

# Estimates of Density and Population Size of African Lions in the Katavi National Park, Tanzania

Shwahibu Massawe<sup>1</sup> , Hillary Thomas Mrosso<sup>2</sup>, Michael Honorati Kimaro<sup>2,3\*</sup> 

<sup>1</sup>Conservation Science Department, Katavi National Park, Tanzania

<sup>2</sup>Tanzania Research and Conservation Organization, Morogoro, Tanzania

<sup>3</sup>GELIFES Institute, University of Groningen, Groningen, Netherlands

Email: \*kimarorcp@gmail.com

**How to cite this paper:** Massawe, S., Mrosso, H.T. and Kimaro, M.H. (2022) Estimates of Density and Population Size of African Lions in the Katavi National Park, Tanzania. *Open Journal of Ecology*, 12, 614-628. <https://doi.org/10.4236/oje.2022.129035>

**Received:** June 16, 2022

**Accepted:** September 20, 2022

**Published:** September 23, 2022

Copyright © 2022 by author(s) and Scientific Research Publishing Inc. This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

<http://creativecommons.org/licenses/by/4.0/>



Open Access

## Abstract

Lion populations are declining globally, including in Tanzania, and Africa. However, Katavi National Park is a landscape with potential for a sustainable and healthy population of African lions (*Panthera leo*), but there is currently limited reliable data indicating density and population size. This hinders the development of conservation action plans, including population monitoring, for this species. To address this data gap, we assessed lions' demography and population estimates (population size and density) in the Katavi National Park using a call-back survey method. In addition, we assessed ecological factors that influenced distribution of lions to the call-back stations. Our estimated population size revealed 84 lions (95% CI 53 - 116), with a density of 5/100 km<sup>2</sup> (95% CI 3.14 - 6.86) in the sampled area, representing 38% of the total park. This resulted in an estimated 214 individuals when extrapolated to the whole park. Sixty-seven percent of lions that responded to the stations were female, and ecological factors that significantly influenced their distribution included elevation, land cover, precipitation, temperature, wind speed, and prey abundance. Our results suggest that female lions are more abundant than males in Katavi National Park and that population size and density estimates, as well as understanding prey-lion relations, are important indices for lion monitoring and identifying conservation priorities. Further, our study suggests that the call-back survey method is an effective, rapid, and less costly population assessment method for lions, may be useful for assessing other social species in the Katavi ecosystem and can be a useful tool for community engagement and contributing to scientific monitoring.

## Keywords

Lions, Population Abundance, Density, Ecological Influencing Factors,

---

## Call-Back Method

---

### 1. Introduction

African lions (*Panthera leo*) are a keystone species in many ecosystems and are globally valued as charismatic megafauna [1]. However, despite their ecosystem importance and conservation efforts, lions continue to experience rapid population decline largely as a result of anthropogenic activities [2] [3] [4]. Over the past two decades, many lion range states in Africa have experienced a high rate of decline, from 30% to 50% [2] [5]. As a result, wildlife authorities, conservationists, and researchers continue to work towards effective conservation actions for the remaining lion populations. In particular, lion population monitoring must be completed, to provide robust data and knowledge on status, threats, and long-term trends [6].

