Seasonal Abundance and Distribution of Elephants in Sioma Ngwezi National Park, southwest Zambia

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Abstract

We conducted wet (January 2004) and dry (August 2004 and October 2005) season aerial surveys of African elephants (*Loxodonta africana*) in Sioma Ngwezi National Park (NP) in southwest Zambia. Most elephant herds occurred in the centre and northern portions of the park during the wet season when water was available in seasonal pans. During the two dry season surveys, most herds were scattered across the northern portion of the park with only a few herds in the southwest corner of the park < 6.5 km of the Kwando River. The average bull herd size was smaller for the wet season than for the two dry season surveys, while family group sizes did not differ among the three surveys. We estimated 1099 elephants (23 herds) for the 4322 km² park in the January 2004 wet season survey, 899 elephants (25 herds) in the August 2004 dry season survey and 385 elephants (nine herds) in the October 2005 dry season survey. Based upon earlier reports of elephant numbers, we believe that elephant populations were greatly reduced in the park during the Angolan Civil War in the 1990s, but our survey results suggest that elephants have recolonized the park, and telemetry studies indicate that elephants readily move between the park, southeastern Angola, the West and East Caprivi Strip in Namibia, and northern Botswana. However, several human-associated factors may still affect elephant numbers in the park and community-based conservation programmes are needed to promote the conservation of wildlife habitats, elephants and other wildlife in the region.

Key words: aerial surveys, Angola, Caprivi Strip, civil war, community-based conservation programmes, fires, herd size, human settlements, Kwando River, movements, strip transects, telemetry, veterinary fences, Western Zambezi Game Management Area

Résumé

Nous avons mené une étude aérienne des éléphants africains (*Loxodonta africana*) pendant la saison pluvieuse (janvier 2004) et la saison sèche (août 2004 et octobre 2005) au Parc National Sioma Ngwezi au sud-ouest de la Zambie. On a trouvé la plupart des troupeaux d'éléphant dans les parties centre et nord du parc pendant la saison pluvieuse quand l'eau était disponible dans les mares saisonnières. Au cours des deux études de la saison sèche, la plupart des troupeaux étaient éparpillés dans la partie nord du parc avec seulement quelques troupeaux dans le coin sud-ouest du parc <6.5 kms de la Rivière Kwando. La taille moyenne du troupeau des mâles était plus petite pour la saison pluvieuse que pour les deux études de la saison sèche, alors que la taille des groupes familiaux n'a pas différé entre les trois études. Nous avons estimé 1099 éléphants (23 troupeaux) pour les 4322 km² de parc dans l'étude de la saison pluvieuse du mois de janvier 2004, 899 éléphants (25 troupeaux) dans l'étude de la saison sèche du mois d'août 2004, et 385 éléphants (9 troupeaux) dans l'étude de la saison sèche du mois d'octobre 2005. En se basant sur les rapports précédents du nombre des éléphants, nous croyons que leurs populations ont été largement réduites dans le parc pendant la guerre civile angolaise dans les années 1990, mais les résultats de notre étude suggèrent que les éléphants ont recolonisé le parc, et

les études de télémétrie indiquent que les éléphants se déplacent aisément entre le parc, le sud-est de l'Angola, l'ouest et l'est de la Bande de Caprivi en Namibie, et le nord du Botswana. Cependant, des facteurs anthropiques peuvent encore affecter le nombre d'éléphants dans le parc, et on a besoin de programmes communautaires de conservation pour promouvoir la conservation des habitats de la faune, des éléphants et des autres animaux dans la région.

Introduction

The 25-year long Angolan Civil War and illegal hunting devastated elephant and other wildlife populations in Sioma Ngwezi NP, southwest Zambia (Muleta et al. 1996; Simasiku et al. 1996; Turpie et al. 1999; Vetter 2001; Hoare 2004). The park's proximity to the Luiana Partial Reserve (PR) across the border in southeast Angola, the base of military operations for UNITA, exposed the wildlife of Sioma Ngwezi NP to extensive poaching. Elephant ivory and rhino horn were used by UNITA to pay for arms and meat to feed its soldiers (Kumleben 1996). Refugees also depended heavily on bush meat to survive (Simasiku et al. 1996). Yet, the full impact of the Angolan Civil War on the elephants of Sioma Ngwezi NP is uncertain because there are few reliable estimates of the park's elephant population. In December 1991, Tembo (1995) reported 1187 elephants from aerial surveys of the park. Yet, by 1996–97, Larry Patterson (pers. comm. 2006) reported seeing few elephants in the park from his limited aerial survey. In 2004, the African Parks Company terminated its agreement with the Zambia Wildlife Authority to manage the park based in part on the scarcity of wildlife in the park. The purpose of this study was to provide historic and current information on the abundance and distribution of elephant and other wildlife populations in Sioma Ngwezi NP.

