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# Changes in African lion demography and population growth with increased protection in a large, prey-depleted ecosystem

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**Abstract**

Large carnivores such as the lion are declining across Africa, in part because their large herbivore prey is declining. There is consensus that increased protection from prey depletion will be necessary to reverse the decline of lion populations, but few studies have tested whether increased protection is sufficient to reverse the decline, particularly in the large, open ecosystems where most lions remain. Here, we used an integrated population model to test whether lion demography and population dynamics were measurably improved by increased protection. We used data from monitoring of 358 individuals from 2013 to 2021 in the Greater Kafue Ecosystem, where prior research showed that lions were strongly limited by prey depletion, but protection increased in several well-defined areas beginning in 2018. In some other areas, protection decreased. In areas with high protection, lion fecundity was 29% higher, and mean annual apparent survival ($\varphi$) was 8.3% higher (with a minimum difference of 6.0% for prime-aged adult females and a maximum difference of 11.9% for sub-adult males). These demographic benefits combined to produce likely population growth in areas with high protection ($\widehat{\lambda} = 1.085$, 90% CI $= 0.97, 1.21$), despite likely population decline in areas with low protection

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($\hat{\lambda} = 0.970$, 90% CI = 0.88, 1.07). For the ecosystem as a whole, population size remained relatively constant at a moderate density of 3.74 (±0.49 SD) to 4.13 (±0.52 SD) lions/100 $km^2$. With the growth observed in areas with high protection, the expected doubling time was 10 years. Despite this, recovery at the scale of the entire ecosystem is likely to be slow without increased protection; the current growth rate would require 50 years to double. Our results demonstrate that increased protection is likely to improve the reproduction and population growth rate of lions at a large scale within an unfenced ecosystem that has been greatly affected by poaching.

KEYWORDS

bushmeat hunting, integrated population model, Kafue, Kavango-Zambezi Trans-Frontier Conservation Area, lion, *Panthera leo*, population dynamics, prey depletion

## 1 | INTRODUCTION

Across Africa and in much of the world, large herbivore populations are in decline (Bolger et al., 2008; Ripple et al., 2015; Western et al., 2009). Because the density of apex carnivores correlates strongly with the density of large herbivores (Hatton et al., 2015; Hayward et al., 2007; Orsdol et al., 1985), large carnivore populations are declining in parallel with their prey (Estes et al., 2011; Ripple et al., 2015). The population density of lions (*Panthera leo*) correlates particularly strongly with prey density (Hatton et al., 2015; Hayward et al., 2007; Packer et al., 2005), and lions are currently declining throughout most of their range (Bauer et al., 2015; Riggio et al., 2015) due to a combination of prey depletion, habitat loss, conflict with humans and livestock, trafficking of skins and parts, and other threats (Bauer et al., 2016; Cushman et al., 2018; Dickman, 2010; Williams et al., 2017). Prey depletion due to bushmeat poaching has been identified as one of the broadest and strongest threats to the lion (Bauer et al., 2022), but despite the magnitude and pervasiveness of this threat (Visser et al., 2023), it has received relatively little direct research for lions or other large carnivores (Creel et al., 2023; Goodheart et al., 2021; Lindsey et al., 2013; Vinks et al., 2020; Vinks, Creel, Rosenblatt, et al., 2021; Vinks, Creel, Schuette, et al., 2021).

The effects of bushmeat poaching on the demography of lions (and other carnivores) are rarely quantified (Vinks, Creel, Schuette, et al., 2021). Broadly, these effects include direct mortality due to snaring by-catch, and indirect effects on survival and reproduction due to prey depletion. By-catch mortality can be appreciable for lions (Becker, McRobb, et al., 2013; Becker, Watson, et al., 2013; Montgomery et al., 2023; Mudumba et al., 2021; White & Van Valkenburgh, 2022), and programs to reduce mortality by removing snares from injured animals can significantly increase a lion population's growth rate (Banda et al., 2023). The effect of prey depletion on lion demography and population dynamics is harder to quantify, but it is likely to be strong because lion density is very tightly correlated with prey density, across a wide range of spatial and temporal scales (Hatton et al., 2015; Packer et al., 2005; Van Orsdol, 1984).

Beyond the well-documented impact of poaching on large herbivore biomass, the specific trends, patterns and consequences of prey depletion are not well described, but are likely to vary among species and ecosystems. Integrated long-term studies in Zambia's Greater Kafue Ecosystem (GKE) and Luangwa Valley Ecosystem (LVE) have begun to clarify the effects of bushmeat poaching and prey depletion on large herbivores and carnivores, showing that: (1) herbivore density is reduced in areas where poaching pressure is high (Rosenblatt et al., 2019; Schuette et al., 2018; Vinks et al., 2020; Watson et al., 2013, 2015); (2) larger herbivores have been more affected by poaching than smaller ones (Creel et al., 2018; Vinks et al., 2020); (3) overlap in large carnivore diets increases where large prey are disproportionately depleted (Creel et al., 2018); and (4) within the large carnivore guild, the distribution, density and demography of both dominant (lions) and subordinate (African wild dogs, *Lycaon pictus*, Leopard, *Panthera pardus*) competitors are negatively affected by prey depletion (Creel et al., 2023; Goodheart et al., 2021; Rosenblatt et al., 2016; Vinks, Creel, Rosenblatt, et al., 2021; Vinks, Creel, Schuette, et al., 2021).

Bushmeat poaching emerges as a threat where budgets are not adequate for the management of protected areas and has increased across Africa coincident with human population growth and increased wealth in urban areas

(Lindsey et al., 2013, 2018). Bushmeat poaching in Africa arises from multiple problems such as food insecurity, poverty, and unemployment, but also represents a significant and profitable economic opportunity for impoverished communities near protected areas. Broadly addressing the bushmeat crisis will require an array of integrated efforts combining both incentives (e.g. community engagement, alternative livelihoods and protein sources, legal game meat) and deterrence (e.g. anti-poaching and anti-trafficking). The single most effective short-term action to reduce bushmeat hunting is thought to be anti-poaching patrolling (Lindsey et al., 2018), but its effectiveness is generally assumed rather than tested.