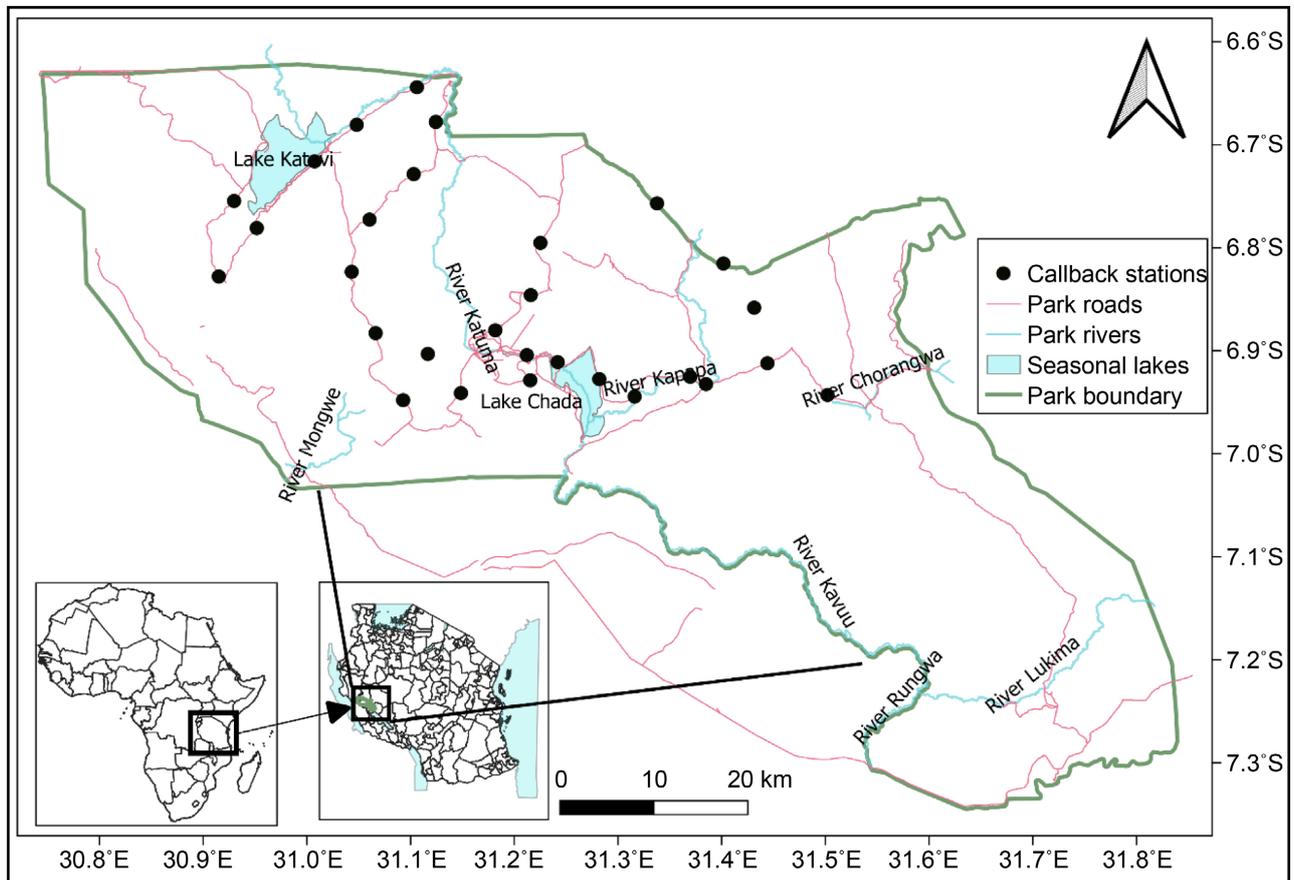
However, the monitoring of animals with low densities like lions is a very challenging task, as their sample sizes are likely to contain fewer individuals than other higher density species, as well as the geographic extent and elusive nature of these animals make monitoring efforts costly and time-consuming [7]. Several methods have been used to estimate lion populations, including spoor counts, camera trapping, and call-back surveys, with promising results [1] [5] [8]. A call-back survey in particular involves broadcasting playback sounds of prey animals during the night to attract lions to stations [9]. The lions that respond are then counted by trained observers and identified based on age and sex. This method is commonly used across many protected areas because of the lower costs and rapid implementation with reliable data to estimate the population and density of lions [1].

Given that Tanzania holds the largest population of African lions [10], and given Katavi National Park's potential lion population, and surrounded by multiple hunting reserves, and experiencing lion mortality induced by human-lion conflict [5] [11], monitoring the population of lions is vital. We used call-back surveys to determine lion demography, population size, and density, as well as ecological factors influencing their distribution from call-back stations. The findings of our study contribute to lion population datasets and monitoring for Katavi National Park, and the development of conservation action for this species.

### 2. Materials and Methods

#### 2.1. Study Area

Katavi National Park is located in western Tanzania and covers 4471 km<sup>2</sup> (Figure 1; [5] [11]). The park is the sixth largest national park in Tanzania. A large portion of the park is situated within the Rukwa Valley and is part of the Zambezi biome, receiving an average annual rainfall of 923 mm [5] [12]. The park



**Figure 1.** Map of Katavi National Park showing call-back stations, water sources, and road networks.

is composed of permanent and seasonal lakes, rivers, and floodplains, and is dominated by miombo woodland vegetation [12] [13]. Katavi National Park is considered an Important Bird Area in Tanzania, estimated to hold 40% of the country's bird species [13], and supports a variety of other species like buffalo, eland, elephant, giraffe, hippopotamus, leopards, cheetah, hyenas and wild dog [13] [14]. Human communities surrounding this park mostly participate in crop cultivation and livestock keeping [11] [13] [15]. Illegal hunting for subsistence or traditional purposes continues, which contributes to the decline in the lion population [15], though hunting in the National Park is strictly prohibited [16].

## 2.2. Data Collection

Our study followed designs in Kruger National Park [17], and Katavi National Park [5]. We established 29 call-back stations, with a total area sampled of 1682 km<sup>2</sup>, accounting for 38% of the Park. The survey team played MP3 audio of buffalo in distress, mixed with sounds of a lion feeding at every call-back station for four rounds. Each round took 10 minutes. After every round, a period of five minutes of silence was followed. After playing the last 4<sup>th</sup> round of recordings, a 10-minute silence period was used for observation. The flash drive containing

the MP3 recording was connected to a 12 V amplifier which was connected to two horn speakers, and the sound was heard 3 kilometers away. Speakers were made by Enjo Sports Inc, Guangdong China, ISO 9001 from TACBAND. Speakers were placed to face opposite directions at 45 degrees angle to make sure that sound was directed in all directions for the period of the call-back. The sound was played from the speaker at the maximum volume possible, with the speaker on the roof of the vehicle at an approximate height of 2.5 meters.

Three trained observers sat on the roof of the vehicle, of which one observer was to operate the sound system and the other two were to document observed animals that responded to the calls. An additional observer was located inside the vehicle in front of the driver. Each observer had a personal flashlight with two strong spotting lights covered with a red filter to reduce the light disturbance to responding animals. In some cases, the red filter on the lights was removed to help in the age and sex identification of the responded animals, especially when the responded lion individuals scared to approach the vehicle. Due to the difficulty of identifying the sex of lion cubs, we only documented the sex of adult and sub-adult lions.

