





Elephant population responses to increased density in Kruger National Park



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The elephant population in the Kruger National Park (KNP) has been increasing since the cessation of culling in the mid-1990s. This contrasts with recent trends in elephant populations in many parts of Africa where poaching continues to decrease numbers. Logistic growth theory predicts that increased competition for vital resources when densities increase should serve to constrain population growth, implying a negative density-growth correlation. We tested this prediction using 28 years of elephant census data to investigate how the growth of the KNP's elephant population responds to increasing elephant density from the period 1985 to 2012. We expected a spatially variable population growth pattern in response to the distribution of elephant densities in the park and thus classified the park into zones with low, medium or high long-term (28 years) average, dry-season elephant density. Zones were named 'peripheral', 'semi-peripheral' and 'core' zones, respectively, and represent proxies of resource availability to elephant herds. Using a Stochastic Ricker growth model, we tested for the presence of negative density-dependence in population growth in the core versus peripheral zones. In response, we only detected density-dependent growth in the core zone. Overall the population grew at 4.1% per year, coupled with local recruitment rates that increased over time, particularly in the peripheral zones. These density-dependent trends support previous observations of homogenisation of elephant distribution and density across the KNP landscapes.

Conservation implications: Density-dependent changes to elephant growth rates are scale-dependent (local vs. park level). Only core areas with long-term high density show signs of density-dependent growth. Overall, the distributions of elephants are homogenising in the KNP. Conservation authorities should monitor the impact of such homogenisation to landscape heterogeneity. The spatial variation of the negative density-growth correlation, especially between the core and peripheral zones, can be considered when developing effective strategies to manage the KNP elephant population.

Keywords: African elephants *Loxodonta africana*; population growth; density dependence; spatial distributions; conservation management.

Introduction

Despite threats of poaching and habitat loss, trends in the numbers of African elephants (*Loxodonta africana*) in southern Africa contrast with their declining numbers in the rest of the continent (Chase et al. 2016). South Africa epitomises these trends with populations increasing in trans-frontier (Selier et al. 2016) and fence protected areas (Pretorius, Garai & Bates 2019). Apart from being a key component of South Africa's natural heritage, elephants are ecological engineers or habitat modifiers because of the substantial influence they exert on the habitats they share with other co-occurring species (Valeix et al. 2011). That is, elephants can change the structure of vegetation whilst browsing and can therefore become a catalyst for landscape state change (Eckhardt, Van Wilgen & Biggs 2000; Trollope et al. 1998). As a result, the influence of elephants on ecosystems has stimulated much debate (Van Aarde, Whyte & Pimm 1999; Van Wyk & Fairall 1969).

The Kruger National Park (KNP) in South Africa is a large, protected area where elephant numbers increased from an estimated 10 animals in the early 1900s to over 17 000 elephants in 2015 (Ferreira, Greaver & Simms 2017). Historically, authorities linked increasing elephant population size to vegetation impact, resulting in action being taken to control elephant numbers through culling (Van Aarde, Whyte & Pimm 1999). Changes in conservation philosophy led to the subsequent cessation of elephant culling in 1995, in favour of allowing density-dependent processes to guide population dynamics over the longer term (Whyte et al. 1999). In the same period (1997), the systematic removal of many artificial water points in the park was implemented to regulate game distributions by returning surface water availability to a more natural state (Pienaar et al. 1997).

The authorities also increased efforts to provide more land for elephants by removing fences from neighbouring private protected areas and international trans-frontier parks since 1996 (Venter et al. 2008). In general, these management actions aim to let the spatial heterogeneity of resources, such as water and vegetation, drive elephant distributions and regulate the impacts elephants exerted on landscape heterogeneity in lieu of directly regulating population size (Owen-Smith et al. 2006; Van Aarde et al. 1999).

To date, the effectiveness of changing elephant management strategies to achieve different biodiversity conservation goals remains open to debate. Elephant distribution in the KNP has become less clumped and more homogeneous as their density has increased (MacFadyen et al. 2019). This is likely because of elephants' responses to local resource and space constraints from crowding and consequent movement into relatively lower quality habitats (MacFadyen et al. 2019; Robson & Van Aarde 2018) or could be a result of artificial water holes still enabling elephants to utilise areas far from natural water sources (Purdon & Van Aarde 2017). Many have argued that this movement into lower quality habitats should result in decreased survival and birth rates and eventually serve to regulate population growth dynamics (Owen-Smith et al. 2006; Robson & Van Aarde 2018). Others have speculated that this has already contributed to lower population growth rates as new management interventions were introduced (Ferreira et al. 2017). Increased elephant density and the spatial variation of climate and vegetation in the park are expected to jointly affect elephant population growth (Robson 2015). On the other hand, as elephants spread further into the landscape, they will also utilise and potentially disturb a much larger part of the vegetation in the park (MacFadyen et al. 2019; Young, Ferreira & Van Aarde 2009a). This will compromise and even counter management goals of letting landscape heterogeneity drive and regulate the distribution of elephants.

Population change rate is dependent on population density, whilst the strength of density-growth correlation should vary across landscapes (Owen-Smith et al. 2006). Large vertebrates typically display convex curves of density-dependent population growth patterns (Sibly et al. 2005). This means that density-dependent growth only becomes evident once the population is close to the carrying capacity of the habitat (Fowler 1981), as is often seen in smaller, fenced reserves. Such density dependence originates from the way large vertebrates respond to aggravating resource constraints. For example, when density increases juvenile survival rates typically decrease followed by reduced reproductive outputs, whilst adult survival rates decrease, culminating in reduced population growth (Eberhardt 2002).

Like most large herbivores, elephants choose landscapes based on water, food, comfort and safety (Boult et al. 2019; Chamaillé-Jammes, Valeix & Fritz 2007; Kinahan, Pimm & Van Aarde 2007; Purdon & Van Aarde 2017; Wittemyer et al. 2017) and make large seasonal movements (e.g. Cook,

Henley & Parrini 2015). During the dry season, the distribution of water is a primary driver of elephant space use (Chamaillé-Jammes et al. 2007; Purdon & Van Aarde 2017). This need for water often exceeds the selection of food resources in water-scarce ecosystems and thus elephants are restricted to habitats near water sources. As elephant breeding herds normally use the same dry season home ranges from year to year (Young, Ferreira & Van Aarde 2009b), we assume the dry season is the key period during which density-dependent processes will activate. As negative density-dependent growth only occurs in areas with high elephant density, we might not be able to detect it at a park-wide scale. As a result, we focus on how local population growth varies spatially in different long-term density zones throughout the park.