Although lions are the most-studied species in the African large carnivore guild (Strampelli et al., 2022), empirical analyses of their demographic responses to management and conservation actions remain rare, and mostly restricted to the effects of trophy hunting (Creel et al., 2016; Loveridge et al., 2007, 2016; Mweetwa et al., 2018; Rosenblatt et al., 2014; Whitman et al., 2004). Vinks, Creel, Schuette, et al. (2021) found that low prey density due to bushmeat poaching in the GKE caused lion density to be low, primarily due to poor cub recruitment (rather than poor adult survival). Unlike legal trophy hunting, which can be directly altered by management decisions that quickly alter lion dynamics (Mweetwa et al., 2018), the response of lions to management actions intended to prevent or reverse prey depletion are likely to be slower, because poaching is less controllable, the recovery of prey populations will lag behind changes in protection, and the demographic responses of lions will lag behind the recovery of prey populations.

The GKE is approximately 66,000 km$^2$, consisting of Kafue National Park (KNP) and surrounding Game Management Areas (GMAs), and comprising approximately 13% of the Kavango-Zambezi Trans-Frontier Conservation Area (KAZA). The GKE holds Zambia's second-largest populations of lions, wild dogs, leopards and spotted hyenas, and its largest population of cheetahs (Creel et al., 2023, Goodheart et al., 2021, Vinks, Creel, Rosenblatt, et al., 2021, Vinks, Creel, Schuette, et al., 2021). However, the densities of large herbivore species in the GKE are from 6 to 20 times lower than has been observed in other miombo ecosystems with similar rainfall (using ground transects that correct for detection) (Schuette et al., 2018; Vinks et al., 2020). A recent assessment of lion populations in protected areas throughout their range found that funding was from 3 to 6 times less than would be needed to effectively protect and maintain existing populations, with Zambian populations facing greater than average shortfalls (Lindsey et al., 2018). The GKE has long had very low management budgets, which has contributed to high levels of poaching and low densities of wildlife, but from 2018 to 2021, the Zambia Department of National Parks and Wildlife (DNPW) received increased anti-poaching investment and support from partners beginning with Game Rangers International (GRI), followed by Panthera, Musekese Conservation (MC), and African Parks Network (APN). Simultaneously, private conservancies and operators of hunting concessions have increased investment in the GMAs surrounding KNP. In 2022, these efforts led to a 20-year agreement between the Zambian government and African Parks for the co-management of Kafue National Park, with expected collective investment across the GKE of $15–20 million/year.

Rigorous assessment of demographic responses of vulnerable species is essential to evaluate the effectiveness of such actions. For lions, there has been considerable debate whether increased funding for protection can be effective without fencing a protected area (Creel et al., 2013; Durant et al., 2015; Packer et al., 2013). Here, we used long-term data from intensive population monitoring of lions in the GKE to test whether lion demography and dynamics have measurably responded to increased investment in protection in a large, unfenced ecosystem. Because we monitored the GKE lion population in the same manner for several years before and several years after a systematic increase in protection (and because protection did not increase in all areas), these data allow an unusually direct test.

## 2 | METHODS

### 2.1 | Study area

We monitored the GKE lion population from 2013 to 2021 across ~8000 km$^2$ in the northern and central portions of the ecosystem (Figure 1). Lions are present in other portions of the ecosystem at densities estimated recently at less than 1 individual/100 km$^2$ (Panthera, 2022), but because our study area held most of the population, dynamics within this area are likely to have driven population trends for the system. To describe population trends since protection efforts increased, we estimated population density for a constant area of 4152 km$^2$ using data from a subset of recent years (2018–2021) over which the intensity of monitoring was constant over a large area (Figure S1). To test for effects on apparent survival, reproduction and population growth, each lion group was assigned a protection level (high, intermediate, or low) based on the exposure to bushmeat poaching, active law enforcement effort, and passive protection due to accessibility and tourist activity (Figure 1). Most high protection prides resided within “Intensive Protection Zones” (IPZs). IPZs were areas in central and

