



Counting cats for conservation: seasonal estimates of leopard density and drivers of distribution in the Serengeti

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Abstract

Large carnivore conservation is important for ecosystem integrity and understanding drivers of their abundance is essential to guide conservation efforts. Leopard (*Panthera pardus*) populations are in a general state of decline, although local studies demonstrated large variation in their population trends and density estimates vary widely across their range. We used spatially-explicit capture-recapture models for unmarked populations with camera trap data from a citizen science project to estimate previously-unknown leopard population densities in Serengeti National Park, Tanzania, and determine potential biological drivers of their abundance and distribution. We estimated leopard densities, at 5.41 (95% CrI = 2.23–9.26) and 5.72 (95% CrI = 2.44–9.55) individuals/100 km², in the dry and wet season, respectively, which confirmed Serengeti National Park as one of the strongholds of this species in Africa. In contrast to abundance estimates, we found that drivers of leopard abundance and distribution varied among the dry and wet seasons, and were primarily affected by interactions with other larger carnivores and cover. The underlying driver of leopard distribution may be the dynamic prey availability which shifts between seasons, leading to an avoidance of dominant carnivores when prey availability is low in the dry season but an association with dominant carnivores when prey availability is high in the wet season. As efforts to conserve large carnivore populations increase worldwide, our results highlight the benefits of using data from citizen science projects, including large camera-trapping surveys, to estimate local carnivore abundances. Using a Bayesian framework allows of estimation of population density, but it is also important to understand the factors that dictate their distribution across the year to inform conservation efforts.

Keywords Competition · Leopard · *Panthera pardus* · Population density · Predator–prey dynamics · Seasonal variation · Spatially explicit capture recapture

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Introduction

Effective conservation for species at risk is dependent on understanding their abundance and drivers affecting it, but these can be difficult to determine for cryptic species such as large carnivores (Gese 2001; Rich et al. 2013; Allen et al. 2018a). Large carnivores occupy the highest trophic levels, and play important roles in ecosystem regulation (Estes and Palmisano 1974; McLaren and Peterson 1994) and disease and population control (Packer et al. 2003; Ripple et al. 2014). Many populations worldwide, however, are declining due to increasing human populations and development, habitat degradation, and unsustainable hunting (Ripple et al. 2014). These anthropogenic effects are accelerating for large carnivores, whose naturally low population densities and birth rates make their populations sensitive to changes in the environment (Ripple et al. 2014). The density and conservation status of large carnivore populations often varies across geographical and jurisdictional ranges (Chapron et al. 2014; Jacobson et al. 2016; Durant et al. 2017), making it important to identify and conserve strongholds of high density populations.

Leopards (*Panthera pardus*) are cryptic solitary carnivores, whose IUCN Red List status has recently been up-listed to Vulnerable (Stein et al. 2020). Leopards suffered a substantial reduction in their range and currently occupy 25–37% of their historic range (Jacobson et al. 2016). Leopard populations across their range are also in a general state of decline with many of the nine leopard subspecies being critically endangered (Jacobson et al. 2016). The density estimates for leopards vary widely, with estimates ranging from 0.1 to 30.3 leopards/100 km² (Grey et al. 2013; Jacobson et al. 2016), and rigorous estimates from sub Saharan Africa ranging from 0.25 to 12.67 leopards/100 km² (Supplementary Material 1). Such high variation in population densities and limited number of regions sampled precludes extrapolation to other parts of their range, particularly because leopards have high variability in home-range size (Jacobson et al. 2016), prey preferences (Hayward et al. 2006), and interactions with humans and larger carnivores (Stein et al. 2020). There is a concurrent lack of research on density and abundance in many parts of leopards range and they are difficult to predict based on estimates from other parts of the range (Jacobson et al. 2016). This for now limits our ability to create range-wide population estimates, and as a result there is currently no robust estimate for the number of leopards across their range (Stein et al. 2020). Thus additional population surveys across the range of leopards, while also examining the effects of potential drivers, is important for both their local and range-wide conservation.

Densities of leopards vary across their range based on anthropogenic (i.e., development, hunting, and conservation activities) and ecological (i.e., competitors, prey, seasons, and habitat) factors (Bailey 2005; Balme et al. 2009; Harihar et al. 2011; Grey et al. 2013; Qi et al. 2015; Rosenblatt et al. 2016). Interactions with humans, including habitat loss and degradation (Jacobson et al. 2016; Stein et al. 2020), prey base depletion (Datta et al. 2008; Gray and Prum 2012), conflicts over livestock (Kissui 2008; Athreya et al. 2011) and unsustainable hunting practices (Packer et al. 2009; Gray and Prum 2012) are a leading cause of mortality and population declines for leopards. Leopard populations can also be suppressed by dominant carnivores, as documented in Asia for tigers (*Panthera tigris*) (Harihar et al. 2011), and suggested in Africa for African lions (*Panthera leo*), and spotted hyenas (*Crocuta crocuta*) (Packer et al. 2011). Besides interference competition, one of the possible mechanism of top-down suppression could be connected with kleptoparasitism, which was shown to reduce reproductive success in African leopards (Balme et al. 2017a).

However, recent research gives equivocal results on the importance of top-down effects and avoidance of dominant carnivores on leopard densities and activity (Steinmetz et al. 2013; Vanak et al. 2013; du Preez et al. 2015; Balme et al. 2017b). This suggests regional differences in the factors driving leopard abundance and further studies are therefore needed also to better understand the importance of interspecific interactions for leopards across their range.