Road networks were identified before fieldwork, and each road was given a unique name. Each road was 50 kilometers long. To avoid double counting, call-back stations were placed at an interval of 8 km from each other, measured by the vehicle odometer, and situated along road networks. Surveys were conducted half an hour after sunset, between 17:30 hours and 00:00 hours, and animals were counted at each station once during the dry season [18]. Climatic data (rainfall, temperature, and wind speed) at each station per specific date was obtained from the National Aeronautics and Space Administration (<https://power.larc.nasa.gov/data-access-viewer/>). A global Positioning System (GPS) receiver was used to record the location and elevation of each call-back station. Habitat type in each call-back station was identified and recorded in the field. The NNjoin plugin from QGIS software was used to estimate the distance from each station to the nearest perennial water source. The team also conducted strip transects the following morning (from 7:00 to 11:00 hours) to identify and count prey species. Transect length representing prey abundance per call-back station was 8 km, and strip width was 300 m (150 m for the left and right sides of the road). The team conducted 29 prey transects, and species names and total numbers encountered were recorded.

### 2.3. Data Analysis

To determine lion demography, descriptive analysis was performed to calculate the mean, range, and sum of lions that responded to the call-back stations. The sex ratio determined by calculating proportion of the observed males to female lions.

The study estimated lion population size by using Ferreira and Funston's study, as shown below;

$$N_j = \frac{A_T \sum_{s=1}^n f_{nc,s}}{n\bar{A}P_{nc,p}P_{nc,i}(1-P_{nc,r})} + \frac{A_T \sum_{s=1}^n f_{c,s}}{n\bar{A}P_{c,p}P_{c,i}(1-P_{c,r})}$$

All constants (probabilities) adopted from Ferreira and Funston’s study, with their definitions are shown in **Table 1**.

Ferreira and Funston’s study included the probabilities that lions in groups with cubs and lions in groups without cubs will respond more than once, however, since we only completed one observation per station these probabilities were not applicable. We instead used the calculated population size and manipulated it to determine the relative density of lions per 100 km<sup>2</sup>. The following formula was used to determine variance of the observed lions, and 95% confidence intervals for population size of lions:

$$\text{var}[N_j] = N_j^2 \left[ \frac{\text{var}[\underline{A}]}{\underline{A}^2} + \frac{X_{nc}^2 \text{cv}^2[X_{nc}] + X_c^2 \text{cv}^2[X_c]}{(X_{nc} + X_c)^2} \right]$$

where

$$X_{nc}^2 = \frac{\sum_{s=1}^n f_{nc,s}}{P_{nc,p}P_{nc,i}(1-P_{nc,r})}$$

$$X_c^2 = \frac{\sum_{s=1}^n f_{c,s}}{P_{c,p}P_{c,i}(1-P_{c,r})}$$

$$\text{CV}^2[X_{nc}] = \frac{n}{n-1} \frac{\sum_{s=1}^n (f_{nc,s} - \bar{f}_{nc})^2}{(\sum_{s=1}^n f_{nc,s})^2} + \frac{\text{var}[P_{nc,p}]}{P_{nc,p}^2} + \frac{1-P_{nc,i}}{P_{nc,i}} + \frac{P_{nc,r}}{1-P_{nc,r}}$$

To assess the ecological factors influencing lion distribution to call-back

**Table 1.** Constants and probabilities adopted from ferreira and funston’s study to lion study in the Katavi national park.

Symbol	Variable definition	Value
<i>r</i>	Radius of call-back station	4.3 km
$\pi$	Pie	3.142
$\bar{A}$	Area of one call station ( $\pi r^2$ )	58 km <sup>2</sup>
$A_T$	Sum of the area sampled (29 stations* $\pi r^2$ )	1682 km <sup>2</sup>
$P_{nc,p}$	Response probability of a lion group responding without cubs	0.734
$P_{c,p}$	Response probability of a lion group responding with cubs	0.286
$P_{nc,i}$	Response probability of a lion in a responding group of lion without cubs	0.902
$P_{c,i}$	Response probability of a lion in a responding group of lion with cubs	0.957

stations, we used the “Performance Analytica” package in R and examined correlations with elevation, habitat type, precipitation, temperature, wind speed, distance to the nearest water source, prey abundance, and total lion counts. No pairs of variables showed strong correlation ( $> \pm 0.7$ ). Generalized Linear Mixed Model (GLMM) with zero inflated Poisson model was used to identify factors that significantly influenced lion distribution to the call-back stations using “pscl” and “glmmTMB” packages in R version 4.0.2 [19]. Fixed effects included in the model were elevation, habitat type, precipitation, temperature, wind speed, distance to the nearest water source, prey abundance, while response variable was lion counts. Random effect was road ID. From the MASS package, we used the “stepAIC” function to determine final or adequate model.

