The status of African elephant populations in South Africa

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Abstract

With an increase in poaching of elephants (*Loxodonta africana*) across Africa, it is vital to know exactly how many elephants remain and where they occur, to ensure that protection and management are planned appropriately. From a nationwide survey, we provide current population and distribution data for elephants in South Africa. We consider the viability of elephant populations in the country, as well as some of the management techniques implemented and how effective these are in controlling elephant numbers. According to our surveys, there were 28,168 elephants in South Africa as of December 2015, with 78% of these occurring in the Kruger National Park (KNP) and reserves bordering and open to the Park. Of the country's 78 discrete that host elephants, 77% have populations of <100 elephants, which could mean they are not genetically viable. We discuss our findings in terms of the conservation value of South Africa's elephant reserves, and the animal welfare implications. We recommend that the current fragmentation of elephant habitat in the country be addressed through a national elephant management strategy that promotes wildlife corridors between existing, neighbouring elephant reserves.

Key words: elephant, welfare, South Africa, population, fences, contraception

Introduction

African elephant (*Loxodonta africana*) categorized as Vulnerable on the IUCN Red List (Blanc, 2008) have been declining rapidly across the continent, largely as a result of increased poaching pressure and competition for resources with humans and livestock (Bouché et al., 2011; Wittemyer et al., 2014; Chase et al., 2016). In stark contrast to this, the elephant population within South Africa (SA) appears to have been increasing since 1992 (Hall-Martin, 1992; Slotow et al., 2005). Since the mid 1980s there has been an increase in the number of smaller, fenced reserves in South Africa that contain elephants, following translocations of juveniles who were spared from the culls conducted in Kruger National Park up to 1996 (Garaï et al., 2004). These smaller reserves, and the elephants within them, are owned and managed by various entities, including national or provincial level state-ownership, as well as communal or private ownership.

The first nation-wide survey of elephant numbers within South Africa was conducted by Hall-Martin in 1992. This was followed by further surveys in 1994 and 2001, conducted by the Elephant Managers and Owners Association (EMOA). These surveys showed a substantial increase in both elephant numbers and distribution since the species was nearly extirpated from South Africa by hunting a century before (Garaï et al., 2004; Slotow et al., 2005). Further national surveys were recently conducted by the Elephant Specialist Advisory Group of South Africa (ESAG). Here we aim to collate this survey information and provide current data on *total* elephant numbers within South Africa, which is timely given the continuing debates regarding the future of ivory trading and the threat of poaching (e.g. Cruise, 2016).

Within South Africa, perimeter fences are used extensively to denote land ownership and contain wildlife within designated protected areas (Snijders, 2012). However, such fences

often cut off the historic movement routes of elephants and change the way they use the landscape, giving rise to artificial distribution patterns and unique management problems. Confining elephants within a closed, fenced area is known to increase localized impact on vegetation, often with a consequent reduction in the available browse for other species such as black rhinoceros (*Diceros bicornis*) (Landman et al., 2013). Hence, elephant populations in fenced reserves need to be limited and controlled, but such population control presents its own ethical challenges (Lötter et al., 2008). Moreover, small elephant population sizes may result in incomplete social structures, which have previously been shown to lead to behavioural abnormalities such as hyperaggression (Slotow et al., 2000).

In open systems, elephant societies are made up of a multi-tiered social structure, with the mother and calf unit at the core (first tier) of a family group (second tier) that consists of a matriarch, her maternal sisters and their adult female daughters and dependent offspring (around 10 individuals on average, Lee and Moss, 1986), with females typically spending their whole lives with other close female relations. Related family groups fuse from time to time as bond groups (third tier) and when several families or bond groups join each other, they form what is known as a clan (fourth tier) (Wittemyer et al., 2005). Bulls start to leave their natal families when they reach adolescence and link up with other bulls to form bachelor herds. As bulls grow older they may become more solitary but still interact with other males to maintain dominance hierarchies (Poole, 1994). However, males of all ages prefer to associate with older bulls, and proximity to mature bulls is thought to play an important role in learning and socialisation (Evans and Harris, 2008).

In order to consider the viability of the discreet, fenced elephant populations within South Africa, we shall assess their genetic viability. Whilst this is very difficult to determine in practice, Franklin (1980) proposed a theoretical minimum number of 50 breeding animals, which keeps inbreeding at 1% per generation. Using this number as a rule of thumb whilst

taking demography and sex ratios into account, Sukumar (1993) suggested a total of 100 elephants per population are needed to ensure a high probability of survival during the next 100 years. Whilst estimates of a minimum viable population size for elephants vary greatly among authors (for example, Armbruster & Lande (1993) argue for a much greater number), here we use Sukumar's figure of 100 animals as a simple proxy to determine how many of South Africa's discreet elephant populations are likely genetically viable at present.

