Accepted Manuscript

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PII: S2351-9894(19)30125-8

DOI: https://doi.org/10.1016/j.gecco.2019.e00651

Article Number: e00651

Reference: GECCO 651

To appear in: *Global Ecology and Conservation*

Received Date: 25 February 2019

Revised Date: 3 May 2019

Accepted Date: 3 May 2019

Please cite this article as: Belant, J.L., Bled, F., Mkasanga, I.J., Wilton, C.M., Mwampeta, S.B., Beyer, D.E., Mwakilema, W., Fyumagwa, R., Track surveys do not provide accurate or precise lion density estimates in serengeti, *Global Ecology and Conservation* (2019), doi: https://doi.org/10.1016/j.gecco.2019.e00651.

Track surveys do not provide accurate or precise lion density estimates in Serengeti

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ABSTRACT

More than 60% of the world's large carnivore species are threatened with extinction. Enumerating species abundance is critical for assessing their conservation status in response to anthropic threats and environmental stochasticity. Track surveys are commonly used to estimate abundance and density of large carnivore species, including lions (*Panthera leo*), but their suitability for estimating species abundance has been challenged. Recently developed regression models for track surveys of African large carnivores offer improvements over previous density estimators but have not been independently validated. We conducted weekly track surveys for lions in southeastern Serengeti National Park during 2015–2016 and applied one of these recent regression models, comparing corresponding lion densities to an independent density estimate in 2015 derived from a repeated call-in survey conducted during the same season. We surveyed 3,289 km for tracks in total with overall lion densities of 41.2 (95% confidence limits [CL] = 31.9–57.9)/100 km^2 in 2015 and 34.6 (26.8–46.0)/100 km^2 in 2016. Within year point estimates of lion density varied up to 56% among weeks, though 95% CLs overlapped. Overall annual CLs from the track survey in 2015 did not overlap with the 95% credible interval from the estimate of lion density using a repeated call-in survey (14.36 lions/100 km^2; 95% CrI = 9.04–29.31), suggesting overestimation of lion densities using track surveys in 2015. High between-year and among-week variation in density estimates from track surveys suggests that lion use of roads for movement varied over time and that other factors (e.g., prey distribution, luminosity) influenced lion movements independent of road distributions. We recommend caution when applying current track survey methods for estimating lion density and support application of survey designs that include direct observation of lions (e.g., call-in surveys), account for imperfect detection in a spatially-explicit framework, and incorporate environmental variables (e.g., prey, land cover) that can influence lion space use and movements.

1. Introduction

More than 60% of the world's large carnivore species are threatened with extinction and 80% of these species have decreasing populations (Ripple et al., 2014). The African lion (*Panthera leo*) is a large carnivore whose global population has reportedly declined 43% from 1993 to 2014 (Bauer et al., 2015a) and is currently restricted to only 8% of its historic range (Riggio et al., 2013). Enumerating large carnivore abundance and associated trends is critical for assessing their conservation status in response to anthropic threats and environmental stochasticity. However, abundance of large carnivores can be notoriously difficult to estimate due to their low density and often cryptic behavior, typically requiring intensive and extensive survey efforts that can be logistically or cost prohibitive. Development of accurate and economically feasible techniques to estimate their abundance would facilitate carnivore conservation and management.

Track surveys have been used to estimate abundance of numerous large carnivore species including gray wolf *Canis lupus* (Linnaeus, 1758; Patterson et al., 2004), tiger (*P. tigris*; Jhala, Qureshi & Gopal, 2011), puma (*Puma concolor* (LinnaeuS; Smallwood & Fitzhugh, 1995), and African large carnivores (Stander, 1998; Houser, Somers & Boast, 2009; Funston et al. 2010). Track surveys employing techniques developed by Funston et al. (2010) are commonly used for lions (e.g., Bouché et al. 2016). Advantages of track surveys include low cost and repeatability, which allows these surveys to be conducted rapidly across large spatial extents. However, the suitability of track surveys for estimating large carnivore abundance has long been questioned (e.g., Norton, 1990; Elliot and Gopalaswamy, 2017). Belant et al. (2016) attempted to refine track surveys using repeated track sessions and N-mixture models but found a poor correlation between track indices and estimated lion abundance.

A reanalysis of data reported by Funston et al. (2010) resulted in the development of new regression models (Winterbach et al., 2016) for estimating densities of African large carnivores. These authors used simple linear regression through the origin and found improved model fit compared with regression models with intercept. In addition to the statistical improvements offered by linear regression through the origin, this approach is ecologically sensible as one would expect no tracks to be detected if no carnivores occur in an area, assuming substrates are available for track deposition and tracks can be detected.

