

University of Groningen

African Lion Population Estimates in Tanzania's Ruaha National Park

Kimaro, Michael; Mrosso, Hillary T.; Chidodo, Simon J.; Chilagane, Nyemo A.; Msigwa, Fenrick F.; Bulenga, George B.; Kicheleri, Rose P.; Mgeni, Charles P.; Kangile, Rajabu J.; Kimambo, Elisante A.

Published in:
Open Journal of Ecology

DOI:
[10.4236/oje.2022.128031](https://doi.org/10.4236/oje.2022.128031)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2022

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Kimaro, M., Mrosso, H. T., Chidodo, S. J., Chilagane, N. A., Msigwa, F. F., Bulenga, G. B., Kicheleri, R. P., Mgeni, C. P., Kangile, R. J., Kimambo, E. A., Hughes, C., Warbington, C., Mchaki, H., Mathayo, D., & Kiwango, H. R. (2022). African Lion Population Estimates in Tanzania's Ruaha National Park. *Open Journal of Ecology*, 12(8), 558-569. <https://doi.org/10.4236/oje.2022.128031>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

African Lion Population Estimates in Tanzania's Ruaha National Park

Michael H. Kimaro^{1,2*}, Hillary T. Mrosso², Simon J. Chidodo², Nyemo A. Chilagane², Fenrick F. Msigwa², George B. Bulenga², Rose P. Kicheleri^{2,3}, Charles P. Mgeni^{2,4}, Rajabu J. Kangile^{2,4}, Elisante A. Kimambo², Courtney Hughes^{2,5}, Camille Warbington^{2,5}, Helen Mchaki⁶, Daniel Mathayo⁶, Halima R. Kiwango⁶

¹GELIFES Institute, University of Groningen, Groningen, Netherlands

²Tanzania Research and Conservation Organization, Morogoro, Tanzania

³CFWT College, Sokoine University of Agriculture, Morogoro, Tanzania

⁴SAEBS College, Sokoine University of Agriculture, Morogoro, Tanzania

⁵University of Alberta, Alberta, Canada

⁶Conservation Science Department, Ruaha National Park, Iringa, Tanzania

Email: *kimarorcp@gmail.com

How to cite this paper: Kimaro, M.H., Mrosso, H.T., Chidodo, S.J., Chilagane, N.A., Msigwa, F.F., Bulenga, G.B., Kichele-ri, R.P., Mgeni, C.P., Kangile, R.J., Kimambo, E.A., Hughes, C., Warbington, C., Mchaki, H., Mathayo, D. and Kiwango, H.R. (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>

Received: June 16, 2022

Accepted: August 15, 2022

Published: August 18, 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

Tanzania is considered a country with the largest number of African lions (*Panthera leo*). However, the continued absence of ecological population estimates and understanding of the associated factors influencing lion distribution hinders the development of conservation planning. This is particularly true in the Ruaha-Rungwa landscape, where it was estimated that more than 10% of the global lion population currently resides. By using a call-back survey method, we aimed to provide population estimates (population size and density) of African lions in the Ruaha National Park, between wet (March 2019) and dry (October 2019) seasons. We also assessed the key factors that influenced the distribution of the observed lions towards call-back stations. Ferreira & Funston's (2010) formula was used to calculate population size and in turn used to estimate density in the sampled area, while the Generalized Linear Model (GLMM) with zero-inflated Poisson error distribution was used to determine factors that influence the distribution of the observed lions to call-back stations. The population size we calculated for the sampled area of 3137.2 km² revealed 286 lions (95% CI, 236 - 335) during the wet season, and 196 lions (95% CI, 192 - 200) during the dry season. The density of lions was 9.1/100 km² during the wet season, and 6.3/100 km² during the dry season. Distance to water source had a significant negative effect on the distribution of the observed lions to the call-back stations, while habitat had a marginal effect. Our findings show that, although lion population estimates were larger during the wet season than the dry season, the season had no effect on

the distribution of the observed lions to call-back stations. We suggest that the proximity to water sources is important in study design. Further, we suggest that density and population size are useful indices in identifying conservation area priorities and lion coexistence strategies.