However, given our knowledge of elephant society, and the evidence from several sources that suggests behavioural problems can manifest in elephants living in abnormal social groups that deviate from the natural pattern (Slotow et al 2000; Bradshaw et al., 2005), we also propose the concept of a *socially*-viable minimum group size. This may be a novel idea in conservation assessments, but it has previously been suggested as necessary by philosohers and animal-welfare researchers (Donaldson and Kymlicka 2011), and we argue it is particularly pertinent to elephants as a highly social species (Byrne et al., 2009, McComb et al., 2001). This suggestion is supported by the evidence that elephants strive to maintain normal social units in the face of population breakdown (Goldenberg et al., 2016) and that the absence of normal social units in a population may result in elephants behaving abnormally or maladaptively (Shannon et al., 2013; Slotow et al., 2005).

If a normal social hierarchy is required in elephants to prevent maladaptive behavoiur, we suggest that each population must include all the main tiers, relationships, and dominance hierarchies that are evident in large, open societies. Thus we suggest here that at least three family groups (i.e. three second tier groups, which can form a bond group and/or a fourth tier clan) and four independent bulls (two young adults and two mature bulls) might form a minimum requirement for a *socially*-viable elephant population (that is, one that gives the elephants access to a 'normal' social hierarchy and so allows for normal social behaviour). Given the average family group size of ten elephants (Lee and Moss, 1986), we therefore

125 suggest that 34 elephants (30 adult cows and dependent offspring, plus 4 independent bulls)
126 is a workable and necessary minimum number to permit normal social behaviour among
127 elephants.

128 Using these proxy figures as minimum numbers for genetically and socially viable
129 populations, we aim to determine (1) how many elephants South Africa has, (2) where they
130 are distributed and, crucially, (3) how many of these populations within South Africa are
131 genetically and socially viable.

132

133 **Methods**

134 Members of the ESAG committee produced a list of reserves in South Africa currently
135 hosting elephants, using data from the previous elephant counts (EMOA 2001, unpublished
136 database; Slotow et al., 2005), as well as information from provincial nature conservation
137 authorities detailing which reserves applied for permits to introduce elephants since 2001. A
138 search was also conducted on Google using the keywords "elephants South Africa" to check
139 whether any reserves previously unknown to us were advertising that they hosted elephant.
140 These combined sources generated a list of 90 reserves and protected areas that were
141 potentially home to free-ranging elephants in 2015.

142 We determined that three reserves have removed all their elephants since 2001, resulting in a
143 list of 87 reserves, protected areas or parks containing elephants within South Africa. Owners
144 and managers from each of these 87 reserves were then contacted between 2012 and 2015
145 and asked to fill in a questionnaire. The questionnaire comprised inquiries about the location
146 and ownership of the property; elephant numbers; counting techniques; population structure;
147 dates elephants were introduced to the reserve; number of introductions, removals and deaths;

148 and the management techniques implemented (including any use of the porcine zona
149 pellucida (PZP) vaccine for immunocontraception of cows, vasectomies of bulls, and/or the
150 use of gonadotropin releasing hormone vaccine (GnRH)).

151 South African National Parks (SANParks), Mpumalanga Tourism and Parks Agency (MTPA)
152 and the Associated Private Nature Reserves (APNR) bordering the Kruger National Park
153 provided us with elephant numbers from aerial elephant counts conducted during the study
154 period in and around the Kruger National Park. Because nine private reserves that border the
155 Kruger National Park are open with the park and elephants are allowed to move between the
156 private reserves and the park, we consider all of these elephants as a single population, which
157 we subsequently refer to as the Greater Kruger elephant population. This means there are 78
158 discreet elephant populations within South Africa. For most of the descriptive analysis,
159 reserves were categorized according to the provinces in which they occurred and whether
160 they were owned by the state or a community or private entity. As, theoretically, the entire
161 South African elephant population was counted, there was no nee to statistically test for
162 changes in elephant numbers from the previous complete census. However, changes in
163 ownership were tested using chi-square statistics.

164 To examine the effect of birth control and fences on elephant population size we used
165 completed questionnaires from the 2012-2015 surveys (three-year interval), and the previous
166 data from 2001 and 2005 (four-year interval). We calculated average annual population
167 increase rates at three to four year intervals for the 27 reserves for which we had complete
168 information on population sizes across these years and who indicated what type of birth
169 control (vasectomy on bulls/ PZP vaccine on cows) they used. These rates were calculated by
170 subtracting the first year of count data available for a re- serve from the second year of count
171 data available, divided by the number of years between the two counts and then ex- pressed
172 as a percentage. To compare rates of population increase between fenced and open

populations we used data on the average annual elephant population-increase rate in the Greater Kruger as part of an open system and published data on long-term studies in Amboseli (Moss, 2001) and Samburu (Wittemyer et al., 2013), also representing open systems. Using a t-test with a one-tailed distribution assuming unequal variances, we compared the difference in population-increase rates between reserves that used birth control and those that did not, as well as between fenced and open systems.

All reserves surveyed made use of aerial counting techniques or had extensive monitoring programmes that made individual identification of all elephants on the property possible. Hence, we assume that all elephant numbers reported during our survey represent a minimum estimate of elephant populations sizes in South Africa as of December 2015.

Results

A total of 45 reserves at least partially answered our questionnaire, and 30 were returned fully completed. Total elephant numbers for the 42 remaining reserves were obtained from either the relevant state conservation authorities (provincial conservation bodies or SANParks) or follow-up telephone calls to private owners.