Winterbach et al. (2016) also called for the collection of independent data to further validate and refine their models. Our objective was to provide the first independent validation of one model developed by Winterbach et al. (2016), comparing estimated lion densities from track surveys with an independent estimate using a call-in survey (Belant et al., 2016) in southeastern Serengeti National Park (SNP), Tanzania. This call-in survey used broadcasted vocalizations to attract lions to approach predetermined sites across multiple sessions and the maximum number of lions detected at each location and session was used to estimate abundance using N-mixture models (Belant et al., 2016; 2017). Secondarily, we were interested in potential short-term variation in lion track deposition and associated densities and therefore applied this same model to estimate variation in lion densities across consecutive weeks.

2 Materials and Methods

2.1 Study Area

We conducted this study in a 1,880 km^2 area of southeastern Serengeti National Park, Tanzania (Fig. 1). Most rainfall in this predominantly savanna system occurs during November–May, increasing from the southeast to northwest (Norton-Griffiths, Herlocker & Pennycuick, 1975). Vegetation response to rainfall results in short-grass savanna in the southeast, transitioning to tall-grass savanna before becoming woodland in the northwest part of the study area (Sinclair, 1979). Woody vegetation is most extensive along rivers and rock outcrops (kopjes) occur throughout the study area.

2.2 Track surveys

Field methods for track surveys were described previously (Belant et al. 2016). We established 10 transects on roads ($\bar{x}$ = 25.3 km, σ = 1.12 km, 253 km total; Fig. 2) and surveyed each transect once each week for 7 and 6 weeks in 2015 (September–November; Belant et al., 2016) and 2016 (September–October), respectively. Transects were established on dirt roads used primarily by commercial wildlife tour operators and SNP personnel. As lion track deposition can vary among road substrates (Funston et al. 2010), we avoided road surfaces that were predominantly gravel or heavily vegetated. We cleared tracks from routes the evening before we surveyed them (typically 1700–1830 hrs) using a tire drag pulled behind a vehicle. Each of the two track survey crews included a driver and experienced tracker positioned on the vehicle bonnet. Surveys typically began at 0700 hr and were completed before 1200 hr to reduce adverse effects of direct sunlight on detecting tracks. Each crew traversed routes at speeds up to 10 km/hr. We alternated the routes crews surveyed each week.

When we detected lion tracks, we identified the number of individuals using track size, juxtaposition, and direction of travel. We then measured the length and width of a representative track of each individual and took an image of each for reference. Following Funston et al. (2010), if we located similar tracks within 500 m of each other and could not distinguish them as unique individuals using our criteria, we did not include the second track. Leopards (*P. pardus*) are rare in our grassland-dominated study area and we distinguished the occasional leopard track from lion tracks using track size, shape of pads, group size (leopards are typically solitary), and location (leopards largely restrict movements to wooded riparian areas). We discarded any track that could not reliably be identified as lion.

As our study area contains deep clay soils (Funston et al., 2010), we estimated lion densities using the regression model 'lion and cheetah on clay through origin' (*observed track density* = 0.54 x *carnivore density*; Winterbach et al., 2016). This model was developed using data from the same study areas as this study (see Funston et al. 2010). As the number of lion tracks detected each week ($\geq$30 tracks) was adequate for estimating lion density (Funston et al., 2010), we calculated weekly lion density estimates each year.

2.3 Reference population estimate

We compared track density estimates in 2015 with an independent estimate of lion density derived using a call-in survey with repeated sessions and N-mixture models (see Belant et al., 2016).

3. Results

We surveyed 3,289 km of roads for tracks overall (1,771 km in 2015 and 1,518 km in 2016), 253 km during each of the 13 weekly sessions. We detected 22.22 tracks/100 km of survey route in 2015 and 18.68 tracks/100 km in 2016. Overall lion density estimates were 41.15 (95% confidence limits = 31.92–57.86)/100 km^2 in 2015 and 34.59 (26.83–46.04)/100 km^2 in 2016, representing a 16% decline from 2015 to 2016. Corresponding lion abundance estimates for the study area during 2015 and 2016 were 773 (600–1088) and 650 (504–866), respectively.

