Received: 25 September 2018 | Revised: 13 January 2020 | Accepted: 19 January 2020

DOI: 10.1111/aje.12728

African Journal of Ecology WILEY

ORIGINAL ARTICLE

Lion (*Panthera leo*) demographics in the south-western Kgalagadi Transfrontier Park

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Funding information
University Research Fund; National Research Fund; Gemsbok National Park's management team; Peace Parks Foundation; Land Rover South Africa; Dr and Mrs Fehlmann; South African National Parks; SATIB Conservation Trust; Botswana's Ministry of Wildlife, Environment and Tourism; CPUT Bursary Fund

Abstract

Changes in demographic features of the lion population in the south-western Kgalagadi Transfrontier Park cause conservation concern. The ratio between adult males and females changed from 1♂:2♀ to 1♂:1♀ over a 32-year period (1977–2010). This is atypical for undisturbed lion populations. We evaluated mechanisms that on their own or together could explain the trend by using both a discrete- and continuous-time capture–recapture model to analyse 2 years of individual-based observation data (May 2013–June 2015). Although most vital rates were within expected parameters, shifts in the sex structure remained similar to that reported for sub-adults previously. The population comprised of 26.9% cubs and juveniles (<2 years), 14.2% sub-adults (2–4 years) and 59% adults (>4 years). Litters had equal sex ratios at first detection. Birth rates were lower (0.44 cubs per female per year) than between 1998 and 2001 (0.69 cubs per female per year). The continuous model indicated a higher survival effect for female cubs, while both models showed higher survival rates/effects for sub-adult and adult females relative to males. However, the sex ratio for sub-adults was male-biased. The shift in demographic signals may associate with changes in age-related immigration rates of sub-adult males.

KEYWORDS

continuous capture-recapture model, discrete capture-recapture model, sex ratios, survival rates

Résumé

Les changements dans les caractéristiques démographiques de la population du lion dans le sud-ouest du parc transfrontalier de Kgalagadi suscitent des préoccupations en matière de conservation. Le rapport entre les mâles et les femelles adultes est passé de 1♂: 2♀ à 1♂: 1♀ sur une période de 32 ans (1977-2010). Ceci est atypique pour les populations de lions non perturbées. Nous avons évalué des mécanismes qui, seuls ou ensemble, pourraient expliquer la tendance en utilisant à la fois un modèle discret et continu de capture-recapture pour analyser deux années de données d'observation individuelles (mai 2013 - juin 2015). Bien que la plupart des taux vitaux se situent dans les paramètres attendus, les changements dans la structure du sexe sont restés similaires à ceux signalés précédemment pour les sous-adultes. La population comprenait 26,9 % d'oursons et de juvéniles (< 2 ans), 14,2 % de

sous-adultes (2 à 4 ans) et 59 % d'adultes (> 4 ans). Les portées avaient des rapports de sexe égaux à la première détection. Les taux de natalité étaient plus faibles (0,44 ourson par femelle et par année) qu'entre 1998 et 2001 (0,69 ourson par femelle et par année). Le modèle continu indiquait un effet de survie plus élevé chez les femelles, tandis que les deux modèles montraient des taux/effets de survie plus élevés chez les femelles sous-adultes et adultes par rapport aux mâles. Toutefois, le rapport entre les sexes des sous-adultes était biaisé chez les mâles. Le changement des signaux démographiques peut être associé à des changements dans les taux d'immigration liés à l'âge des sous-adultes mâles.

1 | INTRODUCTION

Vital rates, such as survival and recruitment, are consequences of environmental and social influences (Gardner, Reppucci, Lucherini, & Royle, 2010; Trimble, Ferreira, & Aarde, 2009) and translate into population growth rates (Trimble et al., 2009; White & Burnham, 1997). Vital rates can thus serve as indicators of change, risk of extinction or resilience to disturbances (Andresen, Everatt, & Somers, 2014; Carroll, Fredrickson, & Lacy, 2013). A skewed sex ratio recorded for African lions (*Panthera leo*) in the south-western Kgalagadi Transfrontier Park (KTP) raised concerns of a pending collapse of the population (Ferreira, Govender, & Herbst, 2013). Previously, demographic parameters for the population had a typical lion age and sex structure (24%–43% males) (Castley, Knight, Mills, & Thouless, 2002; Funston, 2011; Mills, Wolff, Riche, & Meyer, 1978; van Vuuren, Herrmann, & Funston, 2005), but with some age classes having specific abnormalities (Funston, 2011). Lionesses accounted for 80% of the adult population in 2001 (Funston, 2011). By 2010, observed adult sex ratios were equal and sub-adults were male-biased (Ferreira et al., 2013). The persistence of male biases may have undesirable consequences for the persistence of lions in the KTP (Borrego, Ozgul, Slotow, & Packer, 2018; Ferreira et al., 2013; van Vuuren et al., 2005). Even so, population sizes during 2015 derived from mark–recapture (n = 246; 95% CI: 237–256), track indices (n = 242; 95% CI: 176–307) and a registration study (n = 250) (Beukes, Radloff, & Ferreira, 2017a) were greater than those reported previously albeit using different methods: 130 (95% CI: 108–181) (Mills et al., 1978); 131 (95% CI: 106–156) (Castley et al., 2002); 120 (95% CI: 113–131) (Funston, 2002; Funston, 2011); and 130 (95% CI: 91–169) (Ferreira et al., 2013).

Variability in the proportion of males and females is a key element of life history traits for a species (Borrego et al., 2018; Cameron, 2004). Body condition as a result of shifting prey dynamics may influence vital rates resulting in changes in the sex ratio of a population (Cameron, 2004; Ferreira et al., 2013; Trivers & Willard, 1973). Prey availability in the Kalahari Gemsbok National Park (KGNP) (i.e. the south-western KTP) became more constant over time largely because of the provision of permanent water points along two dry river beds (Knight, 1995; Mills, 2015). Prey species such as blue wildebeest (*Connochaetes taurinus*) became more resident and concentrate around these water sources which may improve opportunities for lionesses to regularly catch them and maintain good body condition (see Dunham, 1992). Females with better body condition can potentially produce a greater proportion of male offspring (Holand et al., 2006; Huck, Labov, & Lisk, 1986; Sheldon & West, 2004; Trivers & Willard, 1973). Furthermore, a skew towards males in a polygamous species such as lions increases conflict and can perpetuate male recruitment (Packer & Pusey, 1983; Woodroffe & Frank, 2005; Yamazaki, 1996). In cases where infanticide occurs after coalition changeovers, females are more likely to produce male offspring in their first litter after the takeover (Packer & Pusey, 1983; Woodroffe & Frank, 2005; Yamazaki, 1996). We thus expected male bias in cub sex ratios at birth if female body conditions or incidences of coalition takeovers increased.