Negative density-dependence refers to the decline in population growth rate in response to increasing population size or density (Hixon & Johnson 2009), which is typically associated with the effect of intense resource competition from overcrowding. To identify the effects of density-dependent growth, we consider two lines of evidence. Firstly, we present a statistical test for negative density-dependent growth described by Dennis and Taper (1994) that incorporates logistic growth theory (Tsoularis & Wallace 2002; Verhulst 1845). This approach differs from earlier works that identify changes to growth trends by comparing goodness-of-fit of growth models over different time periods (Ferreira et al. 2017) or identify factors influencing population growth with regression models (Robson 2015). Secondly, we quantify trends in the recruitment rates of elephant calves. Mainstream large vertebrate models often predict juvenile survival as the first demographic variable to respond to resource constraints (Eberhardt 2002; Trimble, Ferreira & Van Aarde 2009). The calves counted during the annual dry season censuses, represent those born and also survived between the previous and present dry season. This recruitment serves as a proxy to evaluate early demographic responses to population density (Eberhardt 2002; Trimble et al. 2009). Here we expect a negative density-dependent recruitment rate from density increases and the resulting resource constraints in the dry season.

Research methods and design

Study area

The KNP is situated in the north-eastern part of South Africa, bordered by Mozambique and Zimbabwe to the east and north, respectively (Figure 1a). It covers an area of approximately 2 million hectares and is comprised of 35 predominantly savanna and woodland ecosystems (Gertenbach 1983) including a number of artificial water points at scattered locations, permanent and seasonal rivers pass through the park and water supply network. The KNP has a summer rainfall season (Gertenbach 1983), with the south-western part receiving higher annual rainfall (Figure 1a; MacFadyen et al. 2018).

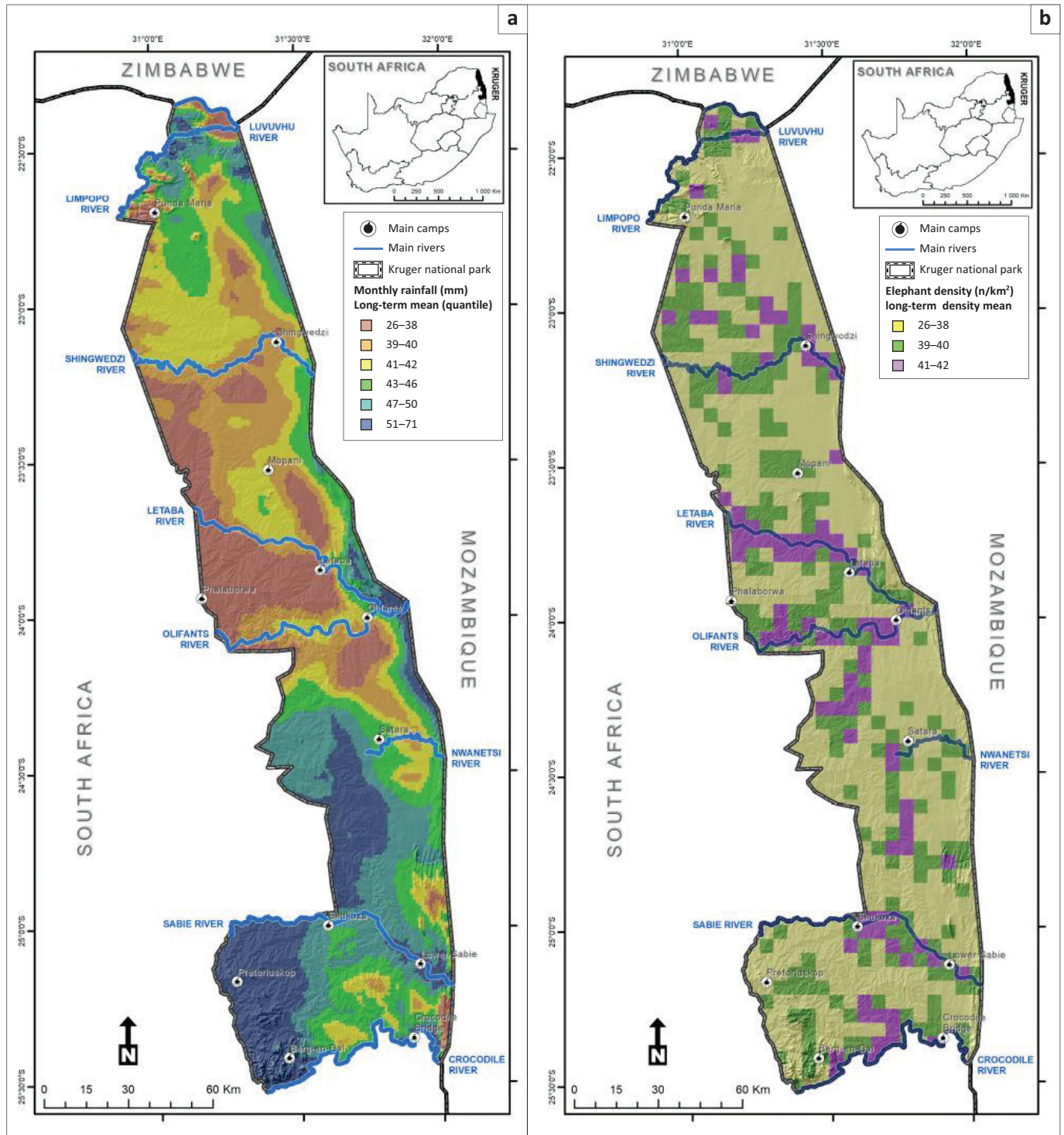


FIGURE 1: (a) The Kruger National Park, South Africa, lies between latitudes 22°19'40" S to 25°31'44" S and longitudes 30°53'18" E to 32°01'59" E. Main rivers (in blue) supply water throughout the year. Rainfall occurs mainly in summer and varies in the park. The long-term average monthly rainfall for areas is indicated in the figure by a colour sequence from red (dry) to blue (wet). (b) Average elephant density observed in each 25 km² grid-cell throughout the study period (1985–2012). Grid-cell colour indicates density of elephants per square kilometre. High density cells are coloured in purple, whilst medium and low-density cells are in green and yellow. The data are from yearly elephant censuses.

Data collection

For this study, we used census data from annual aerial counts conducted in the KNP between 1985 and 2012. All censuses were flown during the dry season (July / August / September), when reduced foliage makes elephant spotting easier (Van Aarde et al. 1999). Counts were conducted using a spotting crew and helicopter that systematically flew over 21

designated census blocks to record all elephants sighted. Each observed herd is recorded with the geolocation, number of elephants in the herd and group type (i.e. bull group or herd group). Bull groups consist of only bull animals whilst herd groups are a mix of cows and bulls of different age classes. In these mixed groups, the number of calves younger than 1 year was also recorded. No information was recorded on elephant deaths, immigrations or emigrations, which

may result in an underestimate of birth rates. These data only represent a winter account of elephant distributions. However, water availability and foraging range are limited to a larger degree in these drier winter months (Codron et al. 2006; MacFadyen et al. 2019; Thomas, Holland & Minot 2008), and it is still the best representation of long-term elephant population distributions in the KNP. See Whyte (2001) for a full description of the census methodology.