The weekly number of lion tracks detected ranged from 44 to 80 in 2015 and 35 to 54 in 2016 Table 1); lion densities were correspondingly variable, ranging from 31.86 (24.72–44.80) to 57.55 (44.64–80.92)/100 km^2 in 2015 and 27.22 (21.03–36.23) to 40.40 (31.34–53.77) /100 km^2 in 2016 (Fig 3). Weekly point estimates of lion density varied up to 55.6% in 2015 and 39.0% in 2016, though within-year weekly 95% CLs overlapped.

The reference lion density estimate for the same study area in 2015 derived from the call-in survey was 14.36 (95% confidence limits = 9.04–29.31)/100 km^2 and lion abundance was 270 individuals (95% credible interval = 170–551) (Belant et al. 2016).

4. Discussion

Annual and weekly lion density estimates obtained from track surveys were consistently greater than our reference density estimate. The overall upper confidence interval from track surveys did not overlap with the 95% credible interval from our call-in survey in 2015. Based on our earlier comparison with past research on lion densities in this study area (see Belant et al. 2016), and our observations of lion prides (J.L. Belant, unpublished data), we are confident our reference estimate is reasonable. Differences in lion density estimates from track sessions among weeks within a year (up to 56%) were even greater than overall density estimates between years (16%). We detected adequate numbers of lion tracks (>30) each week to have good precision in estimates (Funston et al. 2010), yet among-week density estimates within a year varied greatly.

There are several possible reasons alone or in combination that lion densities we estimated using track surveys were greater than expected, including differences in survey methodologies, limited sampling for initial model development, and errors in reference estimates. We note two primary differences in our survey methodologies from those of Funston et al. (2010). First, we drove at speeds up to 10 km/hr, considerably less than the 10–20 km/hr driven in the earlier study. We suggest that increased speed can reduce the probability of detecting lion tracks; during our preliminary surveys we found reduced confidence in our ability to consistently detect tracks at speeds >10 km/hr. Second, we consistently cleared tracks from routes the day before they were surveyed. In contrast, Funston et al. (2010) only counted tracks made during the previous 24-hours for analysis and only cleared tracks from routes when they were surveyed on consecutive days (though in SNP transects were surveyed only once). We were unable to confidently discern track age (e.g., 25-hr old vs. 23-hr old) during our preliminary work and instead standardized the period of track deposition by consistently clearing tracks from routes. We suggest that use of an estimated track age could result in under- or over-estimation of the number of lion tracks (and density) which can vary within or among observers. Additionally, potential differences between studies in assignment of consecutive tracks within 500 m as the same or different lions could influence density estimates.

The original (Funston et al., 2010) and revised (Winterbach et al., 2016) regression models for clay soils were developed from data collected from the same approximate area we surveyed in SNP.

Funston et al. (2010) divided this study area into adjacent short grass and long grass areas and surveyed each during wet and dry seasons. The regression model of Winterbach et al. (2016) we used included lion and cheetah data from this study area, limited to 4 points for each species within temporally- and spatially-dependent surveys. Further, the total distance sampled in these surveys ranged from 66.8 to 375.3 km, more similar to our weekly sessions (253 km) than our annual surveys (1,518 and 1,771 km). If we assume that 30 tracks are needed for reliable (Coefficient of Variation [CV] <20%) estimates of large carnivore densities from track survey data (Funston et al., 2010; Bauer et al. 2017), only 1 of the 8 dependent large carnivore density estimates from SNP reported by Funston et al. (2010) had adequate track data for good precision (lions in long grass during dry season). Thus, the number of tracks recorded and surveys conducted to develop the regression model appear insufficient and call into question the reliability of the corresponding density estimates.

Finally, errors in reference lion density estimates used to develop regression models would result in corresponding errors in density estimates derived from track surveys. Lion and cheetah density estimates from Serengeti National Park reported by Funston et al. (2010) are point values without estimates of precision or the specific time period (season only) for which the data were collected. However, combining lion density reference estimates reported by Funston et al. (2010) for short-grass and long-grass during the dry season resulted in an overall estimate of 13.87 lions/100 km^2, similar to our reference density of 14.36 lions/100 km^2. That our reference lion density estimate was similar to other recent estimates from SNP (see Belant et al., 2016) and that lion populations in this portion of SNP are largely static, with episodic shifts every 10–20 years (Packer et al., 2005), suggests the lion population likely did not change markedly between our survey and those of Funston et al. (2010) and that earlier estimates too are likely reasonable. Thus, we suggest that our inaccurate estimates of lion density from track surveys likely resulted from differences in methodologies between studies, subjectivity of assigning tracks to individuals and estimating track age, and limited data to estimate the relationship in the original and revised regression models.