Survival probability of lions correlates with available prey biomass (Ferreira & Funston, 2010, 2010; Mosser, Fryxell, Eberly, & Packer, 2009; van Orsdol, Hanby, & Bygott, 1985). In addition, cub survival rate associates with group territoriality, pride size as well as synchronous breeding of females (Mosser & Packer, 2009; Packer, Pusey, & Eberly, 2001). Survival probability and social factors are in turn driven by environmental stochasticity (Celesia, Peterson, Peterhans, & Gnoske, 2010). In the KGNP, cub survival in certain areas at different times was as low as 5%, primarily attributed to starvation (Eloff, 1998). Such a low cub survival rate can induce demographic stochasticity, which in turn may skew sex ratios. It is unlikely, though, that such stochasticity remains in favour of only males for an extended period (Goodman, 1987). We thus expected cub survival in the first year to be equal between the sexes in the south-western KTP.

Density-dependent social factors, however, influence sex-specific survival rates at older ages (Mosser & Packer, 2009). Lion life history dictates that sub-adult male lions disperse from their natal territories (Elliot, Cushman, Loveridge, Mtare, & Macdonald, 2014; Funston, 2011) but they typically survive at a reduced rate due to intraspecific competition with older territorial males (Elliot, Valeix, Macdonald, & Loveridge, 2014). In addition, if resource gradients create more favourable patches in a landscape, dispersing animals tend to colonise favourable patches (Ward, 1987). Given the reliable prey availability associated with water provisioning in the dry riverbeds of KGNP (Knight, 1995; Mills, 2015), we expect that new males originating from the Botswana side of the KTP may favour moving westwards into the study area rather than elsewhere.

Adult lion survival rates are typically lower for males compared to females because of the conflict and potential injury associated with coalition takeovers, sub-adult male dispersal (Barthold, Loveridge, Macdonald, Packer, & Colchero, 2016) and the risks of catching prey as a single old male (Starfield, Furniss, & Smuts, 1981). We would thus also expect adult female survival to be higher than that of adult males.

Based on the above, we deduce that the following hypotheses can potentially explain the 2010 observations of an equal sex ratio of adult lions and more males in the sub-adult age class (Ferreira et al., 2013). First, sex ratios are equal at birth and subsequent sex-specific survival rates remain equal from the cub to adult stages, but there is a temporary influx of migrant sub-adult males from elsewhere that explains the sub-adult male bias. Alternatively, sex ratios at birth could favour males, but subsequent survival of females is better than males through the cub to adult stages with an influx of migrant sub-adult males, with some settling in the area, producing the sub-adult male bias and equal adult sex ratio. A third possibility is similar to scenario two, but with the sex ratio equal or in favour of females at birth. It is also possible that follow-up studies to interrogate the observations of Ferreira et al. (2013) find that the previous state no longer exists.

We conducted an exhaustive registration study based on individual lion identification, using whisker spot patterns (Beukes et al., 2017a; Caughley & Sinclaire, 1994; Pennyquick & Rudnai, 1970; Whitman & Packer, 2006) to extract demographic information for the lion population in the south-western KTP. We use the observed age and sex structure of the population and individual capture histories of lions to establish whether: (a) sex ratios favour males at birth; (b) cub and juvenile survival is the same for males and females; (c) sub-adult male survival is similar or higher than that of sub-adult females; and (d) adult female survival rate is higher than that of adult males. We do not have explicit data that allow direct evaluation of sex-specific migration. Instead, we predict that we should encounter more males than females that do not associate with a pride as time elapses, if dispersing sub-adult males show a preference for the south-western KTP with its more stable prey base due to the artificial water provision. These evaluations focus on the mechanisms that could have led to previously observed deviations of age-specific sex ratios (Ferreira et al., 2013; Funston, 2011) from that typically expected for lions (Banerjee & Jhala, 2012; Barthold et al., 2016; Caro, Young, Cauldwell, & Brown, 2009; Castley et al., 2002; Ferreira et al., 2013; Funston, 2011; Funston, Mills, Richardson, & Jaarsveld, 2003; Mills, 1995; Mills et al., 1978; Mudongo & Dipotso 2011; Smuts, 1978; Trinkel, 2013; Woodroffe & Frank, 2005; Yamazaki, 1996). Finally, we define the age and sex structure during our study to evaluate the hypothesis that they do not differ from expectations that sub-adult and adult sex ratios should favour females.

Our results contribute to the understanding of the Kgalagadi lion population demographics, critical to informing conservation management of the species locally. Furthermore, the observations, analyses and interpretation of the results will also contribute to understanding of lion demographics across their range.

2 | MATERIALS AND METHODS

2.1 | Study area

The study took place in the arid south-western Kgalagadi Transfrontier Park (KTP) comprising of the entire Kalahari Gemsbok National Park (KGNP; 9,710 km^2) in South Africa (RSA) and a narrow zone (approximately 20 km) of the Gemsbok National Park (GNP; 26,000 km^2), of Botswana abutting the KGNP to the east (Beukes et al., 2017a, Figure 1). Collectively, the GNP and KGNP make up the greater KTP, an open protected area of some 36,000 km^2. The study area lies between 24°–26°30′ south and 20°–22° east and falls entirely within the Kalahari Duneveld bioregion of the savannah biome (van Rooyen, Van Rooyen, Bothma, & Van den Berg, 2008). Two ephemeral river valleys, the Auob and Nossob, bisect the study area with the Nossob delineating the border between South Africa (KGNP) and Botswana (GNP) (Bothma et al., 1993). Kalahari sand covers the area with a mixture of parallel and irregularly shaped vegetated dunes (van Rooyen et al., 2008). The region is a semi-desert with an average rainfall of 220 mm that varies from 180 mm in the south-west to more than 230 mm in the north (Grist, Nicholson, & Mpolokang, 1997). Temperature extremes range from −5°C in winter to 45°C in summer (Mills, 2015).

2.2 | Field data collection

Data on lion demographics were collected between May 2013 and June 2015 making use of an optimised registration study (Beukes et al., 2017a; Caughley & Sinclaire, 1994; Ogutu & Dublin, 1998; Pennycuik & Rudnai, 1970). We aimed to identify as many lions as possible in the south-western KTP. We drove systematic transects on a monthly basis in the dune and riverbed environments, as well as random transects on management tracks across the extent of the south-western KTP as opportunistically determined by the field crew at the time. Chance encounters, following up on sighting reports, following fresh tracks and following the direction of roars (Stander, 1991) allowed us to opportunistically encounter lions. In addition, seven adult females from seven different prides were fitted with satellite collars (African Wildlife Tracking^{cc}, Pretoria, South Africa) as part of a dietary study (Beukes, Radloff, & Ferreira, 2017b). The collars provided opportunities to locate these lionesses once per month for the duration that the collars were active. We attempted to identify all lions at a sighting and noted their locations using a Garmin GPSMAP 62 (Garmin eTrex, Garmin International).