Data preparation

All statistical analyses were carried out using R version 3.6.1 (R Core Team 2019) and associated R packages referenced in the text. Firstly, we divided the KNP into a grid with 3738 cells of 5 km × 5 km and aggregated the total number of elephants observed in each grid cell for each census year, distinguishing elephants in bull groups, elephants in mixed herd groups and number of calves present. We then calculated: (1) the density of elephants per square kilometre in each grid cell for each year (Equation 1) and (2) the proportion of calves per herd born since the previous census using *raster* (Hijmans 2020). We defined local population density as follows:

$$d_i(t) = \frac{\sum_j n_{ij}(t)}{A_i} \quad [\text{Eqn 1}]$$

where $d_i(t)$ is the density in the i -th grid cell at year t ; A_i the surface area of the i -th grid cell (25 km²); and $n_{ij}(t)$ the total number of elephants in the j -th point observation of an elephant group in grid cell i in year t .

We then determined the long-term average density of elephants for each grid cell in the KNP from 1985 to 2012. That is, for each cell we estimated the average density from annual census records; for cell i , it is the average of $d_i(t)$ over t . Grid cells were then assigned into three zones according to this long-term average density pattern: periphery (0.0–0.5), semi-periphery (0.5–1.0) and core zone (> 1) (units are elephants per square kilometre). We then summarised the growth patterns in grid cells for each zone and produced a map that illustrates the three zones. Throughout our investigation, we made the distinction between time periods when the population was constrained by culling (1985–1995) and when culling was stopped (1996–2012). We did this because culling aimed to maintain the KNP's elephant population at a roughly constant size and would thus have obstructed normal population growth rates.

Growth rates

To estimate the overall growth trends of elephant population numbers, we fitted an exponential growth model to the average, park-wide elephant density from 1985 to 2012 using the least-squares method. We fitted separate exponential models for the two periods: (1) when the population was maintained by culling (1985–1995) and (2) when the population was released from culling (1996–2012):

$$d(t) = d_0 e^{rt} \quad [\text{Eqn 2}]$$

where $d(t)$ is the total elephant population density at time t ; d_0 the initial population density; and r the per-capita annual growth rate.

To identify the effect of elephant population size on growth rate, we used a statistical test for density-dependent growth described by Dennis and Taper (1994). We applied this test first to the time-series of park-wide total population size and then to the time-series of total population size in each of the three zones (core, semi-periphery and periphery). This test assumes growth happens according to a stochastic Ricker model, that is, a discrete-time model of logistic population growth, described as follows:

$$N_{t+1} = N_t \exp(a + bN_t + \sigma N_t Z_t), \quad [\text{Eqn 3}]$$

where N_t is population size at time t ; a and b are growth rate parameters describing the density-independent and density-dependent components of growth, respectively and Z_t is a noise component reflecting added stochasticity in the model. Therefore, if $b < 0$, this indicates a negative density-dependent growth in the population dynamics, suggesting a decline in growth rate in response to the increase of population density (Hixon & Johnson 2009). We tested whether b is significantly less than zero by assessing whether a model assuming $b < 0$ fits the observed population growth significantly better than the null model assuming $b = 0$. We conducted the test separately for the period when the population size was maintained through culling (1985–1995) and the period when the population had no culling (1996–2012).

To assess how well growth models described the observed population growth, we compared our estimated model to observed time-series data. To further uncover any potential patterns in the population growth of different zones, we fitted a smooth line to the time series using a smoothed conditional mean function in *ggplot2* (Wickham 2016).

Recruitment rates

For each observed mixed herd, the number of calves that were born and survived since the previous census year was documented. In this context, we quantified recruitment rate as the ratio of calves to other animals in each group. The subsequent metric represents how productive or fertile cows in each elephant herd and specific grid cell were, as well as how well calves from the previous year survived for a specific year. However, it is worth noting that the calf survival might have been overestimated because of the fact that the census was conducted during the dry season when resources are limited, so some calves could still succumb to resources limitations after the census. We specifically do not refer to *birth rate*, because we have no data on actual calf births or deaths. To estimate yearly recruitment rate, we calculated the proportion of the herd

made up of calves and reported the average for herds in each grid cell as follows:

$$R_i = \frac{\sum_j \frac{n_i c_{ij}}{h_{ij}}}{n_i} \quad [\text{Eqn 4}]$$

where R_i is the average recruitment rate per herd group in the i -th cell, c_{ij} the number of calves in the j -th elephant herd in cell i , and h_{ij} the number of elephants in the rest of the herd. The number of herd-groups in a grid cell is n_i . In this calculation, we excluded bull groups as calves are present only in mixed herds. To check whether recruitment rates differed significantly between grid cells belonging to the three different zones, we used the non-parametric Mann-Whitney U test. This statistical test is robust for data that is not normally distributed, for example, our data had unequal number of cells in the different zones. Furthermore, to reduce skewness in the distribution of recruitment rates, we transformed the recruitment rate by its cube root. We then fitted a smoothed conditional mean to the time series (Wickham 2016) to display recruitment rate trends in the core, semi-peripheral and peripheral zones. A non-parametric Mann-Kendall test was then conducted to test for the presence of a significant trend in elephant recruitment over the study period (between 1985 and 2012). We used this test because elephant recruitment rate was not normally distributed according to a Shapiro-Wilk test.

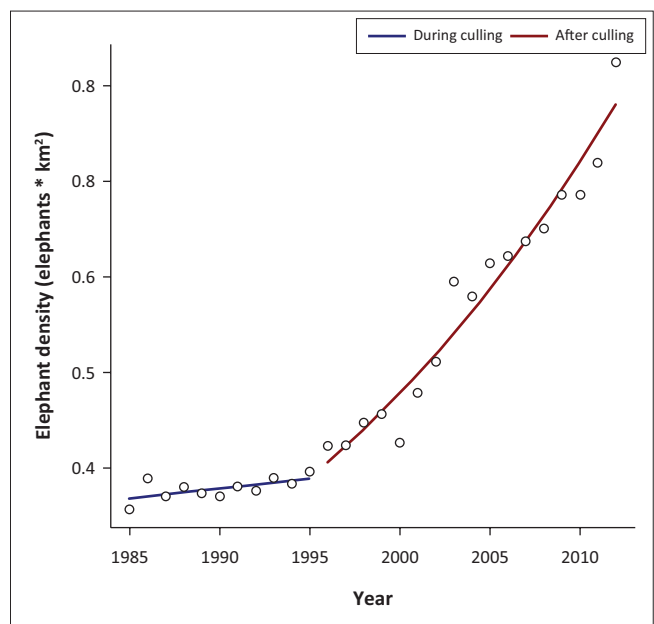
Results

Growth and density-dependence

During the period elephants were culled (1985–1995), the population was maintained at approximately 0.36 elephants per square kilometre (Figure 2; Appendix 1 Table 1-A1; $R^2 = 0.34$, $F(1,9) = 6.16$, $r = 0.006$, $p = 0.035$). In the period after 1995, growth can be described by an exponential model with per capita annual growth rate of 4.1% (Figure 2; Appendix 1 Table 1-A1; $R^2 = 0.95$, $F(1,15) = 278.4$, $r = 0.041$, $p < 0.001$).