As currently conducted, for density estimates from track surveys to be accurate with good precision requires that track deposition rates during surveys are consistent in space and time, suggesting in turn that lion movements are consistent, or that track deposition is random and adequate sampling occurs to account for variation in deposition. We suggest that none of these are true and lion activity and movements in relation to roads will vary spatially and temporally based on other factors such as luminosity (Belant et al., 2016), landscape features to facilitate prey acquisition (Hopcraft, Sinclair & Packer, 2005), and prey abundance (Kittle et al., 2016). Indeed, our study area within SNP is well-known for the annual large migration of ungulates (e.g., Holdo, Holt & Fryxell, 2009) that influences lion movements and distributions (Packer et al., 2005; Moser and Packer, 2009). That lions move in response to prey distributions and availability, among other environmental factors unrelated to roads, would support the considerable among-week and between-year variation in point estimates of lion density we observed that were unrelated to actual changes in lion density within the study area.

We recommend caution when using track surveys for estimating lion density as currently designed and support application of experimental designs that include direct observation of lions (transect or road surveys, call-in surveys), account for imperfect detection in a spatially-explicit framework, and incorporate environmental variables (e.g., prey, land cover) that can influence lion space use and movements (e.g., Belant et al., 2016; 2017; Elliot and Gopalaswamy, 2017). Previous estimates of lion abundance have recently been used as the foundation for large-scale recommendations for lion conservation (e.g., Packer et al., 2013) and inferring population trends used for global conservation assessments (Bauer et al., 2015a; b), which can in turn influence national and international policies (e.g., U.S. Federal Register, 2015). Track surveys were one of the methods used to generate lion abundance estimates for these conservation actions (see Bauer et al., 2015b); based on our study and previous assessments (e.g. Riggio et al., 2016; Elliot and Gopalaswamy, 2017), we suggest that at least some of these population estimates may be in error. We encourage caution when applying these estimates in conservation actions to ensure that scientific rigor is maintained to benefit lion populations.

Acknowledgements

The Tanzania Wildlife Research Institute, Tanzania National Parks, and the Commission for Science and Technology provided permission to conduct this research. Field methods were approved by State University of New York College of Environmental Science and Forestry Institutional Animal Care and Use Committee (180502). Primary funding was provided by Safari Club International Foundation. Project support was provided by M. Eckert, I. Lejora, and M. Lewis. M.-K.W. Belant, N. Isaack, A. Kashindye, P. Kessy, J. Mkwizu, S. Msechu, S. Mwinyimtama, R. Ndaskoi, and M. Nzunda provided field assistance.

References

Bauer, H., Packer, C., Funston, P.J., Henschel, P., Nowell, K. 2015a. *Panthera leo*. The IUCN Red List of Threatened Species 2015: e.T15951A79929984. Available at: http://www.iucnredlist.org (accessed 30 April 2017).

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B., Macdonald, D.W., Packer, C. 2015b. 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.

Bauer, H., Henschel, P., Packer, C., Sillero-Zubiri, C., Chardonnet, B., Sogbohossou, E.A., De Iongh, H.H., Macdonald, D.W. 2017. Lion trophy hunting in West Africa: a response to Bouché et al. PLoS One 12, e0173691.

Belant, J.L., Bled, F., Wilton, C.M., Fyumagwa, R., Mwampeta, S.B., Beyer, D.E., Jr. 2016. Estimating lion abundance using N-mixture models for social species. Scientific Reports 6, e35920.

Belant, J.L., Bled, F., Mwampeta, S.B., Mkasanga, I.J., Wilton, C.M., Fyumagwa, R. 2017. Temporal and spatial variation of broadcasted vocalizations does not reduce lion *Panthera leo* habituation. Wildlife Biology 2017, e00287.

Bouché, P., Crosmary, W., Kafando, P., Doamba, B., Kidjo, F.C., Cermeulen, C., Chardonnet, P. 2016. Embargo on lion hunting trophies from West Africa: an effective measure or a threat to lion conservation? PLoS One 11, e0155763.

Cozzi, G., Broekhuis, F., McNutt, J.W., 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

Cozzi, G., Broekhuis, F., McNutt, J.W., Turnbull, L.A., Macdonald, D.W., Schmid, B. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. Ecology 93, 2590–2599.

Elliot, N.B., Gopalaswamy, A.M. 2017. Towards accurate and precise estimates of lion density. Conservation Biology 31, 934–943.