### 3. Results

#### 3.1. Population Demography

This study covered 1682 km<sup>2</sup>, or 38% of the total park area. Lions were seen at twelve (41%) of the 29 call-back stations, indicating that 59% of call-back stations had no lion response. Number of lions observed ranged from 0 - 7 comprising a total of 42 lions with an average of 1.5 lions per call-back station. Sixty-seven percent of lions that responded to the call-back stations were female. Only six cubs observed, however, the team was unable to identify sex of these individuals, therefore cubs are excluded in sex ratio calculations. The sex ratio of male to female lions was 50% (1:2), indicating that the proportion of male responded was half of the total female responded (**Table 2**).

#### 3.2. Population Size and Density

The estimated population size revealed 84 lions (95%, CI 53 - 116) in the sampled area, and when extrapolated to the whole park, the number of lions became 214 individuals. The estimated density of lions was 5 lions per 100 km<sup>2</sup> (95%, CI 3.14 - 6.86, **Table 3**).

#### 3.3. Ecological Factors That Influencing Distribution of Lions

We found that elevation, habitat type, precipitation, temperature, wind speed,

**Table 2.** Demography of lions responded to the call-back stations.

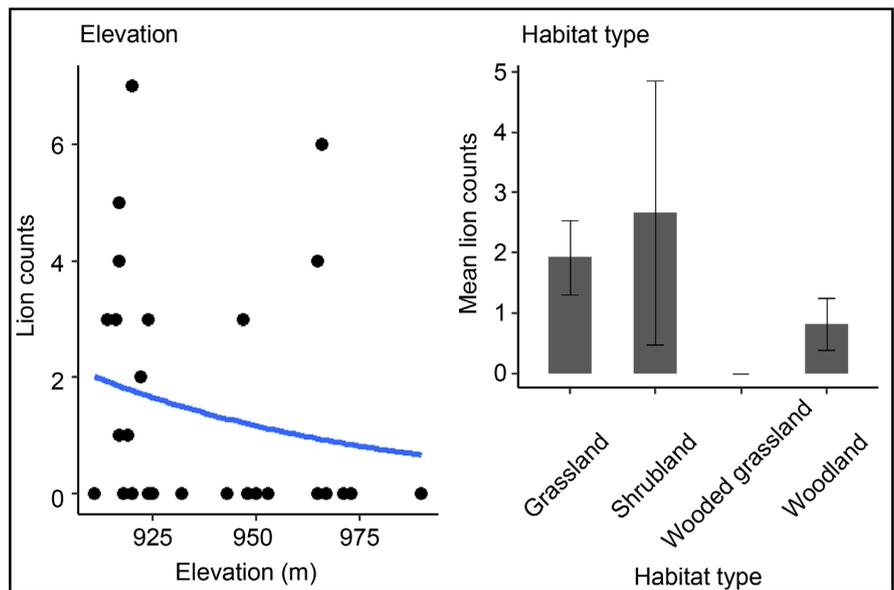
Number of stations	Sightings proportion (%)	Range	Mean per station	Adult	Sub-adult	Cub	Total observed	Male	Female
29	41	0 - 7	1.5	28	8	6	42	12	24

**Table 3.** Estimates of population size and density of lions under 95% confidence interval.

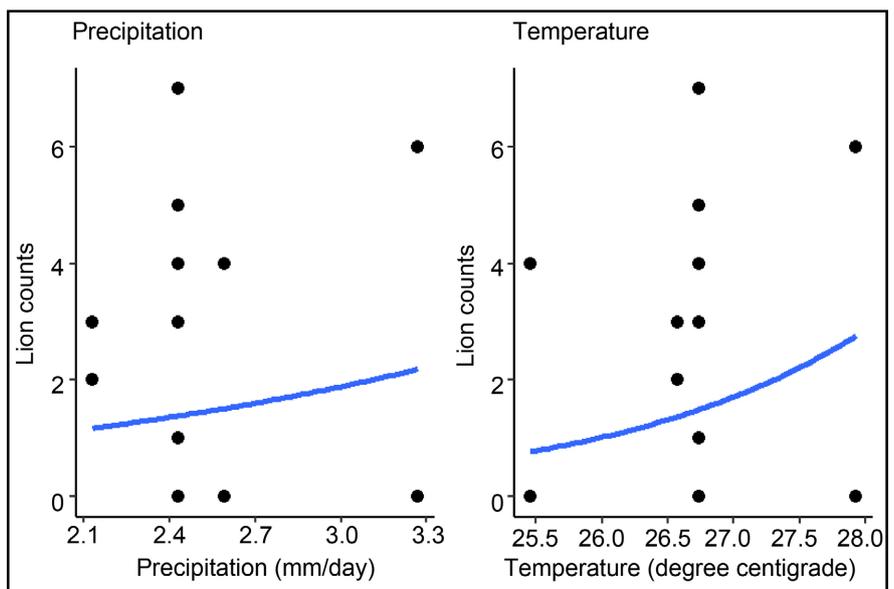
Number observed	Population estimate	Margin Error	95% CI	Density estimate per 100 km <sup>2</sup>	95% CI for density
42	84.26	31.24	53 - 116	5	3.14 - 6.86.

and prey abundance influenced the distribution of lions to the call-back stations. Lion abundance was significantly high in lowlands (GLMM,  $P = 0.03$ ) and in the grassland and shrublands habitat (GLMM,  $P = 0.04$ , **Figure 2**).