During the culling period (1985–1995), the overall population and the zoned populations showed significant negative density-dependent growth (Appendix 1 Table 2-A1, Appendix 1 Figure 1-A1). For the post-culling period, no negative density-dependent growth was observed in the overall population (Figure 3a). That is, b was > 0 in the stochastic Ricker growth model (Eqn 3) and thus we could not reject the null hypothesis ($b = 0$) (see Appendix 1 Table 2-A1). However, we did find a significant ($\alpha = 0.05$) negative density-dependent component for elephant growth in the core zone ($b = -1.4 \times 10^{-4}$). In the semi-peripheral and peripheral zones, the bootstrap confidence intervals for the parameter b included zero, indicating no density-dependent effects.

Elephant densities increased in the core zone after culling practices (red line in Figure 4a). After 2008, elephant densities in these core areas began to stabilise, whereas in the semi-peripheral and peripheral zones elephant densities sharply increased even after 2008 (Figure 4a).



Note: Please see the article, Louw, A.S., MacFadyen, S., Ferreira, S. & Hui, C., 2021, 'Elephant population responses to increased density in Kruger National Park', *Koedoe* 63(1), a1660. <https://doi.org/10.4102/koedoe.v63i1.1660>, for more information.

FIGURE 2: Time series of park-wide elephant density in elephants per square kilometre, as obtained from annual census (circles). Lines represent exponential growth models (Eqn 2) fitted to the census time series for the period with culling (1985–1995) in blue and without culling (1996–2012) in red.

Recruitment rates

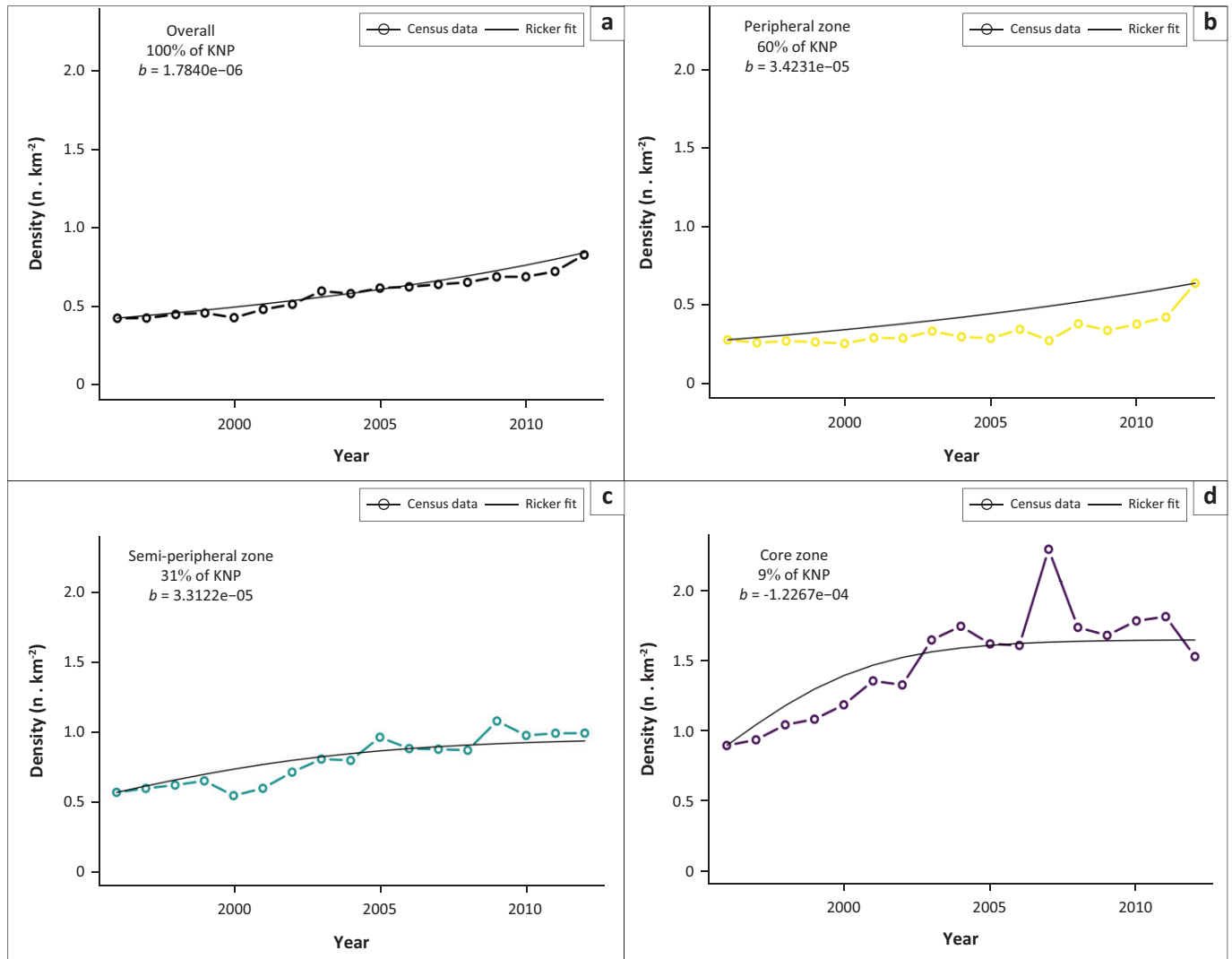
Elephant recruitment rates in the peripheral and semi-peripheral zones had a significant upward trend between 1985 and 2012 (Mann-Kendall tests for trends, $p = 0.017$ and $p = 0.034$, respectively; Table 4-A1). Recruitment rates in the core zone did not have a significant trend ($p = 0.277$) but were in general higher than the rates in the semi-peripheral and peripheral zones. Recruitment rates in the semi-peripheral zone were also higher than in the peripheral zone (Mann-Whitney U tests, Table 3-A1). Over time, however, the trends in recruitment appear to converge and all zones experienced similar recruitment rates by 2012 (Figure 4b).

Discussion

Scale and density-dependent growth

Elephant population growth rates in the KNP were expected to drop in response to management approaches that enhance habitat variability in the landscape (Ferreira et al. 2017). Over time, these reduced growth rates would manifest as reduced birth rates and increased mortality because of increased spatial variability of resources and thus increased competition for space and resources as population density increases (Van Aarde et al. 1999). We observed, however, that the KNP's population has been growing exponentially at an annual rate of 4.1% since culling stopped in 1995. These results are similar to those reported by Ferreira et al. (2017) but lower than the intrinsic growth rate reported during the time of culling (Whyte 2001).