Keywords

Population Size, Density Estimate, Call-Back Survey, African Lion, Conservation

1. Introduction

In Africa, large carnivores including lions are declining rapidly over the past few decades [1]. This decline is often attributed to anthropogenic pressure [2], with an estimated 73% decrease in the African lion (*Panthera leo*) range in Eastern Africa alone [3]. This has resulted in only 10 population strongholds of African lions remaining across the African continent [4]. Depletion of prey base is considered one of the reasons for declining populations of large carnivores [1]. Understanding the key factors influencing the susceptibility to extinction and actual decline of lions is crucial for planning and implementing successful conservation efforts. For this to be done, monitoring of lions' population must occur, in order to provide robust knowledge of status, threats, and trends [5] [6]. However, it is often difficult to obtain precision in population abundance estimates for species with small populations, as sample sizes are likely to contain fewer individuals than sample sizes from species that exist at higher densities [7].

A variety of methods have been used to estimate lion populations, with capture-mark-recapture by using camera traps being one of the most widely used, but is a resource-intensive technique [8] [9]. Given the costs and staffing requirements associated with camera trapping, conservation researchers and managers are shifting their focus to use more inexpensive and rapid approaches, notably spoor or sign counts and call-back surveys [10] [11]. In the case of African lions, a prey distress sound has been used to attract the animal towards the call-back station, and then the species is identified and the numbers present are counted by observers [10]-[19].

The call-back survey method was effective and generated accurate and economical results [11] [20] [21]. Other studies have found that spotted hyenas (*Crocuta crocuta*) respond effectively to call-back stations together with lions [12]; however, the presence of spotted hyenas may affect lions' response to call-back stations [22], and thus must be taken into account during the analysis. Other considerations include lions' active hours, when their calls are broadcasted, and strong light is used to locate the animals [23]. Furthermore, habitat type and luminosity had an impact on lion population estimates in the Serengeti [21], but disease, prey density, and competition with hyenas had a substantial

impact on lion population estimates in Zimbabwe [22].

In southern Tanzania, the Ruaha-Rungwa landscape, which includes the Ruaha National Park, is an important landscape for African lions [24]. It was estimated that the Ruaha-Rungwa ecosystem could hold more than 10% of the global remaining lion population, however, no reliable data is yet available to validate estimation [4]. As such, we conducted call-back surveys in the Ruaha National Park during the wet and dry seasons in 2019 to determine lion population size and densities. In addition to providing population-level information for conservation decision-making, we also determined which factors influenced the distribution of the observed lions to call-back stations, to inform future monitoring.

2. Materials and Methods

2.1. Study Site

The Ruaha-Rungwa ecosystem is approximately 45,000 km² and comprises the Ruaha National Park, neighboring game reserves, Wildlife Management Areas (WMAs), game-controlled areas, and village land [25]. Our study area focused on the Ruaha National Park, over an area of 20,226 km², situated between 6.9°S to 8.7°S and 33.6°E to 35.6°E (**Figure 1**), however, we sampled an area of 3137.2

