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Author(s): Ann Apio, Martin Plath & Torsten Wronski
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RECOVERY OF UNGULATE POPULATIONS IN POST-CIVIL WAR AKAGERA NATIONAL PARK, RWANDA

Ann Apio
Department of Wildlife and Aquatic Resources Management
College of Agriculture, Animal Sciences and Veterinary Medicine
School of Animal Sciences and Veterinary Medicine, University of Rwanda
P.O. Box: 117, Huye, Rwanda
a-apio@gmx.de

Martin Plath
College of Animal Science and Technology, Northwest A&F University
Yangling 712100, Shaanxi Province, P.R. China
mplath-zoology@foxmail.com

Torsten Wronski
School of Natural Sciences and Psychology, Faculty of Science,
Liverpool John Moores University
Liverpool, L3 3AF, UK
&
College of Science and Technology, Department of Biology
School of Sciences, University of Rwanda
P.O. Box 117, Huye, Rwanda
t_wronski@gmx.de

ABSTRACT

Following the 1991–1995 civil war in Rwanda, large parts of Akagera National Park (NP) and the adjacent Mutara Game Reserve were endowed by government to returning war refugees for cattle grazing. In 1997, official degazettement reduced the area covered by these two protected areas by 60% (from 2800 km^2 to 1120 km^2). This study reports trends in population sizes and densities of ungulates in modern Akagera NP (1120 km^2), with a focus on the more common ungulates (impala, topi, zebra, buffalo, waterbuck, and warthog). Data from previous surveys are compared with our 2010–2014 road strip counts using distance sampling. A decline of ungulate populations during the civil war, followed by recovery several years after reduction of the size of the Park, is evident. The ungulate populations show different trends in size in recent years, suggesting that the carrying capacity has been reached for some species.

Keywords: density estimates, distance sampling, protected area reduction, antelopes, post-conflict trend

INTRODUCTION

With a world population of about 7 billion humans in 2015, 1.15 billion of which live in Africa, and a projected increase of the African population to 2.4 billion by 2050 (UNICEF, 2015), competition for natural resources has brought about widespread extirpations of wildlife outside protected areas in recent decades (CMP, 2005; CMP-IUCN, 2007). Nowhere in Africa is this problem more apparent than in the Republic of Rwanda, a country that has not only been plagued by severe overpopulation for centuries, but after the 1991–1997 civil war, Rwanda faced additional problems from hundreds of thousands of returning war refugees (Lorch, 1995; Kanyamibwa, 1998). The war also had implications on law enforcement in Akagera National Park (NP; 2800 km²), leading to a lack of protection activities and loss of wildlife. This loss became most apparent after the civil war, when 1680 km² of Akagera NP and the entire adjacent Mutara Game Reserve (300 km²) were devoted to the grazing of the 600 000–700 000 cattle of returning refugees (Kanyamibwa, 1998; Plumptre *et al.*, 2001). At this time, wildlife in the Akagera NP was decimated (even below numbers at the beginning of the 1991 conflict; see figure 7) by bushmeat poachers and by competition with livestock for food.

In 1997, Mutara Game Reserve (GR) and the northern and western sections (1380 km²) of Akagera NP were officially degazetted. Combined, 1680 km² (60%) of protected area were degazetted (from 2800 km² to 1120 km²). This was one of the largest protected area degazettements in African conservation history (Kanyamibwa, 1998; Bizoza & Madina, 2013; Macpherson, 2013). This led, however, to the re-establishment of effective conservation law enforcement in Akagera NP and highlights the importance of active conservation effort implemented by the new management system.

Several studies have monitored the decline (or persistence) of ungulates in modern Akagera NP and adjacent areas (former Mutara GR and degazetted parts of Akagera NP; Vande weghe & Dejace, 1991; Fourniret, 1994; Chardonet & East, 1995; Williams & Ntayombya, 1999, 2001; Lamprey, 2002; Viljoen, 2010; Apio & Wronski, 2011; Macpherson, 2013). The small size of modern Akagera NP, especially after the park was fenced in 2013 (1120 km²; RDB, 2013), highlights the need for continuous monitoring of ungulate populations in the park. Fencing national parks has become a widespread practice to reduce human-wildlife conflict, but inevitably creates problems for some large mammal species (Boone & Hobbs, 2004; Islam *et al.*, 2009; Ferguson & Hanks, 2010). Fences prevent dispersal and, therefore, can lead to over-stocking, especially if large predators are absent (Goodman, 2003). Lions *Panthera leo* (Linnaeus, 1758) have not been reported for at least 15 years (Lamprey, 2002), while spotted hyenas *Crocuta crocuta* (Erxleben, 1777) and leopards *Panthera pardus* (Linnaeus, 1758) persist in Akagera NP (Macpherson, 2013; authors, pers. obs.).