2.3 | Individual identification

Identifying individuals using vibrissae spot patterns, ear nicks (Elliot, Cushman, et al., 2014; Pennycuick & Rudnai, 1970), nose pigmentation (Whitman et al., 2007) and existing brand marks (Castley et al., 2002; Funston, 2001; M. Ferreira, 2015 Pers.

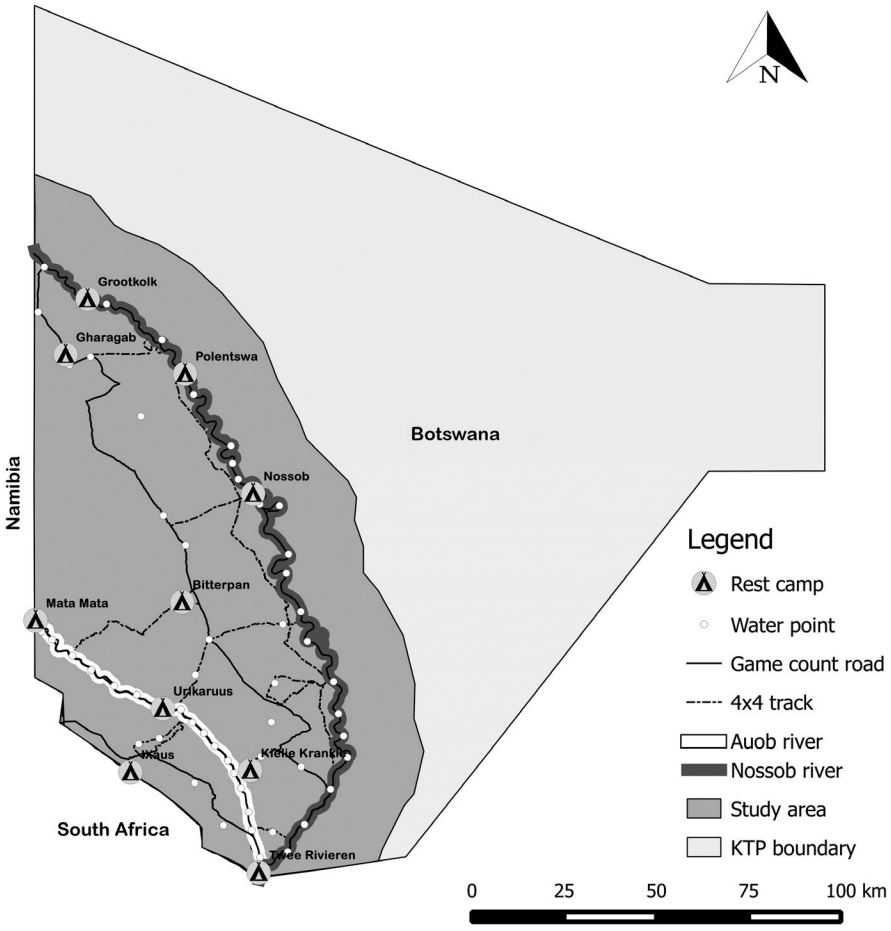

FIGURE 1 The Kgalagadi Transfrontier Park where the study focused on the south-western part (dark grey shaded area)

comm.[1]) allowed us to establish a register of individual lions from which we constructed the age and sex structure of the population. A photographic database of all unique individuals supported individual identification in the field. The search for lions continued until an effort accumulation curve indicated that >90% of lions within the area have been identified (Beukes et al., 2017a). Data of the lion population's historic demographics were extracted from peer-reviewed publications (Funston, 2011; Ferreira et al., 2013; Castley et al., 2002; Mills et al., 1978; Mudongo & Dipotso, 2011) and used for comparative purposes.

2.4 | Data analyses

2.4.1 | Observed age and sex structure

We divided individuals into five discrete age classes on a subjective basis using a lion's relative size, nose pigmentation, tooth wear, leg markings and male mane development (Ferreira & Funston, 2010, 2010; Miller et al., 2016; Whitman & Packer, 2006; Whitman et al., 2007). Individuals considered to be under 1 year old were called cubs; lions between 1 and 2 years old were considered juveniles; and individuals between 2 to 4 years of age were classed as subadults. Adults were animals between 4 and 10 years, and old adults exceeded 10 years of age (van Vuuren et al., 2005; Whitman et al., 2007). Our survey defined six observation occasions each 4 months long. We extracted an age and sex distribution for each of the six occasions and expressed each age class as a percentage of the total number of individual lions recorded during an occasion. We then obtained an average percentage weighted by the total individual lions recorded during an occasion to define the observed age and sex distribution during the study.

2.4.2 | Reproductive characteristics

To derive reproductive schedules, we used observations of cubs being born into prides. We identified the average age of adult females at conception [using a 110-day gestation period (Zuckerman, 1953)] and at birth through backdating from the estimated age of individuals when they were observed with cubs for the first time. When first observed, we also noted litter size and sex structure. Birth rates were the average number of cubs detected per reproductively mature female (>4 years old) per year (Funston, 2011; Lehmann, Funston, Owen, & Slotow, 2008).

[1]Micho Ferreira, Section Ranger, Twee Rivieren, Kalahari Gemsbok National Park, Northern Cape, South Africa. 8800.

2.4.3 | Sex ratios

Sex ratio is defined to be the estimated abundance of males divided by the estimated abundance of females. Defining sex ratio at birth is challenging because cubs are seldom seen before they are three to 12 weeks old (Packer & Pusey, 1987) or even up to 1 year of age if lionesses hide cubs from infanticidal males (Packer et al., 2001). Here, we use the term newborn cub to refer to a newly born, live lion that is less than 3 months old. With this definition, the birth sex ratio is the same as the newborn cub sex ratio.

A newborn cub faces a significant chance of death due to infanticide (Barthold et al., 2016), disease and starvation (African Lion & Environmental Research Trust, 2019) before they become old enough to be detected by our methods. We have limited data on newborn cubs as most of the young cubs in our data set are 3 months old. The recorded cub sex ratio is thus not necessarily equivalent to the sex ratio at birth. If, however, it is assumed that the mortality rates are the same for male and female newborn cubs, then the newborn-to-cub survival probabilities for males and females are proportional to cub survival probability from occasion k to occasion $k+1$. Under this assumption, the birth sex ratio can be estimated with the cub sex ratio.

If, however, this assumption is not made, an estimator developed by Eberhardt (1985) based on the work of Siler (1979) can be computed. Eberhardt (1985) discusses the difficulties of estimating survival at birth when no data are available for animals younger than m time units, the age at which early hazards of death are essentially over. Here, we take this age to be 3 months. If S_m, an estimate of the survival probability of animals of age m, is available, then Eberhardt (1985) argues that an estimate of S_0 can be computed as follows.