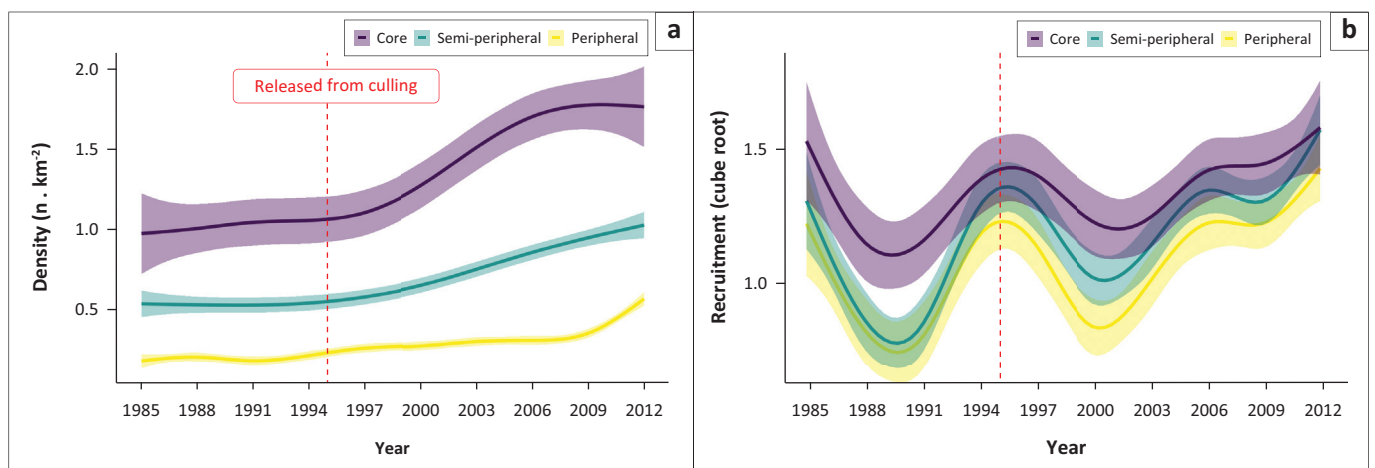
African elephant populations, when left undisturbed, typically experience exponential growth (Slotow et al. 2006). With persistent poaching, however, elephant population growth



Note: Please see the article, Louw, A.S., MacFadyen, S., Ferreira, S. & Hui, C., 2021, 'Elephant population responses to increased density in Kruger National Park', *Koedoe* 63(1), a1660. <https://doi.org/10.4102/koedoe.v63i1.1660>, for more information.

KNP, Kruger National Park.

FIGURE 3: Deterministic component of Stochastic Ricker growth models (Eqn 3) fitted to time series of elephant population in the Kruger National Park (1996–2012). Models shown for overall population (a), and separately for the three zones in the park; peripheral (b), semi-peripheral (c) and core (d). Test for negative density dependent growth reported significant for the core zone (d). Model parameter estimates in Appendix 1 (Table 2–A1).



Note: Please see the article, Louw, A.S., MacFadyen, S., Ferreira, S. & Hui, C., 2021, 'Elephant population responses to increased density in Kruger National Park', *Koedoe* 63(1), a1660. <https://doi.org/10.4102/koedoe.v63i1.1660>, for more information.

FIGURE 4: Time series of (a) elephant density per grid cell and (b) recruitment rate. The solid lines represent a smoothed conditional-means fit to the data in ggplot2. Filled regions show 95% confidence intervals. Grid cells were classified into three zones according to the average elephant density observed in them through the study period. Colour distinguishes the zones (grid cells that had a low average elephant density were classified as 'peripheral' and are shown in yellow, grid cells with medium average density were 'semi-peripheral' and are shown in blue and grid cells with high elephant density were defined as the 'core zone' for elephants and are in purple). A cube root transform is used to reduce skewness in the distribution of the recruitment rates. Recruitment rate is defined as the proportion of calves in a herd and is reported as an average for each grid cell (Eqn 4). Recruitment in the peripheral and semi-peripheral zones had significant upward trend, by Mann-Kendall test for trend (Table 4–A1).

can be disrupted (Chase et al. 2016) to such an extent that many places across the continent now have only 25% of expected elephant numbers (Robson et al. 2017). Different management strategies can also influence natural population dynamics and can disrupt natural density-dependent processes in protected areas. For instance, no density-dependent population growth has been recorded in elephants in the Addo Elephant National Park (AENP) (Gough & Kerley 2006) as various land acquisitions have increased the area available to elephants (Kerley, Boshoff & Knight 2002) and thereby potentially delayed the effect of resource constraints associated with increasing densities. During the culling era in the KNP, authorities aimed to maintain the elephant population size to around 7500 animals (Van Aarde et al. 1999). In practice, to achieve this annual culling, quotas were set based on the number of elephants counted the previous year. In other words, years with high elephant numbers had high culling quotas set the next year (Whyte 2001). In some ways, management's response was itself a density-dependent response. It is thus not surprising that we observed negative density-dependent population growth during the period when the elephant population was maintained at a target population size through regular culling (Appendix 1 Figure 1-A1; Table 2-A1). However, this 'density-dependent' population growth during the culling periods was not in response to resource constraints and once the population was released from culling the population growth rate switched to an exponential pattern (Figure 2). This is similar to observations elsewhere in South Africa (Slotow et al. 2006).

Exponential growth models describe the growth of populations in the absence of density-dependent growth constraints. As the elephant population growth was well described by an exponential growth model, it suggests that the KNP elephant population has not yet reached the point where resource constraints curtail the overall population growth in the park. That is, the population has not yet reached the total carrying capacity of the park (Van Dyken & Zhang 2019). For large vertebrates such as elephants, the effect of density on growth rates might only play out and become notable when population abundances have reached levels close to or above the carrying capacity (Fowler 1981; Sibly et al. 2005). Furthermore, in a large protected area, the total carrying capacity of the habitat becomes difficult to establish as it is then a function of local population growth parameters, habitat heterogeneity and the strength of dispersal (Van Dyken & Zhang 2019). In such cases, the population dynamics and presence of localised density dependence might differ from the dynamics observed for the population as a whole.

The effect of density dependence can therefore be scale-dependent. We failed to observe density-dependent growth at the scale of the entire park (i.e. the overall population growth; Figure 2 and Figure 3a), but we detected density-dependence effects on elephant growth at local scales (i.e. when growth was considered as spatially explicit across 25 km² grid-cells). In particular, in the core zone we

detected significant density-dependent growth (Figure 3d). These significant local-scale density-dependent growths were masked in the overall park-scale growth because of the spatial variation in local density-dependent growth (Figure 3b, 3c). The fact that density dependence was spatially variable suggests that the carrying capacity also varied across the landscape. Previous predictions that variations in local water and food availability, thus local carrying capacity, should influence the distribution and dynamics of elephants in the landscape are thus indirectly supported by our findings (Harris et al. 2008; Owen-Smith et al. 2006; Smit & Ferreira 2010; Young et al. 2009a).