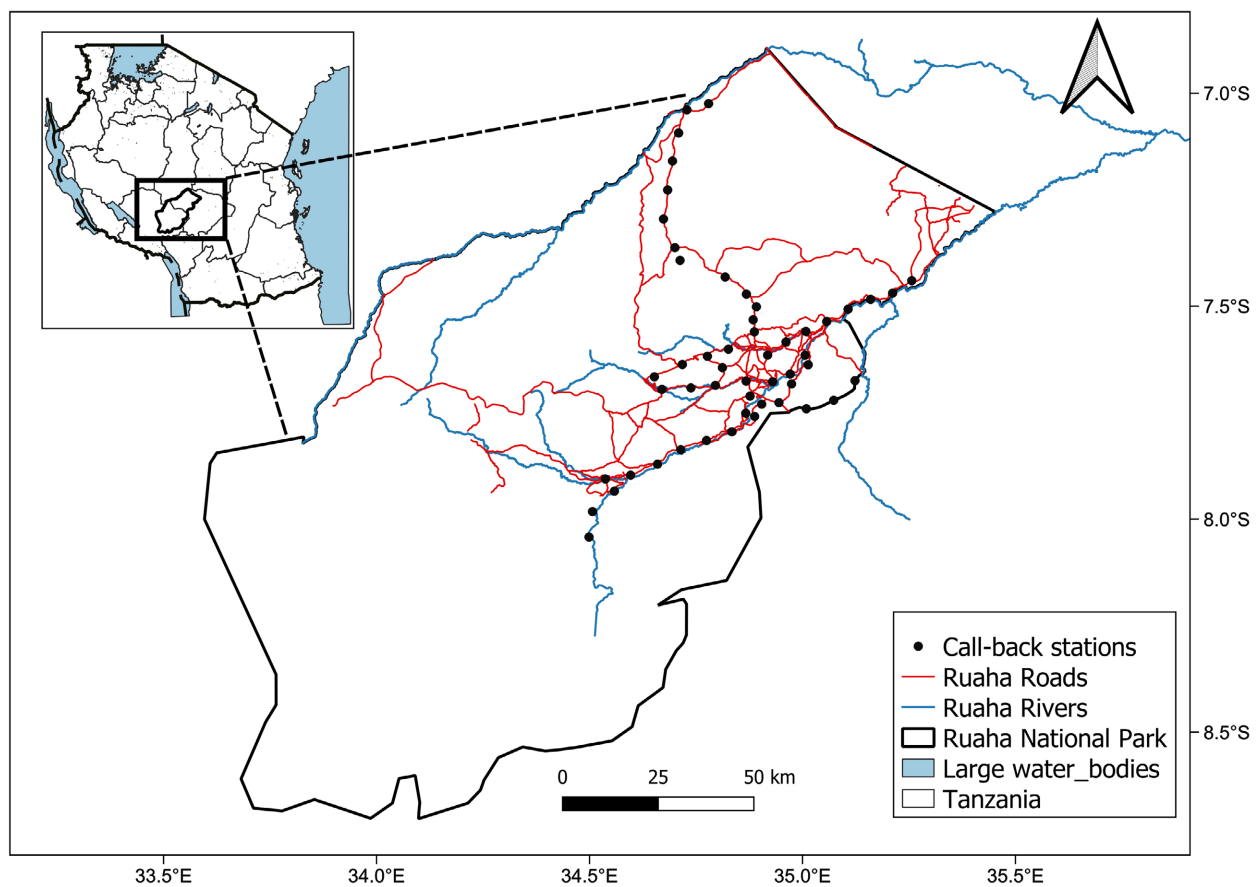


Figure 1. Map showing study area, and calling stations in the Ruaha national park.

km² presenting 18.5 percent of the actual size of the park. Ruaha National Park is among Tanzania's largest national parks and one of the most significant ecoregions in the world given its abundance and diversity of plants and animals [26]. The climate of the area is semi-arid to arid, characterized by dry seasons that typically begin in May to November and wet seasons from December to April [27]. The mean annual rainfall is 500 mm [27], and the temperature ranges from 15°C to 35°C [25]. The main commercial activity in the park is photographic tourism which receives about 21,000 visitors per year [28], which is linked to visitors seeking out iconic species such as African lions.

2.2. Data Collection

This study covered 54 call-back stations in total, which were observed twice (once per season), and the total area covered was 3137.2 km². At each station, we broadcasted vocalization for 70 minutes: a time which is enough for a lion to approach and be detected in the call-back stations [29]. We played a recording of prey animals in distress (buffalo, pigs), mixed with sounds of mobbing spotted hyenas and a lion feeding at every call-back station for four rounds. Each round took 10 minutes. After playing the sound for every round, a period of 5 minutes of silence was followed. After playing the last round of recordings, 10 minute of silence period was used exclusively for observation. Sounds were played from a smartphone (Tecno Pop 1 Pro) and were heard 3 kilometers away. The phone was connected to a 12 V amplifier which was connected to four speakers. 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 aired from the speaker at the maximum volume possible. The speaker was placed on the roof of the vehicle at an approximate height of 2.5 m.

