11 the finite rate of change over 7 years is 1.1, also indicating a 9.5 % increase per year.

Generalised linear models for survey elephant population estimates in the whole study area and in NG11, with normal error structure, retained year as having a statistically significant positive effect ($F = 5.3$, $df_M = 1$, $df_R = 9$, $p < 0.05$) and ($F = 298$, $df_M = 1$, $df_R = 2$, $p < 0.01$) respectively, confirming that the population has significantly increased.

## Simulations

Simulations showed that as sampling intensity increased the root mean square errors (RMSE) decreased and the survey estimate is more precise. The interquartile range (IQR) decreases with increasing sampling intensity from 3 % (IQR = 2600) to 20 % (IQR = 1005) to 40 % (IQR = 743), however, it is still relatively large for all sampling intensities. As sampling intensity increases the RMSE decrease, yet the RMSE are not highly affected by the spatial distribution of animals. However, at lower sampling intensities, the RMSE increases slightly with more clustered distributions of elephants, indicating that surveys with lower sampling intensity are less precise when elephants have a clustered distribution (see Appendix 4).

We are confident in the observed trend that elephant numbers are increasing (i.e. slope of regression) in the study area. The estimated slope from the data lay outside the 95 % confidence limits of the frequency distribution of randomly generated slopes (calculated using simulated means and standard deviations of

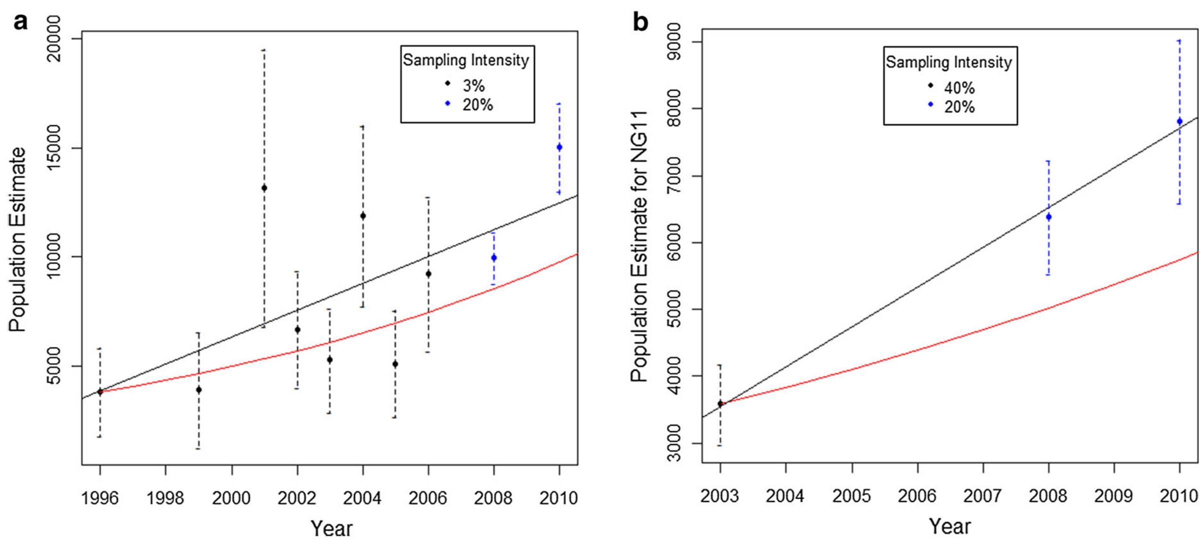


**Fig. 3** Population growth for **a** total study area (NG11, NG12 and NG13) and **b** NG11. *Red line* is projected growth using maximum rate of increase (7 %) for an elephant population (Calef 1988) and *black* is predicted growth from surveys

population estimates for different sampling intensities and spatial distributions of elephants), indicating that the observed trend was not random (see Fig. 4). However, the interquartile range for population estimates calculated from simulations was relatively large for all sampling intensities and, therefore, our population estimates cannot be considered highly accurate.

Consistent patterns were seen when we sampled at a broader spatial scale. The simulations for the whole Kavango region showed RMSE increasing as sampling intensities decreased and the interquartile range of population estimates decreasing as sampling intensity increased. At low sampling intensity the spatial distribution of elephants affected the precision of surveys over the larger study area, with more dispersed distributions resulting in larger RMSE.

### Population growth in relation to HEC incidents

There was no significant relationship between number of elephants or elephant density and number of crop raiding incidents per year.

## Discussion

### Reliability of aerial survey data

Our study reveals the usefulness of using simulations to test the reliability of survey data and plan more efficient surveys. Population estimates from past and current surveys in the Panhandle showed large fluctuations (see Appendix 1) that are biologically unlikely. However, with the aid of simulations, we were able to determine with certainty trends in population numbers that were predicted from this data. Simulations also revealed that such trends do not appear to be significantly affected by sampling intensity of surveys, spatial distribution of elephants or the spatial scale of the survey, indicating that, as long as bias is minimised during survey design and implementation, aerial survey data can be used reliably for predicting population trends despite variations in the above variables. Patterns were consistent across different spatial scales indicating that surveying smaller or larger areas of elephant populations should not significantly affect the precision of abundance estimates.