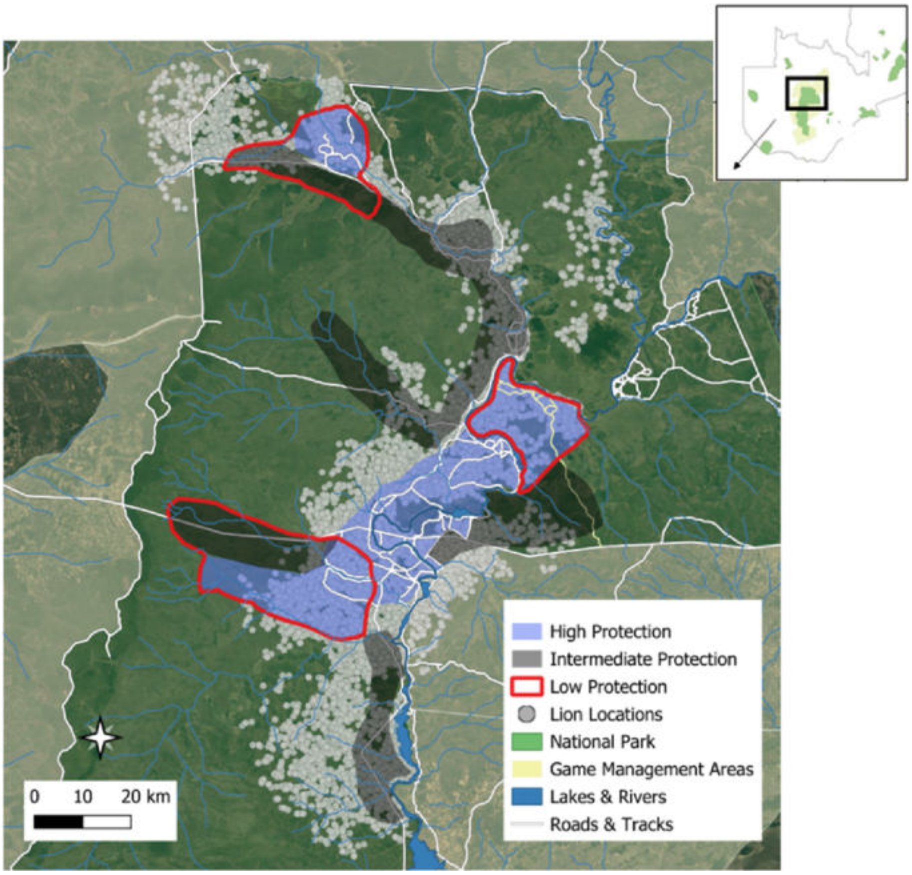

**FIGURE 1** The GKE study area, with Kafue National Park shown in green and adjacent Game Management Areas in tan. Smaller polygons show areas with relatively high protection in blue and intermediate protection in black. All other areas had relatively low protection. During the study, several areas shifted from low to intermediate or high protection, or vice-versa: These areas are outlined in red. The red-outlined area in the North shifted from intermediate (black) or high (blue) protection to low protection. The two other red-outlined areas shifted from low protection to intermediate (black) or high (blue) protection Transparent gray points show lion locations from a single year (2021) to illustrate that our study included lions that were well-distributed over large regions that varied in protection level. Rivers are shown in blue and roads/tracks are shown in white. The inset map shows the study site's location within Zambia.

northern Kafue where DNPW and their law enforcement partners Panthera and Musekese Conservation targeted intensive antipoaching patrols starting in 2018. This increase in patrolling decreased the number of snares and people encountered per kilometer of patrol effort (Panthera, 2022), in locations commonly used by lions and other large carnivores (Figure 1). Other high protection prides had ranges in areas with tourist camps, a network of vehicle tracks, and relatively high levels of tourist activity that resulted in low levels of poaching (Figure 1). Prides with low protection had ranges outside of designated IPZs and high tourism areas, often on the periphery of Kafue National Park or within the adjoining Game Management Areas, where prey depletion due to snaring is severe (Vinks et al., 2020). Prides with intermediate protection had ranges near IPZs and/or moderate levels of tourist activity. The level of protection for a given group was allowed to vary among years if circumstances changed, and more than half of the area designated as high protection changed classification during the study (Figure 1). This temporal variation helps to disentangle the effects of protection from other spatial attributes of a location.

Protection levels for each pride were assigned by six assessors with more than 50 years of collective field experience in the ecosystem: LZ as a patrol commander and Senior Ranger for northern KNP's anti-poaching operations, MB with more than a decade of ground observations of GKE carnivores, including lions, BG and AK, each with 5 years of daily ground observation of GKE carnivores, including lions, and WD and Phil Jeffery, each with extensive ground observations and antipoaching patrol experience in the Musekese area. The six assessors made identical assignments except for two ranges that were initially considered low protection by one observer and intermediate by another. To eliminate this minor ambiguity, we combined the low and intermediate protection levels prior to analysis (hereafter, "low protection"), yielding complete agreement among six assessors who worked for three organizations with a range of perspectives, priorities and activities, including research, photo-tourism, and law enforcement. The assignments of protection level were made prior to fitting the model, without examining the data, and were not subsequently adjusted. SC (who built the IPM and ran the analysis) did not participate in the assignment of protection levels.

## 2.2 | Population monitoring

Our methods of population monitoring for lions and other large carnivores have previously been described in

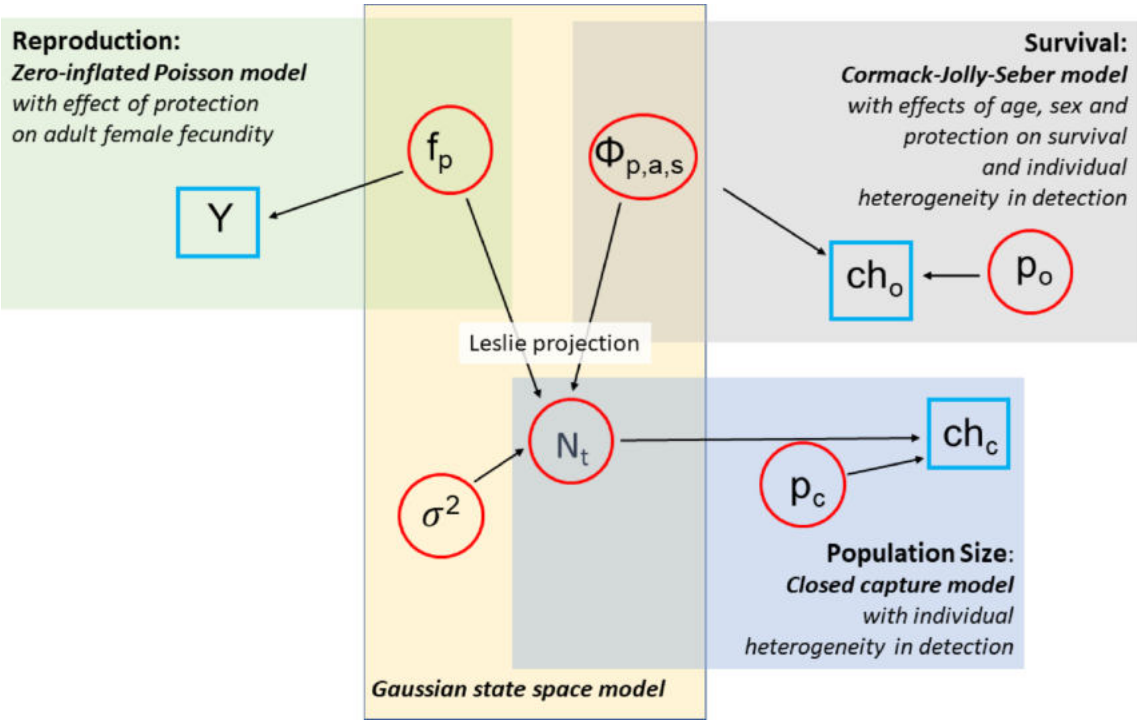

FIGURE 2 The integrated population model's structure, shown as a directed acyclic graph. The four component models are identified by shaded boxes. Data are identified by blue squares, and estimated parameters are identified by red circles. *Data*: $Y$ = one-year old cubs produced per adult female per year, $ch_o$ = capture history for multi-year CJS model, $ch_c$ = capture histories for closed capture model fit separately for each year. *Parameters*: $p_o$ = detection probability for CJS model, $p_c$ = detection probability for closed capture model, $f_p$ = protection level ($p$) specific annual fecundity, $\varphi_{p,a,s}$ = protection level ($p$) specific annual apparent survival for each age-class (a) and sex (s), $N_{A,t}$ = area-specific population size, summed to obtain total population size ($N$) at each time ($t$), $\sigma^2$ = Gaussian sampling error in total population size. All parameters were simultaneously estimated with a single joint likelihood using Bayesian methods.