Population size, distribution and rate of change

Using our survey data and data provided to us by the national and provincial conservation authorities, we calculated that South Africa was home to an estimated 28,168 elephants in total, as of December 2015, across the 87 reserves, parks and protected areas. This figure is substantially higher than the total population of 15,744 as counted in 2001, with an increase of nearly 89% over the 14 years.

The Greater Kruger area hosts 78% of South Africa's elephant (21,657 animals), a similar proportion to the 82% in 2001 (then 12,924 animals). Few elephants are found on community land, with less than 1% (115 animals) of the national population on community-owned land in 2001, rising to just 2.3% (652 animals)in 2015. The proportion of privately owned elephants within SA has changed from 17.5% (2,755 animals)in 2001, to 22.8% (6,430 animals) in 2015, with the actual number of elephants being privately owned more than doubling. Although elephant numbers have significantly increased on private, state and communal land ($p<0.05$) since 2001, the proportion of ownership between these entities have stayed the same ($p>0.05$; Figure 1).

South Africa's elephant populations are spread across seven of the country's nine Provinces (Figure 2). Only the Northern Cape and Free State provinces, in the arid north-west of the country, have no elephants. Gauteng Province is home to a population of just 13 individuals, whilst Limpopo province hosts the majority of the country's elephants, even when excluding those found within the Greater Kruger area. Many of Limpopo's non-Kruger elephants occur on privately owned land (939 animals), the rest being divided between state and community-owned reserves. North-West Province hosts the most state-owned elephant, at 1,246 animals, outside of Greater Kruger (Table 1 and Figure 3).

Between 2001 and 2015, 26 reserves introduced elephant for the first time. As can be seen in table 1, these introductions mainly occurred in the Eastern Cape (80 elephants on 6 reserves), KwaZulu Natal (149 elephants on 5 reserves) and Limpopo (78 elephants on 5 reserves). All of these new reserves are privately owned, and the elephants introduced to them originated from various existing reserves, including in the Greater Kruger area (Table 1).

On average, between 2001 and 2015, elephant population change for all provinces in South Africa, including the Greater Kruger has been positive, with ranges of increase between 1.8% per year (Limpopo private land) and 4.3% per year (Kruger private land) (Figure 4).

Thirty-three reserves answered our questions about non-lethal management interventions. Of these, 13 confirmed that they use the PZP vaccine on elephant cows as a means of birth control, whilst 4 reserves stated that they had vasectomized one or more of their bulls as a means of birth control. Ten reserves have used GnRH on their bulls, and did so in an attempt to decrease aggression and signs of musth, rather than primarily as a contraceptive measure.

As would be expected, the elephant population increase is significantly higher for reserves that do not use birth control (5.53%) compared to reserves that do (0.18%) ($N=27$, $p < 0.05$). However, there was no significant different in population increases between reserves that use birth control and open systems ($N=14$, $p > 0.05$) whereas increase in reserves that did not use birth control were significantly higher than open systems ($N=19$, $p < 0.05$).

Population viability

There are 78 discrete elephant populations in South Africa (considering the ten Greater Kruger reserves as one population). However, currently, these elephant populations can mix and inter-breed only if individual elephants are artificially translocated by human managers (Garaï et al., 2004). Between the 78 reserves, 21 small populations occur on reserves that share a communal boundary fence, which, if opened, would result in nine larger populations. Another eight populations occur on reserves that border a trans-frontier park containing free-roaming elephant populations.

Moreover, of the 78 discrete populations within South Africa, 59% are not socially viable according to our proxy minimum figure of 34 elephants per population. Of the 33 reserves

240 that provided data on elephant age and sex structures, nine reserves hosted either no bulls or
241 only one bull, and 17 had fewer than four bulls; 53% of the elephant populations we know
242 about do not contain socially viable male populations.

243 Furthermore, 77% percent of the populations were not genetically viable according to
244 Franklin (1980) and Sukumar (1993). That is, in 60 reserves the elephant population
245 numbered fewer than 100 individuals. Thirty-eight of the reserves that numbered fewer than
246 100 elephants in 2001, and so could not be considered genetically viable then, remain with a
247 population under 100 today. Only three of the genetically unviable populations are state-
248 owned; one each in of Eastern Cape, Western Cape and Limpopo provinces. All four of the
249 nationally-owned, SANParks-managed populations are genetically viable, with a minimum
250 population size of at least 240 individuals. Conversely, at least 90% of all the privately
251 owned reserves in all seven Provinces contain fewer than 100 elephants.

252 **Discussion**

253 Since Hall-Martin's national elephant survey in 1992, South Africa's elephant numbers have
254 more than tripled and, unlike most countries in Africa where poaching is rife (Chase et al.,
255 2016), the elephant population continues to increase within the country. This increase is true
256 of all provinces that host elephants, and although in some cases it is attributable to the
257 introduction of translocated elephants to new reserves, it is mostly due to population
258 expansion within established ranges.