This study was designed to provide trends of population size and density for several large ungulates in modern Akagera NP. We summarised data from previous surveys and conducted road strip counts with the aim of evaluating the population dynamics of ungulates in this unique African ecosystem.

MATERIAL & METHODS

Four road strip count surveys (13–16 April 2010, 18–20 September 2011, 26–28 May 2012, 14–16 March 2014) were conducted along existing tracks in Akagera NP from a 4 × 4 Land Cruiser. Nine road strips of varying length were established but, for logistic reasons, not all were surveyed during each count. Road strips included during each survey, road strip length, and major habitat types in which road strips were situated are presented in table 1. Habitat types were defined according to Vande weghe (1990) and Williams and Ntayombya (1999), and later integrated into population size estimations (see below). Distances driven in each habitat type were determined during each count using a GPS. Perpendicular distance to each animal (or group of animals) sighted was estimated using a range finder.

Table 1. Road strips included in the four surveys from 2010 to 2014, conducted in the course of our present study, including length and dominant habitat type for each road strip.

Transect	Name	Habitat type	Length [km]	2010	2011	2012	2014
1	Lake Ihema	dry and riverine forest	19.9	x	x	x	x
2	Rwinirabo	moderate slope	27.7	x	x	x	x
3	Southern loops	moderate slope	13.0	x	x	x	
4	Lake Hago/Kivumba	dry and riverine forest	21.3	x	x	x	x
5	Lake Minindi	dry and riverine forest	19.1		x		x
6	Lake Rwamyakizinga	moderate slope	18.1	x		x	x
7	Kilala	moderate slope	18.2	x	x	x	x
8	Nyungwe	moderate slope	13.5	x	x	x	x
9	*Mutumba*	*hill top plains*	*23.7*	*x*	*x*	*x*	

We focused on six ungulate species (taxonomy following Kingdon *et al.*, 2013): southern savanna buffalo, *Synceros caffer caffer* (Sparrman, 1779) (figure 1); topi, *Damaliscus lunatus jimela* Matschie, 1892 (figure 2); defassa waterbuck, *Kobus ellipsiprymnus defassa* Rüppell, 1835 (figure 3); impala *Aepyceros melampus* (Lichtenstein, 1812) (figure 4); plains zebra *Equus quagga* Boddaert, 1785 (figure 5); common warthog, *Phacochoerus africanus* (Gmelin, 1788) (figure 6). Ungulate densities in modern Akagera NP were estimated using the software DISTANCE vs. 6.0 (Thomas & Buckland, 2005; Thomas *et al.*, 2010). Making full use of the power of AIC (Akaike Information Criterion) and information theory, the full data set was explored to determine the model that fit best, *i.e.* the detection function with the lowest AIC. The best model applied the hazard-rate as the key function with a hermite polynomial series expansion (AIC = 6475.0, χ^2 = 0.0002, estimated strip width, ESW = 21 m). Since the χ^2–test was highly significant (<0.01), and outliers occurred at around 500 m, raw distances were binned into four intervals (avoiding cut points that coincided with multiples of 10, *i.e.* 105 m, 195 m, 305 m, and 395 m) and truncated at 400 m. This resulted in an AIC of 746.02, a χ^2 of 0.99 and an ESW of 65 m. All other binning intervals or truncations resulted in smaller (*i.e.* significant) χ^2–values. Subsequently, the overall data set was split into six target species, re-running the analyses with the same settings as above (impala: AIC = 179.3, χ^2 = 0.16; topi: AIC = 198.7, χ^2 = 0.45; buffalo: AIC = 85.1, χ^2 = 0.22; waterbuck: AIC = 117.7, χ^2 = 0.09; zebra: AIC = 99.8, χ^2 = 0.01; warthog: AIC = 65.3, χ^2 = 0.08). The sum of the six AIC values (746.00) was slightly lower than the AIC of the full dataset (746.02), thus supporting the splitting of the dataset and estimating detection functions for each of the six target species. In a second step, raw data for each species were pooled annually to obtain sufficiently large sample sizes and to estimate detection functions for each of the six target species after stratification by year (table 2). In several cases, however, sample sizes were not sufficient to obtain robust population estimates (table 3).