Funston, P.J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D.M., Durant, S., Packer, C., Mosser, A., Ferreira, S.M. 2010. Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. Journal of Zoology 281, 56–65.

Holdo, R.M., Holt, R.D., Fryxell, J.M. 2009. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. American Naturalist 173, 431–435.

Hopcraft, J.G.C., Sinclair, A.R.E., Packer, C. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74, 559–566.

Houser, A.M., Somers, M.J., Boast, L.K. 2009. Spoor density as a measure of true density of a known population of free-ranging wild cheetah in Botswana. Journal of Zoology 278, 108–115.

Jhala, Y., Qureshi, Q., Gopal, R. 2011. Can the abundance of tigers be assessed from their signs? Journal of Applied Ecology 48, 14–24.

Kiffner, K.C., Waltert, M., Meyer, B., Mühlenberg, M. 2008. Response of lions (*Panthera leo* Linnaeus 1758) and spotted hyena (*Crocuta crocuta* Erxleben 1777) to sound playbacks. African Journal of Ecology 46, 223–226.

Kittle, A.M., Bukombe, J.K., Sinclair, A.R.E., Mduma, S.A.R., Fryxell, J.M. 2016. Landscape-level movement patterns by lions in western Serengeti: comparing the influence of inter-specific competitors, habitat attributes and prey availability. Movement Ecology 4, e17.

Lazaridis, E. 2014. Lunar: lunar phase & distance, seasons and other environmental factors. Version 0.1–04. Available at: http://statistics.lazaridis.eu (Accessed 2 January 2016).

Midlane, N., O'Riain, M.J., Balme, G.A., Hunter, L.T.B. 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.

Mosser, A., Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo.* Animal Behaviour 78, 359–370.

Norton, P.M. 1990. How many leopards? A criticism of Martin and de Meulenaer's population estimates for Africa. South African Journal of Science 86, 218–220.

Norton-Griffiths, M., Herlocker, D., Pennycuick, L. 1975. The patterns of rainfall in the Serengeti Ecosystem, Tanzania. African Journal of Ecology 13, 347–374.

Omoya, E.O., Mudumba, T., Buckland, S.T., Mulondo, P., Plumptree, A.J. 2014. Estimating population size of lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* in Uganda's savannah parks, using lure count methods. Oryx 48, 394–401.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., Sinclair, A.R.E. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. Science 307, 390–393.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M., Zander, K.K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C.M., Begg, K.S., Bhalla, S., Bissett, C., Bodasing,T., Brink, H., Burger, A., Burton, A.C., Clegg, B., Dell, S., Delsink, A., Dickerson, T., Dloniak, S.M., Druce, D., Frank, L., Funston, P., Gichohi, N., Groom, R., Hanekom, C., Heath, B., Hunter, L., DeIongh, H.H., Joubert, C.J., Kasiki, S.M., Kissui, B., Knocker, W., Leathem, B., Lindsey, P.A., Maclennan, S.D., McNutt, J.W., Miller, S.M., Naylor, S., Nel, P., Ng'weno, C., Nicholls, K., Ogutu, J.O., Okot-Omoya, E., Patterson, B.D., Plumptre, A., Salerno, J., Skinner, K., Slotow, R., Sogbohossou, E.A., Stratford, K.J., Winterbach, C., Winterbach, H., Polasky, S. 2013. Conserving large carnivores: dollars and fence. Ecology Letters 16, 635–641.

Patterson, B.R., Quinn, N.W.S., Becker, E.F., Meier, D.B. 2004. Estimating wolf densities in forested areas using network sampling of tracks in snow. Wildlife Society Bulletin 32, 938–947.

Reed, D.N., Anderson, T.M., Dempewolf, J., Metzger, K., Serneels, S. 2009. The spatial distribution of vegetation types in the Serengeti ecosystem: the influence of rainfall and topographic relief on vegetation patch characteristics. Journal of Biogeography 36, 770–782.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., Lictenfeld, L., Pimm, S. 2013. The size of savannah Africa: a lion's (*Panthera leo*) view. Biodiversity and Conservation 22, 17–35.

Riggio, J., Caro, T., Dollar, L., Durant, S.M., Jacobson, A.P., Kiffner, C., Pimm, S.L., van Aarde,R.J. 2015. Lion populations may be declining in Africa but not as Bauer et al. suggest. Proceedings of the National Academy of Sciences of the United States of America 113, E107–E108.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J. 2014. Status and ecological effects of the World's largest carnivores. Science 343, 6167.