Serengeti National Park (hereafter Serengeti) is the site of many long-term ecology studies (Mduma et al. 1999; Sinclair et al. 2007) and is a conservation stronghold for many species, but is not immune from the impacts of human encroachment and environmental change (Veldhuis et al. 2019). The leopard population in the Serengeti is anecdotally thought to be robust (Kruuk and Turner 1967; Schaller 1976), but abundance estimates for the leopard population are very rough (e.g., 800–1000) and lacking explanation of methods (e.g., Borner et al. 1987). With a full suite of carnivores and a large diversity of prey, the Serengeti is an ideal area to understand leopard population densities in a large natural system and how interspecific interactions, seasons, and habitat may shape leopard densities. Such knowledge can then be used as a reference to guide conservation efforts aimed to restore carnivore guilds in previously degraded ecosystems (Hayward et al. 2007a; Dalerum et al. 2008).

Although rarely used, the application of modern analytical tools in combination with data generated through citizen-science projects has the potential to improve our understanding of carnivore populations and the factors that affect densities across their range. Our objectives were to estimate leopard population densities in the Serengeti, and determine potential biological drivers of their abundance and distribution. Leopard densities in the Serengeti are unknown, and we used camera trap data from the largest citizen-science project to date (Swanson et al. 2015) to obtain our estimates. We first used spatially-explicit capture-recapture (SECR) models for unmarked populations to estimate a leopard population from the Serengeti in 2012 during both the wet and dry season. In this way we established the baseline information on leopard abundance, to which future surveys could be compared in order to understand population trends and detect potential conservation problems. We then tested 18 zero-inflated Poisson (ZIP) models in an *a-priori* modeling framework using Akaike Information Criterion (AIC) to compare models based on 10 variables (Table 1) to determine the impact of habitat, dominant carnivores and prey availability on leopard abundance documented during camera trapping in each season.

Materials and methods

Study area

The National Park in the Serengeti, established in 1951, is a vast area covering 14,750 km² in northwestern Tanzania. The Serengeti is characterized by a mix of open and dense woodlands in the north and treeless grass plains in the south, interspersed with rivers (Norton-Griffiths et al. 1975; Grant et al. 2005). Grasslands vary in height, depending on species, soil type, and rainfall (Norton-Griffiths et al. 1975). Rocky outcrops or ‘kopjes’ support trees and bushes and are found throughout the Serengeti, often providing the only cover on the plains (Durant 1998). Mean annual rainfall ranges from 350 mm in the southeast to 1200 mm in the northwest, and is concentrated in the wet season (November–May) with very little rain in the dry season (June–October) (Norton-Griffiths et al. 1975; Durant 1998). Ungulates perform long-distance seasonal migrations in the Serengeti

Table 1 Individual variables considered in *a-priori* models of leopard abundance in Serengeti National Park, Tanzania

Name	Abbreviation	Description	Hypothesized effect
Bushbuck abundance	BSBK	The relative abundance of bushbucks at the camera site	Positive (Hayward et al. 2006)
Cover	COVR	The percent of tree and shrub cover available within 1 km ²	Positive (Ray-Brambach et al. 2018; Balme et al. 2019)
Trap nights	DAYS	The number of trap nights	Positive
Dikdik abundance	DKDK	The relative abundance of dikdiks at the camera site	Positive (Hayward et al. 2006)
Spotted hyena abundance	HYAB	The relative abundance of spotted hyenas at the camera site	Negative (Vanak et al. 2013, du Perez et al. 2015)
Impala abundance	IMPL	The relative abundance of impalas at the camera site	Positive (Hayward et al. 2006)
Lion abundance	LNAB	The relative abundance of African lions at the camera site	Negative (Vanak et al. 2013, du Perez et al. 2015)
Distance to river	RIVR	Distance to the nearest river	Positive (Mkonyi et al. 2018; Strampelli et al. 2018)
Shade	SHAD	The amount of shade available	Positive (Bailey 2005)
Thomson's gazelle abundance	THGZ	The relative abundance of Thomson's gazelles at the camera site	Positive (Hayward et al. 2006)

Included in the table is the variable name abbreviation, description, and hypothesized effect; listed alphabetically by abbreviation

leading to strong seasonal patterns in their density and distribution (Sinclair and Arcese 1995; Mduma et al. 1999).

Data collection and preparation

We used data collected by the Snapshot Serengeti Project (Swanson et al. 2015). The project systematically deployed camera traps in a randomly distributed grid using 5 km² intervals, with camera traps placed in strategic locations within 250 m of the center of each grid to maximize wildlife detections. We used data collected during the dry season (June–October; $n = 115$ functioning camera traps) and wet season (November–May; $n = 118$ functioning camera traps) in 2012. The date, time, and camera trap site were recorded for each photograph, and the project used community scientists (historically called “citizen scientists”) to determine the species in the photographs (Kosmala et al. 2016).

To reduce false replicates, we considered photos of the same species at the same camera trap to be the same event if they occurred within 30 min of a previous photo (Rich et al. 2017; Allen et al. 2019). For each event we used the largest number of animals present in the 30 min time period as the number of individuals for that time period. We then calculated the relative abundance (events per 100 trap nights) as:

$$(\text{events}/\text{trap nights}) \times 100$$

for each dominant competitor (African lions and spotted hyenas) and potential preferred

prey (bushbucks, *Tragelaphus sylvaticus*; dik-diks, *Madoqua* sp.; impalas, *Aepyceros melampus*; and Thomson's Gazelles, *Eudorcas thomsonii*).