Table 2. Best-fitting detection functions (key function, series expansion) for the estimation of local population sizes of six ungulate species (impala, topi, buffalo, waterbuck, zebra and warthog) in the modern Akagera NP. AIC = Akaike Information Criterion, χ^2 = chi-square goodness-of-fit; ESW = Effective Strip Width.

Species	Key function	Series expansion	AIC	χ^2	ESW (m)
Impala	hazard-rate	cosine	262.1	0.56	75
Topi	hazard-rate	cosine	155.3	0.85	104
Buffalo	half-normal	cosine	37.5	0.80	198
Waterbuck	half-normal	cosine	130.7	0.52	95
Zebra	hazard-rate	cosine	128.0	0.03	124
Warthog	half-normal	cosine	79.5	0.41	70

Table 3. Estimated densities of six ungulate species (impala, topi, buffalo, waterbuck, zebra, warthog) in the modern Akagera NP. N = number of detections; Ŷ = mean cluster size; D = density of individuals; D (SE) = standard error of density; CV (D) = per cent coefficient of variation; 95% CI = 95% confidence interval; D_g = density of clusters.

Year	N	Ŷ	*D* (km^{-2})	*D* (SE) (km^{-2})	CV (*D*) (%)	95% CI (km^{-2})	D_g (km^{-2})
Impala							
2010	61	14.4	10.1	5.6	55.1	3.6 – 28.4	0.55
2011	31	17.2	5.7	3.6	63.0	1.8 – 18.2	0.28
2012	65	11.9	9.1	5.1	56.4	3.2 – 26.0	0.59
2014	49	12.0	5.9	3.1	52.9	2.2 – 15.9	0.44
Topi							
2010	33	6.9	1.5	1.1	71.6	0.4 – 5.5	0.22
2011	31	11.8	1.2	0.9	72.6	0.3 – 4.5	0.21
2012	39	3.5	0.8	0.6	67.6	0.3 – 2.9	0.26
2014	26	11.9	1.8	1.2	66.1	0.5 – 5.9	0.17
Buffalo							
2010	6	14.5	1.2	1.5	124.9	0.1 – 12.0	0.02
2011	7	19.9	0.7	0.8	109.7	0.1 – 4.8	0.02
2012	5	14.0	0.3	0.3	95.8	0.0 – 2.3	0.02
2014	7	39.2	3.8	8.5	222.9	0.3 – 58.0	0.10
Waterbuck							
2010	11	7.5	0.3	0.2	79.5	0.0 – 1.2	0.08
2011	20	5.5	1.1	0.6	52.8	0.4 – 2.9	0.14
2012	22	4.8	1.0	0.6	60.2	0.3 – 3.2	0.16
2014	19	5.2	0.7	0.4	56.3	0.3 – 2.1	0.14
Zebra							
2010	9	7.3	0.5	0.3	62.6	0.1 – 1.5	0.05
2011	9	7.9	0.5	0.4	77.2	0.1 – 1.9	0.05
2012	28	8.1	1.4	1.0	69.8	0.4 – 4.9	0.16
2014	17	9.5	1.1	0.7	62.7	0.4 – 3.5	0.09
Warthog							
2010	9	3.6	0.2	0.2	51.9	0.1 – 0.8	0.09
2011	14	2.9	0.2	0.2	48.0	0.2 – 1.1	0.14
2012	12	3.9	0.3	0.3	58.6	0.2 – 1.5	0.12
2014	26	3.7	0.5	0.5	56.7	0.3 – 2.6	0.25

There are contradicting designations regarding the area of modern Akagera NP (Williams & Ntayombya, 1999, 2001: 732 km^2; Nahayo & Yansheng, 2009: 900 km^2; Macpherson, 2013: 1120 km^2; Akagera Management Company, 2015: 1200 km^2). Here we followed

Figure 1. Adult male southern savanna buffalo, Synceros caffer caffer. *Drawing by Jonathan Kingdon (Kingdon & Hoffmann, 2013b).*