Furthermore, the density-dependent growth in the core zone aligns well with the expected convex shape suggested by Sibly et al. (2005). That is, density-dependent effects are only realised at high density levels where elephants are likely to experience increased intraspecific competition for space and food resources (MacFadyen et al. 2019). Elephants respond to variation in resources and thus move extensively across the KNP (Cook et al. 2015). Elephants choosing favoured habitats in the core zone could therefore result in increased local intraspecific competition for space/territory (i.e. between elephant herds), which will limit the number of groups that can be present in an area (MacFadyen et al. 2019). This is known to occur when one herd dominates over another (Wittemyer & Getz 2007; Wittemyer et al. 2007), thereby displacing subordinate herds to suboptimal habitats. Such social dynamics could also accelerate herds' response to leave an area before resource conditions deteriorate to the point where a heuristic learning 'good-stay, bad-disperse' dispersal strategy is employed (Hui et al. 2012). This might explain elephant numbers rapidly increasing in the peripheral and semi-peripheral zones at roughly the same time (2008/2009) that elephant growth in the core zone slowed down. We speculate that the peripheral and semi-peripheral zones in our study represent suboptimal habitats, as those areas had lower dry-season herd occurrences over the long term. We did not directly evaluate habitat suitability for elephants in the different density areas, as performed in previous studies (Harris et al. 2008; Young et al. 2009a). The population distribution that results from these responses is a less clumped and more homogenised pattern as elephant densities increase (MacFadyen et al. 2019; Young et al. 2009a).

How elephant herds with calves distribute in the landscape may also be explained by the aforementioned social dynamics and the distribution of resources. We observed that per-herd recruitment rates (the ratio of new calves to other herd members) were highest in the core zone (Figure 4b; Wilcoxon Rank Sum Test Table 3-A1). We expect that herds prefer to keep young calves in areas with good quality habitat, that is, close to water sources and lush vegetation, as noted elsewhere in the region (Harris et al. 2008). Yet, recruitment in peripheral and semi-peripheral zones had an upward trend (Mann-Kendall tests: Table 4-A1). Recruitment patterns that initially differed in the core and peripheral zones, thus began to converge around 2012 (Figure 4b). This most likely reflects

how herd groups with calves moved into suboptimal habitat as intraspecific competition for resources and space intensified (MacFadyen et al. 2019). Recruitment rates also fluctuated over time, a pattern expected given the association of first year survival with environmental conditions, for example, rainfall (Trimble et al. 2009). Indeed, Robson (2015) found this to be true as variation in the proportion of elephants less than 1 year old was related to changes in vegetation productivity (NDVI), which itself was driven by rainfall in the KNP. For example, the recruitment rates increased sharply after 2000, which was also a year of exceptional rainfall in the park (MacFadyen et al. 2018) (Figure 4b). Years with high rainfall might also have an effect on recruitment in following years and future work could investigate the dynamic relationship between recruitment and rainfall.

The spatial pattern of herds with calves raises the question of how fecundity and young calf survival respond to resource constraints in areas with suboptimal habitat. Owen-Smith et al. (2006) suggested that variation in resource availability can put pressure on herds in areas where resources are more limiting. This can lead to reduced population growth through elevated mortality or hampered recruitment rates. African elephants may respond to resource constraints by reducing birth rates (Trimble et al. 2009). However, we observed that over time the proportion of calves in herds increased in semi-peripheral and peripheral zones. This suggests that conditions and resource availability in lower quality landscapes have yet to hamper fecundity and calf survival, as was predicted by Trimble et al. (2009). Purdon and Van Aarde (2017) have suggested that artificial water holes could have influenced the movements of elephants in the park and possibly reduced the effect that natural resource variation had on the elephant distribution. The effects of water holes on the population dynamics of elephants should thus be investigated in future studies.

An alternative theory is that increasing density does not reduce the survival of calves until only after they are weaned (Young & Van Aarde 2010) at 3–4 years of age (Lee & Moss 1986). If this is the case, calves may be most vulnerable to resource constraints shortly after weaning (Young & Van Aarde 2010). Comparative results between several populations elsewhere in Africa highlighted that with increased daily walking distances and higher density, mortality of weaned calves does increase (Young & Van Aarde 2010). Our census dataset did not report weaned calf mortalities, so we could not test this prediction.

In addition to the age-specific fecundity and survival data, we acknowledge the limitations of the census data as winter snapshots of elephant distributions and densities. These annual surveys (Whyte 2001) do not account for how elephants may move around throughout the year in response to seasonal changes of resources, an aspect well recorded using collared animals in the KNP (Loarie, Van Aarde & Pimm 2009) and elsewhere (Cook et al. 2015; Roever, Van

Aarde & Leggett 2012). All results reflect a dry-season snapshot of elephant distribution and abundance patterns. However, these dry-season months are expected to limit water availability and foraging range so it may also reflect to some degree territorial distributions (Codron et al. 2006; MacFadyen et al. 2019; Thomas et al. 2008). We report our findings as the long-term changes in dry-season elephant distributions and offer insights into how elephants are responding to changing conditions over time, as illustrated in previous studies using the same dataset (e.g. MacFadyen et al. 2019; Young et al. 2009a, 2009b).

As restoring resource gradients are expected to have park-wide effects on elephant responses (Venter et al. 2008), thus a key management approach is to focus on approaches that induce spatial variations in resources that affect how elephants use landscapes at scales within the core, semi-peripheral and peripheral zones. These include, restoring food, water and comfort (e.g. shade) resource gradients (Owen-Smith et al. 2006; Purdon & Van Aarde 2017), as well as safety or danger gradients (Douglas-Hamilton, Krink & Vollrath 2005; Goldenberg, Douglas-Hamilton & Wittemyer 2018; Ihwagi et al. 2018). As discussed in Carruthers (1995), a key element of how intensely elephants use a landscape also includes human disturbance as predicted from the theories such as 'landscape of fear' (Cromsigt et al. 2013). Adding to this, incorporating movement and migration patterns may help further elucidate the role of local versus regional habitat constraints on the spatial distribution and recruitment dynamics of the elephant herds in the KNP.

Conclusion

Although density dependence in elephant population growth was realised in the core zone, it coincided with the increase of elephants in the peripheral zones. This pattern could lead to a situation where elephants are more homogeneously distributed throughout the park, as also mentioned in previous studies (e.g. MacFadyen et al. 2019). A homogenised distribution of elephants in response to density-dependent factors is in direct contrast with a conservation paradigm that promotes landscape heterogeneity as an important regulator of biodiversity maintenance (Katayama et al. 2014). Our results, however, only present the population dynamics up to 2012 and could be extended to include recent census data (conducted at a biennial pace, 2015, 2017 and 2019).