The 95 % CIs expressed as a percentage of a population estimate are used as a measure of precision. Data from past aerial surveys show that surveys conducted at lower sampling intensities are less precise, because these 95 % CIs were larger. Our simulations confirmed that precision of estimates increase with higher sampling intensities, as found in previous studies using simulation (e.g. Khaemba et al. 2001; Ferreira and van Aarde 2009). Our simulations also showed, however, that sampling at lower intensities is sufficient for reliably observing trends in population changes over time (Ferreira and van Aarde 2009). At higher sampling intensity, the precision of survey estimates was slightly lower with more clustered distributions of elephants in our simulations. It has been found in previous simulation surveys that precision of abundance estimates increases marginally with increasing sampling intensity when animal herds are clumped (Khaemba et al. 2001) and it has been predicted that sampling intensities as high as 50–70 % are actually required to improve precision when herds are clumped (Ferreira and van Aarde 2009). Depending on the purpose of the survey, knowledge of animal distributions may be important prior to survey design to determine whether an increase in sampling intensity to improve precision outweighs the cost of a high intensity survey. If the main purpose of the survey is to identify population trends, however, then our simulations indicate that the distribution of elephants should not affect the ability to identify such trends.

Alternatively, if the intention of monitoring is to gain accurate estimates of population abundance for management strategies such as establishing hunting quotas or identifying sustainable harvesting numbers for population control then both precision and accuracy of population estimates need to be maximised. This requires surveys to be conducted at the highest sampling intensity possible (i.e. 40 %) using the narrowest transects width possible (i.e. 400 m). However, time and financial constraints would need to be considered to assess the viability of conducting such surveys. If the purpose of the survey is to estimate trends in elephant population abundance, however, then our study shows that longitudinal studies at even the smallest sampling intensity are adequate.

### Population growth

Our study has shown that although we cannot consider past and present elephant population estimates to be highly accurate in the Okavango Delta Panhandle (as

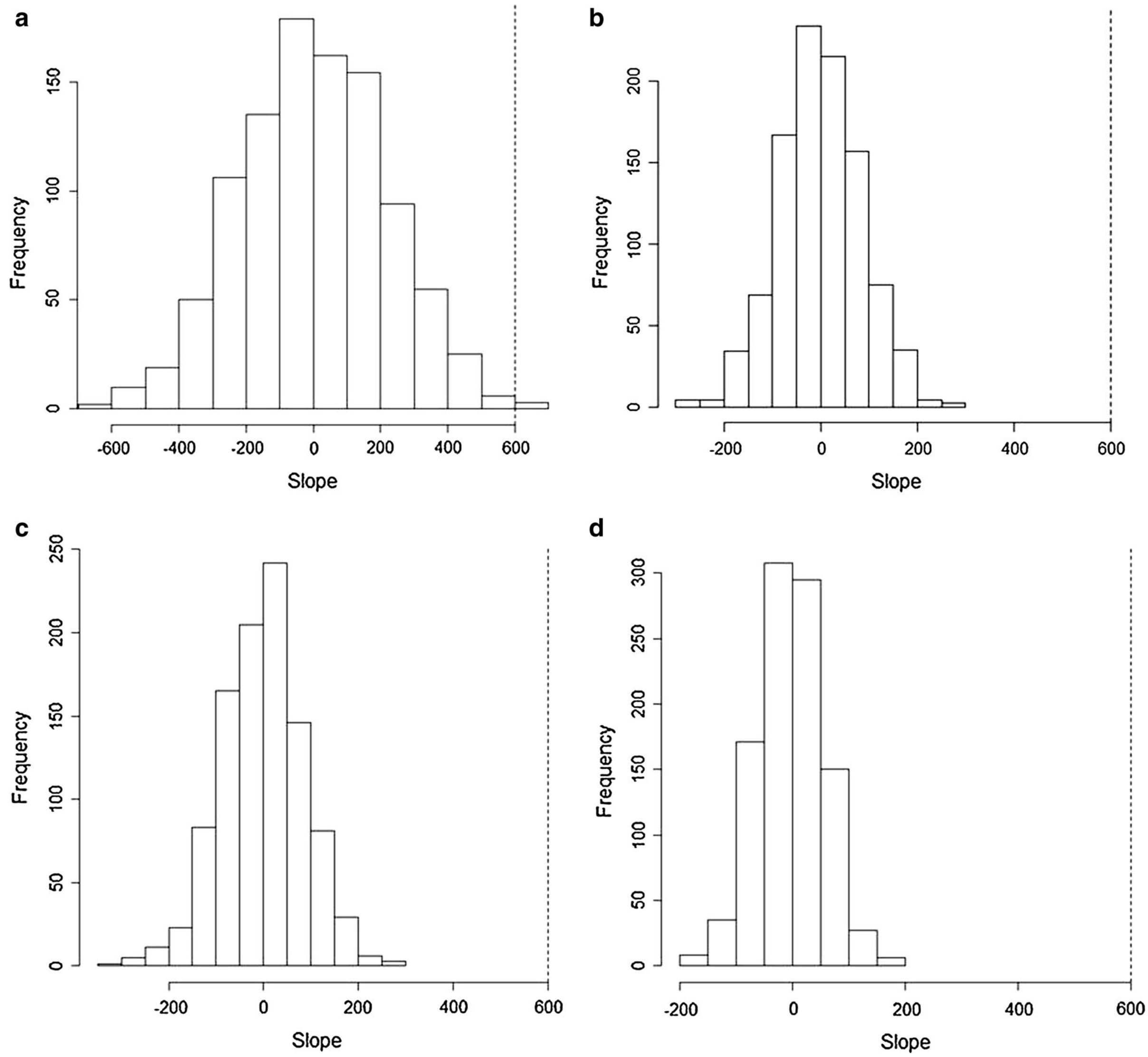


**Fig. 4** Frequency distributions of randomly distributed slopes for a simulated clustered distribution of elephants (r = 0.006) at different sampling intensities **a** 3 %, **b** 10 %, **c** 20 % and **d** 40 %. *Dotted line* represents actual slope calculated for aerial survey over total study area