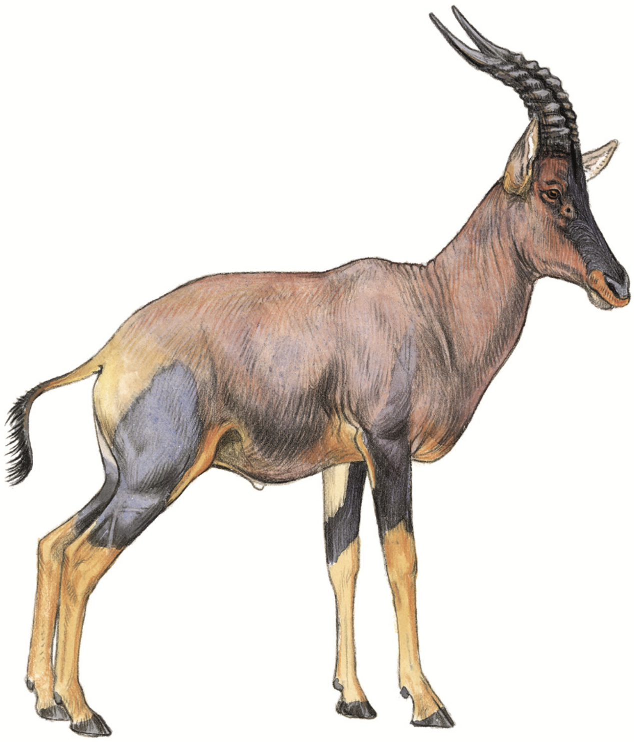


Figure 2. Adult male topi, Damaliscus lunatus jimela. *Drawing by Jonathan Kingdon (Kingdon & Hoffmann, 2013b)*.

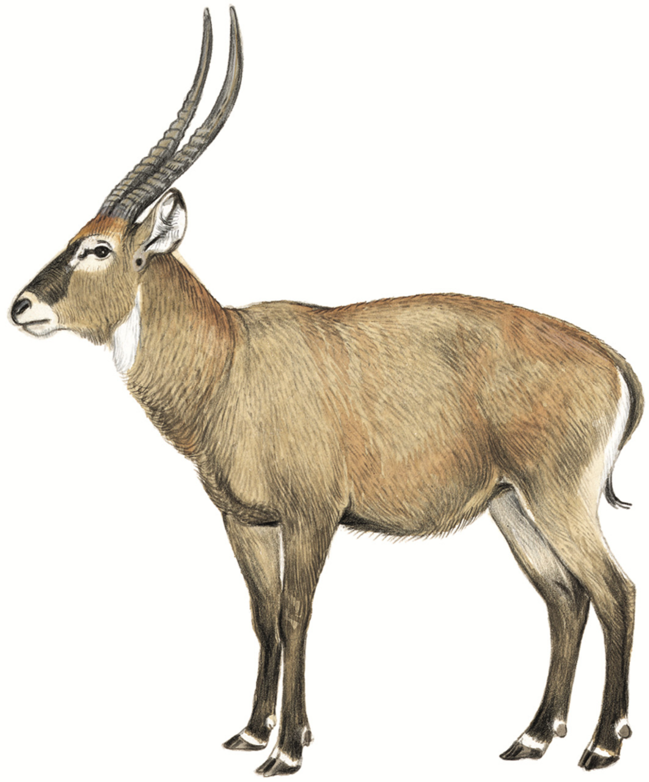


Figure 3. Adult male defassa waterbuck, Kobus ellipsiprymnus defassa. *Drawing by Jonathan Kingdon (Kingdon & Hoffmann, 2013b)*.

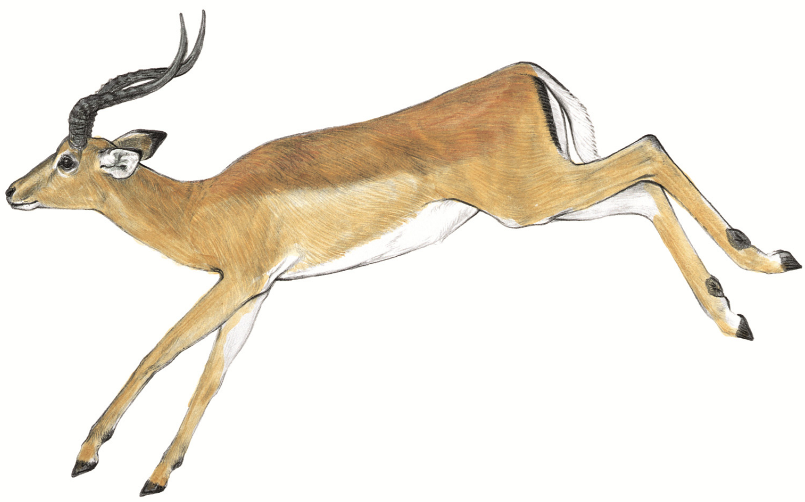


Figure 4. Adult male impala Aepyceros melampus. *Drawing by Jonathan Kingdon (Kingdon & Hoffmann, 2013b)*.