Let $S_{\{age>m\}}$ be the survival probability over u time units of lions just older than m. Here, survival probabilities are computed over intervals of 4 months, so, u is 4 months and $m=3/4$. We take $S_{\{age>m\}}$ to be $S_{juveniles}$. Then, $\hat{S}_0=\exp(-a_1)$ where $a_1=-\log(\hat{S}_m)+m\log(\hat{S}_{\{age>m\}})$, and hence,

$$\hat{S}_0=\hat{S}_m/\hat{S}^m_{\{age>m\}}.$$

In other words, the survival rate at birth is approximated by the probability of survival at age m inflated by the probability of survival at ages greater than m raised to the m^{th} power. The idea is to use available survival estimates to approximate the decrease in survival rate from age 0 to age m. Eberhardt (1985) does not give this estimator a name.

Using this estimated value of newborn cub survival, the abundance of newborn cubs can be estimated with $\hat{v}_0^G=n^G/(1.-\exp(-\hat{S}_0 m))$ since all lions of gender $G(=M,F)$ in the sample were newborn cubs at one time in their life. Finally, an estimate of the sex ratio of newborn cubs is $\hat{v}_0^M/\hat{v}_0^F$.

The ratio of male cubs to female cubs is N_m/N_f where N_m and N_f are the number of male and female cubs, respectively, at first encounter. There are, however, N_u cubs of unknown gender. We modified the above estimator to account for the additional cubs of unknown sex adapted from Nichols, Kendall, Hines, and Spedelow (2004). Let π be the probability that a detected cub is male. Estimate π with $N_m/(N_m+N_f)$. An estimate of the cub sex ratio can now be formed as $\hat{r}=(N_m+\hat{\pi}N_u)/(N_f+(1-\hat{\pi})N_u)$.

McDonald and Amstrup (2001) give an abundance estimator for the i^{th} capture occasion, $i=2,\ldots,T$. The estimator is $\hat{N}_i=\sum_{j=1}^{n}\frac{I_{ij}}{\hat{p}_{ij}}$ where I_{ij} is 1.0 if the j^{th} animal is actually encountered and 0 otherwise. The value $\hat{p}_{ij}$ is the estimated model-based probability of detecting animal j during occasion i. Here, we use our estimated detection probabilities (see later) for the last occasion and for lions observed in at least two occasions to estimate the sex ratio for juveniles, sub-adults and adults, respectively (Table 1). We restrict the estimator to only those lions observed on at least two occasions. Because the probability of detection is not defined for the first occasion, we excluded lions only encountered then (see McDonald & Amstrup, 2001). Note that survival probabilities do not enter into this estimator—only detection probabilities.

2.4.4 | Survival

We consider two approaches—a discrete-time capture–recapture model (Barker, Burnham, & White, 2004) following results from Schwarz and Stobo (1999) and a continuous-time capture–recapture model (Hwang & Chao, 2002). Note that both models estimate apparent survival, the aggregate of survival and emigration. The discrete model provides explicit estimates of apparent survival rates, while the continuous model provides assessment of apparent survival effects. Assessing the suitability of the approaches provides some challenges because Akaike information criterion (AIC) scores typically used for model evaluation (Johnson & Omland, 2004) are not directly comparable. Both the discrete model (Barker et al., 2004) and the continuous model (Hwang & Chao, 2002) maximise a conditional likelihood rather than the full likelihood which is not known because it would require

TABLE 1 Estimated sex ratios (the estimated abundance of males divided by the estimated abundance of females) for five age classes of lions in the south-western Kgalagadi using discrete- and continuous-time models

Age class	Discrete-time Model	Continuous-time Model
Newborn cubs	1.101 (0.945–1.287)	1.016 (0.944–1.127)
Cubs	0.867 (0.758–1.045)	0.867 (0.774–1.000)
Juveniles	0.701 (0.465–1.253)	0.843 (0.631–1.016)
Sub-adults	1.000 (0.667–2.000)	2.574 (1.889–3.558)
Adults	0.454 (0.365–0.541)	0.845 (0.753–0.948)

Note: We also provide the estimated 95% confidence intervals in brackets.

observations on all lions not captured at least once. We could, however, use model goodness of fit (GOF) that ignore model complexity and focus exclusively on the model's fit to data to compare the discrete and continuous models. This allowed us to retain the benefits of explicit apparent survival rate estimates, while also elucidating age-specific apparent survival effects scaled by the different values that the two models bring to our understanding of lion apparent survival in the south-western KTP.

Discrete-time model

Say there are T sampling occasions. Let p_{ij} be the detection probability at the i^{th} occasion of the j^{th} lion, and S_{ij} be the survival probability at the i^{th} occasion of the j^{th} lion, $j=1,\ldots,n$. Let $\mathbf{h}_j$ be the encounter history vector of the j^{th} lion. The components of $\mathbf{h}_j$ are either 0 (not detected) or 1 (detected). Extending the Cormack, Jolly and Seber (CJS) capture–recapture model, the probability of an observed encounter history is proportional to

$$\begin{aligned}&P(H=h_j)\propto\\&P(\text{survival to } l|\text{first released at } k_j)\\&\times P(\text{resighting history in } [k,l)|\text{survival to } l)\\&\times P(\text{capture history in } (k,l]|\text{survival to } l)\\&\times P(\text{encounter history after } l|\text{encounter history in } [k,l]).\end{aligned}$$

Here, assuming a closed population, and no recovery of dead lions, the above is as follows

$$P(\text{survival to } l_j|\text{first released at } k_j)=\prod_{i=k_j}^{l_j-1}S_i$$

where k_j is the index of the occasion of first detection ('release').

$$P(\text{resighting history in } [k_j,l_j)|\text{survival to } l_j)=\prod_{i=k_j}^{l-1}R_i^{y_{ij}}(1-R_i)^{1-y_{ij}}$$

where y_{ij} equals 1 if the j^{th} lion is re-sighted at least once during the interval $[i,i+1)$ and 0 otherwise. Note that all re-sightings of lion j within an occasion after the first such re-sighting are ignored.

$$P(\text{capture history in } (k_j,l_j]|\text{survival to } l_j)=\begin{bmatrix}1&0\end{bmatrix}\times\left\{\prod_{i=k_j}^{l_j-1}\left\{\begin{bmatrix}p_{i+1,j}&0\\0&0\end{bmatrix}I_{\{h_{ij}=1\}}(h_{ij})+\begin{bmatrix}(1-p_{i+1,j})&0\\0&1\end{bmatrix}I_{\{h_{ij}=0\}}(h_{ij})\right\}\right\}\begin{bmatrix}1\\1\end{bmatrix}.$$

Survival probability is linked to sex and age with the logit link:

$$\text{logit}(S_{ij})=\beta_{\{\text{gender}_j,\text{age\_class}_{ij}\}}$$

where age_class is 1 (cub) for lions aged 3–12 months old, 2 (juvenile) for lions aged 1 to 2 years old, 3 (sub-adult) for lions aged 2 to 4 years old, and 4 (adult) for lions aged four or more years old. For example, the probability that lion j, a male cub survives from occasion i into occasion $i+1$ is $S_{ij}=\beta_{\text{male,cub}}$. Detection probability is linked to detection method:

$$\text{logit}(p_{ij})=\gamma_0+\gamma_1 I_{\{\text{radio}\}}(\text{method}_{ij})$$

where method_{ij} is either radio or nonradio.