detail (Goodheart et al., 2021; M'soka et al., 2016; Mweetwa et al., 2018; Rosenblatt et al., 2014; Vinks, Creel, Schuette, et al., 2021). Briefly, we used direct observation of GPS and VHF collared lions and their group mates to record 4303 monthly sightings (i.e., multiple sightings of an individual within a month were collapsed) of 358 known individual lions in 37 prides and 32 male coalitions from 2013 to 2021. We identified lions by whisker-spot patterns, nose-pigmentation patterns, scarring, and tooth wear (Pennycuick & Rudnai, 1970), using a database of digital photographs. For lions whose age was unknown, age was estimated using calibrated standards for nose-pigmentation pattern, tooth wear and coloration, and facial scarring (Miller et al., 2016; Whitman et al., 2004). We validated the accuracy of age assignments with known-age individuals in this population and in another Zambian population with a longer-running study (Mweetwa et al., 2018). Lions were collared with a combination of VHF, GPS store-on-board, and Iridium satellite-GPS collars (Telonics, Arizona, USA), with at least one lion collared per pride or coalition. A Zambian-registered wildlife veterinarian deployed all collars in collaboration with the Department of National Parks and Wildlife, using procedures approved by the Montana State University Animal Care and Use Committee and DNPW. Though lions live in a fission–fusion society, the frequency of pride fission is low when pride sizes are small (Mbizah et al., 2019). Because most prides were small in the GKE (Vinks, Creel, Schuette, et al., 2021) we obtained regular sightings of most non-collared pride members of all age-sex classes by tracking collared lions. Photographs from commercial guides, professional hunters, conservation partners, and tourists provided additional observations of known lions, and as described below (see "Integrated Population Model"), our modeling approach accounted for individual variation in detectability, thus accounting for lower detection rates for animals of some age-sex classes or in less accessible areas. Survival rates did not differ detectably for collared and uncollared lions.

## 2.3 | Integrated population model

To test whether differences in protection were associated with measurable benefits, we fit a Bayesian integrated population model (IPM) to describe the demography and dynamics of lions in areas with high and low protection (Figure 2). IPMs integrate the analysis of multiple datasets that are informative about population size, survival, and reproduction. Consequently, parameter estimates from an IPM can be more precise and less biased than estimates of the same parameters from independent analyses of each dataset (Chandler & Clark, 2014; Schaub & Abadi, 2010). We used Leslie projection to link three submodels: a Cormack–Jolly–Seber model of age-, sex-, and protection-specific apparent survival rates (i.e. the rate at which individuals survived and remained within the study population); a zero-inflated Poisson model of protection-specific adult female fecundity; and a standard state-space model of population size that used estimates from a closed capture-mark-recapture model as the counts from which population size was estimated as a latent variable (Schaub & Kery, 2022). Because the state-space model estimated uncertainty in population size, we did not propagate the variance of closed-capture estimates forward in the IPM; rather, we simply replaced biased population counts with unbiased estimates of N as the left-hand-side input for the state-space model. This IPM's structure does not estimate any parameters for which there were no empirical data. The model was fit in R and JAGS using the jagsUI package (Kellner, 2021) with three MCMC chains of 6000 steps, a burn in of 1000 steps and an adaptive phase of 300 steps. JAGS code for the IPM is provided in the supplemental material.

Within the IPM, we estimated apparent survival rates with a Cormack-Jolly-Seber model using capture histories with three 2-month time bins (May–October, when dry conditions provided good detection rates) in each year, for a total of 27 occasions over 9 years (2013–2021). We modeled annual apparent survival rates ($\varphi$) in areas with high and low protection for males and females of four age classes (cub: 0–1.99 years, sub-adult: 2–3.99 years, prime adult: 4–5.99 years, old adult: ≥6 years). An individual's protection level was allowed to vary through time if the individual moved between regions. Protection levels were also re-assigned for lions in four groups with home-ranges that changed from low to high and for one group that changed from high to low (Figure 1). We did not model an interaction between the effects of protection and age/sex class. We modeled detection probability ($p$) with an individual-level random effect that was normally distributed on the logit scale, using uninformative flat priors with bounds suggested by Schaub and Kery (2022). As with prior analysis of similar data (Goodheart et al., 2021, Vinks, Creel, Schuette, et al., 2021), we used a Q–Q plot to confirm that this detection model fit the data well (i.e., accurately described variation in detectability).

Area-specific fecundity was estimated with a zero-inflated Poisson generalized linear model (GLM) fit to data on the number of first-year cubs per adult female. For GKE lions, the distribution of fecundity had an excess of zeros relative to the Poisson distribution, because females with surviving cubs from the prior year did not reproduce, as is typical for lions. To account for this pattern, the GLM combined a Bernoulli distribution of zero inflation and a Poisson model, with uninformative wide priors for both parameters using bounds suggested by Schaub and Kery (2022). In a separate analysis, we used a Poisson general linear model to test for changes through time in the number of cubs born and raised per pride (*n.b.*, fecundity was not zero-inflated at the pride level, as it was at the individual level).