Four observers were seated on the roof of the car, of which one observer was to operate the sound system and the other three observers were there to look over attracted animals. One more observer was located inside the car in front near the driver. Every observer had a strong light torch, and we had 2 strong spotting lights covered with a red filter to reduce the disturbance of light to the oncoming animals. Sometimes the red filters on the light were removed to help in the age and sex identification of the responded animals. Animals that arrived were categorized by species including spotted hyenas. Due to difficultness of sex identification of lion cubs, we excluded documenting the sex of lion cubs. No bait was used in this survey.

In order to evade double counting, call-back stations were placed at an interval of 8 km from each other, measured by car odometer, and situated along road networks available in the park as sampling units. Two to five stations were sampled per night. Surveys were carried out at least half an hour after sunset between 17:30 hours and 02:00 hours because this is the time when they are expected to be active for lions [30]. Climatic data of call-back stations (rainfall, temperature, and wind speed) were acquired 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 based on general observations, which presents a limitation of this study for not classifying the habitats by using specific metrics. The NNjoin plugin from QGIS software was used to estimate the distance from each station to the nearest perennial river. Wet season data were collected from the end of February to the end of March, and dry season data were collected from mid-October to mid-November, 2019.

2.3. Data Analysis

We estimated lion population size by using the formula of Ferreira and Funston's study [17] as follows:

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

All constants adopted from Ferreira and Funston study and their definitions are shown on **Table 1**.

From **Table 1**, the $P_{c,r}$ and $P_{nc,r}$ is the probabilities that lions in groups with cubs and lions in groups without cubs would respond more than once, however, since our study focused on playback sound that played once per season, these probabilities were not applicable. The formula assumes no habituation and low or no double counting due to >6 km spacing of stations. We used the calculated population size in the sampled area and manipulated it to determine the relative density of lions per 100 km². The following formulas were used to determine

Table 1. Constants adopted from Ferreira and Funston's study to our study in the Ruaha National Park, Tanzania.

Symbol	Variable definition	Value
r	Radius of the playback sound from call-back stations.	4.3 km
π	Mathematical pie for calculating the area of circle <i>i.e.</i> call station.	3.142
\underline{A}	Effective sampled area <i>i.e.</i> area of one call station (πr^2).	58 km ²
A_T	Sum of the effective area sampled (54 stations* πr^2).	3137.2 km ²
$P_{nc,p}$	is the response probability of a lion group responding without cubs.	0.734
$P_{c,p}$	is the response probability of a lion group responding with cubs.	0.286
$P_{nc,i}$	is the response probability of a lion in a responding group of a lion without cubs.	0.902
$P_{c,i}$	is the response probability of a lion in a responding group of a lion with cubs.	0.957

variance and 95% confidence intervals for population size and manipulated to determine the confidence interval for density of lions;

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

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

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

Hmisc package in R software [31] was used to examine the correlation among selected variables. Variables included in the correlation matrix were a season, rainfall, temperature, wind speed, distance to the nearest river, habitat types, elevation, and the number of hyenas that responded per station. For pairs of variables with strong correlation ($>\pm 0.7$), one variable was retained for further analysis, and later substituted by the variable excluded. Rainfall, season, wind speed, and temperature were all strongly correlated variables. A generalized Linear Mixed Model (GLMM) with a zero-inflated Poisson model was used to identify factors that influenced the distribution of the observed lions in the call-back stations by the utilization of “pscl” and “glmmTMB” packages. Station ID was treated as a random variable. We used the “drop1” function to determine the most significant variables, and the best model with the lowest AICc score was determined by the utilization of the “AICc” function from the “AICcmodavg” package.

3. Results

3.1. Population Size Estimates

A total of 128 lions were encountered in the wet season from all call-back stations. A total of 46 adult males, 68 adult females, and 14 cubs responded. Lions were observed at 30 of the 54 stations, accounting for 56% of the total stations. The estimated number of lions at a call-back station ranged from 0 to 11. The mean number of lions that responded per station was 2.4. We found a population size of 286 lions (95% CI, 236 - 335) for the sampled area of 3137.2 km² (Table 2) in the wet season. The wet season lion density is estimated to be 9.1 lions per 100 km².

Table 2. Estimates of population size and density of lions in the sampled area during wet season based on Ferreira & Funston formula from Kruger National Park.