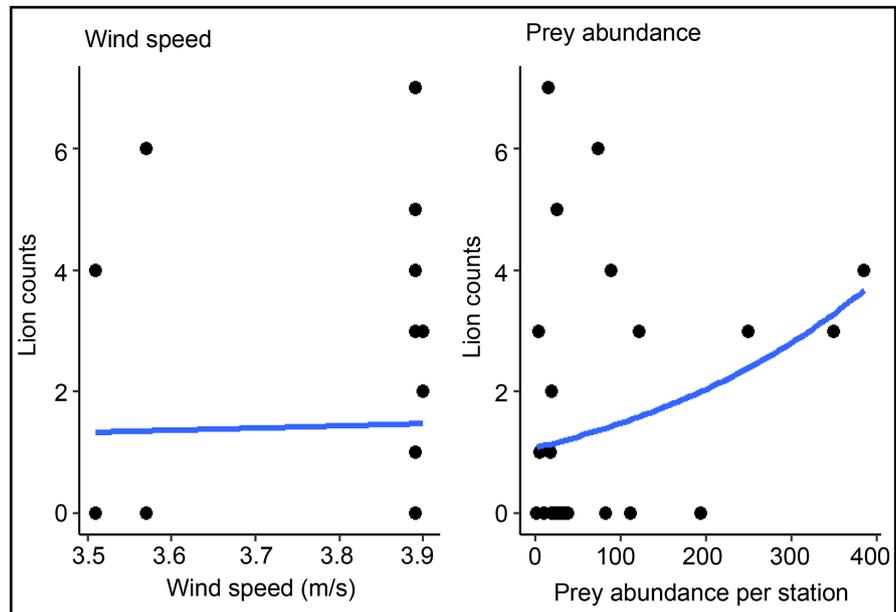
Lion abundance significantly increased with an increase of precipitation (GLMM,  $P = 0.033$ ) and temperature (GLMM,  $P = 0.004$ , **Figure 3**). This is consistent with correlation analysis as we found a weak positive correlation between precipitation and temperature ( $r = 0.33$ ), which had positive correlation with lion abundance (**Figure 3**). Average precipitation and temperature from all call-back stations was 2.5 mm/day and 26.6°C/day, respectively. Most



**Figure 2.** Relationships of lion counts with elevation and habitat types.



**Figure 3.** Relationships between lion counts and variable precipitation and temperature per day per call-back station.



**Figure 4.** Relationships of wind speed and prey abundance on the observed lions at call-back stations.

lions responded to stations with average precipitation and temperature, compared to stations with lower or higher precipitation and temperature values. This suggests precipitation and temperature may be important factors to consider when assessing lion populations, and that using mean value is a better index than minimum or maximum values since both had similar patterns.

There was a significant increase of lion abundance with an increase of wind speed (GLMM,  $P = 0.009$ ) and prey abundance (GLMM,  $P = 0.002$ , **Figure 4**). This suggests that areas with higher wind speed carried playback sounds a greater distance, which may attract more lions. Understandably, areas with higher prey abundance had greater lion response to playback calls. The most abundant prey species in the park are buffalo followed by impala and giraffe (**Supplemental Table S1**).

#### 4. Discussion

This study used call-back surveying in Katavi National Park to determine local lion demography, population size, and density, and to examine factors that may influence lion distribution. We found more female lions responded to the call-back stations compared to males and based on Kruger's study [17] response probabilities, we determined a total of 84 lions (95% CI 53 - 116) present at 29 call-back stations with an estimated lion density of 5/100 km<sup>2</sup> (95% CI 3.14 - 6.86) over our 1682 km<sup>2</sup> sampling area. Lions responded 41% of the time to the 29 stations, which is relatively higher than in Katavi National Park where 27% of lions responded [5]. Factors influencing the lion distribution in the park included habitat type, elevation, temperature, precipitation, wind speed, and prey abundance.

When extrapolated to cover the entire park (4471 km<sup>2</sup>), we estimate the lion

population size of 214 individual lions. This is relatively higher than the estimate from previous Katavi study that found the park holds 168 individuals [5]. However, we found a relatively similar lion density as the previous study [5], as well as that in Kruger National Park, South Africa [17]. Katavi lion density was also found to be relatively higher than lion density in Zimbabwe's Gonarezhou National Park, at 1.5 individuals per 100 km<sup>2</sup> [9]. The lion density here was relatively lower compared to the Serengeti National Park (14.4 individuals per 100 km<sup>2</sup>, [20] and Maasai Mara National Reserve, Kenya (20 individuals per 100 km<sup>2</sup>; [21]), which may be based on prey availability in the Serengeti-Mara ecosystem. Determining population size and density are important for conservation planning because both are critical parameters needed for the assessment of wildlife population viability and assessment of conservation efforts [22] [23].

We found that the sex ratio of responding lions (excluding cubs) was similar to that of previous study in Katavi [5], and that of Maasai Mara Reserve in Kenya [21], although we combined both adults and sub-adults in our analysis. Our findings support the fact that female lions outnumber males in the pride 2:1, which is relatively uniform to other prides [24] though we acknowledge this may differ under alternative ecological or physiological conditions [21] [25]. That said, given we conducted our study between September and November, this may have affected our sex ratio results in Katavi if the growth rate of sub-adults vary like that of the Maasai Mara Reserve, where the survival of sub-adult lions are influenced by wildebeest migration [21]. Future efforts could examine sub-adult lion growth and survival rates in Katavi based on herbivore availability in the park. We also suggest it is possible a lower number of male lions in Katavi National Park could be associated with illegal lion killings by local people [5] [11]. This too would be worthy of future investigation.