Our analyses of annual census data highlighted that exponential population growth typifies elephants in the KNP at a park-wide scale after authorities stopped culling up to 2012. Per capita recruitment rate of calves less than 1 year old into the population varied over the study period but was higher in the core areas. At the park-wide scale, the expected pattern of negative density-dependent growth did not occur. We, however, detected significant negative density-dependence in elephant population growth in the core zone. The mechanism of this density dependence can be demographic responses of fecundity and survival rates and/or movements

of elephants to the local density. The spatially varied growth patterns and the apparent change in density trends after 2008, suggest a more pronounced future density-dependent response by elephants to local resource constraints. Such responses reflect a gradual spread of elephants into less optimal habitats during the dry season and are likely to have consequences for other species in the park.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

A.S.L., S.M. and C.H. developed the ideas, A.S.L. ran analyses and wrote the article under the guidance of C.H., S.M. and S.F.A.S.L., S.M. and C.H. and S.F. helped improve the final manuscript.

Ethical considerations

This article followed all ethical standards for research without direct contact with human or animal subjects.

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Data availability

The authors confirm that the data supporting the findings of this study are available within the article.

Disclaimer

The views and opinions expressed in this article are those of the authors and do not necessarily reflect the official policy or position of any affiliated agency of the authors.

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Appendix 1

TABLE 1-A1: Exponential growth model parameter estimates and model statistics (Eqn 2).

Model parameters	Parameter estimates	
	Cull Model	No-cull Model
Per-capita annual growth rate	0.006**	0.041***
r	0.002	0.002
Initial population density	0.368**	0.407**
d_0	(4.542)	(4.894)
Observations	11	17
R^2	0.406	0.949
Adjusted R^2	0.340	0.945
Residual standard error	0.024	0.049
df	9	15
F-Statistic	6.158**	278.423***
df	1; 9	1; 15

df , degree of freedom.

*, $p < 0.1$; **, $p < 0.05$; ***, $p < 0.01$.

TABLE 2-A1: Parameter estimates of stochastic Ricker model fitted to the time series of elephant population size, as part of test for negative density-dependent growth.

Time period	Model parameters	Parameter estimates: Density classes (elephants per square km)			
		Overall	Peripheral (0.0–0.5)	Semi-peripheral (0.5–1.0)	core (> 1)
Culling period (1985–1995)	a	1.20	0.90	1.44	1.26
	95% bootstrap CI	0.347–1.607	0.246–1.813	0.909–2.189	0.833
	b	-1.2E-4†	-4.0E-4†	-4.4E-4†	-7.2E-4†
	95% bootstrap CI	-2.2E-04 – -5.0E-05	-8.2E-04 – -1.4E-04	-6.8E-04 – -2.8E-04	-1.1E-03
	Observations	11	11	11	11
	Bootstrap samples	2000	2000	2000	2000
Post-culling period (1996–2012)	a	0.02	-0.071	0.19	0.334
	95% bootstrap CI	-0.163–0.179	-0.669–0.670	-0.077–0.367	0.120
	b	1.8E-06	3.4E-05	-3.3E-05	-1.2E-4†
	95% bootstrap CI	-1.2E-05–1.9E-05	-1.9E-04–2.1E-04	-6.8E-05–2.5E-05	-2.3E-04
	Observations	17	17	17	17
	Bootstrap samples	2000	2000	2000	2000

Note: a and b are growth rate parameters describing the respective density-independent and density-dependent components of growth. Results shown for models fitted to overall growth, as well as in the zones divided according to long-term average density (peripheral, semi-peripheral and core). Models fitted for culling period (1985–1995) and the post-culling period (1996–2012) [Eqn 3]. CI, confidence interval.

†, Show b estimates for which $H_0: b = 0$ is rejected at $\alpha = 0.05$, in favour of $H_a: b < 0$.

TABLE 3-A1: Test statistics of Mann–Whitney U tests for difference in recruitment rates in the three long-term density zones. p -values corrected for multiple comparison by Holm method.

Group1	Group2	n1	n2	Statistic	p	p.adj	p.adj.signif
Peripheral	Core	2810	1108	1 388 345	2.97E-08	8.91E-08	***
Semi-peripheral	Core	2984	1108	1535289.5	0.000182	0.000364	***
Core	Semi-peripheral	2810	2984	4 032 359	0.005	0.005	***

Note: Pairwise Wilcoxon rank sum test. p -values adjusted for multiple comparison with Holm method. Alternative Hypothesis: group 2 shifted to the right of group 1.

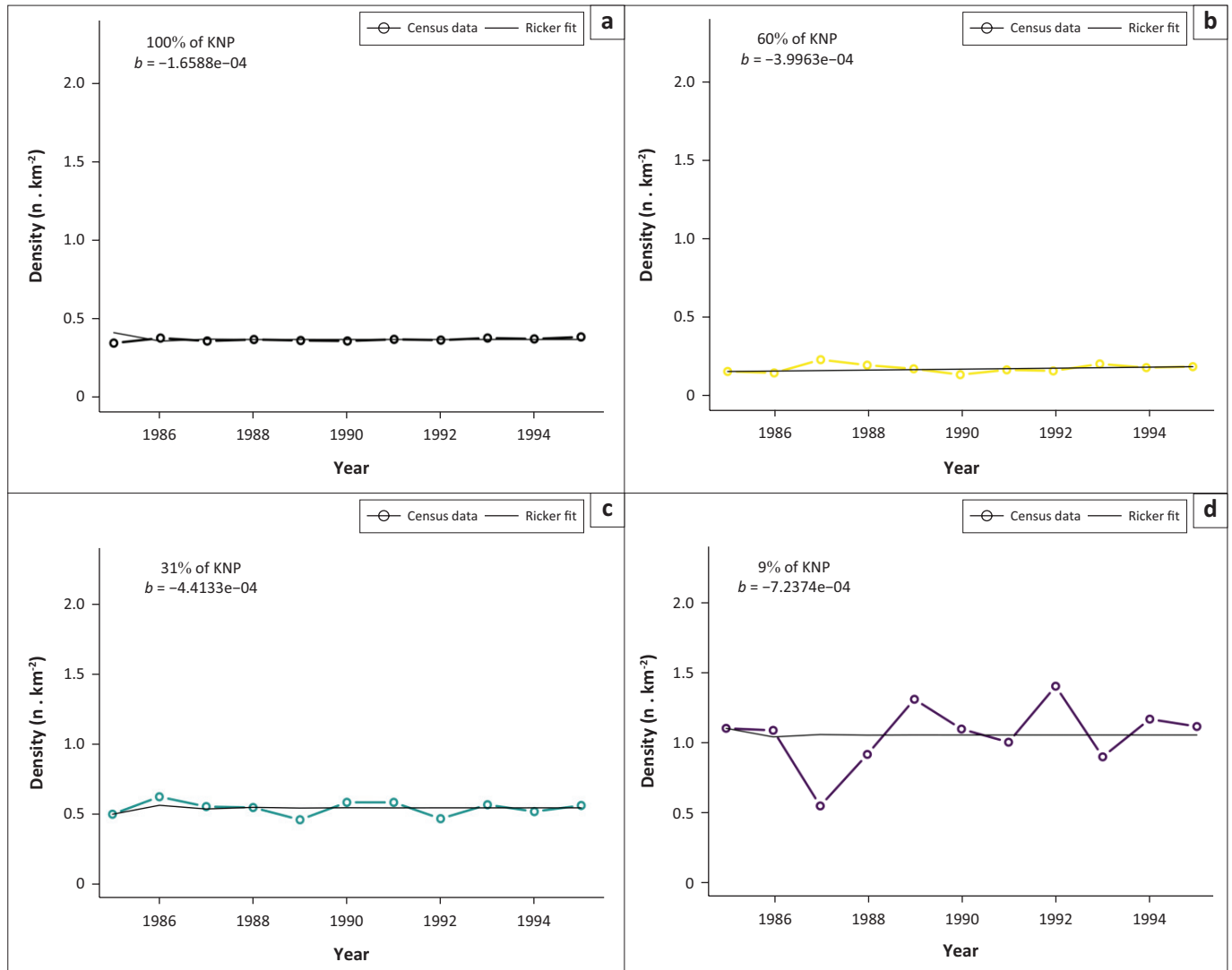
p.adj, adjusted p -values; p.adj.signif, significance level of adjusted p -values.