evident from the large standard errors around the mean), we can be certain about the estimated trend in population numbers. From past and current surveys in this area it appears that the elephant population is increasing at a fast rate of 9.5 % per year. Rapid population increases have been found in elephant populations throughout Africa. For example, population growth rates as high as 13.3 % per year have been reported in Addo National Park, South Africa (Whitehouse and Hall-Martin 2000), > 11 % in Amboseli National Park, Kenya (Moss 2001), 10 % in Hwange National Park, Zimbabwe (Dudley et al. 2001) and 7.1 % in Tarangire National Park, Tanzania (Foley and Faust 2010). Such rapid population growth has been attributed to a number of environmental and social factors such as high rainfall, low population density, high resource availability and release from stresses such as poaching and drought (Dudley et al. 2001; Moss 2001; Trimble et al. 2009; Foley and Faust 2010). Severe droughts were recorded throughout much of southern Africa during 1981–1984 and 1992–1995 (Walker et al. 1987), which caused a lot of drought related mortality of elephant in the region (Dudley et al. 2001). Therefore, one explanation for the high population growth rates we are seeing in the Okavango Delta Panhandle could be a response to such declines before 1996.

Rates of increases in closed populations, however, even with unlimited resources, depend on the structure of the population. For example, a population composed largely of adult females will have a higher rate of increase than one with many young non-breeders. To fully understand the dynamics of the eastern Panhandle elephant population we would need to gain a greater understanding of the survival and productivity rates of the population (Milner-Gulland and Rowcliffe 2007). Demographic fluctuations in elephant populations can result from variations in conception rate, prenatal survival, first year survival and cumulative juvenile survivorship (Trimble et al. 2009), which can be affected by environmental conditions and often show intra- and inter-population differences (van Aarde and Jackson 2007). Evidently, further investigations into elephant population dynamics and recruitment rates are needed in our study area either from direct observations or indirect techniques such as aerial survey photos to truly understand the drivers of change in numbers.

Another explanation for the large annual increases in elephant numbers in the Panhandle, could indicate that elephants are entering the population through immigration (as well as birth) from other areas of the elephant range with little emigration out of the area (and few deaths). For example, Calef's (1988) calculated maximum rate of increase is based on a population with a stable age structure and does not include other demographic rates that also contribute to changes in population size, such as immigration and emigration (Milner-Gulland and Rowcliffe 2007). To determine if this process is responsible for the population changes, we would need to be able to incorporate extrinsic parameters such as immigration and emigration into a population dynamical model. However, in such a wide ranging population it would be difficult to make direct observations and distinguish immigrants from established individuals making it difficult to estimate the rate of immigration (Abadi et al. 2010). If we had a better understanding of immigration and emigration rates, we would however, be able to identify what the Okavango Delta Panhandle elephant population's role is in the larger population of the Kavango region, such as whether it is a source or a sink population (Pulliam 1988; Thomas and Kunin 1999). Satellite telemetry studies are currently underway to start investigating this further and understand what is influencing elephant movements in the area.

If elephants are moving into the Panhandle from surrounding areas, one fundamental question is why? What is attracting elephants to the Panhandle or alternatively deterring elephants from other areas? One explanation could be that elephants are coming from Namibia (if they can cross the fence), possibly to move away from human disturbance in the Caprivi region (Chase and Griffin 2009). However, from a review of population estimates in the Caprivi over the past 20 years there does not appear to be a pattern of population fluctuations between the Panhandle and the Caprivi. Yet, if we review population estimates from the Okavango Delta (south of the northern buffalo fence), there is a clear pattern of Okavango Delta numbers decreasing where Okavango Panhandle numbers increase and vice versa (see Appendices 5, 6). From past survey estimates, it appears that elephant numbers decreased in 2002 and 2005 in the Panhandle concurrently with population increases in these years in the delta, while in 2004 and 2006 numbers increased in the Panhandle and decreased in the delta. Possible explanations for elephants moving from the Delta to the Panhandle could be to access certain food, water and mineral resources or in response to disturbance from past hunting concessions south of the buffalo fence (Blanc et al. 2007). Surface-water availability was found to be a key driver of elephant distribution in Zimbabwe (Chamaille-Jammes et al. 2007), so elephants may be moving to access the main Okavango River in the Panhandle. Several studies have also linked elephant movements with vegetation type and density (Merz 1986; Barnes et al. 1991; Verlinden and Gavor 1998), so it may be that elephants are migrating in search of certain food types including seasonal fruits (White 1994) or moving away from areas where elephant densities are higher i.e. Chobe National Park due to impacts of high elephant density on woody vegetation (Cassidy et al. 2013; Rutina and Moe 2014).