Total observed	Number of call-in stations	Mean abundance estimate per station	Estimated population	95% CI	Density estimate per 100 km ²	95% CI for density
128	54	2.4	286	235.7 - 335.3	8.8	6.7 - 10.9

A total of 87 lions were encountered in the dry season from all call-back stations. A total of 18 adult males, 42 adult females, and 27 cubs responded. Lions were observed at 34 of the 54 stations, accounting for 63% of the total stations. Similar to the wet season, the estimated number of lions at a call-back station ranged from 0 to 11. A mean number of lions that responded per station was 1.6. We found a population size of 196 lions (95% CI, 192 - 200) for the sampled area of 3137.2 km² (Table 3) for the dry season. During the dry season, lion density was estimated to be 6.3 lions per 100 km².

3.2. Factors Influencing the Distribution of the Observed Lions to Call-Back Stations

Factors included in the analysis were a season, rainfall, temperature, wind speed, distance to the nearest river, habitat types, elevation, and the number of hyenas that responded per station. The zero inflation model revealed that the distribution of the observed lions to the calling stations was mostly related to the distance to the nearest river. Specifically, the number of the observed lions decreased with an increase in distance to the nearest river (Estimate = $-15.18 \pm 5.73SE$, $Z = -2.73$, $P = 0.01$, Figure 2).

Table 3. Estimates of population size and density of lions in the sampled area during the dry season based on Ferreira & Funston formula from Kruger National Park.

Total observed	Number of call-in stations	Mean abundance estimate per station	Population estimate	95% CI	Density estimate per 100 km ²	95% CI for density
87	54	1.61	196	193 - 200	6.29	6.2 - 6.4

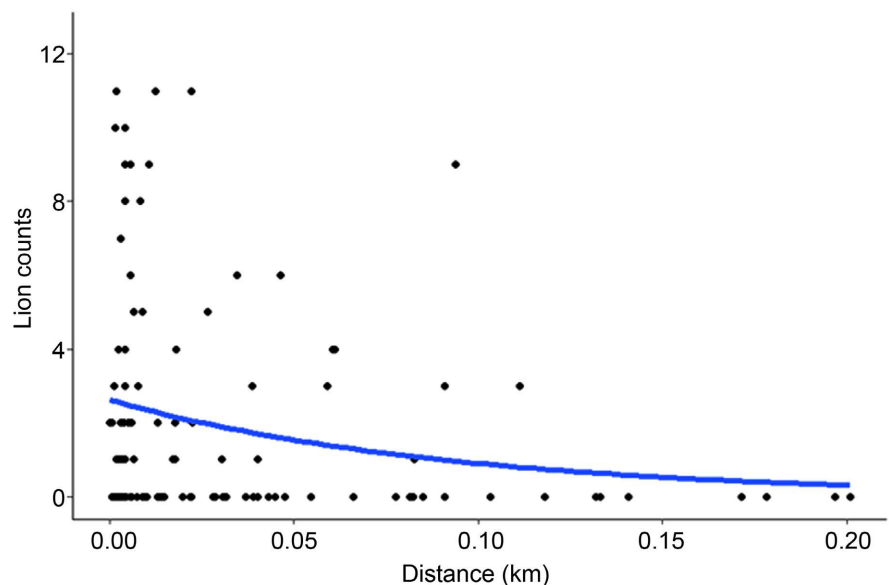


Figure 2. Distribution of the observed lions with a distance to the nearest river in the Ruaha National Park.

4. Discussion

The seasonal population size, and density of lions in the Ruaha National Park, and assessed factors that influenced the distribution of the observed lions to call stations by probability estimates derived from Funston & Ferreira's study [17] and Poisson (GLMM) techniques respectively. The size or density of lion populations was higher during the wet season than during the dry season, but the difference was not significant, and there was no significant difference in the number of observed lions in the call-backs station between the wet and dry seasons. The distance to the water source was the key element that determined the distribution of the observed lions to the call-back stations. Our findings thus imply that population estimates (population size and density) of lions in the Ruaha landscape may likely vary due to variations in water availability.