We determined habitat variables (Table 1) for each camera trap. Shade was estimated on an ordinal scale at each camera trap. We calculated other habitat variables using layers in Arc GIS (Environmental Systems Research Institute, Redlands, CA). For percent of forest cover, we created a 1 km² buffer around the camera trap and determined the percent of forest cover within the buffer using land cover information (available from https://geoportal.rcmrd.org/layers/servir%3Atanzania_sentinel2_lulc2016). For rivers we calculated the Euclidian planar distance from the camera trap to the nearest river. River features were available from a hydrology layer produced from LANDSAT TM images (available from <https://www.fao.org/geonetwork/srv/en/main.home>).

Statistical analyses

We used unmarked SECR analyses based on (Chandler and Royle 2013; Royle et al. 2013). SECR methods are generally non-invasive, using information from camera trapping and genetic sampling to unstructured methods or other data (Royle et al. 2013; Broekhuis and Gopalaswamy 2016). SECR methods allow estimation of heterogeneously distributed populations by creating site-specific density estimates (Chandler and Royle 2013). A base assumption of marked SECR analyses is that all marked individuals are identified correctly at every incident, while partially marked SECR analyses assume that all marked individuals are identified correctly, and only unmarked individuals remain unknown. Individual leopards are identifiable based on their unique spot patterns (Gray and Prum 2012; Grey et al. 2013), but for all individuals to be identified it is necessary to have two camera traps placed parallel in order to record both sides of the individual's body (Rovero and Zimmermann 2016). This was not possible in our study, but other studies have used data from the side of the body captured more often (Strampelli et al. 2020). While this approach works to determine an estimate, it also removes over half of the data (one side of the body and blurry or otherwise unidentifiable photographs) and in doing so likely leads to higher rates of error estimation than using all of the data collected in a Bayesian framework (Chandler and Royle 2013; Royle et al. 2013).

In our model we assumed that each individual (i) had an activity center (s_i) that was distributed within the study area (i.e. our state space, S). To define S , we used a portion of our study area representing a square grid (13 camera traps \times 13 camera traps), and used a buffer equaling two scale parameters (σ ; see below) around the outermost coordinates of our camera traps (e.g., Royle et al. 2013) for an S (including our buffer area) of 2420 km². We used three monitoring periods of 15 days each in both seasons, using the 15th day and the 7 days on either side of it for January, February, March, and July, August, September, respectively. We used the 15-day monitoring periods instead of daily periods because leopards are spatially dispersed and relatively infrequently caught on camera traps, and detection rates close to zero can lead to estimation errors in SECR models (Rich et al. 2014). We also limited the data to a period of 3 months to meet the assumption of population closure. We documented the number of detections for leopards for each camera trap location during each trapping period. In our model we assumed that the number of detections of a given leopard (i) at a given camera trap (j) during a given encounter occasion (k), y_{ijk} , was a Poisson random variable with mean encounter rate λ_{ij} . We then calculated the mean encounter rate for individuals as a function of the distance (d_{ij}) from the given trap (x_j) to the individual's activity center (s_i), using a half-normal encounter rate

model. The half-normal encounter rate model was based on the detection rate (Ψ) and encounter rate for a hypothetical camera trap (λ_0), and σ which we assumed was constant across all encounter occasions. In general, the whole model is

$$Y_{jk} = \sum_i y_{ijk} \sim \text{Poisson}(\Lambda_j)$$

$$\Lambda_j = \sum_i \lambda_{ij}$$

$$\lambda_{ij} = \lambda_0 \exp\left\{-\frac{\|x_j - s_i\|^2}{2\sigma^2}\right\} z_{ij}$$

$$z_{ij} \sim \text{bernoulli}(\psi)$$

where z_{ij} is the indicator of detection, $z_{ij} = 1$ if individual i is able to be detected by camera trap j ; otherwise $z_{ij} = 0$.

We did not have data from our study area for our prior model parameters (Ψ , λ_0 , σ) so we performed literature searches for studies from similar nearby systems to estimate the parameters, and used the same parameters for each season. For Ψ we used estimates from (O'Brien and Kinnaird 2011); daily Ψ of 0.0595), (Swanepoel et al. 2015); six daily Ψ values ranging from 0.003 to 0.039), and (Chapman and Balme 2010); Ψ across 4 days of 0.112). We translated this to a detection rate for our 15-day monitoring period using $1 - (1 - \Psi)^{15}$, to arrive at a mean of 0.322 and a range of 0.044–0.602, which we used to create the beta distribution of our prior distribution. We based λ_0 on our detection rates and number of detections, to create a gamma distribution for our prior distribution. The half-normal detection function we assumed in our model implies a bivariate normal model of space use, which allowed us to translate σ into a 95% home-range radius, r , using the formula

$$r = \sigma \times \sqrt{5.99}$$

(Royle et al. 2013). To estimate home range sizes we used the two closest studies to our study area (Hamilton 1981; Mizutani and Jewell 1988), and used the values from all adult leopard home ranges to calculate a mean and 95% CI (mean = 27.07, 95% CI 20.52–33.63). To ensure inclusion of the home range centers from all possible sampled leopards, we used the value for the radius from the home range at the upper limit of our calculated 95% CI multiplied by 1.5 to account for home range centers not being uniformly distributed in a home range as our upper limit, and converted to a normal distribution for our prior distribution.