The carcass ratio (the proportion of dead elephants to all dead and alive elephants) results for this study area support the explanation of low emigration rates and possible immigration of live elephants into the population as a driver of high rates of population increase. Low carcass ratios in the eastern Panhandle (2 %) indicate relative elephant mortality is low. Douglas-Hamilton and Burrill (1991) model for determining population trends, therefore, predicts that a population with such low mortality could be increasing at a rate of 17.9 % (95 % CI: 7.4–29.4 %) per year. Our estimated population increase falls within the 95 % CI of this predicted range. A low carcass ratio may indicate a low mortality rate, or it may be low as a result of low emigration rates and more live elephants entering the population through immigration (Douglas-Hamilton and Burrill 1991). Survival among adult elephants is high (Owen-Smith 1988) and elephants have few natural predators [apart from young occasionally being hunted by lion (*Panthera leo*) or hyeana (*Crocuta crocuta*)]. The highest cause of mortality in elephant populations is, therefore, either human induced (Eltringham 1982) or through malnutrition during periods of drought (Walker et al. 1987; Dudley et al. 2001; van Aarde and Jackson 2007). Currently, there are no legal elephant hunting quotas (community or commercial) in the wildlife management areas of the eastern Okavango Delta Panhandle, so human induced elephant mortality is limited to problem animal control activities in this area. Poaching levels are also considerably lower than neighbouring countries, owing to strict policy and legislation implementation and an effective anti-poaching unit in the Botswana Defence Force. No incidents of drought related mortality have been recorded in the Panhandle recently either, which could also explain the low carcass ratios.

Despite the increase in elephant numbers in the Panhandle, there was no statistically significant relationship between elephant numbers or elephant density and crop-raiding incidents per year. In Zimbabwe, however, Hoare (1999) found that elephant density was significantly (but weakly) correlated to the number of problem elephant incidents. This difference could be attributed to different contributing factors associated with different study sites or it may be due to the spatial scale used for analysis. Hoare (1999) calculated elephant density and problem elephant incidents per ward rather than for the whole study area. Our results found no correlation between crop-raiding incidents and elephant numbers or density. This correlation is, however, difficult to make when survey estimate precision is low as a result of low survey intensity. A survey of community perception of HEC in this area (Songhurst 2012) revealed that many people believe their problems with elephants are being intensified because the elephant population is increasing, therefore despite the lack of correlation between crop-raiding incidents and population numbers, it is still evident that an increasing elephant population is exacerbating the full extent of HEC.

## Management implications

The management of burgeoning elephant populations in some southern African countries (such as Botswana) and resulting conflicts with humans living on the edge of wetlands and expanding elephant ranges, are important conservation issues. The ability to reliably estimate population numbers, trends and densities of elephants has, therefore, a very important role in helping to guide effective and appropriate wetland conservation and management. Our simulations have provided a viable and cost-effective method to plan efficient aerial surveys. Our findings have implications for the management of elephants in the Okavango Delta Panhandle, and call upon, for example, the serious consideration of fence realignments to effect the objectives of the KAZA TFCA initiative and relieve the regions elephant population pressure. With an increasing elephant population and an expanding human population in the Panhandle requiring more land for agricultural uses, incidents of HEC are widespread. Failure to recognise the importance of connectivity of the elephant population in the Panhandle to the Okavango on a daily basis puts, for example, serious pressure on critical movement corridors as a result of agricultural expansion and habitat conversion (Songhurst et al. in press). Failure to protect these critical habitats for elephant will certainly exacerbate HEC in the Okavango region. It is also imperative to understand why the elephant population numbers are increasing in order to design appropriate management strategies to address both population pressures and HEC. If elephants are migrating into the Panhandle when the fences are damaged, then once fences are repaired this could be effectively trapping elephants within this area. In this scenario, an effective management intervention would be to remove or realign the fences to allow free migration from the Okavango Delta into the Kwando and Linyanti wetlands. This management decision would also alleviate ecological and HEC pressures if the population is increasing rapidly because of low mortality in the area. Further research on the population dynamics and movements of elephants is on going in this area, under the Ecoexist Project, data from which will help us differentiate between the two possible causes of elephant population increases identified in this paper and will also help determine the kind of management decisions that should be taken to address future elephant population management.

**Acknowledgments** We thank the Botswana Ministry of Environment, Wildlife and Tourism, and the Namibian Ministry of Environment for granting permission for these surveys to take place and we are grateful to the Botswana Defence Force for granting permission for allowing the surveys to cross the international border between Botswana and Namibia. We are sincerely thankful to the Wildlife Conservation Society, Wilderness Wildlife Trust and Elephants Without Borders who provided funding for the survey. Thank you to the surveying team, including K. Landen for her observer skills and photo-correction analysis, and to the pilots namely A. Parnass and M. Holding for providing both their planes and piloting services to the project.

## Appendix 1

See Table 3.

**Table 3** Herd number, type and mean herd size by observer on strip transects

| Observer | Year | No. herds observed | No. un-class. herds | No. bull herds | No. family groups | X bull herd size (SE) | X family herd size (SE) |
|---|---|---|---|---|---|---|---|
| L | 2008 | 143 | 3 | 62 | 52 | 3.03 (0.4) | 11.59 (0.8) |
| L | 2010 | 173 | 0 | 82 | 91 | 2.17 (0.26) | 14.74 (1.36) |
| R | 2008 | 121 | 4 | 65 | 78 | 2.54 (0.3) | 11.98 (1.2) |
| R | 2010 | 158 | 0 | 70 | 88 | 2.3 (0.3) | 12.4 (1.35) |
| L/R | 2008 | 1 | 0 | 0 | 1 | – | – |
| Both | 2008 | 265 | 7 | 127 | 131 | 2.8 (0.3) | 11.8 (0.7) |
| Both | 2010 | 331 | 0 | 152 | 179 | 2.23 (0.2) | 13.59 (0.96) |

## Appendix 2

See Table 4.