Population size and the population growth rate were estimated in the final sub-model of the IPM. First (outside of the IPM), we fit a closed capture-mark-recapture model to estimate total population size in each year, using individual encounter histories with the same time bins and logit-normal individual random effect on $p$ as in the CJS model. Comparing the number of known individuals to posterior probability distributions for population estimates ($\widehat{N}$) for 2019 to 2021 from this sub-model (Figure S3A–C) suggests that detection probability changed over time. With such changes in detection, an IPM that includes a state-space model fit to population estimates that corrects for detection provides a better fit than an IPM that includes a state-space model fit to uncorrected population counts (Schaub & Kery, 2022, section 4.3). Posterior probability checking confirmed that the detection component of this closed capture model fit the data well (Figure S3D), so we used the median of the posterior probability distribution as a point estimate of population size for each year. Then, Leslie matrices incorporating estimated rates of reproduction and (age- and sex-specific) survival for areas with high and low protection were used to estimate the number of yearlings and adults expected in each year in the absence of immigration or emigration ("growth in place"). We used uninformative flat priors for the number of individuals of each age in areas with high and low protection, using guidance for bounds from Schaub and Kery (2022). Finally, we fit a state-space model that related the closed-capture estimates of total population size to the summed number of individuals (of all ages and both sexes, in areas with high and low protection) from Leslie projection, with normally distributed sampling variance to account for error in the population estimates. Local population growth rates were then derived for areas with high and low protection. This approach rolled all variance in population estimates into the state-space model, and simultaneously allowed for the possibility that population size

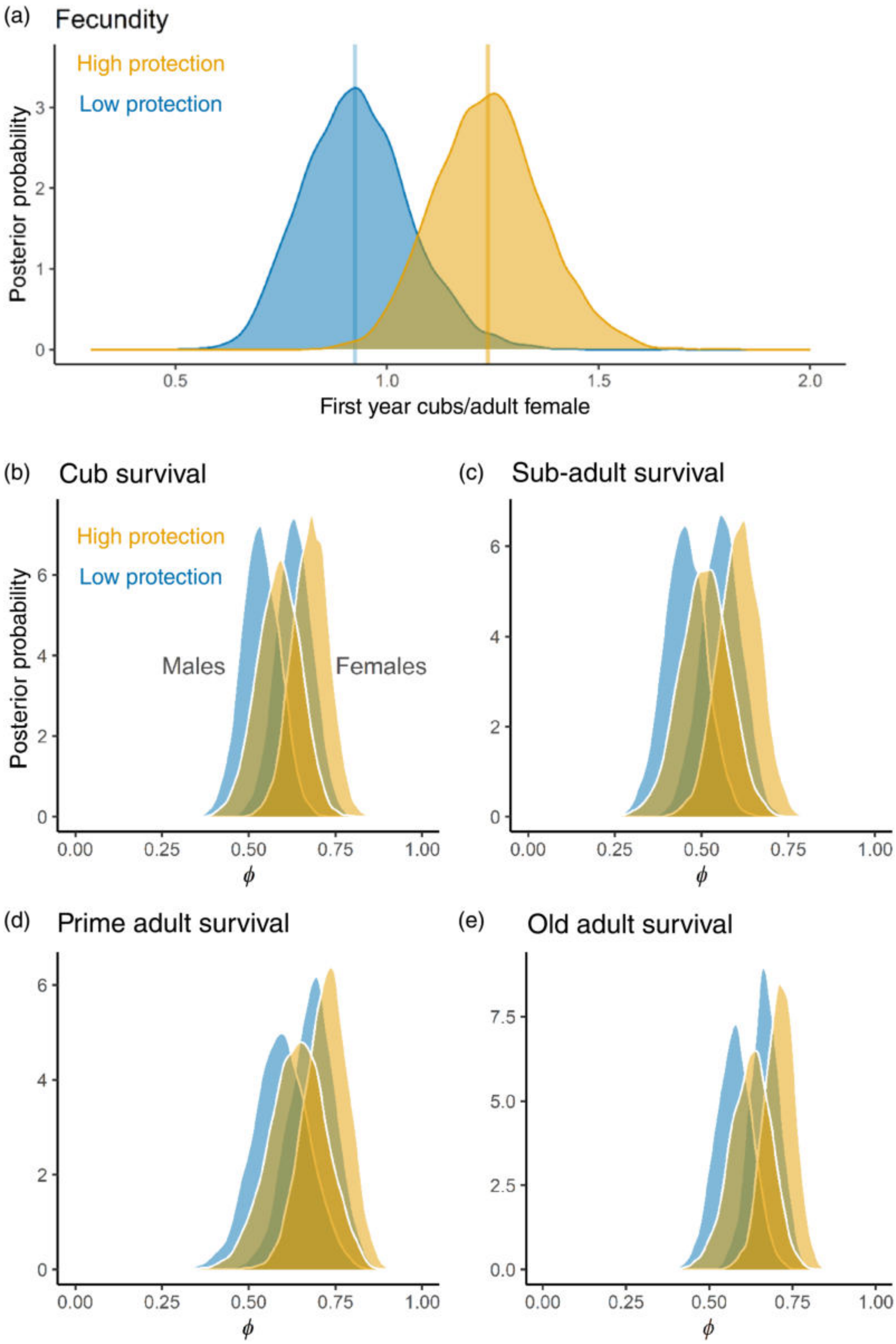

**FIGURE 3** Posterior probability distributions for demographic parameters for lions in areas with high protection (yellow) or low protection (blue) from illegal bushmeat poaching. (a) Adult female fecundity, measured as first year cubs per female. (b–e) Annual apparent survival ($\varphi$) for four age classes: Cubs (0–1.99 years), sub-adults (2–3.99 years), prime adults (4–5.99 years) and old adults(≥6 years). Males (with lower survival rates) are to the left of females in panels b–e. The model estimated effects of age and sex on survival, but did not include an interaction between the effects of age and sex.

could be over- or under-estimated (as is apparent in Figure S3A–C) due to imperfect estimation of the probability of detection in the closed capture-mark-recapture model, less than complete population closure, or imperfect estimation of the area that was used by the population.

Because the exact area under study varied from year to year as groups formed and failed and our sampling effort expanded, direct comparison of population sizes from the IPM might not provide an accurate description of population trends. Therefore, we converted annual estimates of population size ($\widehat{N}$) to estimates of density $\widehat{D}$ by dividing by the area ($\widehat{A}$) occupied by prides included in the estimate of population size, which was determined by the 80th percentile isopleth of a kernel utilization distribution fit to GPS locations from all adult female lions monitored in that year, following methods from Vinks, Creel, Schuette, et al. (2021) (Figure S1, and see Section 4). We examined population trends for a 4-year period from 2018 to 2021 with relatively constant sampling effort ($\overline{X} = 4152\,\text{km}^2$, see Figure S1 and Vinks, Creel, Schuette, et al. (2021)) by testing for changes through time in these densities.