We estimated the population density of leopards using data augmentation in a Bayesian framework and used Markov chain Monte Carlo (MCMC) method to sample from the posterior distributions using their full conditional distributions. We implemented MCMC code (Supplementary Material 2) in the program R version 3.5.1 (R Core Team 2018), adapted from the code developed by (Royle et al. 2013). In our MCMC model we used three chains, with 100,000 total iterations and 20,000 iterations in each chain used as burn-in. We considered models to have converged if trace plots exhibited adequate mixing and if

point estimates of the Gelman–Rubin statistic were < 1.01 (Gelman and Rubin 1992). We then used our density results to model the site level population density across the study area by plotting the activity centers (s_i) of each individual (i) across the state space (S) for each of the model iterations, and then scaling these numbers to derive a mean of the density for each camera trap. We report the estimates, naïve SE, and 95% CrI for each variable in each season.

To determine the drivers of the spatial distribution and abundance of leopards we tested ZIP models using the *pscl* package (Zeileis et al. 2008). We used ZIP models because the histogram of our leopard detection data revealed more zeros than expected in a Poisson distribution, and ZIP models effectively account for detection rates using the presence of non-informative, structured zeros in a binomial model followed by a Poisson model with non-informative zeros accounted for (Zeileis et al. 2008). We used the same months as in

Table 2 *A-priori* candidate models for leopard abundance in Serengeti National Park, Tanzania

Variables	Reason
COVR	Leopards will select for forested habitat with cover
RIVR	Leopards will use areas based on availability of water
SHAD	Leopards will use areas based on availability of shade
COVR + RIVR	Leopards will use areas based on availability of cover near water
SHAD + RIVR	Leopards will seek out cool areas near water for thermoregulation
COVR*SHAD	Leopards will select for forested habitat with shade for thermoregulation and camouflage
COVR*SHAD*RIVR	Leopards will select for forested habitat with cover and shade near water
LION	The larger sympatric African lion will exclude the smaller and subordinate leopard
HYNA	The larger sympatric spotted hyena will exclude the smaller and subordinate leopard
LION*HYNA	Larger social carnivores will exclude the smaller and solitary leopard
COVR*LION*HYNA	Leopards will select for areas with forest and shrub cover to mitigate the negative effects of larger pack carnivores
THGZ	Leopards will seek out areas where their preferred prey, Thomson's gazelle, are most abundant
THGZ + IMPL	Leopards will seek out areas where their top two preferred prey, Thomson's gazelle and impala, are most abundant
THGZ + IMPL + BSBK + DKDK	Leopards will seek out areas where their four common prey are most abundant
COVR + RIVR + THGZ + IMPL	Leopards will seek out areas with cover near water and high availability of their preferred prey for hunting
COVR*SHAD + THGZ + IMPL	Leopards will seek out areas with cover and shade for camouflage with a high availability of their preferred prey for hunting
Null	Selection of areas used by leopards is independent of variables we considered
Global	The selection of areas used by leopards is complex and can only be explained by a combination of all of the variables

Included in the table are the combination(s) of variables and reasoning for each model

our population estimate for our ZIP models, but used the data from the entire month and accounted for variation in the number of trap nights among cameras. For each season we considered trap nights as the predictor of non-informative zeros in the binomial process, and tested along with the variables for each of 18 *a-priori* models in the Poisson process (Table 2). We compared the models in an AIC framework using AIC weight (w) after removing models that did not converge from our comparisons, and considered any model with < 0.90 cumulative w to be a top model (Burnham and Anderson 2003).