Our analysis also revealed that stations with a high prey abundance had a high lion response. The influence of prey availability in our study is consistent with previous studies in Katavi [5] as well as in the Maasai Mara [21] and Kruger National Park [17]. We also found that lion response was higher in the lowlands, however, prey abundance did not differ between lowlands and highlands ( $t = -0.303$ ,  $p > 0.05$ ). This may indicate that lions target certain prey species likely to occur in lowland areas, such as waterbuck (*Kobus ellipsiprymnus*; [5], which appear to have a higher predation risk from lions [26]; **Supplemental Table S1**). Further, we found that lions appeared to utilize more grassland and shrub habitats than other habitat types, similar to the Serengeti National Park [20]. This suggests future conservation planning should include the monitoring of prey population change and lion-prey relationships, as well as the potential for land cover change in the park. However, habitat selection is not mutually exclusive, rather lion habitat selection is driven by a combination of multiple factors including prey availability [27]. Lastly, temperature and precipitation appeared to influence lion abundance in Katavi, which is consistent with Kolowski and Holecamp's findings [28], though contrary to the Serengeti study [20]. We suggest

that future consideration be given to the possible impacts of climate change on the distribution and abundance of lions, as well as prey species given habitat effects [29].

## 5. Conclusion

To conclude, our study suggests that the call-back survey method can be a cost-effective and rapid technique to monitor large carnivores like lions, with proper training of observers prior to fieldwork. Indeed, estimating lion population size and density can help assess conservation efforts' successes across the landscape. We suggest that using sex ratio as an index of assessing conservation efforts is possible, however, caution is warranted as sex ratio variation can be influenced by both natural and anthropogenic factors. Also, with the sex ratio obtained from this study, the population can still be viable but there is a need for a close monitoring to study the rate of pride male exchange as it may be critical for population growth. We also suggest that the call-back method may be an effective way to engage local communities, including pastoralists (*i.e.*, livestock keepers), in enhancing their awareness and knowledge, and developing skills in scientific processes, as well as build better relations with community members to, in hopes, stem illegal lion killing both within and beyond protected area boundaries [30]. Indeed, engaging communities in lion monitoring (and that of other large carnivores or wildlife) is important to help address human-lion conflict but also human wellbeing needs [31] [32], because population estimates and wildlife distribution may have management implications [33] [34]. These data can be used as a baseline to track changes of the lion population over time, and assess the effectiveness of conservation efforts in Katavi National Park, and link the impacts of lion hunting (legal and illegal) to the population viability analysis.

## 6. Study Limitations

Our study adopted probabilities generated from the Kruger National Park study [17], and did not perform its own calibrations to generate probabilities for Katavi National Park. This study also referred to the design of Katavi study [5] regarding the placement of stations, and we acknowledge there may be a more optimal solution for Katavi that can be explored in future. Other studies suggested that illumination (*i.e.*, moon lights; [20]), diseases (*i.e.*, bovine tuberculosis; [17]), and the presence of hyenas [9], may affect lion response to call-back stations, and we did not consider these factors in our study.

## Acknowledgements

We would like to pass our sincere and heartfelt appreciations to the Tanzania National Park Authority (TANAPA) for funding this research project. This work would not have become a success without tireless efforts and commitments invested by the field team notably the field Assistants, especially Frank Riziki and our driver Hamdan Mheluka. We thank Dr. Courtney Hughes for the review of

manuscript before its submission to the journal.

### Author Contributions

S.M designed the study, collected data, and was lead author for this manuscript. M.K and H.M performed data analysis. Both S.M., H.M, and M.K contributed to writing and revisions of the manuscript. Both authors have given their approval for publication of this manuscript.

### Funding Statement

This study was funded by the Government of Tanzania, through Tanzania National Parks Authority (TANAPA).

### Conflicts of Interest

At a time conducting this study, S.M was an employee who works for TANAPA, and played part as an ecologist from the Conservation Science Department of the Katavi National Park, but funder did not have any influence on the publication of this article. Both authors declare absence of conflict of interest.