259 Our total population estimate for South Africa (28,168) is substantially more than the
260 estimates recently published for the country as part of the Great Elephant Census (GEC)
261 (17,433) (Chase et al., 2016). The GEC figure was based a transect count over the Kruger
262 National Park whereas our figure includes all the private reserves adjacent to and open with
263 Kruger, as well as fenced parks and reserves in the rest of the country. Although we do

acknowledge the limitations of our population estimates in that, other than for the GEC, different pilots and counters were used in the aerial counts conducted by each reserve, we believe that even allowing for potential errors introduced by inexperienced counters, our estimate at the least gives a true representation of the *minimum* number of elephants in the country.

However, mere numbers and general population statistics do not always reflect the stability of a species, particularly one with such complex social structures and spatial requirements as the African elephant. Elephant societies in an open landscape are multi-tiered (Wittemyer et al., 2005) with genetic relatedness and the presence of experienced elders playing an important role in the stability and functioning of the society (Gobush and Wasser 2009; Goldenberg et al., 2016; McComb et al., 2001, McCombe et al 2011). We have shown that South Africa's elephant are widely fragmented, and most populations consist of only single families, and/or incomplete bull hierarchies.

In an initial attempt to measure and assess the potential impacts of this fragmentation, we introduced the concept of a socially viable population. Much has been written about the problems associated with keeping elephants in unnatural social groups (Bradshaw et al. 2005; Gobush and Wasser 2009), and it is apparent that elephants that do not have access to the kind of society found in large, open elephant populations often demonstrate abnormal, possibly aggressive, or maladaptive behaviour (e.g. see Slotow et al., 2000; Shannon et al., 2013)). We argue, therefore, that the concept of a *socially-viable* group is necessary for the improved management of elephants in fenced reserves. By allowing elephants to live in societies that better mimic natural social patterns and hierarchies, there is good reason to think that fewer behavioural problems will manifest. The minimum socially-viable population size of 34 individuals that we used here was defined according to average family sizes in natural elephant populations, and the minimum number of family groups and bulls

289 that together could provide the same hierarchical structure known in open elephant
290 populations. However, we must be clear that this figure is, at this stage, purely an estimate
291 and further research is required to both validate the utilty of the concept, and determine the
292 most appropriate minimum figure. However, based on current arguments and knowledge, it is
293 clear that the majority of elephant reserves in South Africa do not have the number of
294 elephants required for normal social functioning. Many populations are not genetically or
295 socially viable.

296 In South Africa wildlife may be privately owned, and many reserves keep elephants for the
297 economic benefits of photographic safaris and/or hunting. Such reserves dedicate large tracts
298 of land to conservation which might otherwise be used for farming or other commercial
299 purposes (Cousins et al., 2008), but the social requirements of species within these reserves
300 must also be taken into consideration. Currently, the *National Norms and Standards for the*
301 *Management of Elephant in South Africa* (Department of Environmental Affairs, 2008) does
302 not include any mention of keeping socially and genetically viable populations. We strongly
303 recommend that such standards be included in future.

304 In accordance with the findings of Delsink et al. (2006), our analysis shows that currently
305 used techniques of birth control (namely the PZP vaccine and vasectomy of bulls) are
306 effective in reducing elephant population increases, as is often required on small reserves.
307 However, it is apparent from our surveys that a third of the reserves who completed the
308 questionnaire use GnRH with the sole aim of reducing aggression in elephant bulls (De Nys
309 et al., 2010). The probable cause of this negative aggression – namely the lack of complete
310 and normally functioning bull hierarchies – is generally ignored, even though
311 hyperaggression in young adult elephant males in the absence of older experienced bulls has
312 been well described (Slotow et al., 2000). Given that little is known about the long-term

313 consequences of GnRH use on fertility, we caution against using this as a simple remedy for
314 male aggression, and encourage managers to consider the underlying causes of any
315 aggressive behaviour.

316 We believe that emphasis should now be placed on opening the fences between neighbouring
317 elephant reserves to increase population and range sizes, and reduce the need for intensive
318 artificial management. An increasing number of reserves across the African continent are
319 now erecting (or considering the use of) fences in order to manage and contain elephant and
320 other wildlife populations (Durant et al., 2015; Woodroffe et al., 2014). We urge policy
321 makers to at least consider the impacts on population viability when making such decisions in
322 the future. With the numbers of elephants plummeting across the continent (Chase et al.,
323 2016), we must make sure that as many populations as possible are and remain viable, and
324 accurately counting elephant populations is a necessary first step towards this goal.

325 Despite the increases in South Africa's elephant population in the last century, the country
326 has a mixed history of interaction with elephant: indiscriminate hunting of elephant for ivory
327 in the late 19th century, proclamation of fenced provincial and national parks hosting
328 elephant in the early 20th century, culling of elephant to control numbers in these fenced
329 parks in the mid 20th century, translocation of elephant to new fenced reserves in the late
330 20th century, contraception of elephant cows and vasectomy of elephant bulls since the
331 beginning of the 21st century, and most recently use of hormonal vaccines to modify
332 behaviour (Scholes and Mennell, 2008). We hope the next era of elephant history in South
333 Africa will be one of defragmentation of elephant habitat and formation of corridors to
334 facilitate the restoration of viable, functioning elephant societies.

335

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Authors' Contributions

YP and MG conceived the study, designed the methodology and collected the data. YP and LB analysed the data. All authors contributed to writing and revision of the article and approved the final version for publication.