Figure 5. Plains zebra Equus quagga. *Drawing by Jonathan Kingdon* (*Kingdon & Hoffmann, 2013a)*.

Figure 6. Adult male common warthog, Phacochoerus africanus*. Drawing by Jonathan Kingdon (Kingdon & Hoffmann, 2013b)*.

Macpherson (2013; 1120 km^2), including both terrestrial and aquatic habitats. Based on maps (Akagera Management Company, 2015), the terrestrial area of modern Akagera NP is *ca.* 794 km^2. This value was the basis for all population density estimates given here.

In addition, we included population estimates obtained between 1991 and 2013, collected by various scientists using different sampling methods (table 4). Those population estimates were set in relation to the area of the terrestrial park at the time (1991–1998: 2170 km^2, 1999–2014: 794 km^2) to obtain the population densities presented here. Thus, the data set presented here is from 1991 to 2014.

Table 4. Previous studies from which population estimates were obtained, including references, study area in and around the modern Akagera National Park, and methods applied to count wildlife.

Reference	Survey area	Year	Count method
Vande weghe & Dejace (1991)	old Akagera NP	1990	ground count (?*)
Williams & Ntayombya (1999, 2001)	modern Akagera NP & degazetted parts	1997, 1998	aerial total count
Lamprey (2002)	modern Akagera NP	2002	systematic reconnaissance flight
Viljoen (2010)	modern Akagera NP	2010	systematic reconnaissance flight
Macpherson (2013)	modern Akagera NP	2013	aerial total count

* information on type of sampling not available

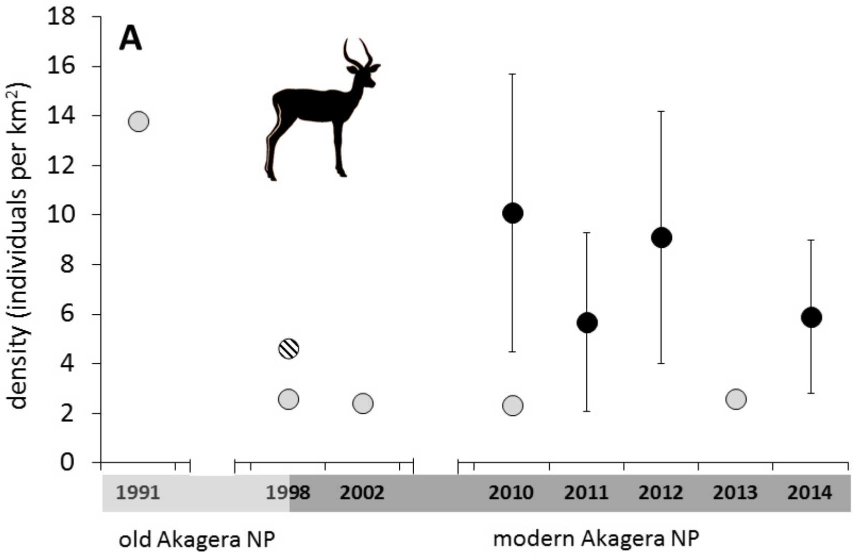
RESULTS

Two major trends can be inferred: (*i*) a negative effect of the civil war on all species, and (*ii*) ungulate population sizes and densities increased substantially several years after 1997, *i.e.* after the park was reduced in size (figure 7, table 3). Warthog (figure 7f) exhibit a steady increase in population density over the study period (*i.e.* after 2010), while topi, buffalo and zebra (figure 7b, c, e) show a decline until 2012, followed by an increase. Impala (figure 7a) densities increased substantially after the war until 2010, then declined. Similarly, waterbuck (figure 7d) recovered, only to decline after 2011.