*, $p < 0.1$; **, $p < 0.05$; ***, $p < 0.01$.

TABLE 4-A1: Test statistics of Mann–Kendall test for trend in the average elephant recruitment rates in areas belonging to different zones.

Zone	Statistics				
	Tau	two-sided p	Kendall score (S)	Denominator	Variance of S
Peripheral	0.28571	0.03452	108	378.00003	2562
Semi-peripheral	0.32275	0.01682	122	378.00003	2562
Core	0.14814	0.27721	56	378.00003	2562

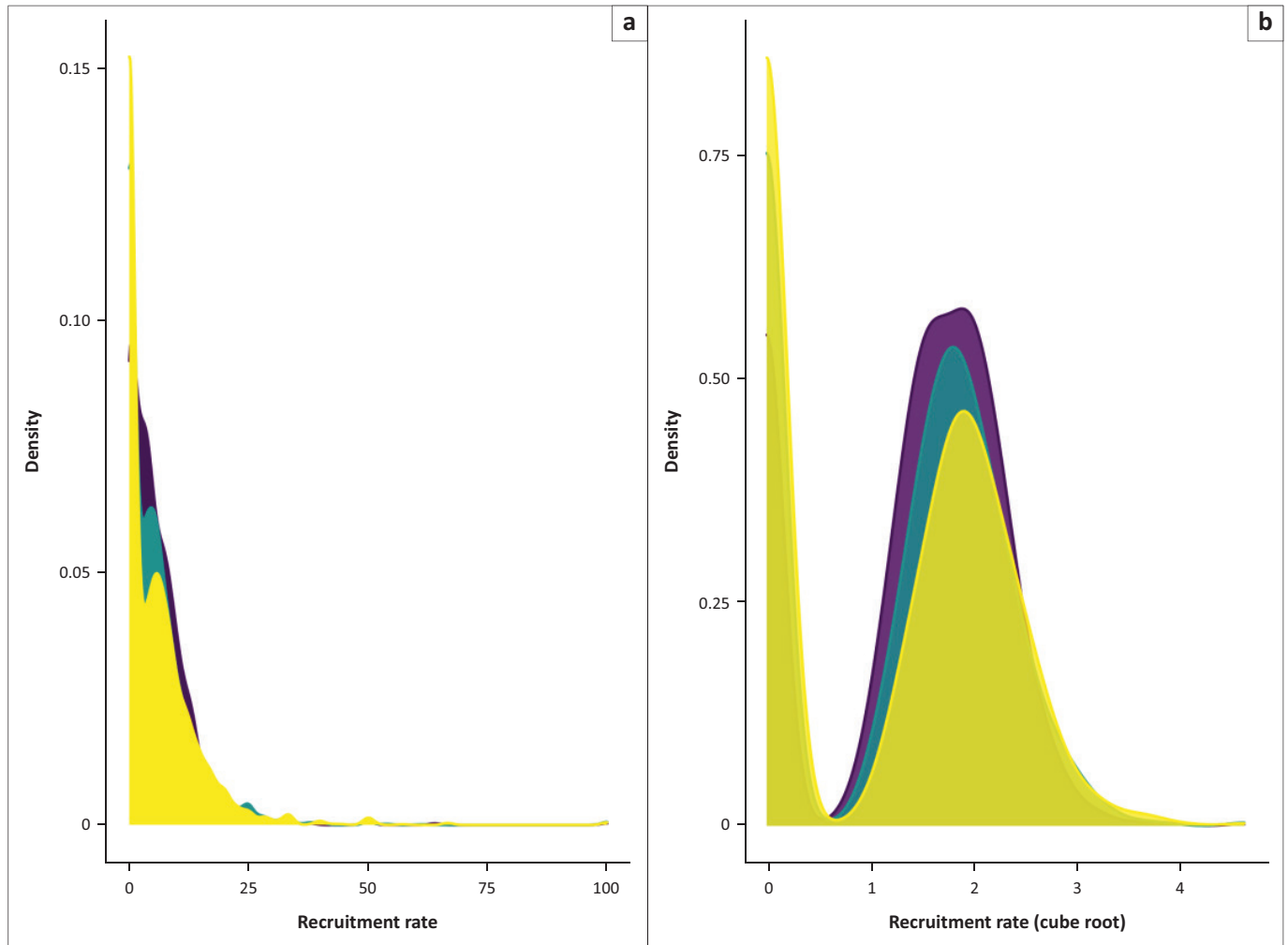
Note: Mann–Kendall tests for trend in the recruitment rates of the three density groups.



Note: Please see the article, Louw, A.S., MacFadyen, S., Ferreira, S. & Hui, C., 2021, 'Elephant population responses to increased density in Kruger National Park', *Koedoe* 63(1), a1660. <https://doi.org/10.4102/koedoe.v63i1.1660>, for more information.

KNP, Kruger National Park.

FIGURE 1-A1: (a) Overall, (b) peripheral zone, (c) semi-peripheral zone and (d) core zone. Deterministic component of Ricker growth models (Eqn 3) fitted to time-series of elephant population in Kruger National Park during the period of regular culling (1985–2012). Model parameter estimates in Appendix 1 (Table 2-A1). Models shown for overall population, and separately for three zones in the park having low medium or high long-term average elephant density (denoted as 'peripheral', 'semi-peripheral' and 'core' zones for elephants). Test for negative density-dependent growth reported significant for all the zones, and the population overall.



KNP, Kruger National Park.

FIGURE 2-A1: Distribution plots of Recruitment rate observations. (a) Shows recruitment rates are skewed and (b) shows a cube root transformation of the recruitment rates, to reduce skewness.