Results

Population density

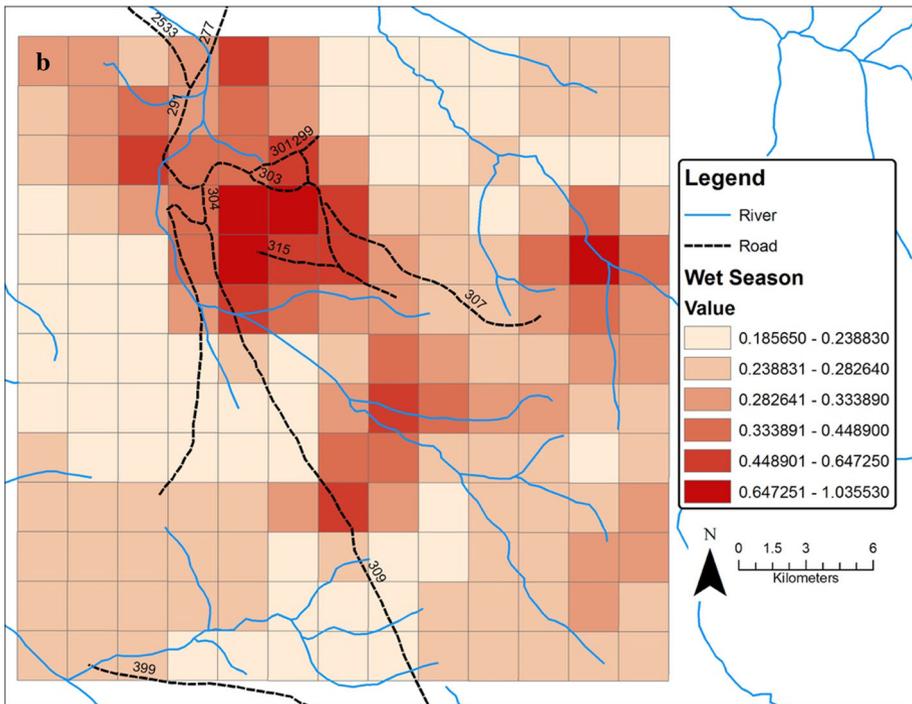
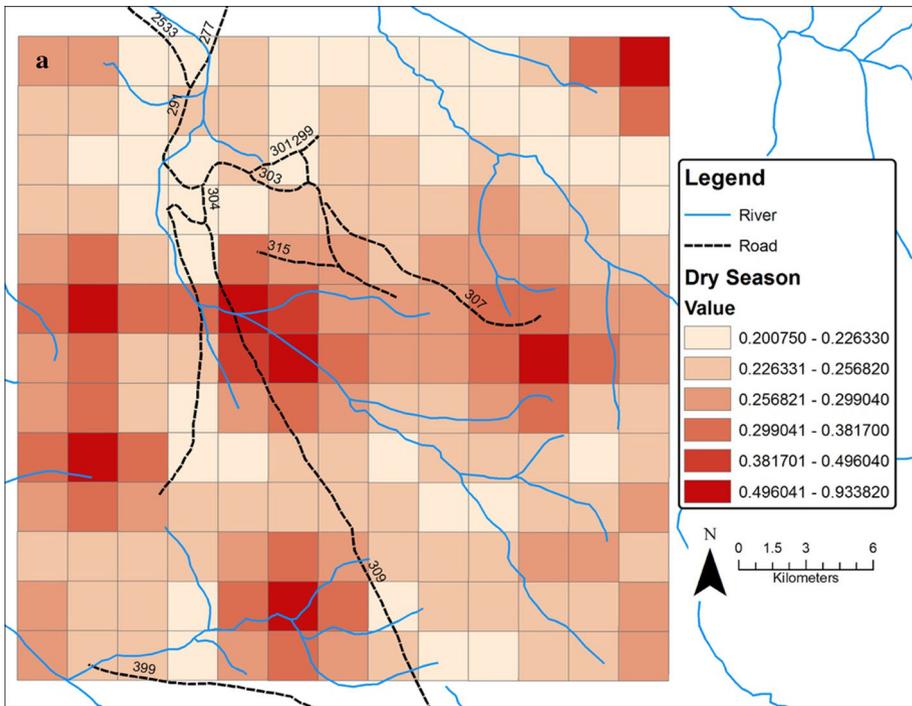
In the dry season, our posterior mean estimate of the leopard density in the study area was 5.41 (± 0.004 SE, 95% CrI = 2.23–9.26) individuals/100 km². Leopards were heterogeneously distributed during the dry season with the posterior mean number of leopards/km² per camera trap being 0.276 (range = 0.201–0.934; Fig. 1a). We found that σ was not updated by the model with a posterior mean of 1.22 km (± 0.0004 SE, 95% CrI = 0.80–1.65), similar to the prior mean and distribution. In contrast, both λ_0 and Ψ were updated by the model. The mean λ_0 was 0.069 (± 0.0001 SE, 95% CrI = 0.018–0.194), lower than the prior mean and distribution. The mean Ψ was 0.37 (± 0.0003 SE, 95% CrI = 0.15–0.63), slightly higher than the prior mean and distribution. The mixing of the model was even (Fig. 2) and the Gelman–Rubin convergence statistic was < 1.01 for each parameter.

In the wet season, our posterior mean estimate of the leopard density in the study area was 5.71 (± 0.004 SE, 95% CrI = 2.44–9.55) individuals/100 km². Leopards were heterogeneously distributed during the wet season with the posterior mean number of leopards/km² per camera trap being 0.298 (range = 0.186–1.036; Fig. 1b). We found that σ was updated by the model with a posterior mean of σ was 1.34 km (± 0.0004 SE, 95% CrI = 0.95–1.75), slightly larger than the prior mean and distribution. We found that λ_0 was updated by the model, with a posterior mean of 0.078 (± 0.0001 SE, 95% CrI = 0.025–0.197); lower than the prior mean and distribution. We found that Ψ was also updated by the model with a posterior mean of 0.39 (± 0.0003 SE, 95% CrI = 0.17–0.65), slightly higher than the prior mean and distribution. The mixing of the model was even (Fig. 3) and the Gelman–Rubin convergence statistic was < 1.01 for each parameter.

Drivers of density

During the dry season, the global model was our highest ranking model ($w = 0.70$), 15 times higher than the next closest model (Table 3, Supplementary Information 3). In this model, BSBK had significant positive effect ($\beta = 0.92 \pm 0.28$, $p = 0.011$); and DKDK had a significant negative effect ($\beta = -0.82 \pm 0.36$, $p = 0.02$) on leopard density. SHAD had a marginally significant positive effect ($\beta = 0.51 \pm 0.28$, $p = 0.07$), while LION had a marginally significant negative effect ($\beta = -0.17 \pm 0.11$, $p = 0.12$).