$$\begin{aligned}&P(\text{encounter history after } l|\text{encounter history in } [k,l])\\&=P(\text{resighting history in } [l,l+1)|\text{encounter history to } l)\times\\&P(\text{never encountered after } [l,l+1)|\text{encounter history in } [k,l+1)).\end{aligned}$$

The first probability, above, is $S_lR_l+(1-S_l)R'_l$, and the second probability is

$$1-f_i-\sum_{g=i+1}^{T}\left\{\alpha_{ig}\prod_{h=i}^{g-1}S_i(1-R_i)\right\}-\sum_{g=i+1}^{T}\left\{f_i\beta_{ig}\prod_{h=i}^{g-1}S_h(1-R_h)\right\}$$

if the last encounter with lion j was by capture, or

$$-\frac{\phi_i}{\beta_{ii}}\left\{\sum_{g=i+1}^{T}\left\{\alpha_{ii}\prod_{h=i}^{g-1}S_i(1-R_i)\right\}-\sum_{g=i+1}^{T}\left\{f_i\beta_{ii}\prod_{h=i}^{g-1}S_h(1-R_h)\right\}\right\}$$

if the last encounter with lion j was by re-sighting. In the above,

$$f_i=S_iR_i+(1-S_i)R'_i,\phi_i=(S_iR_i)/\left[S_iR_i+(1-S_i)R'_i\right],$$

$$\alpha_{ig}=\begin{bmatrix}1&0\end{bmatrix}\left\{\prod_{h=i}^{g-2}\begin{bmatrix}p_{h+1,j}&0\\0&0\end{bmatrix}\right\}\begin{bmatrix}(1-p_{g,j})&0\\0&1\end{bmatrix}\begin{bmatrix}1\\1\end{bmatrix},$$

and,

$$\beta_{ig}=\begin{bmatrix}1&0\end{bmatrix}\left\{\prod_{h=i}^{g-2}\begin{bmatrix}p_{h+1,j}&0\\0&0\end{bmatrix}\right\}\begin{bmatrix}1\\1\end{bmatrix}.$$

This model has 13 parameters: eight survival probabilities, R , R', two detection probability parameters, and f_T. For some of the lions in the data set, the observed age changes across occasions. This is represented in the model by having the *age* covariate be dependent on occasion. The re-sighting probability, R_i, is the probability that an animal captured in occasion i is re-sighted again in occasion i.

For estimation, we used the likelihood function, $L(\phi,\mathbf{p}|\mathbf{h}_1,\ldots,\mathbf{h}_n)\propto\prod_{j=1}^{n}P(H_j=\mathbf{h}_j)$. We maximise the logarithm of this function with the COBYLA algorithm of Powell (1992) as implemented in SAS (SAS, 2019). This algorithm does not use derivatives of the objective function.

We conduct a Monte Carlo (MC) hypothesis test of the model's fit to our data set. We build a contingency table consisting of the eight

populations (columns) by the six occasions (rows). Each cell holds the observed number of detected lions and, under the estimated model, the expected number of detected lions. Then, a chi-squared test statistic is computed, but its *p*-value is found from an MC technique because there are dependencies across occasions (see Agresti, 2013). To do this, $n_{MC} = 1000$ MC data sets are simulated using the estimated model. The test statistic is computed for each of these data sets. The *p*-value is the fraction of these test statistic values that exceed the observed test statistic value (Waller, Smith, Childs, & Real, 2003).

A 95% confidence interval for each parameter is computed with the delete-*d* Jackknife procedure (Hall, Boogaard, Fernando, & Mynett, 2004; Shao & Wu, 1989). The value of d is fixed at $n^{0.608} = 254^{0.608} = 29$ and 250 Jackknife samples are drawn. We report a population estimate given the detection probabilities that we estimated from this model.

Continuous-time model

The continuous-time model follows Hwang and Chao (2002) that allows us to include covariates such as radio collars or variance in behaviour of individual lions. The model uses an intensity function of the i^{th} lion defined as $\lambda_i(t) = \lambda_i(t)\gamma + \log(\phi)X_i(t)$, where $\lambda_i(t) = \exp(f(\boldsymbol{\beta}, \mathbf{Z}_{it}))$ is a parameterised function in animal-specific covariates and time, and $X_i(t)$ is the indicator function for the event that lion i was captured in the interval $(0, t)$. Let the entire experimental period be the interval $[0, \tau]$. As we have placed all individual lion effects into the λ parameter, we fix γ to the value 1.0.

The parameter ϕ is the effect on the intensity function due to the behaviour of all animals towards the device used by the experimenters for captures. Such devices include animal traps, cameras or radio collars. Typically, this parameter accounts for 'trap-shy' or 'trap-happy' behaviours across all animals. Because lions are photographed from a distance, we assume no behavioural response to the camera between the first and subsequent encounters. Hence, we fix the value of ϕ to 1.0.

We need to account for imperfect detection chance across all lions, some of the lions wearing intermittently functioning radio collars, sex differences and lions ageing during the experiment period. We represent these effects as follows. First, let $\mathbf{Z}_{it} = (\text{gender}_i, \text{age}_{it})'$. Next, we define $f(\boldsymbol{\beta}, \mathbf{Z}_{it}) \equiv \beta_p + \beta_c I_{\{\text{lion } i \text{ is collared at } t\}}(i) + \beta_{d_{it}}$, where β_p is an overall imperfect detection effect, $d_{it} = 4I_{\{\text{lion } i \text{ is male}\}}(i) + \sum_{l=1}^{4} l I_{\{\text{lion } i \text{ is in age class } l \text{ at } t\}}(i)$, and $l = 1, \ldots, 4$ indexes the age classes of cub, juvenile, sub-adult and adult, respectively. This model has 10 parameters.

For estimation, we let $\mathbf{h}_i = (t_{i1}, \ldots, t_{i,m_i})'$ be the vector of capture times of the i^{th} lion. The conditional log-likelihood is

$$l(\boldsymbol{\beta}, |\mathbf{h}_1, \ldots, \mathbf{h}_n) = \sum_{i=1}^{n}\sum_{j=1}^{m_i} \log(\lambda_i(t_{ij})) + m_i \log(\gamma) + (m_i - 1)\log(\phi) + \left[-\phi\gamma\Lambda_i(\tau) + (\phi - 1)\gamma\Lambda_i(t_{i1})\right] - \log\left(1 - \exp(-\gamma\Lambda_i(\tau))\right)$$

where $\Lambda_i(t) = \int_0^t \lambda_i(u)du$ is the cumulative intensity (hazard of being captured) function. The value of τ is set to the range of sighting times plus 12 months. Doing so allows lions sighted for the first time late in the experiment period to have a positive value of $\Lambda_i(\tau)$. Conditioning is on those animals actually observed (see also equation (5) in Yip and Wang (2002)). Parameter estimates are found by maximising this log-likelihood.