Study Area

Sioma Ngwezi NP, situated in the southwest corner of Zambia, is one of Zambia's most remote and seldom visited parks. The park shares a 62 km border with the Luiana PR in southeast Angola, along the Kwando River, and an 18 km border with the Caprivi Strip of Namibia to the south (Fig. 1). The park encompasses 4322 km² and is surrounded on the east, north and northwest by the Western Zambezi Game Manage-

ment Area (38,070 km²). The park is not fenced and there is no official entry point or tourism infrastructure. The Game Management Area consists of communal lands where hunting is permitted through a licensing system administered by the Zambia Wildlife Authority. However, Muleta et al. (1996) reported that the game management area was now largely devoid of wildlife due to poaching and lack of management, except for wildlife migrating through it towards the Zambezi River.

The park has a tropical savannah climate with three seasons: a hot dry season (August–October), a hot wet season (November–April), and a cool dry season (May–July). Mean annual rainfall ranges from 600 to 800 mm and is strongly concentrated from November to April (Van Gils 1988). The mean maximum temperature is between 27° and 30°C and the mean minimum temperature ranges from 9° to 12°C (Vetter 2001).

The northern part of the park is a complex of open grassy plains dominated by Leptochloa uniflora, Oplismenus hirtellus, Panicum heterostachyum, and Setaria homonyma (Werger and Coetzee 1978). Moving south towards the centre of the park, Baikiaea woodlands dominate (Werger and Coetzee 1978). In the south of the park, Baikiaea plurijuga is dominant, forming dense, dry, semi-deciduous forests with trees up to 20 m in height. Within these forests, there is a dense shrub layer that develops from frequent fires that penetrate the Baikiaea forests and woodlands, especially in the late dry season (Vetter 2001). Along the Kwando River there are extensive, open floodplains and patches of mixed riparian woodlands that occur on seasonally flooded islands and along the river.

There are numerous seasonal pans throughout the park during the wet season (Fig. 1); however, only the Kwando and Zambezi Rivers (25 km east of the park) provide water during the dry season. There are numerous subsistence agricultural settlements within the park along the Kwando River and to a lesser degree, along the eastern and northern borders (Fig. 1).

Methods

Three aerial surveys were flown over the entire park (4322 km²), including one wet season and two dry season surveys. The wet season survey occurred over five days (19–23 January) in 2004 (Jan04), and the dry season surveys took six days (20–25 August) in 2004 (Aug04) and four days (4–7 October) in 2005 (Oct05).

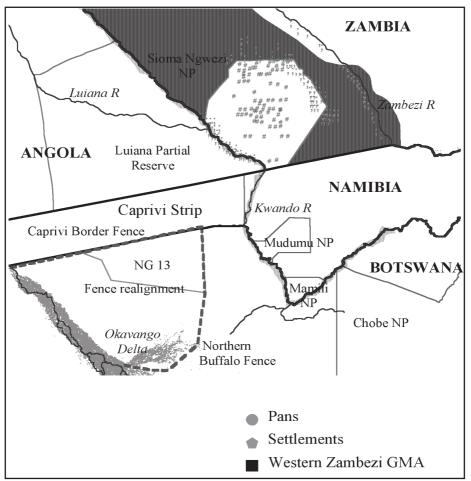


Figure 1. Seasonal pans with water recorded during the January 2004 wet season survey and human settlements recorded on three surveys of Sioma Ngwezi National Park, Zambia.

Prior to flying, all flight transects were mapped as routes on a digital map. We used GPS receivers and DNR Garmin software (Minnesota Department of Natural Resources) to navigate along transects. Transects were systematically flown with a Cessna 182/206 along generally east/west axes, corresponding to the perpendicular gradient of major watercourses.