In the wet season our top models were COVR*LION*HYNA ($w = 0.37$) and LION*HYNA ($w = 0.36$; Table 3, Supplementary Information 3). In the first model, the effects of each variable were positive (COVR $\beta = 2.95 \pm 1.88$, $p = 0.11$; LION $\beta = 1.28 \pm 0.44$, $p = 0.004$; HYNA $\beta = 0.80 \pm 0.30$, $p = 0.008$), all of the single interactions were negative ($\beta_{\text{COVR:LION}} = -2.07 \pm 0.97$, $p = 0.03$; $\beta_{\text{COVR:HYNA}} = -$



◀ **Fig. 1** Leopard density estimates during the dry (a) and wet (b) seasons within our camera grid in Serengeti National Park, Tanzania

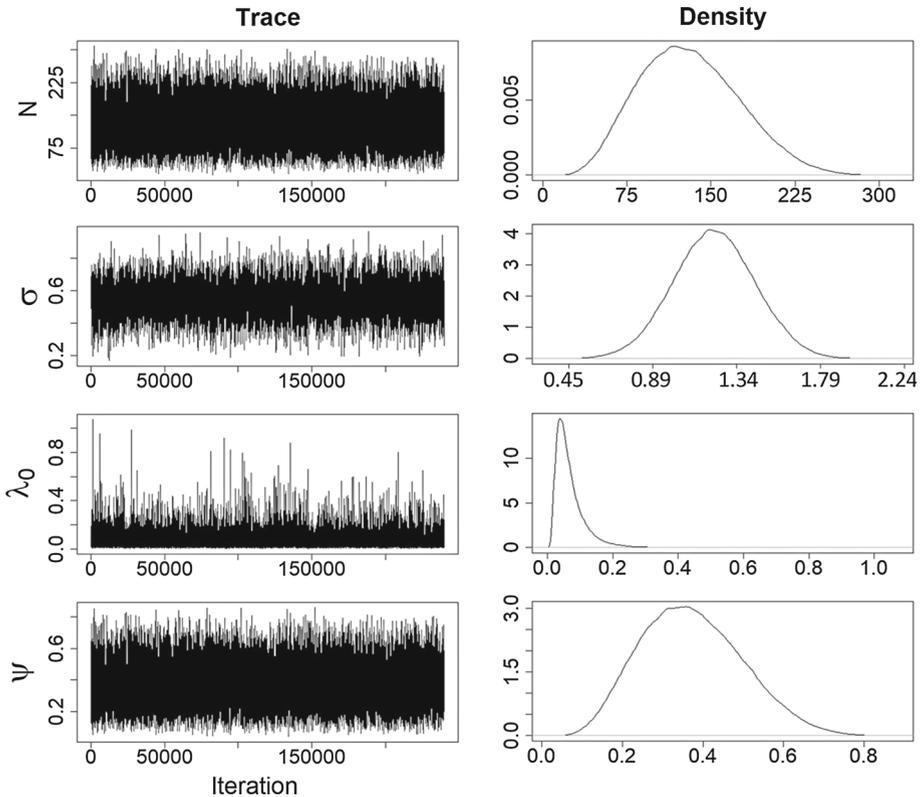


Fig. 2 Trace plots (left) and posterior density plots (right) of the posterior estimates for each model parameter, including σ , λ_0 , Ψ and total abundance (N), of leopards during the dry season in Serengeti National Park, Tanzania

0.82 ± 0.39 , $p = 0.04$; $\beta_{\text{LION:HYNA}} = -0.19 \pm 0.12$, $p = 0.12$), and the COVR:LION:HYNA interaction was positive but not statistically significant ($\beta = 0.23 \pm 0.28$, $p = 0.42$). In the second best model, the effects of each variable were positive (LION $\beta = 0.33 \pm 0.09$, $p = 0.0002$; HYNA $\beta = 0.20 \pm 0.06$, $p = 0.002$), but the LION:HYNA interaction was negative ($\beta = -0.04 \pm 0.01$, $p = 0.005$).

Discussion

We determined the seasonal population density of leopards in the Serengeti and examined the ecological factors that may be affecting site-level abundance. Densities showed minimal variation among seasons, with 5.41 individuals/100 km² in the dry season and 5.72 individuals/100 km² in the wet season, but the drivers of abundance changed among seasons. These densities are slightly higher than many other areas (Fig. 4), as would be expected in a large protected area. But importantly, the seasonal variation in drivers indicates that leopard density is affected by ecological factors including dominant