Our population size or density for lions had precise estimates due to narrow confidence intervals. Many studies lack an analytical assessment of this method for both seasons. Higher estimates during the wet season than dry season conform with the hypothesis that lion distribution is negatively correlated with prey availability [12] since precipitation is considered as an indirect measure of prey density variable. Furthermore, higher population estimates of lions during the wet season compared to the dry season could be supported by the behavior of lions that often utilize dry lands like roads to avoid stepping on wet areas, and their known behavior of using roads for travel when they are within their core home range [17], indicating potential bias of using roads for population estimate of lions. Although the wet season had larger population estimates than the dry season, the season had no effect on the lions' observations to the call-back stations, indicating that population estimates at any season will offer reliable data. In addition, the positive lion response towards the call-back stations when the sound played indicates that they have a common stimulus towards food availability [12]. As a result, the call-back method can be used to cover the entire Ruaha-Rungwa ecosystem and other savannah-protected areas.

Our dry season estimates are comparable to estimates from other studies, as most studies performed call-back surveys during the dry season only. Our dry season density of 6.3 lions per 100 km² was approximately half of the density of lions reported in Serengeti National Park, Tanzania (14.4 lions per 100 km², [21]), and was one-fifth of lions reported from Maasai Mara Game Reserve [12]. In addition, our dry season density was comparable to 5.0 lions per 100 km² of Kruger National Park, South Africa [17] and Katavi National Park, Tanzania [32]. Our dry season density was higher than 1.5 lions per 100 km² of Gonarezhou National Park, in Zimbabwe [22]. This generally implies that the Ruaha-Rungwa ecosystem holds a potential population of lions as reported by Rigio & Pimm's study [4].

With regards to factors that influenced the distribution of the observed lions, proximity to water sources was determined as the main influencing factor. Our findings are supported by other studies (see [21] [33] [34]). In Serengeti Nation-

al Park, luminosity had a significant effect on lion responses to the call-back station [21], while in Kruger National Park, disease severity affected the distribution and response of lions in the call-back stations [17], which implies they are important variables to consider in savannah ecosystems, although those data were not available for our study. In addition, other studies found that the response or presence of spotted hyenas to the call-back stations may have a significant effect on lion responses [23]. However, our findings found that the presence of hyenas had no strong effect on the distribution of the observed lions, which is in line with the study from Maasai Mara Game Reserve [12].

To conclude, it is worth using a call-back method as it is a quick, inexpensive, and effective method for long-term monitoring of lion populations. Such monitoring is important, especially in areas where trophy hunting operates, and where human-large carnivore conflict is intense like in the Ruaha-Rungwa ecosystem. The population size, density, and population trends of lions are important to the management of protected areas and the adjacent unprotected regions because they can be used as a proxy to measure the success or failure of conservation techniques or policies [35] [36]. With this study, successful application of the call-back method requires consideration of important variables to take into account during study design such as water proximity.

5. Study Limitations

Our study has important implications for the long-term monitoring of lions, as well as conservation decision-making. Specifically, population size or density are dynamic aspects and not static, hence, require long-term monitoring. Similarly, the findings imply that a call-back survey method can be adopted to assess lion population estimates, however, there are key aspects to consider. For instance, Kruger National Park, prey density, and areas with and without diseases were included in the model [17], while in Serengeti National Park [21] the luminosity variable was included models. We acknowledge that disease severity and luminosity data could help us improve our models, however, these data were not available for our study. Our study used rainfall from each call-back station as a correlated variable with prey abundance due to the absence of prey data, but we acknowledge that using real prey abundance data rather than correlations might improve our models (see [12] [34] [37]). Despite the lack of critical data that could help us improve our models, our research gives precise population estimates and identifies crucial elements that influenced the observed lions' distribution, and this is the first time a call-back method has been used in the Ruaha National Park.