### References

- [1] IUCN SSC Cat Specialist Group (2018) Guidelines for the Conservation of Lions in Africa. Version 1.0. International Union for Conservation of Nature (IUCN), Muri/Bern, 147 p.
- [2] IUCN SSC Cat Specialist Group (2006) Regional Conservation Strategy for the Lion (*Panthera leo*) in Eastern and Southern Africa. International Union for Conservation of Nature (IUCN), Gland.
- [3] Bauer H., Chapron G. and Nowell K. (2015) Lion (*Panthera leo*) Populations Are Declining Rapidly across Africa, Except in Intensively Managed Areas. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 14894-14899. <https://doi.org/10.1073/pnas.1500664112>
- [4] Williams, V.L., Loveridge, A.J., Newton, D.J. and Macdonald, D.W. (2017) A Roaring Trade? The Legal Trade in *Panthera leo* Bones from Africa to East-Southeast Asia. *PLOS ONE*, **12**, Article ID: e0185996. <https://doi.org/10.1371/journal.pone.0185996>
- [5] Kiffner, C., Meyer, B., Mühlenberg, M. and Waltert, M. (2009) Plenty of Prey, Few Predators: What Limits Lions *Panthera leo* in Katavi National Park, Western Tanzania? *Oryx*, **43**, 52-59. <https://doi.org/10.1017/S0030605307002335>
- [6] Wilson, G.J. and Delahay, R.J. (2001) A Review of Methods to Estimate the Abundance of Terrestrial Carnivores Using Field signs And Observation. *Wildlife Research*, **28**, 151-164. <https://doi.org/10.1071/WR00033>
- [7] Yoccoz, N.G., Nichols, J.D. and Boulinier, T. (2001) Monitoring of Biological Diversity in Space and Time. *Trends in Ecology & Evolution*, **16**, 446-453. [https://doi.org/10.1016/S0169-5347\(01\)02205-4](https://doi.org/10.1016/S0169-5347(01)02205-4)
- [8] Strampelli P., Andresen L., Everatt K.T., Somers M.J. and Rowcliffe J.M. (2018) Leopard *Panthera pardus* Density in Southern Mozambique: Evidence from Spatially Explicit Capture-Recapture in Xonghile Game Reserve. *Oryx*, **54**, 405-411. <https://doi.org/10.1017/S0030605318000121>

- [9] Groom, R. J., Funston, P. J. and Mandisodza, R. (2014) Surveys of Lions *Panthera leo* in Protected Areas in Zimbabwe Yield Disturbing Results: What Is Driving the Population Collapse? *Oryx*, **48**, 385-393. <https://doi.org/10.1017/S0030605312001457>
- [10] Smitz, N., Jouvenet, O., Ambwene, F., Crosmary, W.G., Ikanda, D., Chardonnet, P., et al. (2018) A Genome-Wide Data Assessment of the African Lion (*Panthera leo*) Population Genetic Structure and Diversity in Tanzania. *PLOS ONE*, **13**, Article ID: e0205395. <https://doi.org/10.1371/journal.pone.0205395>
- [11] Mgawe, P., Mulder, M.B., Caro, T., Martin, A. and Kiffner, C. (2012) Factors Affecting Bushmeat Consumption in the Katavi-Rukwa Ecosystem of Tanzania. *Tropical Conservation Science*, **5**, 446-462. <https://doi.org/10.1177/194008291200500404>
- [12] Engilis, A., Lalbhai, P.S. and Caro, T. (2009) Avifauna of the Katavi-Rukwa Ecosystem, Tanzania. *Journal of East African Natural History*, **98**, 95-117. <https://doi.org/10.2982/028.098.0107>
- [13] Caro, T. (2008) Decline of Large Mammals in the Katavi-Rukwa Ecosystem of Western Tanzania. *African Zoology*, **43**, 99-116. <https://doi.org/10.1080/15627020.2008.11407412>
- [14] Caro, T.M. (2003) Umbrella Species: Critique and Lessons from East Africa. *Animal Conservation*, **6**, 171-181. <https://doi.org/10.1017/S1367943003003214>
- [15] Ceppi, S.L. and Nielsen, M.R. (2014) A Comparative Study on Bushmeat Consumption Patterns in Ten Tribes in Tanzania. *Tropical Conservation Science*, **7**, 272-287. <https://doi.org/10.1177/194008291400700208>
- [16] United Republic of Tanzania (2009) The Wildlife Conservation Act. The Ministry of Natural Resources and Tourism, Dar es Salaam, 91 p
- [17] Ferreira, S.M. and Funston, P.J. (2010) Estimating Lion Population Variables: Prey and Disease Effects in Kruger National Park, South Africa. *Wildlife Research*, **37**, 194-206. <https://doi.org/10.1071/WR09030>
- [18] Hayward, M.W. and Slotow, R. (2009) Temporal Partitioning of Activity in Large African Carnivores: Tests of Multiple Hypotheses. *South African Journal of Wildlife Research*, **39**, 109-125. <https://doi.org/10.3957/056.039.0207>
- [19] R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>.
- [20] Belant, J.L., Bled, F., Wilton, C.M., Fyumagwa, R., Mwampeta, S.B. and Beyer, D.E. (2016) Estimating Lion Abundance Using *N*-Mixture Models for Social Species. *Scientific Reports*, **6**, Article No. 35920. <https://doi.org/10.1038/srep35920>
- [21] Ogutu, J.O. and Dublin, H.T. (2002) Demography of Lions in Relation to Prey and Habitat in the Maasai Mara National Reserve, Kenya. *African Journal of Ecology*, **40**, 120-129. <https://doi.org/10.1046/j.1365-2028.2002.00343.x>
- [22] Henle, K., Sarre, S. and Wiegand, K. (2004) The Role of Density Regulation in Extinction Processes and Population Viability Analysis. *Biodiversity & Conservation*, **13**, 9-52. <https://doi.org/10.1023/B:BIOC.0000004312.41575.83>
- [23] Shaffer, M.L. (2019) Population Viability Analysis. In: Decker, D.J., Krasny, M.E., Goff, G.R., Smith, C.R., Gross, D.W., Jenkins, R.E., et al., Eds., *Challenges in the Conservation of Biological Resources*, Routledge, New York, 107-118. <https://doi.org/10.4324/9780429046650-12>
- [24] Schaller, G.B. (1972) *The Serengeti Lion*. University of Chicago Press, Chicago
- [25] Hewison, A.M. and Gaillard, J.M. (1996) Birth-Sex Ratios and Local Resource Competition in Roe Deer, *Capreolus capreolus*. *Behavioral Ecology*, **7**, 461-64.