Using standard methodology for strip transect sampling (Norton–Griffiths 1978), only elephants observed within the interval were counted and recorded when herds were as nearly perpendicular to the plane as possible. Observers kept their eyes at a consistent height, thereby maintaining consistent interval widths for each observation. We recorded numbers of elephants, herd type (bull or family group), GPS waypoint, and height above ground level for each

herd observed. The same two observers were used on the Aug04 and Oct05 surveys (each with >350 hrs of previous survey experience), while one new observer from the Zambia Wildlife Authority with previous aerial survey experience participated in the Jan04 survey. Considering there was little information on other wildlife species in the park, we also recorded observations of other wildlife in addition to elephants (Appendix 1).

For the three surveys, we attached two wands to each of the wing struts of the plane to delineate a 250-m interval for recording elephant observations at an altitude of 91 m. The 250-m strip intervals were calibrated and confirmed prior to flying transects by placing markers on the ground and conducting several flyover tests. Repeated fly—overs across these markers allowed observers to record the distances that

coincided with the two wands, and photos were taken to verify the interval distances. When necessary, the wands were adjusted to provide a 250-m wide strip at 91 m altitude. The aluminium wands were semi-permanently attached to the struts for the duration of each survey.

Our sampling strategy differed between the Jan04 and two subsequent surveys (Aug04 and Oct05). The first transect was randomly chosen within 3 km of the southernmost boundary of the study area (Jan04) or stratum (Aug05, Oct05) (Fig. 2). For the Jan04 survey, transects were spaced between 2 and 5 km apart throughout the park. More transects were concentrated along the Zambia/Namibia border where we expected higher elephant numbers, providing a sampling coverage of 14.4% for the entire park with a search rate of 0.75 km²/min. The same flight transects were flown for the Aug04 and Oct05 surveys, and were systematically spaced 3 km apart within three strata. Strata were arbitrarily delineated to reduce transect lengths to <30 km, thereby reducing observer fatigue, resulting in 11.4%, 13.1%, and 12.2% coverage and 0.83 km²/ min, 0.85 km²/min, and 0.75km²/min search rate for the three strata, respectively from south to north (Fig. 2). All transects were flown at 100 knots, and 91 m above ground level using a radar altimeter. Surveys were flown during the morning hours.

To verify herd size and the sighting of herds within the interval defined by the wands during subsequent analyses, a window-mounted camera was used

on each side of the plane during the Jan04 and Oct05 surveys, but this was not available for the Aug04 survey. Each camera used an 18 mm/20 mm wide-angle lens and camera back with a time code generator. Typically, observers took a picture for each elephant herd >5 in Jan04 and for each elephant observation in Oct05, and a GPS time code and date were recorded to the second for every frame exposed.

Data analyses

Photo-interpretation

Digital images of each herd photographed were interpreted and compared to the observers' counts. This method verified and/or corrected observers' herd counts and the presence of elephants within the strip interval.

Strip transect sampling

Following the guidelines developed by Norton–Griffiths (1978), we adjusted for altitude and calculated abundance estimates for all strata combined. Estimates for an individual stratum were not calculated because the boundaries of strata were arbitrarily delineated for flight logistics, not for any relevant stratification variables. We used the traditional Jolly's Method II for unequal sized sampling units to calculate variance (Jolly 1969). If the lower limit of the confidence interval was less than the actual number of elephants counted within the strip, the latter was used as the lower limit of the 95% range.

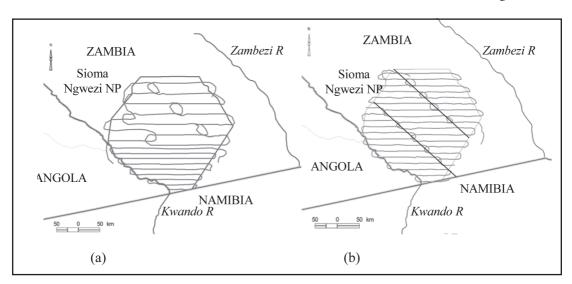


Figure 2. Aerial survey transect flight lines for (a) wet (Jan04) and (b) dry season (Aug04, Oct05) surveys of Sioma Ngwezi National Park, Zambia.