Goodness of fit tests for IPMs that incorporate a state-space model of population dynamics are not well resolved (Schaub & Kery, 2022). Therefore, we confirmed the model's fit in several ways. First, we confirmed that trace plots were well mixed for all parameters. Second, we confirmed that $\widehat{R}$ values were near one (≤1.01) for all parameters. Third, we used a Q–Q plot to confirm that variation in the probability of detection in the survival model was well described by an individual random effect that was normally distributed on the logit scale. Fourth, we confirmed that the observed distribution of fecundity was well described by the zero-inflated Poisson distribution used in the fecundity model. Fifth, we confirmed that estimates from the IPM for survival and fecundity were similar to results from the same models run in isolation (Schaub & Kery, 2022).

## 3 | RESULTS

### 3.1 | Reproduction

Fecundity was 29% greater for females in areas with high protection than in areas with low protection (Figure 3a) (*high*: posterior median = 1.24 first year cubs/adult female, 90% CI = 1.04, 1.46; *low*: posterior median = 0.93, 90% CI = 0.73, 1.14), and there is a 78% probability that fecundity was greater in high protection areas than in low protection areas. From 2018 to 2021, the known number of cubs raised to 1 year per pride increased substantially (Figure S1, Poisson GLM, $b = 0.29$ cubs raised/pride/year, SD = 0.12, $z = 2.53$, $p = .012$). For the same prides over the same period, the number of litters produced per pride decreased slightly but significantly (Figure S2, Poisson GLM, $b = -0.35$ litters/pride/year, SD = 0.14, $z = 2.51$, $p = .012$), and the number of cubs born per pride decreased slightly but significantly (Figure S2, Poisson GLM $b = -0.26$ cubs born/pride/year, SD = 0.08, $z = -3.42$, $p = .0006$). An increase in cub recruitment would be expected to cause a decrease in the number of cubs and litters born, because female lions do not ovulate while they have nursing cubs (due to lactational infertility).

### 3.2 | Survival

After accounting for higher survival in females than males and higher survival in adults than subadults and cubs, there was a weak tendency for lions in areas with high protection to survive better (Figure 3b–e). For male cubs, median annual apparent survival ($\varphi$) was 0.59 (90% CI = 0.48, 0.69) with high protection and 0.53 (90% CI = 0.44, 0.62) with low protection. For female cubs, annual apparent survival ($\varphi$) was 0.68 (90% CI = 0.59, 0.76) with high protection and 0.63 (90% CI = 0.54, 0.72) with low protection. For male subadults, annual apparent survival ($\varphi$) was 0.51 (90% CI = 0.39, 0.62) with high protection and 0.45 (90% CI = 0.35, 0.55) with low protection. For female subadults, annual apparent survival ($\varphi$) was 0.61 (90% CI = 0.51, 0.70) with high protection and 0.56 (90% CI = 0.46, 0.65) with low protection. For male prime adults, annual apparent survival ($\varphi$) was 0.64 (90% CI = 0.51, 0.77) with high protection and 0.59 (90% CI = 0.46, 0.72) with low protection. For female prime adults, annual apparent survival ($\varphi$) was 0.73 (90% CI = 0.62, 0.82) with high protection and 0.68 (90% CI = 0.57, 0.79) with low protection. For male old adults, annual apparent survival ($\varphi$) was 0.63 (90% CI = 0.52, 0.72) with high protection and 0.57 (90% CI = 0.48, 0.66) with low protection. For female old adults, annual apparent survival ($\varphi$) was 0.71 (90% CI = 0.63, 0.78) with high protection and 0.67 (90% CI = 0.59, 0.74) with low protection.

Overall, the estimates of median annual apparent survival ($\varphi$) were 6.0% to 11.6% higher in areas with high protection, relative to annual apparent survival for individuals of the same age and sex in areas with low protection (male cubs: 9.6%, female cubs: 7.2%, male subdaults: 11.9%, female subadults: 9.0%, male prime adults: 8.0%, female prime adults: 6.0%, male old adults: 8.5%, and female old adults: 6.4%). Across all age-sex classes, the median survival rate was 8.3% higher in areas with high

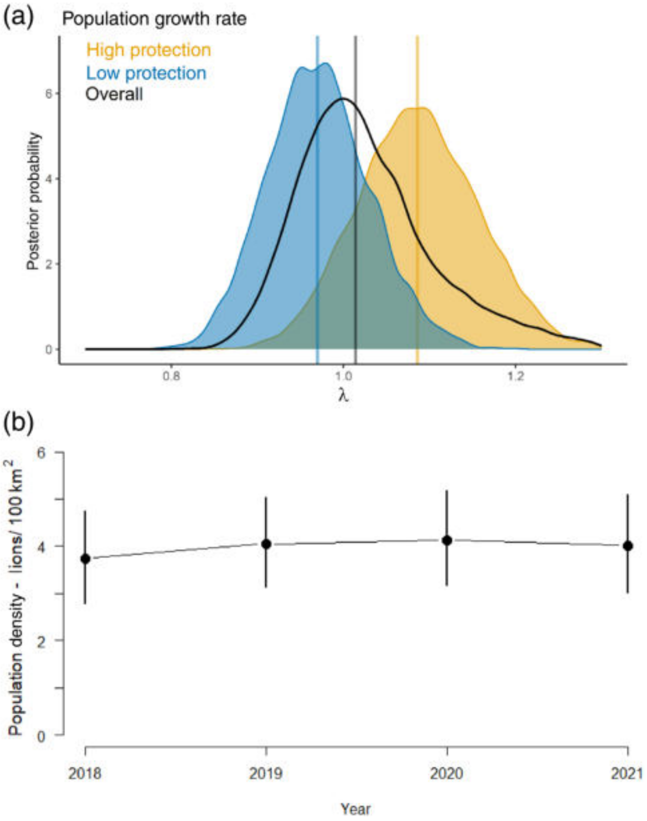

**FIGURE 4** (a) Posterior probability distributions for annual population growth rates ($\lambda$) for lions in areas with high protection (yellow) or low protection (blue) from illegal bushmeat poaching, and for the GKE lion population as a whole (black). (b) The population trend from 2018 to 2021. Density was estimated by the integrated population model, for an area of 4152 km$^2$ including both high and low protection. Points show means from the posterior probability distribution for each year, and error bars show 95% credible intervals.

protection, but posterior distributions overlapped greatly for survival in high protection and low protection areas.