**Table 4** Estimates of elephant numbers in the eastern Okavango Panhandle by block/strata, 1996–2010

| Source | Block/strata | Year | Area | No. animals observed | Population estimate | SE | 95% range | $t$ | 95% CI | 95% CI as % estimate | Density | Strip width | Transect space | Sampling intensity (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DWNP (1996) | Total | 1996 | 9835 | 114 | 3782 | 2021 | 114–8131 | 2.15 | 4349 | 115 | 0.384 | 400 | 12 | 3.01 |
| DWNP (1999) | Total | 1999 (Wet) | 9835 | 222 | 7353 | 3243 | 368–14,338 | 2.15 | 6985 | 95 | 0.748 | 400 | 12 | 3.02 |
| DWNP (1999) | Total | 1999 (Dry) | 9835 | 126 | 3886 | 2647 | 126–9598 | 2.16 | 5712 | 147 | 0.395 | 400 | 12 | 3.24 |
| DWNP (2001) | Total | 2001 | 9919 | 458 | 13,173 | 6355 | 458–26,873 | 1.04 | 13,700 | 104 | 1.328 | 400 | 12 | 3.48 |
| DWNP (2002) | Total | 2002 | 9919 | 218 | 6660 | 2681 | 866–12,454 | 0.87 | 5794 | | 0.671 | 400 | 12 | 3.27 |
| DWNP (2003) | Total | 2003 | 9919 | 211 | 5261 | 2393 | 211–10,417 | 0.98 | 5156 | 98 | 0.53 | 400 | 12 | 4.01 |
| DWNP (2004) | Total | 2004 | 9841 | 447 | 11,870 | 4151 | 2849–20,891 | 0.76 | 9021 | 76 | 1.206 | 400 | 12 | 3.77 |
| DWNP (2005) | Total | 2005 | 9142 | 177 | 5088 | 2440 | 177–10,380 | 1.04 | 5292 | 104 | 0.557 | 400 | 12 | 3.48 |
| DWNP (2006) | Total | 2006 | 9919 | 280 | 9212 | 3556 | 1566–16,858 | 0.83 | 7646 | 83 | 0.929 | 400 | 12 | 3.04 |
| Songhurst (2012) | Total | 2008 | 9732 | 1927 | 9963 | 1170 | 7642–12,284 | 1.984 | 2321 | 23.3 | 1.14 | 500 | 3.2 | 19.7 |
| Songhurst (2012) | Total | 2010 | 9732 | 2771 | 15,027 | 2008 | 11,043–19,011 | 1.984 | 3984 | 25.7 | 1.72 | 500 | 3.2 | 19.2 |
| Jackson et al. (2008) | NG11 | 2003 (Dry) | 5952 | 1806 | 3579 | 604 | 2373–4785 | 1.997 | 1206 | 33.7 | 0.71 | 800 | 2 | 40 |
| Jackson et al. (2008) | NG11 | 2004 (Wet) | 5280 | 456 | 1060 | 250 | 561–1559 | 1.997 | 499 | 47 | 0.21 | 800 | 2 | 40 |
| Songhurst (2012) | NG11 | 2008 | 5140 | 1555 | 6383 | 846 | 4692–8074 | 1.999 | 1691 | 26.5 | 1.24 | 500 | 2 | 23.7 |
| Songhurst (2012) | NG11 | 2010 | 5140 | 1800 | 7580 | 1120 | 5346–9824 | 1.999 | 2239 | 29.5 | 1.47 | 500 | 2 | 23.1 |
| Songhurst (2012) | NG12 | 2008 | 1092 | 270 | 1303 | 292 | 700–1906 | 2.064 | 603 | 46.2 | 1.19 | 500 | 2.5 | 18.6 |
| Songhurst (2012) | NG12 | 2010 | 1092 | 593 | 2937 | 1054 | 762–5112 | 2.064 | 2175 | 74 | 2.69 | 500 | 2.5 | 18.1 |
| Songhurst (2012) | NG13 | 2008 | 2500 | 102 | 1219 | 425 | 293–2145 | 2.179 | 926 | 75.9 | 0.49 | 500 | 5 | 10.3 |
| Songhurst (2012) | NG13 | 2010 | 2500 | 378 | 4591 | 1253 | 1861–7321 | 2.179 | 2730 | 59.4 | 1.84 | 500 | 5 | 10 |
| Songhurst (2012) | Cumulative total | 2008 | 8732 | 1927 | 8905 | – | – | – | – | – | 1.02 | 500 | 3.2 | 19.7 |
| Songhurst (2012) | Cumulative total | 2010 | 8732 | 2771 | 15,429 | – | – | – | – | – | 1.73 | 500 | 3.2 | 19.2 |

## Appendix 3

See Fig. 5.

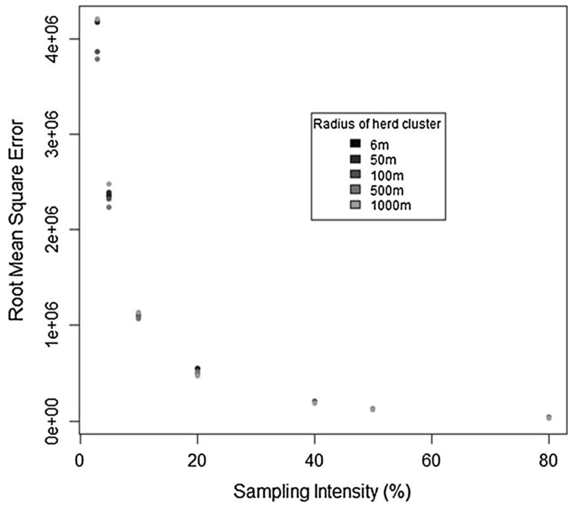


**Fig. 5** Plot showing root mean square errors at different sampling intensities, different shades represent varying degrees of spatial clustering in elephant distribution (radius of herd)

## Appendix 4

See Table 5.