Using these estimated values, a Horvitz–Thompson estimator of the abundance of lions of sex g and age k at the end of the experiment period is

$$\hat{v}_{g,k} = \sum_{i=1}^{n_{g,k}} 1/\hat{P}(\text{at least one lion captured in } [0, \tau])$$

where only lions of sex g and age k are included in the sum, and

$$P(\text{at least one lion captured in } [0, \tau]) = 1 - \exp(-\gamma\Lambda_i(\tau)).$$

If a lion was observed at only a few time points that were close together, the value of $\hat{\Lambda}_i(\tau)$ would be small. Such a small value of this cumulative intensity function results in a small value of $P(\text{at least one lion captured in } [0, \tau])$. This, in turn, causes the abundance estimator to return an inflated abundance estimate. Therefore, to avoid inflation of the abundance estimator from such lions, in the abundance computation, if the range of sighting times of a lion is less than 0.01τ, its cumulative intensity function value is re-set to the value 10,000. Doing so results in each of these lions contributing the value 1.0 to the abundance estimate.

Lion i's sightings are partitioned into the time intervals defined by the occasions used with the discrete-time model. Then, the expected number of sightings of lion i within each of these occasions is found. Finally, two, two-way contingency tables are constructed by summing these observed and expected cell counts, respectively, within each of the eight populations defined by combinations of sex and age within occasion. Note that the continuous-time model also allowed us to estimate total abundance given the detection probabilities estimated.

Identifying transient lions

We defined transient lions as individual lions that do not associate clearly with a pride. We then compared the sex-specific frequency of encounters for both sub-adults and adults.

3 | RESULTS

3.1 | Age structure and population estimates

The observed age structure of the population during the study period comprised 59% adults, 14.2% sub-adults, 3% juveniles and 23.9% cubs (Figure 2). The discrete-time model provided a population estimate of 467 (95% CI: 432–493), while the continuous-time model estimated 292 (95% CI: 289–296).

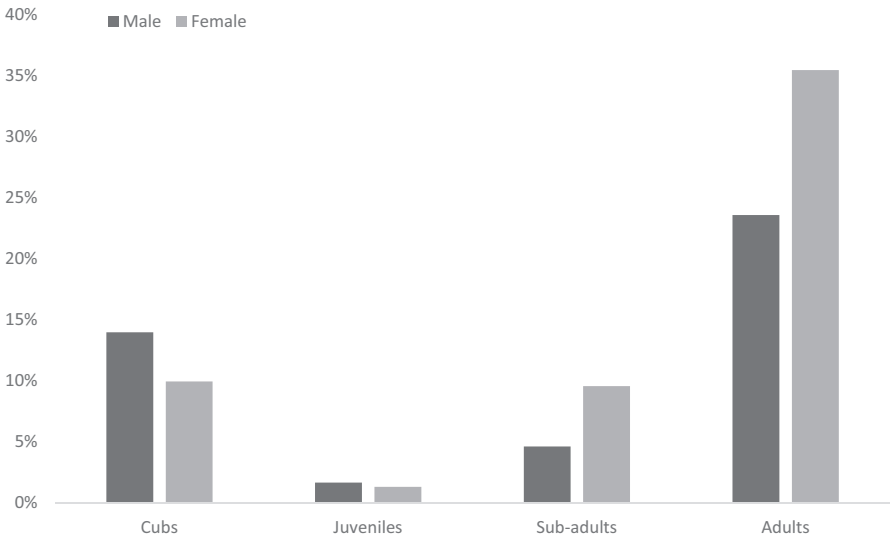

FIGURE 2 Observed sex and age class structure of the south-western KTP lion population noted between May 2013 and June 2015

TABLE 2 Estimated sex-specific survival rates from the discrete-time model and sex-specific survival effects from the continuous-time model

	Survival rates		Survival effects	
Age class	Males	Females	Males	Females
Cubs	1.000 (1.000–1.000)	1.000 (1.000–1.000)	1.075* (0.946–1.184)	1.431* (1.324–1.514)
Juveniles	0.922 (0.893–0.957)	0.834 (0.793–0.881)	0.993 (0.896–1.146)	1.212 (0.992–1.379)
Sub-adults	0.807* (0.769–0.838)	0.922* (0.894–0.946)	−0.485* (−0.704 - −0.285)	0.915* (0.765–1.103)
Adults	0.842* (0.821–0.860)	0.917* (0.904–0.932)	0.660* (0.567–0.757)	1.007* (0.941–1.088)

Note: We also provide the 95% confidence intervals.

*Indicates significant difference between males and females. Note that high values of survival effects mean a high chance of survival. Low values mean a low chance of survival.

3.2 | Reproductive characteristics

Thirty-seven per cent of the observed adult females (n = 31) produced cubs shortly before or during the study period. The minimum average litter size derived from first observations of cubs was 2.39 (SD = 0.72; Range = 1–4). This translated to an average birth rate of 0.44 cubs per female per annum. No females gave birth more than once during our study period.

3.3 | Sex ratios

During the study period, 51 cubs were younger than 3 months (18 ♂♂, 21♀♀, 12 unknown) and a further 24 younger than 12 months (14 ♂♂, 9♀♀, 1 unknown) when first encountered. If we consider re-sighting and detection probability, as well as detection effects, our models predicted that newborn cubs would slightly favour males based on point estimates. Confidence intervals, however, included equal sex ratios (Table 1). The large survival effect of cubs (females surviving much better than males) resulted in both models highlighting some female bias in the cub and juvenile age classes.

The discrete-time model found no difference in sex ratio of sub-adults, while the continuous-time model noted substantially more sub-adult males [72.0% (95% CI: 65.4%–78.1%] than sub-adult females. The difference in the sub-adult sex ratio between the two models, however, should be tempered by noting that the two confidence intervals overlap. By the time lions reach adulthood, females were significantly more numerous than males (Table 1). The discrete-time model estimates that 68.8% (95% CI: 64.9%–73.3%) of adult lions are female, while the continuous-time model estimate 54.2% (95% CI: 51.3%–57.1%).

3.4 | Survival

The model using discrete time produces a goodness-of-fit value of 96.01 and p-value of .322. This estimated lion re-sighting probability as 0.457 (95% CI: 0.441–0.474), but whether a lion was part of a pride that had a collar influenced detection probability. If a lion had

a collar, the detection probability was considered as 1, but without a collar that reduced to 0.551 (95% CI: 0.531–0.570).

The model using continuous time returned a goodness-of-fit value of 18.90 and *p*-value of .406. Under a continuous model, the chance of detecting a lion with a collar (3.332, 95% CI: 3,675–4,086) was significantly higher than for lions without a collar (−6.353, 95% CI: −6.411 to −6.305).