References

Armbruster, P. & Lande, R. (1993). A population viability analysis for African elephant (*Loxodonta africana*): How big should reserves be? *Conservation Biology* 7(3):602-610.

Blanc, J. (2008) Loxodonta africana. In The IUCN Red List of Threatened Species 2008: e.T12392A3339343 Http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T12392A3339343.en [accessed 28 September 2017].

Bouché, P., Douglas-Hamilton, I., Wittemyer, G., Nianogo, A.J., Doucet, J.L., Lejeune, P. & Vermeulen, C. (2011). Will elephants soon disappear from West African savannahs? *PLoS One,* 6(6), e20619.

Bradshaw, G. A., Schore, A. N., Brown, J. L., Poole, J. H. & Moss, C. J. (2005). Elephant breakdown. *Nature,* 433(7028), 807-807.

359 Byrne, R.W., Bates, L.A. & Moss, C.J. (2009) Elephant cognition in primate perspective.
360 *Comparative Cognition & Behavior Reviews*, 4, 65-79.

361 Chase, M.J., Schlossberg, S., Griffin, C.R., Bouché, P.J., Djene, S.W., Elkan, P.W., Ferreira,
362 S., Grossman, F., Kohi, E.M., Landen, K. & Omondi, P. (2016). Continent-wide survey
363 reveals massive decline in African savannah elephants. *PeerJ,* 4,e2354.

364 Clubb, R., Rowcliffe, M., Lee, P., Mar, K.U., Moss, C. & Mason, G.J. (2008). Compromised
365 survivorship in zoo elephants. *Science,* 322(5908), 1649-1649.

366 Cousins, J. A., Sadler, J. P. & Evans, J. (2008). Exploring the role of private wildlife ranching
367 as a conservation tool in South Africa: stakeholder perspectives. *Ecology and Society,* 13(2),
368 43.

369 Cruise, A. (2016). Breaking: Pro-Ivory Trade Country's Change of Heart Upends Elephant
370 Debate. *National Geographic* http://news.nationalgeographic.com/2016/10/elephants-ivory-
371 trade-botswana-cites/

372 Delsink, A. K., J. J. Van Altena, D. Grobler, H. Bertschinger, J. Kirkpatrick, andR. Slotow.
373 (2006). Regulation of a small, discrete African elephant population through
374 immunocontraception in the Makalali Conservancy, Limpopo, South Africa. *South African*
375 *Journal of Science* 102(9), 403-408.

376 De Nys, H.M., Bertschinger, H.J., Turkstra, J.A., Colenbrander, B., Palme, R. & Human, A.
377 M. (2010). Vaccination against GnRH may suppress aggressive behaviour and musth in
378 African elephant (*Loxodonta africana*) bulls: a pilot study. *Journal of the South African*
379 *Veterinary Association,* 81(1),8-15.

380 Department Of Environmental Affairs And Tourism (2008) National Norms and Standards
381 for the Management of Elephants in South Africa in terms of section 9 of the National

382 Environmental Management: Biodiversity Act, 2004 (Act No. 10 of 2004).

383 Donaldson, S. & Kymlicka (2011) *Zoopolis: A Political Theory of Animal Rights*. Oxford
384 University Press, Oxford, UK.

385 Durant, S.M., Becker, M.S., Creel, S. Bashir, S., Dickman, A.J., Beudels-Jamar, R.C.
386 Lichtenfeld, L., Hilborn, R., Wall, J., Wittemyer, G. & Badamjav L. (2015). Developing
387 fencing policies for dryland ecosystems. *Journal of Applied Ecology,* 52(3), 544-551.

388 Evans, K. E., & Harris, S. (2008). Adolescence in male African elephants, *Loxodonta*
389 *africana*, and the importance of sociality. *Animal Behaviour,* 76(3), 779-787.

390 Franklin, I.R. (1980). Evolutionary change in small populations. In *Conservation Biology: An*
391 *Evolutionary Perspective* (eds M.E. Soulè B.A. Wilcox), pp 135. Sinauer Associates,
392 Sunderland.

393 Garaï, M.E., Slotow, R., Carr, R.D. & Reilly, B. (2004). Elephant reintroductions to small
394 fenced reserves in South Africa. *IUCN,* 3, 27.

395 Gobush, K.S. & Wasser, S.K. (2009). Behavioural correlates of low relatedness in African
396 elephant core groups of a poached population. *Animal Behaviour,* 78(5), 1079-1086.

397 Goldenberg, S.Z., Douglas-Hamilton, I. & Wittemyer, G. (2016) Vertical transmission of
398 social roles drives resilience to poaching in elephant networks. *Current Biology*, 26, 75–79.

399 Hall-Martin, A. J. (1992). Distribution and status of the African elephant *Loxodonta africana*
400 in South Africa, 1652-1992. *Koedoe,* 35(1), 65-88.

401 Landman, M., Schoeman, D.S. & Kerley, G.I.H. (2013) Shift in black rhinoceros diet in the
402 presence of elephant: evidence for competition? *PLoS ONE*, 8(7), e69771.