**Table 5** Population estimates within the potential elephant range of the Okavango Panhandle population, including the Okavango Delta, the West Caprivi and South East Angola

| Year | Population Okavango Panhandle | Population Okavango Delta | Source | Population West Caprivi | Source | Population SE Angola | Source |
|---|---|---|---|---|---|---|---|
| 1987 | – | – | – | 1037 | Rodwell et al. (1994) | – | – |
| 1988 | – | – | – | – | – | – | – |
| 1989 | – | – | – | 902 | Rodwell et al. (1994) | – | – |
| 1990 | – | – | – | – | | – | – |
| 1991 | – | – | – | – | | – | – |
| 1992 | – | – | – | – | | – | – |
| 1993 | – | – | – | 4332 | Rodwell et al. (1994) | – | – |
| 1994 | – | – | – | 4733 | Rodwell et al. (1994) | – | – |
| 1995 | – | – | – | – | | – | – |
| 1996 | 3782 | 26,795 | DWNP (1996) | – | | – | – |
| 1997 | – | – | – | – | | – | – |
| 1998 | – | – | – | 3068 | Craig (1998) | – | – |

**Table 5** continued

| Year | Population Okavango Panhandle | Population Okavango Delta | Source | Population West Caprivi | Source | Population SE Angola | Source |
|---|---|---|---|---|---|---|---|
| 1999 | 7353 (Wet) | 30,971 | – | – | – | – | – |
| | 3886 (Dry) | | DWNP (1999) | | – | | – |
| 2000 | – | – | – | – | | – | |
| 2001 | 13,173 | 18,175 | DWNP (2001) | – | – | 126 | Chase and Griffin (2009) |
| 2002 | 6660 | 28,550 | DWNP (2002) | – | | – | – |
| 2003 | 5261 | 19,079 | DWNP (2003) | 4136 | Chase and Griffin (2003) | 350 | Chase and Griffin (2003) |
| 2004 | 11,870 | 27,917 | DWNP (2004) | 4868 | (MET 2004) | – | – |
| 2005 | 5088 | 37,351 | DWNP (2005) | 3456 | Chase and Griffin (2009) | 1550 (Dry)<br>2030 (Wet) | Chase and Griffin (2006) |
| 2006 | 9212 | 31,191 | DWNP (2006) | 4332 | Chase and Griffin (2006) | – | – |
| 2007 | – | – | – | – | – | – | – |
| 2008 | 8905 | – | This study | 4136 | MET (2008) | 7500 | Chase and Griffin (2009) |
| 2009 | – | – | – | – | – | – | – |
| 2010 | 15,113 | – | This study | – | – | – | – |

## Appendix 5

See Fig. 6.

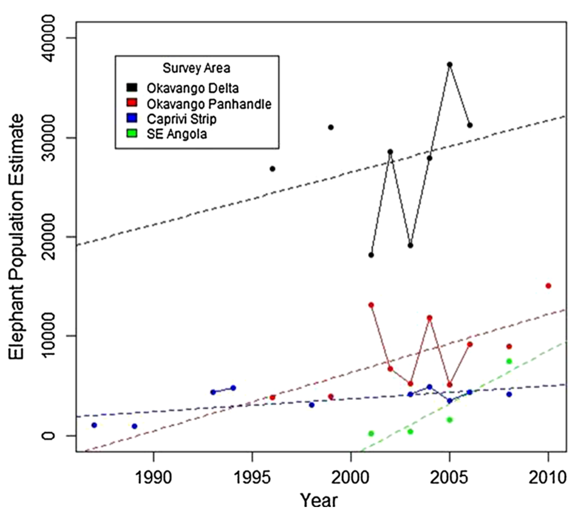


**Fig. 6** Population estimates from the Okavango Delta, Okavango Panhandle, West Caprivi and South East Angola, (see Appendix 4 for data used)

## References


Abadi F, Gimenez O, Ullrich B, Arlettaz R, Schaub M (2010) Estimation of immigration rate using integrated population models. J Appl Ecol 47:393–400

Anon (2012) Strategic environmental assessment for the Okavango delta ramsar site (ODRS). Department of Environmental Affairs and SAREP, Gaborone

Baddeley A, Turner R (2010) Spatstat 'Package': spatial point pattern analysis, model fitting, simulation, tests. CRAN

Barnes RFW, Barnes KL, Alders M, Blom A (1991) Man determines distribution of elephants in the rainforest of north-eastern Gabon. Afr J Ecol 29:54–63

Baumgartener MF (1997) The distribution of risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. Mar Mamm Sci 13:614–638

Blanc JJ, Barnes RFW, Craig GC, Dublin HT, Thouless CR, Douglas-Hamilton I, Hart JA (2007) African elephant status report 2007. Occasional paper series of the International Union for Conservation of Nature Species Survival Commission. African Elephant Specialist Group IUCN, Gland

Booth VR, Dunham KM (2014) Elephant poaching in Niassa Reserve, Mozambique: population impact revealed by combined survey trends for live elephants and carcasses. Oryx. doi:10.1017/S0030605314000568

Buckland ST, Anderson DR, Burnham KP, Laake JL (1993) Distance sampling: estimating abundance of biological populations. Chapman & Hall, London

Calef GW (1988) Maximum rate of increase in the African Elephant. Afr J Ecol 26:323–327

Cassidy L, Fynn R, Bongani S (2013) Effects of restriction of wild herbivore movement on woody and herbaceous vegetation in the Okavango Delta Botswana. Afr J Ecol 51(4):513–527