### 3.3 | Population dynamics

The median population growth rate ($\lambda$) was 1.085 for areas with high protection (90% CI = 0.97, 1.21), but only 0.970 for areas with low protection (90% CI = 0.88, 1.07). In areas with high protection, the annual probability of population growth was 89.3%, but in areas with low protection the probability of growth was only 30.2%. There is a 63% probability that the population growth rate was greater in high protection areas than in low protection areas, and the fraction of the posterior distribution with $\lambda > 1$ was 2.96-fold larger for high protection areas than for low protection areas. For the population as a whole, the median growth rate was 1.014 (90% CI = 0.92, 1.19): population growth in areas with good protection offset population decline in less protected areas, yielding a population that was essentially stable (Figure 3). This inference is supported by estimates of population density (Figure 4), which remained quite constant from 2018 to 2021. Population density ranged from a minimum of 3.74 (±0.49 SD) lions/100 km$^2$ in 2018 to a maximum of 4.13 (±0.52 SD) lions/100 km$^2$ in 2020, and the 95% credible intervals for all years overlapped substantially (Figure 4). These changes in density are very small when compared to the range of variation in lion density (from <1 to >10 lions/100 km$^2$) that is observed among ecosystems.

## 4 | DISCUSSION

This study provides a rigorous evaluation of demographic responses to changes in protection for a large carnivore population that is strongly limited by prey depletion from bushmeat poaching. Our results demonstrate that increasing protection is likely to improve lion demography over large areas. In particular, fecundity and cub recruitment were substantially higher in well-protected areas, and increased in recent years with increased protection effort. Increased cub recruitment was accompanied by a decrease in the number of cubs and litters born per pride, which is expected as a result of lactational infertility among lionesses with a dependent cub (Packer et al., 1988; Pusey & Packer, 1994). Survival rates were higher in areas with good protection, but differences in survival were considerably smaller than the difference in fecundity, as is expected for a long-lived, iteroparous animal on the basis of life history theory (Fisher, 1958; Williams, 1966) and has been suggested previously for lions (Vinks, Creel, Schuette, et al., 2021).

Our results confirm that cub recruitment is a useful leading indicator of lion dynamics and their response to conservation efforts (or threats), but survival rates are probably less useful. Similar effects on lion demography were observed during a three-year moratorium on trophy hunting of lions in the LVE, which allowed the lion population to increase substantially, primarily due to increased cub recruitment (Mweetwa et al., 2018). The response of lion dynamics to a hunting moratorium was more rapid than we detected here. Prior to the hunting moratorium, LVE lions were limited by high mortality in trophy-aged males, leading to high turnover of the males associated with female prides, leading to increased infanticide, low cub recruitment, low subadult and adult male survival, and a senescing female population (Mweetwa et al., 2018; Packer & Pusey, 1983; Rosenblatt et al., 2014; Whitman et al., 2007). For LVE lions, this cascade of demographic responses to excessive trophy hunting was rapidly reduced through changes in policy. For GKE lions, Vinks, Creel, Schuette, et al. (2021) identified a simpler pattern, low cub recruitment, as the demographic signature of a population limited by prey depletion. Our results support this prior inference that GKE lions are limited by prey depletion, because the effect of increased protection on survival was small, whereas a large effect on survival would be expected if direct mortality due to snaring had a larger effect than that of prey depletion. Although estimates of large carnivore density usually exclude dependent offspring, our inclusion of cubs in the IPM was critical to identify the importance of cub recruitment for GKE lion dynamics, and, our results reinforce the inference that measuring cub recruitment might provide a simple tool to assess the status of lion populations.

Our results show that recovery from prey depletion can be relatively rapid in areas with concentrated protection: with density independent growth, the finite rate of increase ($\lambda$) of 1.085 that we observed in areas with high protection would yield a doubling time of 10 years. However, ecosystem-wide recovery for large unfenced ecosystems like the GKE (~66,000 km$^2$), with limited resources and vast areas to patrol, will likely be much slower should the current protection levels remain unchanged: the finite rate of increase of 1.014 that we observed for the study area as whole would (if constant) yield a doubling time of 50 years. Population growth was slightly negative in areas with low protection, which offset growth in areas of high protection and yielded stable dynamics with slight growth at the ecosystem level. This result is as expected for a population that is limited by prey depletion (Creel et al., 2018; Schuette et al., 2018; Vinks et al., 2020; Vinks, Creel, Schuette, et al., 2021), because large herbivore dynamics require time to respond to increased protection, and lion recovery will lag the recovery of their prey (Packer et al., 2005). Nevertheless, areas of high protection provided ecological conditions that yielded an 89.3% probability of annual growth and a high median growth rate (8.5%), so expanding these efforts into areas of low protection should be a top priority to address prey depletion in the GKE.

When assessing the effect of protection on demography and dynamics, one must recognize that active protection by patrolling and passive protection by tourism are usually directed to areas with high animal densities. This pattern can make it difficult to assess whether density is high because of protection, or vice-versa. In this study, more than half of the areas with high protection changed designation at some point in the study, both from low to high and from high to low (Figure 1). By examining changes in protection in fixed areas, causal inferences are strengthened, because other important ecological attributes of the area do not change (e.g., vegetation type, distance to water, location within the ecosystem). In addition, the areas of high and low protection in this study were similar with respect to vegetation type and distance from permanent water, which are the main ecological drivers of large herbivore density (Vinks et al., 2020). Finally, we have previously found that vegetation type has little effect on lion survival in Kafue (Vinks, Creel, Schuette, et al., 2021). For these reasons, we consider it likely that the observed effect of protection on lion population dynamics is causal. Our analysis does not directly reveal which aspects of protection are most beneficial to lions, but prior research shows that prey depletion due to poaching has strong effects on the density, distribution, diet and demography of lions and other large carnivores in the GKE and other Zambian ecosystems (Becker et al., 2023; Creel et al., 2018, 2023, 2024; Goodheart et al., 2021, 2022; Rosenblatt et al., 2016, 2019; Schuette et al., 2018; Vinks et al., 2020; Vinks, Creel, Rosenblatt, et al., 2021; Vinks, Creel, Schuette, et al., 2021).