Acknowledgements

We would like to thank Tanzania National Park Authority through Ruaha National Park Chief Park Warden, Mr. Msinday for his approval and support of funding to conduct this study successfully. We also appreciate and thank the

Conservation Science Department for their constant unlimited support, time and inspiration. We also acknowledge all park drivers, rangers, and many thanks to assistants Mr. Cosmas, and Mr. Ally Kikula for their great support.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

- [1] Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B. and Packer, C. (2015) Lion (*Panthera leo*) Populations Are Declining Rapidly across Africa, Except in Intensively Managed Areas. *Proceedings of the National Academy of Sciences*, **112**, 14894-14899. <https://doi.org/10.1073/pnas.1500664112>
- [2] Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. and Mace, G.M. (2004) Human Population Density and Extinction Risk in the World's Carnivores. *PLoS Biology*, **2**, e197. <https://doi.org/10.1371/journal.pbio.0020197>
- [3] Henschel, P., Azani, D., Burton, C., Malanda, G.U.Y., Saidu, Y., Sam, M. and Hunter, L. (2010) Lion Status Updates from Five Range Countries in West and Central Africa. *Cat News*, **52**, 34-39.
- [4] Riggio, J.S. and Pimm, S.L. (2011) The African Lion (*Panthera leo leo*): A Continent-Wide Species Distribution Study and Population Analysis. Master of Environmental Management Thesis, Duke University, Durham.
- [5] Manley, P.N., Zielinski, W.J., Schlesinger, M.D. and Mori, S.R. (2010) Evaluation of a Multiple-Species Approach to Monitoring Species at the Ecoregional Scale. *Ecological Applications*, **14**, 296-310. <https://doi.org/10.1890/02-5249>
- [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] Loveridge, A.J., Searle, A.W., Murindagomo, F. and Macdonald, D.W. (2007) The Impact of Sport-Hunting on the Population Dynamics of an African Lion Population in a Protected Area. *Biological Conservation*, **134**, 548-558. <https://doi.org/10.1016/j.biocon.2006.09.010>
- [9] Rosenblatt, E., Becker, M.S., Creel, S., Droge, E., Mweetwa, T., Schuette, P.A. and Mwape, H. (2014) Detecting Declines of Apex Carnivores and Evaluating Their Causes: An Example with Zambian Lions. *Biological Conservation*, **180**, 176-186. <https://doi.org/10.1016/j.biocon.2014.10.006>
- [10] Buckland, S.T., Summers, R.W., Borchers, D.L. and Thomas, L. (2006) Point Transect Sampling with Traps or Lures. *Journal of Applied Ecology*, **43**, 377-384. <https://doi.org/10.1111/j.1365-2664.2006.01135.x>
- [11] Midlane, N., Justin O'Riain, M., Balme, G.A. and Hunter, L.T. (2015) To Track or to Call: Comparing Methods for Estimating Population Abundance of African Lions *Panthera leo* in Kafue National Park. *Biodiversity and Conservation*, **24**, 1311-1327. <https://doi.org/10.1007/s10531-015-0858-z>
- [12] Ogutu, J.O. and Dublin, H.T. (1998) The Response of Lions and Spotted Hyenas to