The continuous model fitted the data better than the discrete model (GOF *p*-value = .406 vs. GOF *p*-value = .322) and also has fewer parameters (10 vs. 13). The continuous-time model noted significant differences in sex-specific apparent survival effects for cubs, sub-adult and adults (Table 2). For cubs, sub-adults and adults, the apparent survival effects are substantially greater for females than males, that is females of cub, sub-adult or adult age have a much better chance at surviving than male cubs of similar age. Our estimation process maximised cub survival for the discrete-time model. For sub-adults and adults, however, the discrete-time model confirmed the sex-specific apparent survival effects identified by the continuous-time model (Table 2).

3.5 | Transient lions

Of the identified individual lions, 225 (86%) could be associated with prides. Only 36 known individuals could not be associated with any particular pride and were considered to be transient. Transient individuals were identified at 14 of the 299 sighting events and comprised of 16 adult and 14 sub-adult males, as well as three adult and three sub-adult females.

4 | DISCUSSION

Concerns for the persistence of the lions in the Kgalagadi Transfrontier Park (Ferreira et al., 2013) did not result in a reduction in numbers by the end of 2015 (Beukes et al., 2017a). This is supported by the model results presented here that accounted more robustly for re-sighting and detection probabilities. The much larger total abundance estimates of the discrete model (467 vs. 292) may be due to, firstly, the detection probability being a single value (0.551) for all un-collared lions and, secondly, only the first re-sighting, if any, is included in the discrete-time model's parameter estimation (Barker et al., 2004). The continuous-time model on the other hand uses the exact sighting times rather than discretised versions of them, includes both survival and detection effects in its abundance estimate and uses all recapture observations in its parameter estimation (Hwang & Chao, 2002). As a result, model evaluation using a goodness-of-fit approach highlighted that the continuous-time model fitted the data better than the discrete-time model. The continuous-time model's abundance estimate correlates well with the spoor count and registration study estimates of Beukes et al. (2017a).

In addition to the unexpectedly higher population size estimates calculated by Beukes et al. (2017a) that is supported by the results presented here, we also did not find the sex ratio favouring particularly sub-adult males to be as apparent as found by Ferreira et al. (2013). The observed sub-adult sex ratio calculated for this study do not portray a male bias (Figure 2), but the discrete-time model suggests an equal sub-adult sex ratio, while the continuous-time model recorded a strongly male-biased sex ratio for sub-adult lions. Given the goodness of fit of the two models, we place heavier weighting on the continuous model results—the sub-adult age class was most likely dominated by males. A higher preponderance of males in the sub-adult age class is uncharacteristic for lion populations as, large undisturbed lion populations typically have between two to three sub-adult and adult females for each sub-adult and adult male (Bertram, 1973; Castley et al., 2002; Funston, 2011; Funston et al., 2003; Mills et al., 1978; Smuts, 1976; Stander, 1991).

The predictions that male-favoured litters may result from good female body condition during gestation (Trivers & Willard, 1973) and/or more regular pride takeovers (Díaz-muñoz, Duval, Krakauer, & Lacey, 2014; Packer & Pusey, 1987; Yamazaki, 1996) were not supported by the observed sex ratio of cubs when first encountered 3–12 months after birth. When we used the estimated survival rates of the discrete-time model, there were 10% more males than females at birth. The results from the continuous-time model suggest there were 2% more males than females at birth. Given the better goodness of fit of the continuous-time model, it is likely that sex ratios of newborns are not favouring any of the sexes. However, female cubs aged 3 months to a year outnumber their male counterparts, suggesting that male cubs between ages 0 and 3 months experience higher mortalities than females of similar age. This result was similar for both models.

Although both analyses suggest that females aged 3 months to a year survive substantially better than males, our modelling approach does not allow estimation of sex-specific cub survival. Nevertheless, we can get some approximation of cub survival irrespective of sex. From direct observations of 67 cubs, 7 were confirmed dead suggesting that survival at maximum was 89.6%. Another 22 cubs were never seen again and could either have died or managed to evade further detection. If all of the unaccounted individuals died, cub survival can be as low as 56.7%.

Birth rates of 0.44 cubs per female per year during our study were lower than the 0.67 to 1.33 cubs per female per year during 2001 (van Vuuren et al., 2005). Our observed birth rates were also substantially less than elsewhere. These ranged between 0.8 and 1.4 cubs per female per year in Kenya (Woodroffe & Frank, 2005), Namibia (Orford, Perrin, & Berry, 1988), South Africa (Lehmann et al., 2008), Tanzania (Caro et al., 2009) and Zambia (Yamazaki, 1996). Low birth rates in the south-western KTP are surpassed only by the *Panthera leo persica* subspecies of the Gir Forest, India (0.37 cubs per female per year) (Banerjee & Jhala, 2012).

Overall, our results suggest reproductive constraints—birth rates are low. Immigration aside, annual survival must be high to result in recent increases (Beukes et al., 2017a) assuming no methodological biases in comparing lion population estimates. We approximated annual survival for cubs between 56.7% and 89.6% irrespective of

sex. This overlaps with populations in Kruger National Park, South Africa (40%–80%; Funston et al., 2003), but is higher than at Etosha National Park in Namibia (40%). Generally, lion cub survival rates are variable and tend to correlate strongly with lean season prey abundance (Celesia et al., 2010). It is likely that lean season prey abundance is relatively higher and less variable in the south-western KTP than elsewhere (see Beukes et al., 2017b). Synchronous breeding of females in prides may also contribute to increased cub survival due to allo-caring of cubs (Packer & Pusey, 1997; Packer et al., 2001). More than half of known cubs were born into three large pride cohorts during the study period. Within our study area and period of study, cub survival was much higher than observed in the northern KGNP in 1978 (5%) (Eloff, 1980), but similar to that noted during 2001 (61%) (Funston, 2011).

The apparent survival rate estimate for juveniles did not differ between sexes and neither did any of the sexes have a different apparent survival effect. There is a significant sex difference in apparent survival probability for sub-adult lions with males having lower chances of survival. Elsewhere, the dispersal of sub-adult males imposed higher mortality on them than on adult females (e.g. Etosha National Park in Namibia, Stander, 1991). Lion social dynamics in undisturbed populations predicts lower survival rate of sub-adult males resulting from various risks encountered when emigrating from natal areas (Hanby & Bygott, 1987) such as reduced hunting success (Funston, Mills, & Biggs, 2001) or reduced opportunities to acquire territories (Funston et al., 2003). Apparent survival rates for adult females were significantly higher than that of adult males. Elsewhere, adult male and female survival rates are typically similar (Ferreira & Funston, 2010, 2010; Starfield et al., 1981; van Vuuren et al., 2005). These results suggest that apparent survival rates did not contribute to the anomalous sex ratio for sub-adult lions noted in our study, as well as previous studies (Ferreira et al., 2013; Funston, 2011).