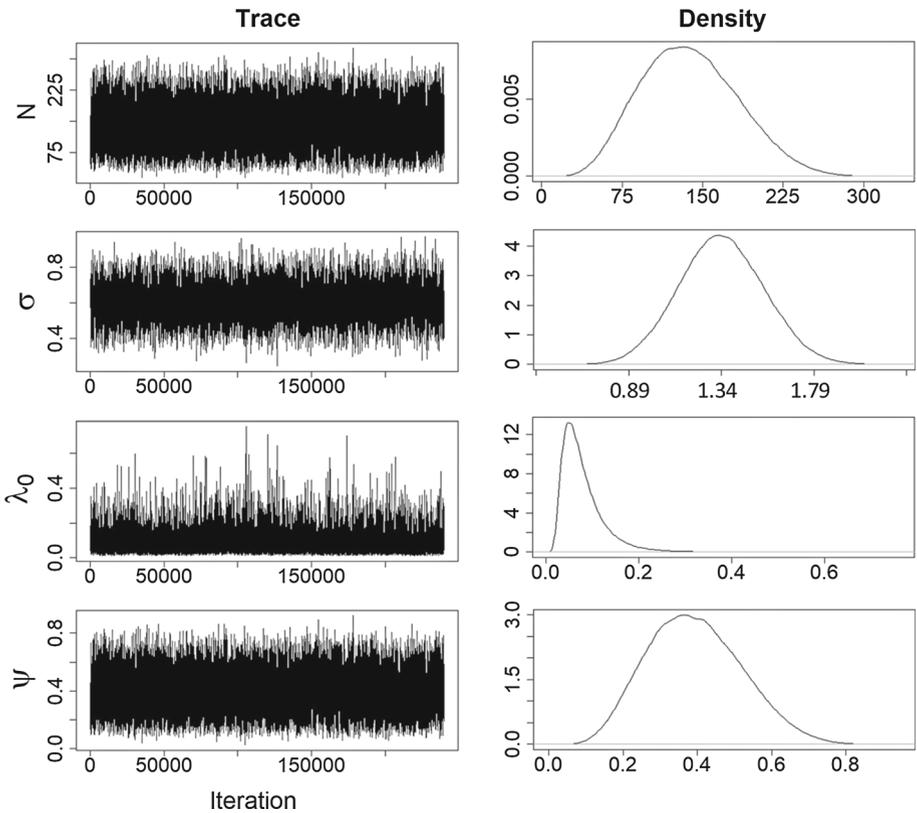


Fig. 3 Trace plots (left) and posterior density plots (right) of the posterior estimates for each model parameter, including σ , λ_0 , Ψ and total abundance (N), of leopards during the wet season in Serengeti National Park, Tanzania

Table 3 Model selection results of top *a-priori* models ranked by their AIC weight (w) for drivers of leopard density in the dry season and wet season in Serengeti National Park, Tanzania

Rank	Poisson variables	AIC	Δ AIC	wAIC	Cumulative wAIC
<i>Dry season</i>					
1	Global	119.26	0.00	0.64	0.64
2	RIVR	124.70	5.43	0.05	0.75
3	SHAD	124.90	5.64	0.04	0.79
4	LION	125.32	6.05	0.03	0.82
5	SHAD + RIVR	125.65	6.38	0.03	0.85
6	HYNA	125.79	6.53	0.03	0.88
<i>Wet season</i>					
1	COVR*LION*HYNA	107.91	0.00	0.37	0.37
2	LION*HYNA	107.99	0.09	0.36	0.73

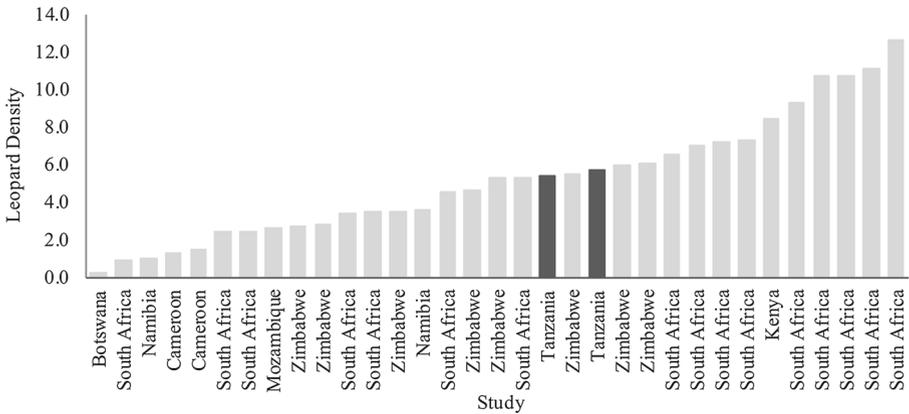


Fig. 4 A comparison of leopard densities from rigorous peer-reviewed studies from sub Saharan Africa. The densities of studies are shown in ascending order in gray, and our density estimates from the wet and dry season in the Serengeti are shown in black

carnivores and access to water and other resources. Density estimates for leopards vary widely across their range (Grey et al. 2013; Jacobson et al. 2016), making local studies of density and their drivers important for understanding the species' conservation status. The relatively high leopard densities in the Serengeti suggest that leopards are a successful species in natural conditions when not faced with human-related mortality (e.g., Balme et al. 2019), even if faced with high densities of dominant carnivores. The Serengeti is a conservation stronghold for many species, and our study confirms anecdotal reports that it is a stronghold for leopards as well (Kruuk and Turner 1967; Schaller 1976). Considering the substantial range-wide contractions for leopards (Jacobson et al. 2016), the Serengeti leopard population may be particularly important for their future conservation.

When compared to other leopard studies from sub Saharan Africa, the densities from the Serengeti are fairly robust (Fig. 4), but we must consider how methodology and size of study areas affect estimates. Smaller study areas (i.e., < 1000 km²) have been shown to have higher densities in Africa (e.g., 10.2 leopards/100 km²; (Grey et al. 2013), but these small areas can be biased towards prime habitat, exclude surrounding areas with no leopards present or be inflated due to artificial factors, such as fences, habitat modifications, artificially increased ungulate density or extermination of larger competitors (Power 2002; Hayward et al. 2007b; Mysterud 2010). Non-spatial population density models have also been found to overestimate leopard density compared to spatial population models (Devens et al. 2018), indicating our density estimates may be even larger relative to some other areas. However, leopards vary at least 300-fold in their densities across their range and it is important to understand leopard density across different landscapes for their effective conservation (Jacobson et al. 2016). Much of the variation is based on habitat productivity and prey populations (Jacobson et al. 2016), but the size of study areas should also be considered when comparing density estimates.