- Sound Playbacks Is a Technique for Estimating Population Size. *African Journal of Ecology*, **36**, 83-95. <https://doi.org/10.1046/j.1365-2028.1998.113-89113.x>
- [13] McGregor, P.K. (2000) Playback Experiments: Design and Analysis. *Acta Ethnological*, **3**, 3-8. <https://doi.org/10.1007/s102110000023>
- [14] Mills, M.G.L., Juritz, J.M. and Zucchini, W. (2001) Estimating the Size of Spotted Hyena (*Crocuta crocuta*) Populations through Playback Recordings Allows for Non-Response. *Animal Conservation*, **4**, 335-343. <https://doi.org/10.1017/S1367943001001391>
- [15] Giannatos, G., Marinos, Y., Maragou, P. and Catsadorakis, G. (2005) The Status of the Golden Jackal (*Canis aureus* L.) in Greece. *Belgian Journal of Zoology*, **135**, 145-149. <https://doi.org/10.1007/s10344-013-0765-0>
- [16] Whitman, K. (2006) Modeling, Monitoring & the Sustainable Use of Lion Populations in Tanzania.
- [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] Hansen, S.J.K. (2015) Pairing Call-Response Surveys and Distance Sampling for a Mammalian Carnivore. *Journal of Wildlife Management*, **79**, 662-671. <https://doi.org/10.1002/jwmg.865>
- [19] Winterbach, C.W., Ferreira, S.M., Funston, P.J. and Somers, M.J. (2016) Simplified Large African Carnivore Density Estimators from Track Indices. *PeerJ*, **4**, e2662. <https://doi.org/10.7717/peerj.2662>
- [20] Henschel, P., Coad, L., Burton, C., Chataigner, B., Dunn, A., MacDonald, D. and Hunter, L.T.B. (2014) The Lion in West Africa Is Critically Endangered. *PLOS ONE*, **9**, e83500. <https://doi.org/10.1371/journal.pone.0083500>
- [21] 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>
- [22] 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>
- [23] Macdonald, D.W. and Loveridge, A.J. (2010) Biology and Conservation of Wild Felids.
- [24] Dickman, A.J. (2008) Key Determinants of Conflict between People and Wildlife, Particularly Large Carnivores, around Ruaha National Park, Tanzania. Ph.D. Diss., University of London, London.
- [25] Abade, L., Macdonald, D.W. and Dickman, A.J. (2014) Assessing the Relative Importance of Landscape and Husbandry Factors in Determining Large Carnivore Depredation Risk in Tanzania's Ruaha Landscape. *Biological Conservation*, **180**, 241-248. <https://doi.org/10.1016/j.biocon.2014.10.005>
- [26] Olson, D.M. and Dinerstein, E. (1998) The Global 200: A Representation Approach to Conserving the Earth's Most Biologically Valuable Ecoregions. *Conservation Biology*, **12**, 502-515. <https://doi.org/10.1046/j.1523-1739.1998.012003502.x>
- [27] Walsh, M. (2000) The Development of Community Wildlife Management in Tanzania. *Conference African Wildlife Management in the New Millennium*, Mweka, 13-15 December 2000, 13-15.
- [28] Kabuga, S.B. (2018) Tourism and Poverty Reduction in "Southern Circuits" of Tanzania: Experiences of Communities at the Gateway of Ruaha National Park.

Innsbrucker Bericht, **19**, 153-173.

- [29] Cozzi, G., Broekhuis, F., McNutt, J.W. and Schmid, B. (2013) Density and Habitat Use of Lions and Spotted Hyenas in Northern Botswana and the Influence of Survey and Ecological Variables on Call-In Survey Estimation. *Biodiversity and Conservation*, **22**, 2937-2956. <https://doi.org/10.1007/s10531-013-0564-7>
- [30] 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>
- [31] R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org>
- [32] 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>
- [33] Mosser, A., Fryxell, J.M., Eberly, L. and Packer, C. (2009) Serengeti Real Estate: Density vs. Fitness-Based Indicators of Lion Habitat Quality. *Ecology Letters*, **12**, 1050-1060. <https://doi.org/10.1111/j.1461-0248.2009.01359.x>
- [34] Abade, L., Macdonald, D.W. and Dickman, A.J. (2014) Using Landscape and Bioclimatic Features to Predict the Distribution of Lions, Leopards, and Spotted Hyenas in Tanzania's Ruaha Landscape. *PLOS ONE*, **9**, e96261. <https://doi.org/10.1371/journal.pone.0096261>
- [35] Crosmary, W.G., Ikanda, D., Ligate, F.A., Sandini, P., Mkasanga, I., Mkuburo, L. and Chardonnet, P. (2018) Lion Densities in Selous Game Reserve, Tanzania. *African Journal of Wildlife Research*, **48**, Article ID: 014001. <https://doi.org/10.3957/056.048.014001>
- [36] Hughes, C., Steenweg, R.J., Vander Vennen, L.M., Melnycky, N.A., Fullerton, L., Witiw, J.T. and Morehouse, A. (2021) Working Together for Grizzly Bears: A Collaborative Approach to Estimate Population Abundance in Northwest Alberta, Canada. *Frontiers in Conservation Science*, **2**, Article No. 64. <https://doi.org/10.3389/fcosc.2021.719044>
- [37] Hopcraft, J.G.C., Sinclair, A.R.E. and Packer, C. (2005) Planning for Success: Serengeti Lions Seek Prey Accessibility Rather than Abundance. *Journal of Animal Ecology*, **74**, 559-566. <https://doi.org/10.1111/j.1365-2656.2005.00955.x>