- <https://doi.org/10.1093/beheco/7.4.461>
- [26] De Boer, W.F., Vis, M.J., De Knegt, H.J., Rowles, C., Kohi, E.M., Van Langevelde, F., et al. (2010) Spatial Distribution of Lion Kills Determined by the Water Dependency of Prey Species. *Journal of Mammalogy*, **91**, 1280-1286.  
<https://doi.org/10.1644/09-MAMM-A-392.1>
- [27] Sargent, R., Deere, N.J., McGowan, P.J., Bunnefeld, N. and Pfeifer, M. (2022) Room to Roam for African Lions *Panthera leo*. A Review of the Key Drivers of Lion Habitat Use and Implications for Conservation. *Mammal Review*, **52**, 39-51.  
<https://doi.org/10.1111/mam.12262>
- [28] Kolowski, J.M. and Holekamp, K.E. (2006) Spatial, Temporal, and Physical Characteristics of Livestock Depredations by Large Carnivores along a Kenyan Reserve Border. *Biological Conservation*, **128**, 529-541.  
<https://doi.org/10.1016/j.biocon.2005.10.021>
- [29] Peterson, A.T., Radocy, T., Hall, E., Peterhans, J.C.K. and Celesia, G.G. (2014) The Potential Distribution of the Vulnerable African Lion *Panthera leo* in the Face of Changing Global Climate. *Oryx*, **48**, 555-564.  
<https://doi.org/10.1017/S0030605312000919>
- [30] Treves, A., Wallace, R.B., Naughton-Treves, L. and Morales, A. (2006) Co-Managing Human-Wildlife Conflicts: A Review. *Human Dimensions of Wildlife*, **11**, 383-396.  
<https://doi.org/10.1080/10871200600984265>
- [31] Sibanda, L., van der Meer, E., Johnson, P.J., Hughes, C., Dlodlo, B., Parry, R.H., et al. (2021) Evaluating the Effects of a Conservation Intervention on Rural Farmers' Attitudes toward Lions. *Human Dimensions of Wildlife*, **26**, 445-460.  
<https://doi.org/10.1080/10871209.2020.1850933>
- [32] Sibanda, L., Johnson, P.J., van der Meer, E., Hughes, C., Dlodlo, B., Mathe, L.J., et al. (2021) Effectiveness of Community-Based Livestock Protection Strategies: A Case Study of Human-Lion Conflict Mitigation. *Oryx*, **4**, 537-545.  
<https://doi.org/10.1017/S0030605321000302>
- [33] Chomba, C., Simpamba, T., Kampamba, G. and Nyirenda, V. (2014) Does the Luangwa Hippo Population Size and Density Distribution Vary between Upper and Lower Study Blocks? What Are the Management Implications of Such Distribution Pattern? *Open Journal of Ecology*, **4**, 262-280.  
<https://doi.org/10.4236/oje.2014.45025>
- [34] Kimaro, M., Mrosso, H., Chidodo, S., Chilagane, N., Msigwa, F., Bulenga, G., Kicheleri, R., Mgeni, C., Kangile, R., Kimambo, E., Hughes, C., Warbington, C., Mchaki, H., Mathayo, D. and Kiwango, H. (2022) African Lion Population Estimates in Tanzania's Ruaha National Park. *Open Journal of Ecology*, **12**, 558-569.  
<https://doi.org/10.4236/oje.2022.128031>

## Supplementary Materials

**Table S1.** Abundance of prey species per station as encountered during the road transect surveys.

Transect	Species	Counts
A	Giraffe	8
	Impala	90
	Roan	2
	Topi	10
	Warthog	10
	Bushbuck	4
	Hartebeest	3
	Zebra	20
	Warthog	2
	Bushbuck	2
B	Eland	27
	Giraffe	6
	Bushbuck	2
	Roan	6
	Impala	165
	Warthog	5
	Topi	98
	Zebra	96
	Elephant	12
	Hippo	6
C	Buffalo	98
	Eland	5
	Reedbuck	2
	Zebra	47
	Buffalo	362
	Warthog	31
	Elephant	27
	Impala	78
	Giraffe	8
	Waterbuck	12
Roan	18	

**Continued**

---

	Topi	29
	Impala	26
	Warthog	20
	Zebra	109
	Waterbuck	26
D	Giraffe	9
	Hartebeest	11
	Roan	18
	Hartebeest	3
	Lesser Kudu	2
	Bushbuck	1
	Duiker	1
	Impala	65
	Giraffe	7
	Topi	55
	Buffalo	374
E	Waterbuck	7
	Warthog	5
	Zebra	55
	Eland	13
	Roan	2

---