Caughley G (1974) Bias in aerial surveys. J Wildl Manag 38:921–933

Caughley G, Grigg GC (1981) Surveys of the distribution and density of kangaroos in the Pastoral Zone of South Australia, and their bearing on the feasibility of aerial surveys in large and remote areas. Aust Wildl Res 8:1–11

Chamaille-Jammes S, Valeix M, Fritz H (2007) Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. J Appl Ecol 44:625–633

Chase MJ (2007) Home ranges, transboundary movements and harvest of elephants in northern Botswana and factors affecting elephant distribution and abundance in the Lower Kwando River Basin. PhD, University of Massachusetts

Chase M (2011) Dry season fixed-wing aerial survey of elephants and wildlife in Northern Botswana, September–November 2010. Elephants Without Borders, Kasane

Chase MJ, Griffin CR (2003) Ecology, population structure and movements of elephant populations in northern Botswana. Conservation International, Kasane

Chase MJ, Griffin CR (2006) Elephant distribution and abundance in the Lower Kwando River Basin and West Caprivi. Final report. US Wildlife and Fisheries, Kasane

Chase MJ, Griffin CR (2009) Elephants caught in the middle: impacts of war, fences and people on elephant distribution and abundance in the Caprivi Strip, Namibia. Afr J Ecol 47:223–233

Craig GC (1998) Aerial survey of northern Namibia. Ministry of Environment and Tourism, Windhoek

Crawley M (2007) The R book. Wiley, Chichester

Douglas-Hamilton I, Burrill A (1991) Using elephant carcass ratios to determine population trends. Afr Wildl Res Manag 1:98–105

Dudley JP, Craig GC, Gibson D, Haynes G, Klimowicz J (2001) Drought mortality of bush elephants in Hwange National Park, Zimbabwe. Afr J Ecol 39:187–194

DWNP (1996) Aerial census of wildlife and some domestic animals in Botswana. Dry season report. Department of Wildlife and National Parks, Government of Botswana, Gaborone

DWNP (1999) Aerial census of wildlife and some domestic animals in Botswana. Dry and wet season report. Department of Wildlife and National Parks, Government of Botswana, Gaborone

DWNP (2001) Aerial census of wildlife and some domestic animals in Botswana. Dry season report. Department of Wildlife and National Parks, Government of Botswana, Gaborone

DWNP (2002) Aerial census of wildlife and some domestic animals in Botswana. Dry season report. Department of Wildlife and National Parks, Government of Botswana, Gaborone

DWNP (2003) Aerial census of wildlife and some domestic animals in Botswana. Dry season report. Department of Wildlife and National Parks, Government of Botswana, Gaborone

DWNP (2004) Aerial census of wildlife and some domestic animals in Botswana. Dry season report. Department of Wildlife and National Parks, Government of Botswana, Gaborone

DWNP (2005) Aerial census of wildlife and some domestic animals in Botswana. Department of Wildlife and National Parks, Government of Botswana, Gaborone

DWNP (2006) Aerial census of wildlife and some domestic animals in Botswana. Department of Wildlife and National Parks, Government of Botswana, Gaborone

Elphick CS (2008) How you count counts: the importance of methods research in applied ecology. J Appl Ecol 45:1313–1320

Eltringham SK (1982) Elephants. Blandford Books Ltd., Poole

Eltringham SK (1991) The illustrated encyclopaedia of elephants: from their origins and evolution to their ceremonial and working relationship with man. Salamander, London

Ferreira SM, van Aarde RJ (2009) Aerial survey intensity as a determinant of estimates of African elephant population sizes and trends. South Afr J Wildl Res 39:181–191

Foley CAH, Faust LJ (2010) Rapid population growth in an elephant *Loxodonta africana* population recovering from poaching in Tarangire National Park, Tanzania. Oryx 44:205–212

Gumbricht T, Wolski P, Frost P, McCarthy TS (2004) Forecasting the spatial extent of the annual flood in the Okavango delta, Botswana. J Hydrol 290:178–191

Hargrove JW, Borland CH (1994) Pooled population parameter estimates from Mark-recapture data. Biometrics 50:1129–1141

Hoare RE (1999) Determinants of human–elephant conflict in a land-use mosaic. J Appl Ecol 36:689–700

Hone J (2008) On bias, precision and accuracy in wildlife aerial surveys. Wildl Res 35:253–257

Jachman H (2002) Comparison of aerial counts with ground counts for large African herbivores. J Appl Ecol 39:841–852

Jackson TP, Mosojane S, Ferreira SM, Aarde RJV (2008) Solutions for elephant *Loxodonta africana* crop raiding in northern Botswana: moving away from symptomatic approaches. Oryx 42:83–91

Jolly GM (1965) Explicit estimates from capture–recapture data with both death and immigration—stochastic model. Biometrika 52:225–247

Jolly JM (1969) Sampling methods for aerial censuses of wildlife populations. East Afr Agric For J 34:46–49

Khaemba WM, Stein A, Rasch D, de Leeuw J, Georgiadis N (2001) Empirically simulated study to compare and validate sampling methods used in aerial surveys of wildlife populations. Afr J Ecol 39:374–382

Laake J, Dawson MJ, Hone J (2008) Visibility bias in aerial survey: mark-recapture, line-transect or both? Wildl Res 35:299–309

Marsh H, Sinclair DF (1989) Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. J Wildl Manag 53:1017–1024

Marsh H, Harris ANM, Lawler IR (1997) The sustainability of the indigenous Dugong fishery in Torres Strait, Australia/Papua New Guinea. Conserv Biol 11:1375–1386