Statistical analyses

ANOVA tests (SYSTAT® 10.2) were used to compare mean bull and family group sizes between the three surveys.

Extent of fires

The aerial extent of fires in the park for the periods July–November in 2004 and 2005 were obtained from the Web Fire Mapper MODIS Rapid Response System. The grids for each year were downloaded into ArcView 3.2, filtered for the five dry season months and plotted.

Results

For the entire 4322 km² survey area, 28 transects were flown in Jan04 (1595 km) and 39 transects in Aug04 (1474 km) and Oct05 (1433 km). Flight altitude averaged 91.34 m (range 85–96 m), 93.6 (range 87–112), and 90.45 (range 82–98) for herd observations, respectively. In Jan04, 23 elephant herds were observed, 25 herds in Aug04, and 9 herds in Oct05.

Elephant distribution

For the Jan04 wet season survey, most of the elephant herds occurred in the centre and northern portions of the park (Fig. 3). Many of these elephants were in close proximity to large seasonal pans with water. Four herds were observed near the northern park boundary. Only two herds were observed near the Kwando River in the southwest corner of the park, 12 km east of the river. We observed no elephants in the centre of the park during our Aug04 dry season survey (Fig. 3) in contrast to the Jan04 wet season survey. In Aug04, most herds were scattered across the northern portion of the park and three herds occurred in the southwest corner of the park within 6.5 km of the Kwando River (Fig. 3). Similarly, in the Oct05 dry season survey, seven of the nine herds seen occurred in the northwest corner of the park, while only two herds occurred within 5 km of the Kwando River (Fig. 3) in the southwest corner of the park. During the two dry season surveys, we recorded no seasonal pans with water along our flight transects and the herds typically occurred in open grassland habitats; however, we suspect that the larger pans still contained some water during the Aug04 survey. Furthermore, for both dry season surveys, considerable areas in the south and centre of the park were burnt: 924 km² in Aug04 and 2934 km² in Oct05 (Fig. 4).

Herd observations and abundance

The number of herds seen per 1000 km of transect flown increased from 14.4 herds/1000 km for the Jan04 wet season survey to 17.0 herds/1000 km in the Aug04 dry season survey, and then decreased to 6.3 herds/1000 km for the second dry season in Oct05 (Table 1). The majority of herds seen on each survey were bulls (range 56%–74%). The numbers of family groups seen on surveys remained relatively constant in comparison to bull herd numbers. The maximum family group herd size in Oct05 dry season (n=25) was a third as large as the maximum family group size in Jan04 wet season (n=76).

Average bull herd size differed between the three surveys (F=5.73, df=39, P=0.006) with the smallest average bull herd size occurring in the Jan04 wet season survey (1.6), less than half of the average bull herd sizes in the two dry season surveys (Table 1). In contrast, there were no differences in average family group sizes for the three surveys (F=8.49, df=16, P=0.448); however, in comparison to the Jan04 survey, average family group size decreased by 31% in the Aug04 survey and by 55% in the Oct05 survey.

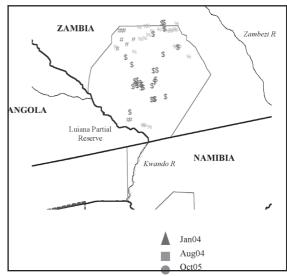


Figure 3. Elephant herds observed on three aerial surveys, Sioma Ngwezi National Park, Zambia.

Combining herd observations for both observers and accounting for the average flight altitudes, strip transect sampling from the Jan04 survey provided an estimate of 1099 elephants [P(223 < N < 1957 = 0.95)] for the entire park (4322 km²). The park-wide estimate declined to 899 elephants [P(144 < N < 1654 = 0.95)]

Table 1. Numbers and mean sizes for bull herds and family groups during three aerial surveys of Sioma Ngwezi National Park, Zambia

Survey date (season) (km flown)	No. bull herds	Bull herd size (SD) [range]	No. of fam- ily groups	Family group size (SD) [range]
Jan04 (wet) (1595)	17	1.6 (1) [1-4]	6	29 (26.9) [2-76]
Aug04 (dry) (1474)	18	3.8 (2.5) [1-10]	7	19.9 (15.6) [7-50]
Oct05 (dry) (1433)	5	3.4 (1.5) [2-5]	4	13 (9.1) [6-25]

for the Aug04 survey, nearly a 20% decline. On the last dry season survey in Oct05, we estimated 385 elephants [P(67 < N < 774 = 0.95)] in Sioma Ngwezi NP, a 65% decline from our first aerial survey.