Density estimates showed considerable variation across studies and years (table 3). Lower density estimates were obtained from aerial counts than from our road counts in the case of impala (figure 7a) and topi (figure 7b). By contrast, buffalo (figure 7c), waterbuck (figure 7d), zebra (figure 7e), and warthog (figure 7f) estimates from our road counts were well below those obtained from aerial surveys.

DISCUSSION

The main conclusion of this study is that the populations of six large mammal species examined here (*i.e.* impala, topi, African buffalo, waterbuck, zebra and warthog) have recovered since the civil war, highlighting the effectiveness of conservation and law enforcement activities of the park management (African Parks, 2016). The general scarcity of large predators (Goodman, 2003; Macpherson, 2013), has likely contributed to the fast population recovery in those species. Other ungulates, however, like roan *Hippotragus equinus* (É Geoffroy Saint-Hilaire, 1803) and eland *Tragelaphus oryx* (Pallas, 1766), which


A
density (individuals per km^2)
18
16
14
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2012
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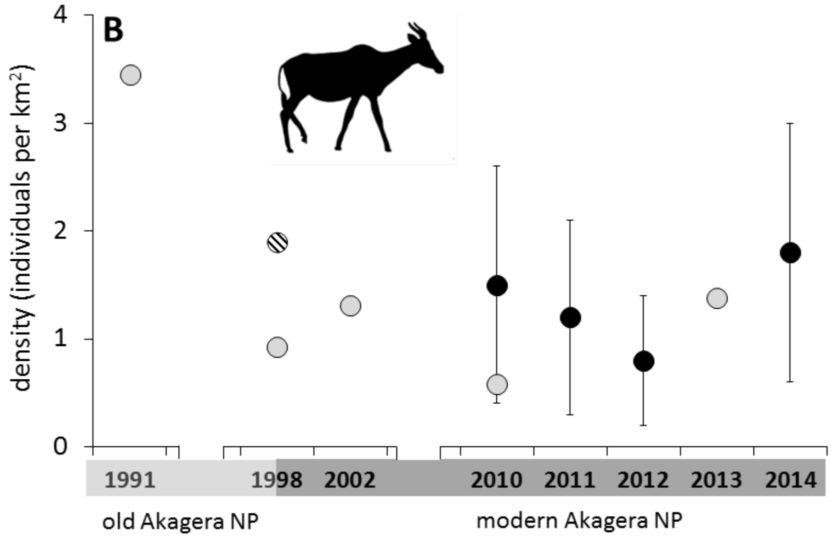
2014
old Akagera NP
modern Akagera NP


B
density (individuals per km^2)
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3
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2012
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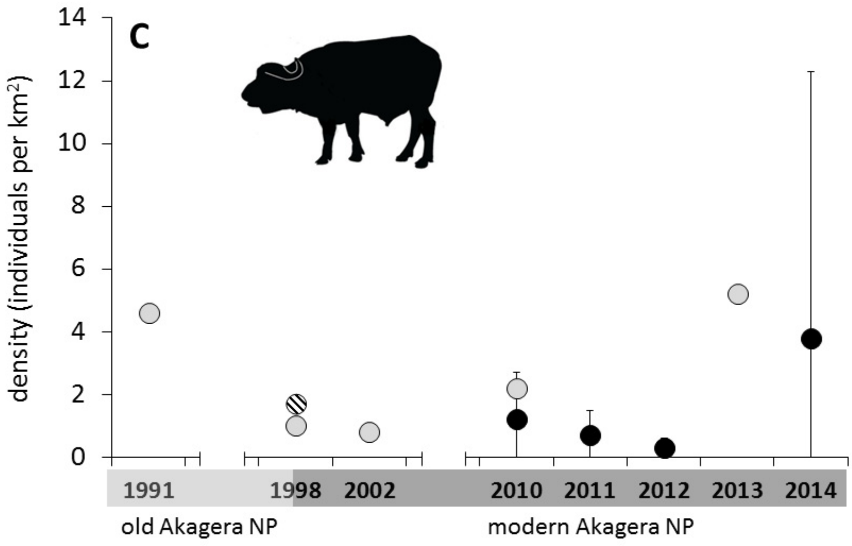
old Akagera NP
modern Akagera NP