Integrated population models are a powerful tool to describe population dynamics with a model that aligns estimates of population size with data on survival and reproduction (Schaub & Abadi, 2010; Schaub & Kery, 2022), an approach that is likely to improve the robustness of inferences (Tenan et al., 2017). For large carnivores like the lion this is important, because population estimates that depend on a single type of data are often imprecise. For large carnivores, the data that underlie population estimates often remain sparse despite intensive sampling effort (Elliot & Gopalaswamy, 2017), so that reliance on as single type of data can suggest biologically implausible rates and patterns of population growth. Our results show that an IPM approach is both feasible and useful for coherent inferences about the effectiveness of conservation actions for large carnivores.

Within our IPM, we used a sequential approach to estimate density by estimation of population size and area, rather than the simultaneous approach that would have been adopted by a "spatially explicit" sub-model of density. This sequential approach allowed us to model individual variation in detection probability in a manner that provided a good fit to the data (Figure S3), and allowed us to model the area used by the study population in a manner that also provided a good fit to the data (Figure S1). Spatially explicit (SECR) models of density are commonly applied to data from lions (Elliot & Gopalaswamy, 2017) and might also have provided a good fit to the data for the density component of the IPM, but most analyses of large carnivore density using SECR models assume that each animal has a single center of activity and a bivariate-normal pattern of space use (or another simple monotonically decreasing function), which is usually not realistic (Worton, 1987). Future work with large carnivores should examine the assumptions and performance of the space use models that underlie estimates of density to better understand the consequences for inferences, in both standalone and IPM analyses (Efford & Schofeild 2022). Our approach aimed to sidestep this concern by fitting a flexible and widely-used model of space use to determine the area sampled (Figure S1), coupled with a flexible and well-fit model of individual detectability within that area (Figure S3). This approach could perhaps create a different concern, namely that one could choose a different isopleth from the utilization distribution to define the study area. Making this choice explicit largely eliminates this concern, by allowing the same choice to be made for each density that is compared. Finally, the state-space sub-model of the IPM treated estimates of population size from the other sub-models as counts with sampling variance that might cause them to be too high or too low (due to imperfect estimation of individual detection or the area used by the population). By estimating population size as a latent variable within a state-space model, the IPM's structure accounted for sampling variance in population estimates more completely than is typical for large carnivores.

Beginning in 2018, the Zambia Department of National Parks and Wildlife, Panthera, Musekese Conservation, Game Rangers International, African Parks, and the Zambian Carnivore Programme significantly increased antipoaching patrols focused on areas where large carnivores and their prey are most affected by bushmeat poaching. Focused anti-poaching patrols were targeted using location data from intensive monitoring of lions, wild dogs, and cheetahs. Combined with de-snaring of individuals (Banda et al., 2023), this field-based protection (or 'halo effect') method can have positive demographic impacts on carnivore populations (Becker et al., 2023). Although this collective work has had positive results, a continued and expanded effort will be needed to reverse prey depletion and allow lion recovery at even larger scales. The signing of a 20-year management agreement between African Parks and the Government of Zambia represents such an effort for KNP, but parallel efforts will be needed for the vast GMA complexes surrounding the national parks. These areas are probably demographic sinks for carnivores due to their low protection levels and high rates of prey depletion, human encroachment and land-use change (Creel et al., 2024; Lindsey et al., 2014; Watson et al., 2015). Improved community conservation partnership models under development between the Government of Zambia, the Nature Conservancy, and partners could help facilitate lion recovery in the GMAs.

African lions have been in decline across much of their range for many years (Bauer et al., 2015, 2016, 2022; Bauer & Van Der Merwe, 2004; Riggio et al., 2013, 2015). Because the density of lions correlates very strongly with the density of prey (Hatton et al., 2015; Orsdol et al., 1985; Packer et al., 2005), a strong driver of the lion's decline has been the decline of large herbivore populations (Bolger et al., 2008; Ripple et al., 2015; Western et al., 2009), in large part due to bushmeat poaching (Lindsey et al., 2011, 2013; Ripple et al., 2016; Rogan et al., 2017). Although there has been some debate over the most effective strategies to mitigate or reverse the lion's decline (Creel et al., 2013; Durant et al., 2015; Packer et al., 2013), there is strong consensus that increased investment in antipoaching protection is necessary. Despite this consensus, there has been very little empirical research testing whether increased investment in protection is sufficient to reverse the lion's decline, or at what scale. Our study shows that increased protection is likely to improve lion reproduction and dynamics in a large, unfenced, ecosystem that has been strongly affected by bushmeat poaching (Creel et al., 2018; Goodheart et al., 2021, 2022; Schuette et al., 2018; Vinks et al., 2020; Vinks, Creel, Rosenblatt, et al., 2021; Vinks, Creel, Schuette, et al., 2021). By targeting protection to reverse prey depletion in ecosystems that remain large carnivore strongholds, managers can appreciably mitigate the impacts of bushmeat poaching, even in the large unfenced systems that hold most of the remaining lions in Africa. Combining improved protection with improved programs for community conservation and coexistence in and around the communities living with these populations should substantially improve the prospects for lion conservation.

## AUTHOR CONTRIBUTIONS

Scott Creel and Matt Becker conceived the ideas, designed the methodology and obtained funding; Ben Goodheart, Anna Kusler, Milan Vinks, Stephi Matsushida, Kachama Banda, Ruth Kabwe, Chase Dart, Kambwiri Banda, Luka Zyambo and Will Donald collected the data; Ben Goodheart, Milan Vinks and Scott Creel processed the data; Scott Creel, Ben Goodheart and Matt Becker analyzed the data; Scott Creel led the writing of the manuscript. Cat Sun contributed to interpretation and writing. Peter Indala, Clive Chifunte and Adrian Kaluka provided research integration with the Zambia Department of National Parks and Wildlife, and Craig Reid provided research integration with African Parks. All authors contributed critically to the concepts and drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Code is provided as supplemental material, and data will be deposited in Dryad upon acceptance.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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