Discussion

Elephant distribution

There was a considerable difference in herd distribution between the wet and dry season surveys. While most of the herds were in the centre of the park during the Jan04 wet season survey, during the two dry season surveys

most of the herds were scattered along the northern portion of the park. We believe this difference in distribution between the wet and dry seasons is related to the availability of water in seasonal pans and occurrence of human settlements. During the wet season when there is water in the numerous seasonal pans throughout the park, elephants may be concentrating in the centre of the park where there are no human settlements (Fig. 1) and associated disturbance. Whereas in the dry season when water in pans is more limited, elephants shift their distribution to the northern portions of the park where there are few human settlements. Although we observed numerous pans with water in the northern portion of the park during the Jan04 wet season survey, we did not record water in any of these pans during the two dry season surveys. However, the northern part of the park with its seasonally flooded grasslands is wetter and we suspect that some of the larger pans held water late into the dry season although we did

not record these pans on our aerial transects. In addition, elephants may be using water from well points in the communities across the northern boundary of the park. For all three surveys, relatively few herds were observed in proximity to the Kwando River in the southwest corner of the park despite the occurrence of perennial water in the river. We suspect that the low numbers of elephants in proximity to the river, especially during the dry season, is due to the extensive human settlements that occur along the river (Fig. 1).

At the request of the Zambia Wildlife Authority, we extended our aerial transects east of the park within the Western Zambezi Game Management Area during the Jan04 survey. The transects extended east to west from the eastern park boundary towards the Zambezi River beginning 35 km north of the Namibian border and extending northward 35 km coinciding with the northern boundary of the park. Although no elephants were seen on 546 km of transects flown in the game management area in the Jan04 survey, we did observe three bull herds in the area in August 2006 when we were collaring elephants in the region. There are also reports of human-elephant conflicts in the communities along the Zambezi River (Muleta 1996). We believe that the numerous human settlements along the Zambezi River and along the eastern boundary of the park probably limit elephant distribution within this portion of the game management area.

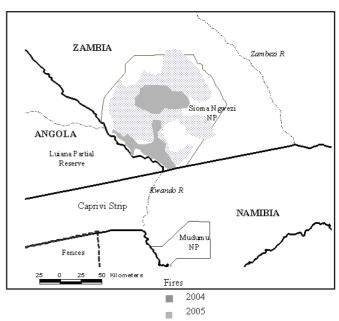


Figure 4. Areas burnt from bush fires during the 2004 and 2005 dry seasons in Sioma Ngwezi National Park, Zambia.

Herd observations and abundance

The large difference in herd density between the two dry season surveys (17.0 and 6.3 herds/1000 km) is most likely due to differences in rainfall and the extent of bush fires between the two years. Rainfall (1096 mm) was 51% higher during the 2003/04 wet season (November-April) than during the 2004/05 wet season (534 mm) (Botswana Meteorological Services 2006). This rainfall difference affected the availability of water in the seasonal pans, especially the length of time that water persists into the dry season. Furthermore, the Oct05 survey occurred six weeks later into the dry season than the Aug04 survey. Additionally, bush fires are common during the dry season (May-October) in the park, and were particularly severe during the 2005 dry season. Approximately 46% more of the park was burnt during the 2005 dry season (68% burnt) than in the 2004 dry season (22% burnt) (Fig. 4).

Our average bull herd sizes were larger in the two dry season surveys than in the wet season survey (Table 1). In contrast, the average family group sizes decreased by 31% and 55% respectively, in the two dry season surveys compared to the Jan04 wet season survey. Typically, both bull and family group sizes decreased from the wet to dry seasons (Western and Lindsay 1984; Sukumar 2003). The reasons for our larger average bull herd sizes during the dry season survey are unknown, but may be related to the dispersal of bulls in musth searching for females in oestrus during the wet season as reported by Hall–Martin (1987) for elephants in Kruger National Park, South Africa. Sukumar (2003) suggested that human disturbance can increase elephant herd sizes. Our average herd sizes may be under-estimated because we only recorded elephants within the survey strip interval. Thus for herds that overlapped the interval boundary, some herd members were excluded from our herd counts.