403 Lee, P.C., & Moss, C.J. (1986). Early maternal investment in male and female African
404 elephant calves. *Behavioral Ecology and Sociobiology,* 18(5), 353-361.

405 Lötter, H.P.P. (2008). Ethical considerations in elephant management. In *Elephant*
406 *management: a scientific assessment of South Africa (eds* R.J. Scholes & K. Mennell). Wits
407 University Press. Johannesberg.

408 Mccomb, K., Moss, C.J., Durant, S.M., Baker, L. & Sayialel, S. (2001) Matriarchs as
409 repositories of social knowledge in African elephants. *Science*, 292, 491–494.

410 Moss, C.J. (2001) The demography of an African elephant (Loxodonta africana) population
411 in Amboseli, Kenya. *Journal of Zoology*, 255, 145–156.

412 Poole, J. H. (1994). Sex differences in the behaviour of African elephants. In *The differences*
413 *between the sexes* (eds R.V. Short & E. Balaban), pp 331-346, Cambridge University Press.
414 United Kingdom.

415 Scholes, R. J., & Mennell K. (eds.). (2008). *Elephant management: a scientific assessment of*
416 *South Africa.* Wits University Press. Johannesburg.

417 Shannon, G., Slotow, R., Durant, S.M., Sayialel, K.N., Poole, J., Moss, C. & McComb, K.
418 (2013) Effects of social disruption in elephants persist decades after culling. *Frontiers in*
419 *Zoology*, 10, 62.

420 Slotow, R., van Dyk, G., Poole, J., Page, B. & Klocke, A. (2000). Older bull elephants
421 control young males. *Nature,* 408(6811), 425-426.

422 Slotow, R., Garaï, M.E., Reilly, B., Page, B. & Carr, R.D. (2005). Population dynamics of
423 elephants re-introduced to small fenced reserves in South Africa. *South African Journal of*
424 *Wildlife Research,* 35(1), 23-32.

425 Snijders, D. (2012) Wild property and its boundaries—on wildlife policy and rural
426 consequences in South Africa. Journal of Peasant Studies, 39, 503–520.

427 Sukumar, R. (1993). Minimum viable populations for elephant conservation. *Gajah* 11.

428 Wittemyer, G., Daballen, D. & Douglas-Hamilton, I. (2013) Comparative demography of an
429 at-risk African elephant population. *PLoS ONE*, 8(1), e53726.

430 Wittemyer, G., Douglas-Hamilton, I. & Getz, W. M. (2005). The socioecology of elephants:
431 analysis of the processes creating multitiered social structures. *Animal behaviour,* 69(6),
432 1357-1371.

433 Wittemyer, G., Northrup, J.M., Blanc, J., Douglas-Hamilton, I., Omondi, P. & Burnham, K.
434 P. (2014). Illegal killing for ivory drives global decline in African elephants. *Proceedings of*
435 *the National Academy of Sciences,* 111(36), 13117-13121.

436 Woodroffe, R., Hedges, S. & Durant, S.M. (2014). To fence or not to fence. *Science,*
437 344(6179), 46-48.

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439 **Biogeographical sketches**

440 Yolanda Pretorius's research focuses on foraging ecology and welfare of African elephant,
441 including rehabilitation of captive elephant into the wild. Marion Garaï's research interests
442 include behaviour of translocated elephant in South Africa and welfare of elephants in
443 European zoos. Lucy Bates's research focuses on cognition and the differences in social
444 behaviour of African elephant across the continent. All authors are on the steering committee
445 of the Elephant Specialist Advisory Group (South Africa).

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448 **Table 1**: The number, provincial location and ownership of elephants in South Africa in
449 2015. The number of additional reserves that have introduced elephant between 2001 and
450 2015 are shown, as well as those sold or removed their elephants. Numbers in brackets
451 indicate those that are owned by the state (at National or Provincial level)

Region	Elephant status 2015		Elephant range expansion 2001 - 2015		Elephants removed 2001-2015	
	Number of reserves hosting elephants (No. owned by the state)	Number of elephants (No. owned by the state)	Number of additional reserves	Number of elephants introduced	Number of reserves ceasing to hold elephants	Number of elephants affected
Eastern Cape	11 (2)	918 (663)	6	80	0	0
Gauteng	1 (0)	13 (0)	1	12	0	0
KwaZulu Natal	20 (5)	1,873 (1299)	5	149	0	0
Limpopo	32 (4)	2,226 (635)	5	78	2	17
Mpumalanga	5 (2)	186 (155)	2	14	0	0
North-West	4 (2)	1,262 (1246)	1	7	1	22
Western Cape	4 (1)	33 (2)	4	31	0	0
Greater Kruger	10 (1)	21,657 (17086)	2		0	0
TOTAL	87 (17)	28,168 (21086)	26	371	3	39