The reproductive and survival schedules in recent years resulted in adult lions irrespective of sex accounting for 59% of the population. The contribution of adults to the lion population structure is relatively high compared to other studies. Adults comprised 40.0%–53.3% of the population in Kruger National Park (KNP), South Africa (Ferreira & Funston, 2010, 2010; Smuts, 1976), and 41% of the population in Etosha National Park (ENP), Namibia (Stander, 1991). Forty-one per cent of the lions in our study population are four years or younger compared to 46%–58% and 59% in KNP and ENP, respectively (Ferreira & Funston, 2010, 2010; Smuts, 1976; Standers, 1991). Similarly, cubs and juveniles occupied a small proportion of the population (26.9%) compared to the KNP (39.6%; Ferreira & Funston, 2010; Ferreira & Funston, 2010), but is higher in proportion than found in the ENP, which ranged between 16.8% and 21.3% between 1987 and 1989 (Stander, 1991).

In relation to our predictions, the results refute predictions 1–3 in the sense that: (a) the sex ratio is equal at birth and do not favour males; (b) male cubs most likely survive worse than females, and hence cub survival is not the same for both sexes; and (c) sub-adult male survival is worse and not better, or equal to that of sub-adult females. However, adult female survival rate was shown to be higher than that of adult males as stated in prediction four. The higher (continuous model) or equal (discrete model) portion of sub-adult males that we noted, when we accounted for re-sighting and detection probabilities, are anomalies from that expected of natural lion populations as already mentioned, and may result from transient dynamics. We noted that sub-adult and adult males are more 'transient' than females. In addition, it is also highly likely that we have missed a number of transient individuals. Even so, such movements into our study area need to be ongoing. It is likely that the direction of dispersion of young males is out of the larger KTP of Botswana westwards into the study area driven by factors such as stable prey availability associated with the two river beds and provision of water at boreholes (Knight, 1995; Mills, 2015). The likely net movement of young males into the study area may thus lead to the observed sub-adult sex ratio anomaly.

The high preponderance of males in the sub-adult age class may result from unintended consequences of management interventions. The long-term consequences of providing water within the south-western KTP resulted in several previously transient or migratory lion prey species now being resident year-round (Knight, 1995; Mills, 2015). Predictable resident prey most likely improves hunting opportunities and success of females that should improve body condition. These better conditioned females may then produce a greater proportion of male offspring (Trivers & Willard, 1973). However, we could find no conclusive evidence in our study of male-favoured litters at birth, but a key requirement to test for this conclusively is to associate variation in individual female body condition with variation in sex ratios of individually associated litters.

Changes in parameters such as immigration, dispersal, coalition change and social interaction may also cause changes in demographic parameters (Ferreira et al., 2013; Packer & Pusey, 1987). A key element associated with the survival of sub-adult males deals with human–lion conflict (Daigle, Brown, Carlstead, & Pukazhenthi, 2015; Ferreira et al., 2013; Mills et al., 1978; Sogbohossou et al., 2014; van Vuuren et al., 2005). Lions in the south-western KTP come into conflict with commercial livestock farmers living next to the park (van Vuuren et al., 2005). Lion demographic profiles may be altered through retribution killing and management actions in response to transgressing lions (Everatt, Andresen, & Somers, 2014; Ferreira et al., 2013; Funston, 2011; van Vuuren et al., 2005). Lions, which transgress the park boundary, whether fenced or unfenced, are often subject to retribution killing in response to livestock losses (Funston, 2002).

In recent times, however, management protocols seek to retrieve the lion or lions and translocate them back into the park interior (Funston, 2002). This activity of retrieval increased over time. For instance, between 1998 and 2001, authorities noted 114 transgressing lions with 34 of these killed during a period of low retrieval (Funston, 2002). Between 2012 and 2017, 107 lions transgressed the boundary of the park. In that period, authorities retrieved 98, while only 9 lions were killed. Due to increased management interventions in retrieving transgressing lions, a decrease

in mortality due to persecution appears to have been achieved. These actions may increase sub-adult male survival. We are aware of one case study that recorded highly skewed adult sex ratios towards females when hunting of males was intense. Sex ratios normalised after a period of low hunting—survival rates increased leading to increases in the number of adult males and male coalition sizes (Loveridge et al., 2016). This type of responses may play out whether management interventions target sub-adult or adult age classes. In our study, only 15 transgressors were sub-adult (9 male and 6 female) and of these 4 males and 2 females were killed (M. Ferreira, 2015 Pers.comm.[2]).

In contrast to the argument that sub-adult male numbers might be increased by management, there are also mechanisms that may impose higher mortality on sub-adult male lions. For instances, retrieved transgressing lions are often released within the territories of nonassociated prides (see the protocol, Funston, 2011; Pers. Obs. 2013–2015). The outcomes of interactions between resident and relocated lions in the south-western KTP are uncertain, but may result in conflict, particularly between males. Such conflict may lead to coalition changeovers, infanticide and consequences for survival and sex ratios at birth (Pusey & Packer, 1987; Yamazaki, 1996), although only one takeover was observed during the time of this study. Relocating transgressors carry several challenges (Borrego et al., 2018) such as becoming habitual transgressors (Funston, 2002) and impacting resident lions (Massei, Quy, Gurney, & Cowan, 2010).

The recent higher lion estimates compared to before (Beukes et al., 2017a) may falsely lead conservationists to conclude that the lion population of the south-western KTP is not under immediate threat due to a male-biased sub-adult population. Furthermore, no other populations showing similar shifts to higher proportions of males (Mills, 1995) have experienced significant declines. The speculated mechanisms leading to unexpected higher proportion of males in the cub and sub-adult age categories in 2001 (Funston, 2001; van Vuuren et al., 2005) and greater proportion of sub-adult males observed in this and the 2010 study of Ferreira et al. (2013) require explicit investigation. It needs to be established whether natural (Celesia et al., 2010; Trimble et al., 2009) or anthropogenic (Trinkel, 2013; Woodroffe & Frank, 2005) drivers cause the higher than expected sub-adult male preponderance.

ACKNOWLEDGEMENTS

We would like to acknowledge the contributions made by South African National Parks, Botswana's Ministry of Wildlife, Environment and Tourism, the Gemsbok National Park's management team, Peace Parks Foundation, Dr and Mrs Fehlmann, Land Rover South Africa, B. Courtenay and the SATIB Conservation Trust. Research grants were from the CPUT Bursary Fund, the National Research Fund and University Research Fund.

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CONFLICT OF INTEREST

The authors do not recognise any potential sources of conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from South African National Parks data repository. Restrictions apply to the availability of these data, which were used under licence for this study. Data are available from Judith Botha, SANParks (judith.botha@sanparks.org), or the first author Dr. Sam Ferreira (sam.ferreira@sanparks.org) with the permission of South African National Parks.

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How to cite this article: Ferreira SM, Beukes BO, Haas TC, Radloff FGT. Lion (*Panthera leo*) demographics in the south-western Kgalagadi Transfrontier Park. *Afr J Ecol*. 2020;58:348–360. https://doi.org/10.1111/aje.12728