Elephant numbers were highest in the wet season (Jan04) survey and decreased for the two subsequent dry season surveys. Due to limited water availability and access to the Kwando River caused by extensive human settlements, elephants may need to disperse out of the park during the dry season, especially in low rainfall years when there is no water in seasonal pans. From his telemetry study of elephants in the Caprivi Strip, Rodwell (1995) reported that one of his collared female elephants in Mudumu NP dispersed into Sioma Ngwezi during the 1993/4 wet season, but

she returned to Mudumu at the beginning of the dry season. Similarly, all five elephants (three bulls and two females) that we had tagged with satellite collars in Sioma Ngwezi NP in mid-August 2006 had moved out of the park by late September 2006 with four moving north into the Zambezi Game Management Area and one west into the Luiana PR (Chase 2006). The especially low numbers of elephants in the park in our second dry season survey was probably due to extensive dispersal out of the park caused by poor rainfall during the previous wet season and extensive fires throughout the park.

The elephant population estimate for our first survey (n=1099) was similar to that reported by Tembo (1995) (n=1187) in Dec. 1991. However, by 1996, Simasiku et al. (1996) believed that elephant numbers declined greatly after this time due to illegal hunting and activities relating to the Angolan Civil War. This decline was substantiated by the few elephants recorded by Larry Patterson (pers. comm. 2006) during his limited aerial survey in 1996-7. We believe that the relatively high numbers of elephants observed on our January 2004 survey, in comparison to Patterson's observations, suggests that elephants are probably recolonizing the park. The cessation of the Angolan Civil War in 2002 coincided with the dispersal of elephants from Namibia into Angola and Zambia across the Kwando River (Chase and Griffin 2006). Two elephants we tagged in southwest Zambia in August 2006 showed repeated movements between Sioma Ngwezi and Luiana across the Kwando River, extending into the Caprivi Strip. In addition, four tagged elephants moved from southwest Zambia into East Caprivi with two continuing south into Botswana into the Chobe Enclave west of Chobe National Park (Fig. 5).

Conservation implications

Although we believe elephant numbers have increased in the park since the late 1990s, several factors may be limiting elephant numbers in Sioma Ngwezi. First, other than the perennial Kwando River, there are no other permanent water sources in the park and the dense human settlements along this river may restrict elephant access to water. Second, there is much human-elephant conflict in the communities along the Kwando and Zambezi Rivers, which erodes local tolerance of elephants and impedes conservation efforts (Simasiku et al. 1996). Furthermore, illegal hunting is difficult to control in these areas. Third,

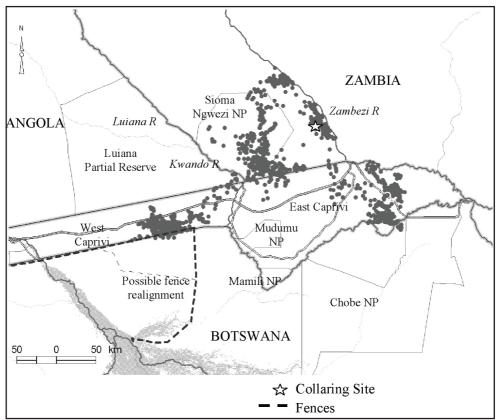


Figure 5. Movements of one adult bull elephant collared in Sioma Ngwezi National Park, southwest Zambia, Aug 2006-Jun 2008 (M. Chase, unpublished data).

the park is highly susceptible to bush fires during the late dry season when farmers burn their fields, thereby affecting the distribution and abundance of elephants. Fourth, there is little tourism and no tourist facilities within the park, thereby restricting the economic potential of the park. Lastly, the Caprivi border and Northern Buffalo Fences in Botswana restrict transboundary wildlife movements from northern Botswana into West Caprivi (Albertson 1998; Scott Wilson Resource Consultants 2000; Chase and Griffin 2003; Jackson and Erasmus 2005; Martin 2005), thereby possibly affecting elephant movements eastward into southeast Angola and southwest Zambia.