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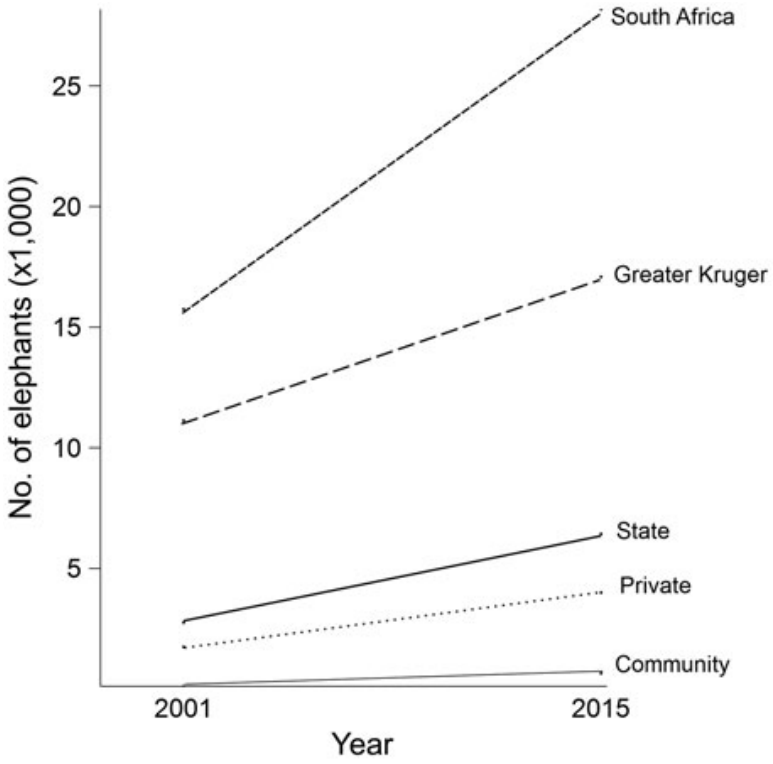
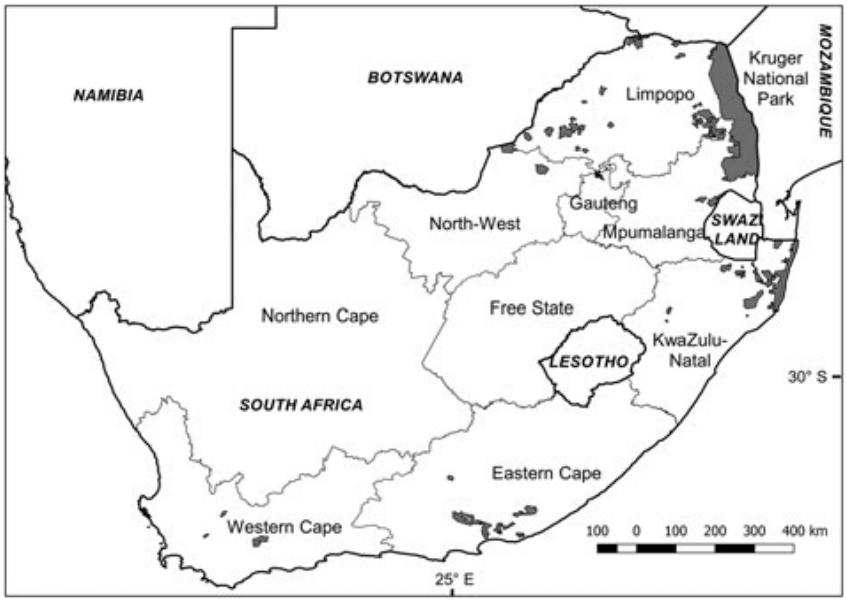


Figure 1: Increases in elephant numbers in the Greater Kruger area and on additional communal, state, and privately owned land across South Africa between 2001 and 2005.



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460 **Figure 2**: Distribution ofelephants in South Africa in 2015 (grey shading). Spatial data

461 supplemented by ESAG and the South African National Biodiversity Institute.

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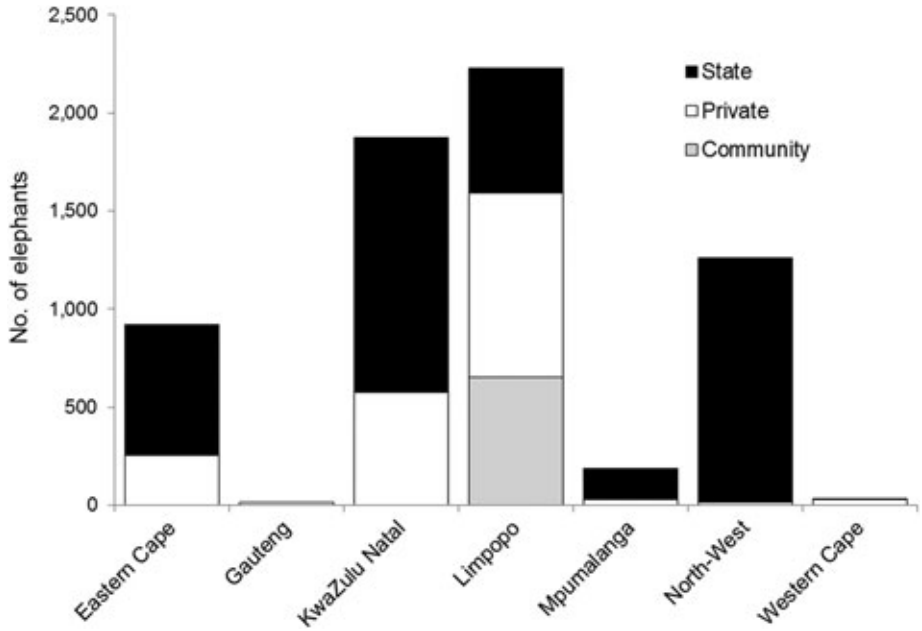

464

465 **Figure 3:** Number of elephants outside of Greater Kruger on state-, private- and communal

466 land in South Africa's provinces in 2015.