C
density (individuals per km²)
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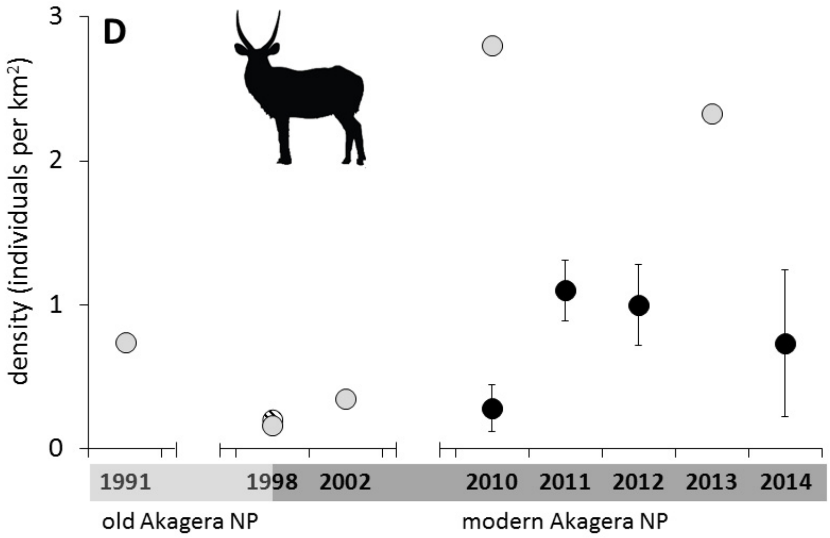
modern Akagera NP


D
density (individuals per km²)
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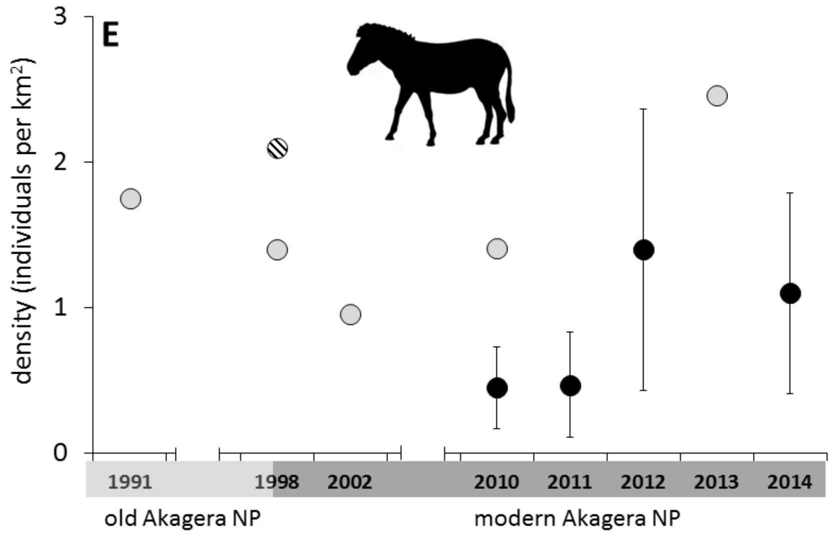

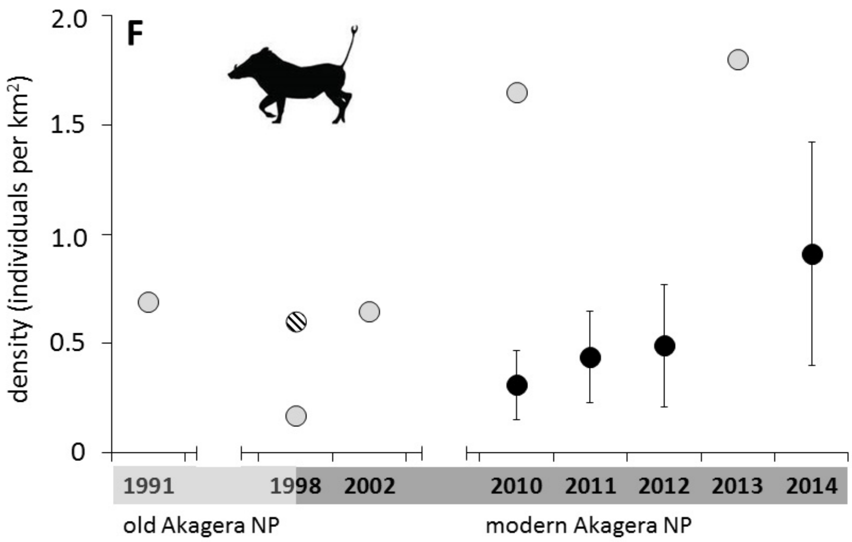

Figure 7. Density estimates [mean numbers of individuals per km² ± standard error, if applicable] of terrestrial ungulates (A. impala, B. topi, C. buffalo, D. waterbuck, E. zebra, F. warthog) derived from studies using different count methods (● this study, ⊘ other studies in the old Akagera NP, ◯ other studies in modern Akagera NP; see table 3).