Community-based conservation programmes need to be established by people living in and adjacent to the park and within the Western Zambezi Game Management Area. There is a critical need to initiate programmes that promote the conservation of wildlife habitats while improving rural livelihoods through economic development. Such conservancy

programmes could facilitate elephant access to the Kwando and Zambezi Rivers; implement strategies for mitigating human-elephant conflicts in communities; reduce illegal hunting and the incidence of bush fires; and provide sources of income to communities through ecotourism. The proximity of the park to Victoria Falls, a regional tourism hub, and to Chobe NP in Botswana provides the potential to market the park as a major regional tourist attraction. Such conservation-based enterprises were successfully developed across the border in the Caprivi Strip of Namibia (Ashley 1995). Development of community conservancies in combination with effective park management, including land use management and anti-poaching programmes, are essential to the conservation of elephants and other wildlife in the park. In addition, barriers to wildlife movements from northern Botswana to the Caprivi Strip, the Caprivi Border and Northern Buffalo Fences need to be realigned to widen the conservation corridor along the Kwando River (Scott Wilson Resource Consultants 2000). Removing portions of the fences to align them with the NG13 concession boundary (Fig. 1) would extend the width of this conservation corridor and increase transboundary wildlife movements into southern Angola and Zambia. Finally, although our ongoing satellite telemetry study of elephants in southern Zambia will provide additional information on factors affecting the seasonal dispersal of elephants, we recommend that additional aerial surveys be conducted. These surveys should extend beyond the park boundaries to include the Zambezi Game Management Area and be co-ordinated with additional surveys in southeast Angola, and in West and East Caprivi. Additional wet and dry season surveys will provide information on elephant abundance and distribution, and help to evaluate the efficacy of proposed conservation programmes within the region (Martin 2006).

Acknowledgements

We thank the Zambian Government for permission to initiate this study and gratefully acknowledge the

support and collaboration of Isaac Longwe, Jones Masonde, Ellie Mwiya and Lisa Mwiinga from the Zambia Wildlife Authority. This project was funded by the following: the Department of Interior US Fish and Wildlife Service, African Elephant Conservation Fund, Gale Family Foundation, Shikar Safari Club, Elephants Without Borders, Conservation International and African Wildlife Foundation. We thank our pilots, Mike Holding, Alan and Kim Parnass and Peter Pearlstein, who flew long hours over new terrain. We sincerely appreciate the help and support of Gavin Johnson from Royal Barotse Safaris and his management couple, Jonathan and Fancisca, at Mutemwa Lodge. We also thank Mike Musgrave, Alan Sparrow and Nina Gibson for their help. Leo Braack and Shannon Charlton from Conservation International are acknowledged for their administrative support. We express our gratitude and thanks to John Hanks for his encouragement and support to initiate this project in southwest Zambia.

Appendix 1. Survey dates and wildlife population estimates for Sioma Ngwezi National Park, Zambia

Species	Dec. 1991 ^a	Jan.	Jan. 2004 ^b		Aug. 2004 ^b		Oct. 2005 ^b	
	N (SE)	N (SE)	95% CL	N (SE)	95% CI	N (SE)	95% CL	
Elephant	1,187 (481)	1,099 (426)	223- 1975	899 (525)	215- 1,654	385 (189)	67-774	
Sable (Hippotragus niger)	389 (151)	297 (103)	40-346	50 (14)	23-85	56 (18)	8-106	
Kudu (<i>Tragelaphus</i> strepsiceros)	195 (81)	235 (90)	50-420	120 (77)	62-223	135 (85)	65-175	
Warthog (Phacochoerus aethiopicus)	156 (53)	124 (36)	49-199	82 (36)	43-168	112 (53)	45-168	
Eland (<i>Taurotragus</i> <i>oryx</i>)	136 (78)	20 (9)	2-40					
Giraffe (Giraffa camelopardalis)		211 (68)	70-351	80 (28)	37-150	26 (11)	4-54	
Impala (Aepyceros melampus)		89 (75)	45-244	30 (11)	7-46	54 (28)	35-86	

^a From Tembo (1995)

^b This study

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