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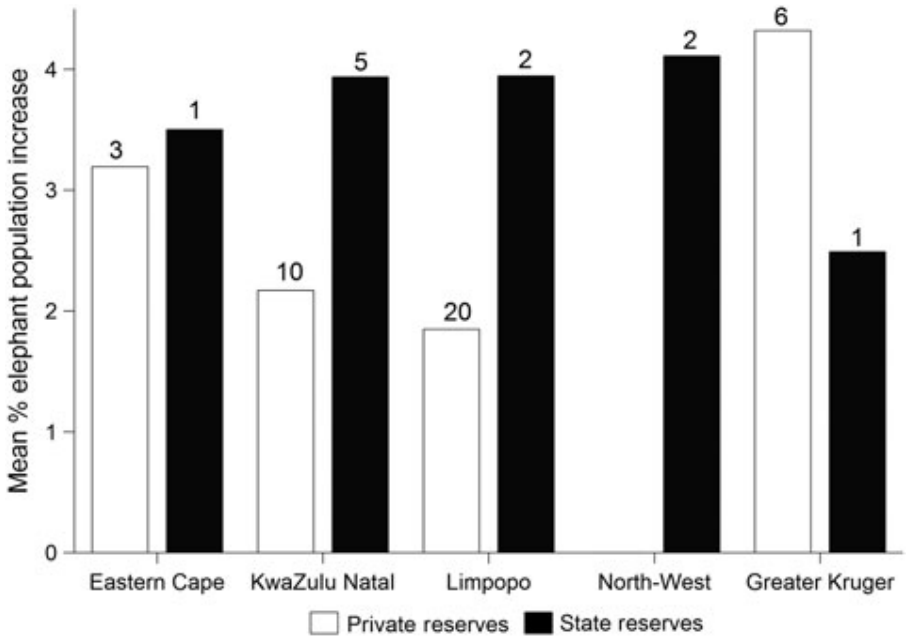

468

469 **Figure 4:** Mean annual population increase of elephants in South Africa between 2001 and
470 2015 (by province), with numbers of reserves for which data were available indicated over
471 the bars.

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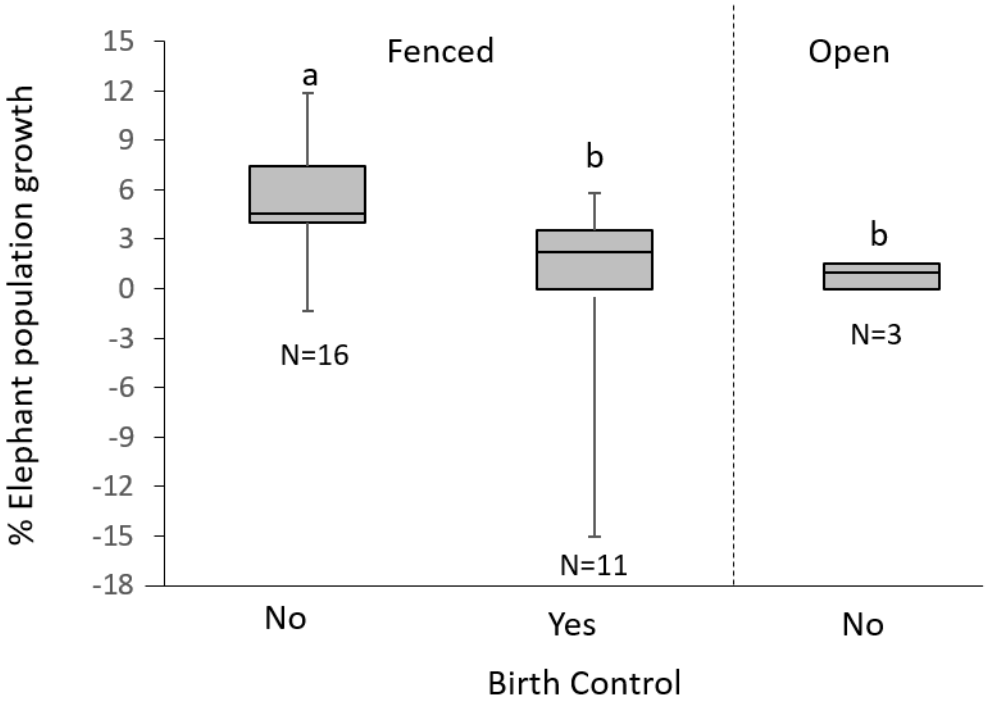

474

475 **Figure 5:** Difference in mean annual percentage elephant population increase between
476 reserves using birth control, reserves that do not, and open and fenced systems (boxes
477 indicate the lower and upper quartile, and whiskers the lowest and highest percentage
478 increases; a is significantly higher than b).

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