were not included in our analysis of population densities, remain uncommon. One herd of roan (approximately 83 individuals) occurs in the northern parts of the park, and about 193 eland inhabit the open plains and hill tops in the north of the park (Macpherson, 2013).

Recent slight declines in the populations of some ungulates (impala, waterbuck, and zebra) may indicate that the carrying capacity has already been reached (compare carrying capacity estimates in Goodman (2003): impala 5.67, topi 1.13, African buffalo 1.76, waterbuck 0.04, zebra 1.39, and warthog 0.54 individuals/km^2). Over-stocking may put these populations at jeopardy due to resource competition and increased parasite transmission (Cabaret & Hugonnet, 1987; Wobeser, 2005). Reintroducing lions, as recently attempted by the park management (Hall, 2015; Toovey, 2015), may provide a partial solution to this problem. Monitoring programs should continue to survey the large ungulates in modern Akagera NP, especially because these animals are prevented from dispersing from the park due to the fence.

Increasing bush in Akagera NP can especially affect grazing species (Averbeck, 2001; Archer, 2010; J. Gruner, *pers. comm.*). For example, stable isotope studies of tooth enamel characterized impala in Akagera NP primarily as grazers (Copeland *et al.*, 2009; but see Dunham, 1982; Wronski, 2002, 2003, for impala in other areas). The downward population trend of this species in recent years may be linked to bush encroachment and a decreasing availability of grass. The absence of larger browsers such as black rhinoceros *Diceros bicornis* (Linnaeus, 1758), which was extirpated during or after the civil war (Lamprey, 2002), and the scarcity of elephants could lead to a further increase in bush (Macpherson, 2013). Reintroducing black rhinoceros, as now planned (Wally, 2016; Karuhanga, 2016), should help reduce the bush cover.

Aerial survey methods can lead to under-estimates of population size for some species, while ground surveys tend to over-estimate population size of some species (Bothma, 2002). In this study, population size estimates from aerial surveys were lower for impala and topi, while higher estimates were obtained for buffalo, waterbuck, zebra and warthog. As such, our discussion of population trends (see above) needs to be considered with caution. How can the disparity between density estimates obtained from aerial and ground surveys be explained? Roads and tracks in protected areas do not usually cover landscape types in a random manner; rather, they follow valleys and plains. This is especially the case in open landscape types where roads access areas that tourists are likely to encounter large mammals. Surveys along these roads and tracks can lead to a higher encounter frequency of certain (*e.g.* plains-dwelling) ungulate taxa as compared to aerial surveys, which cover the entire study area in a more random and systematic fashion. This probably explains the higher densities obtained for impala and topi by ground surveys (Bothma, 2002). On-the-other-hand, lower density estimates for impala derived from aerial surveys (Lamprey, 2002; Viljoen, 2010; Macpherson, 2013) may represent an under-estimation of density, as this small-bodied antelope can easily be overlooked from an aircraft. Impala are typically associated with bush (Jarman, 1979), and aerial surveys can fail to detect small herds that are hidden under trees.

Population estimates for buffalo, particularly for the 2014, should be viewed with caution: the increase in density estimates from 2012 to 2014 fits well with that obtained from the 2013 aerial survey (Macpherson, 2013) but shows an extreme standard error. This may be attributed to the fact that buffalo were encountered in only three large groups (*i.e.* a small number of detections) along only two road transects (*i.e.* Kilala, Lake Rwamyakizinga). This caused the coefficient of variation, as well as standard error and confidence interval, to indicate considerable uncertainty and thus a weak population estimate (table 3).

In summary, population trends of six ungulate species in Akagera NP suggest that some of the large mammals have largely overcome the dramatic decline during the civil war. Increasing human-wildlife conflict after the return of war refugees appears to have been mitigated, probably due to the construction of an electro-fence. In some taxa, the carrying capacity may be reached, highlighting the need for continued monitoring of population trends and possibly, population management.

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