The prior mean and distribution that should be considered most strongly in future studies is the λ_0 , which may vary among study areas or based on habitat, season, or other variables. The posterior means and distributions for λ_0 was lower than the prior means and distributions in both seasons, likely due to the cryptic nature of leopards and the difficulty of documenting them. These could possibly be limited because the camera traps were not set specifically for leopards, but instead were placed to document all wildlife species in the

Serengeti which notably enhances the data gained for a similar amount of effort (Rich et al. 2019). However, there are often sex-biased patterns in detection of leopards and other large felids with the greater mobility of males and avoidance of trails by females leading to male-biased detection (Gray and Prum 2012; Allen et al. 2016; Harmsen et al. 2017; Ray-Brambach et al. 2018). This is likely to affect detection in any SECR or camera trap study, and may lead to underestimates in λ_0 and abundance. In contrast, the posterior means and distributions of Ψ were slightly higher than the prior means and distributions in both seasons, with the wet season being slightly higher than the dry season. This contrasts with previous studies that found Ψ was higher in the dry season (Mkonyi et al. 2018). The posterior means and distributions of σ were updated from the prior means and distributions to be slightly higher in the wet season, but were still relatively small. This is because the prior σ we used was specific to the Serengeti, where the home ranges of leopards are among the smallest documented (leopard home ranges vary from 8 to over 2000 km²; (Marker and Dickman 2005). Our small σ may be specific to the study area and larger values should be expected in other areas with larger home ranges, and study area specific prior values should always be considered in SECR models.

We used a SECR model for an unmarked population (Chandler and Royle 2013; Royle et al. 2013), which tend to have larger variation than partially marked SECR or marked SECR analyses (Chandler and Royle 2013; Royle et al. 2013), but are more accurate than many estimates made using frequentist frameworks (e.g., Strampelli et al. 2020). The low sample sizes and detection rates for large carnivores tend to lead to larger variation and confidence intervals in estimates of their density (Gray and Prum 2012), and our study was no exception. However, our posterior abundance estimates appear robust (Figs. 2 and 3) and provide the first rigorous, peer-reviewed population density estimates for leopards in the Serengeti. Our low λ_0 rates indicate the difficulty and infrequency of capturing leopards on camera, which is one of the limitations of studying many large carnivores. Estimates provided in this study highlight the benefit of analyses using a Bayesian framework and data collected with citizen-science projects for understanding populations, but a worthwhile follow up study would be a comparison of all population methods using the same dataset.

The distribution of animals often matches their resources, but also reflects a tradeoff of risk vs. reward. Leopards had different relationships with the abundance of dominant carnivores during the dry and wet seasons, which may indicate changes in risk for leopards in the different seasons or be an indication of prey abundance. During the dry season, our top model indicated leopard density was negatively affected by the abundance of lions, but during the wet season both of our top models indicated a positive effect of lion and hyena abundance on leopard density. Other studies have found unexpected positive relationships among carnivores (Rich et al. 2017; Allen et al. 2018b; Davis et al. 2018; Lamichhane et al. 2019), and specifically leopards exhibiting no avoidance of lions (Vanak et al. 2013; Balme et al. 2017b, 2019; Strampelli et al. 2018). However, the underlying driver of leopard distribution may be the dynamic prey availability which shifts on the landscape between seasons. When prey availability is low, as in the dry season, it appears that leopards avoid areas with more lions, an effect which has been found among other subordinate carnivores on the Serengeti (Swanson et al. 2014, 2016). During the wet season when prey is abundant, there is less competition for prey and thus leopard abundance is positively associated with lions which may be a proxy for prey availability in this system (Steinmetz et al. 2013; Strampelli et al. 2018), as positive associations among competing carnivores can also be result of their shared habitat affinities (Davis et al. 2018). We did not test for the causation of the effects of dominant carnivores, but (Balme et al. 2019) found

that leopard detections correlated with areas with high hyena detections was actually caused by hyenas seeking out and following leopards in order to kleptoparasitize their killed prey. Lions and hyenas kleptoparasitize leopards, which can have negative effects on leopard reproductive success (Balme et al. 2017a) and cause leopards in areas with higher abundance of dominant carnivores to feed on smaller prey (Hayward et al. 2006) and cache more of their prey in trees to avoid loss of food (Stein et al. 2015; Balme et al. 2017a).

Our study demonstrates the benefits of large, generalized camera-trapping surveys to provide abundance estimates for a variety of species. Projects involving citizen scientists can be used to provide density estimates for elusive carnivores from areas lacking species-focused studies. Equally important, such databases can provide important information on drivers of local abundances. In our case, our seasonal analyses of the distribution of leopards revealed season-specific relationships among large predators and various habitat characteristics. The conservation efforts for one species can negatively affect others (Krofel and Jerina 2016), and the Serengeti is known for robust populations of many large carnivores. Our study shows that the Serengeti is also a stronghold for leopard conservation, but that leopards are also affected by dominant carnivores. In areas where it is important to conserve or restore entire guild of large carnivores, a key step may be ensuring that there is a sufficiently large prey base throughout the year and we suggest that Serengeti could serve as a reference for such efforts.

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