Marsh H, Lawler IR, Kwan D, Delean S, Pollock K, Alldredge M (2004) Aerial surveys and the potential biological removal technique indicate that the Torres Strait dugong fishery is unsustainable. Anim Conserv 7:435–443

Matérn B (1986) Spatial variation. Springer, New York

McIntosh TE, Rosatte RC, Hamr J, Murray DL (2009) Development of a sightability model for low-density elk populations in Ontario, Canada. J Wildl Manag 73:580–585

Mendelsohn J, El Obeid S (2004) Okavango River: the flow of a lifeline. Struik, Cape Town

Merz G (1986) Movement patterns and group size of the African forest elephant (*Loxodonta africana cyclotis*) in the Tai National Park, Ivory Coast. Afr J Ecol 24:133–136

MET (2008) Aerial survey of north east Namibia. Ministry of Environment and Tourism (MET), Namibian Government, Windhoek

MET, M.o.E.a.T. (2004) Aerial survey of north east Namibia, 11 August–19 September 2005. Ministry of Environment and Tourism, Windhoek

Milner-Gulland EJ, Rowcliffe JM (2007) Conservation and sustainable use: a handbook of techniques. Oxford University Press, Oxford

Mosepele K, Moyle PB, Merron GS, Purkey DR, Mosepele B (2009) Fish, floods, and ecosystem engineers: aquatic conservation in the Okavango Delta, Botswana. Bioscience 59:53–64

Moss C (1988) Elephant memories. Morrow, New York

Moss C (1996) Getting to know a population. In: Kangwana KF (ed) Studying elephants. African Wildlife Foundation, Nairobi, pp 58–74

Moss C (2001) The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. J Zool London 255:145–156

Moss CJ, Poole JH (1983) Relationships and social structure in African elephants. In: Hinde RA (ed) Primate social relationships. Blackwell Scientific, Oxford, pp 315–325

Norton-Griffiths M (1978) Counting animals. African Wildlife Leadership Foundation, Nairobi

Owen-Smith N (1988) Megaherbivores. The influence of very large body size on ecology. Cambridge University Press, Cambridge

Pearse AT, Reinecke KJ, Dinsmore SJ, Kaminski RM (2009) Using simulation to improve wildlife surveys: wintering mallards in Mississippi, USA. Wildl Res 36:279–288

Pollock KH, Marsh HD, Lawler IR, Alldredge MW (2006) Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. J Wildl Manag 70:255–262

Pulliam HR (1988) Sources, sinks and population regulation. Am Nat 132:652–661

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Redfern JV, Viljoen PC, Kruger JM, Getz WM (2002) Biases in estimating population size from an aerial census: a case study in the Kruger National Park, South Africa. South Afr J Sci 98:455–460

Rivest LP, Potvin F, Crepeau H, Daigle G (1995) Statistical methods for aerial surveys using double-count technique to correct for visibility bias. Biometrics 51:461–470

Rodwell TC, Tagg J, Grobler M (1994) Wildlife resources in the Caprivi, Namibia: the results of an aerial census in 1994 in comparison with past surveys. Ministry of Environment and Tourism, Windhoek

Rutina LP, Moe SR (2014) Elephant (*Loxodonta africana*) disturbance to Riparian Woodland: effects on tree-species richness, diversity and functional redundancy. Ecosystems 17:1384–1396

Samuel MD, Pollock KH (1981) Correction of visibility bias in aerial surveys where animals occur in groups. J Wildl Manag 45:993–997

Songhurst A (2012) Competition between people and elephants in the Okavango Delta Panhandle, Botswana. Ph.D., Imperial College

Songhurst A, McCulloch G, Coulson T (in press) Finding pathways to human–wildlife coexistence—a risky business. Oryx

Southwell C, Low M (2009) Black and white or shades of grey? Detectability of Adelie penguins during shipboard surveys in the Antartic pack-ice. J Appl Ecol 46:136–143

Stein A, Georgiadis N (2006) Spatial marked point patterns for herd dispersion in a Savanna wildlife herbivore community in Kenya. In: Baddeley A, Gregori P, Mateu J, Stoica R, Stoyan D (eds) Case studies in spatial point process modelling. Springer, Berlin, pp 261–273

Tawana Land Board (2005) Land use plan for Ngamiland. Tawana Land Board, Maun

Thomas CD, Kunin WE (1999) The spatial structure of populations. J Anim Ecol 68:647–657

Trimble MJ, Ferreira S, van Aarde RJ (2009) Drivers of megaherbivore demographic fluctuations: inference from elephants. J Zool 279(1):18–26

van Aarde RJ, Jackson TP (2007) Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. Biol Conserv 134:289–297

Verlinden A, Gavor IKN (1998) Satellite tracking of elephants in northern Botswana. Afr J Ecol 36:105–116

Walker BH, Emslie RH, Owen-Smith RN, Scholes RJ (1987) To cull or not to cull: lessons from a southern African drought. J Appl Ecol 24:381–401

White LJT (1994) Biomass of rain forest mammals in the Lope Reserve, Gabon. J Anim Ecol 63:499–512

Whitehouse AM, Hall-Martin AJ (2000) Elephants in Addo Elephant National Park, South Africa: reconstruction of the population's history. Oryx 34:46–55

Wittemyer G (2001) The elephant population of Samburu and Buffalo Springs National Reserves, Kenya. Afr J Ecol 39:357–365

Wright IE, Reynolds JE, Ackermann BB, Ward LI, Weigle BL, Szelistowski WA (2002) Trends in manatee (*Trichechus manatus latirostris*) counts and habitat use in Tampa Bay 1987–1994: implications for conservation. Mar Mamm Sci 18:259–274