Sinclair ARE. 1979. The Serengeti environment. In: Sinclair ARE, Norton-Griffiths M, eds. *Serengeti: dynamics of an ecosystem* Chicago: University of Chicago Press, 31–44.

Smallwood, K.S., Fitzhugh, E.L. 1995. A track count for estimating mountain lion *Felis concolor californica* population trend. Biological Conservation 71: 251–259.

Stander PE. 1998. Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology* 35: 378–385.

US Federal Register. 2015. Endangered and threatened wildlife and plants; listing two lion subspecies. *Available at: http://www.federalregister.gov/articles/2015/12/23/2015-31958/endangered-and-threatened-wildlife-and-plants-listing-two-lion-subspecies#t-1* (accessed 30 April 2017).

Winterbach, C.W., Ferreira, S.M., Funston, P.J., Somers, M.J. 2016. Simplified large African carnivore density estimators from track indices. PeerJ 4, e2662.

Table 1
Weekly number of tracks detected during surveys to estimate lion abundance, Serengeti National Park, Tanzania, 2015–2016.

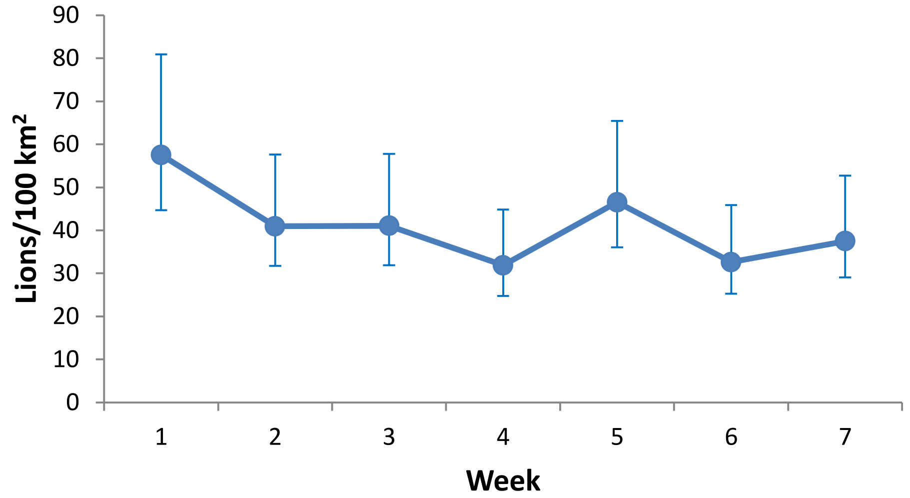
	Number of tracks detected						
Year	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7
2015	80	56	56	44	64	45	51
2016	47	42	35	54	48	46	N/A

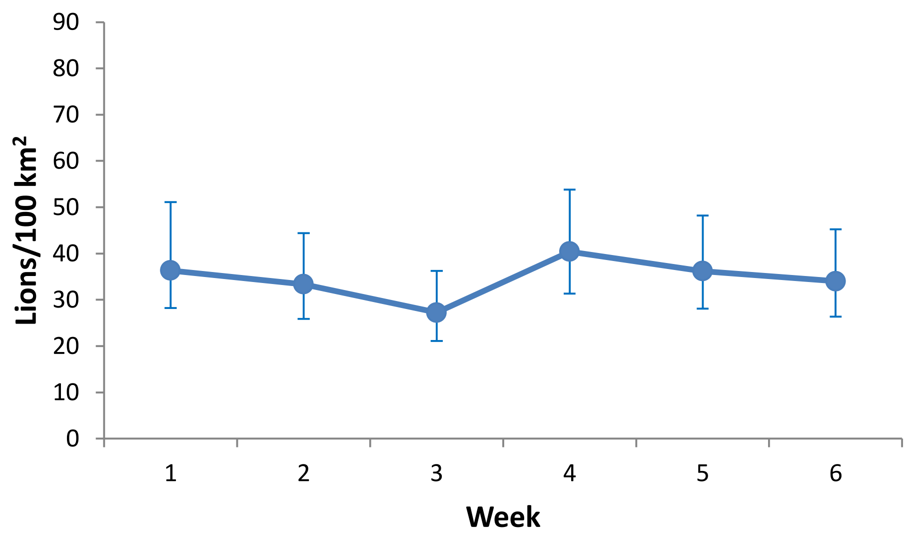
Figure titles

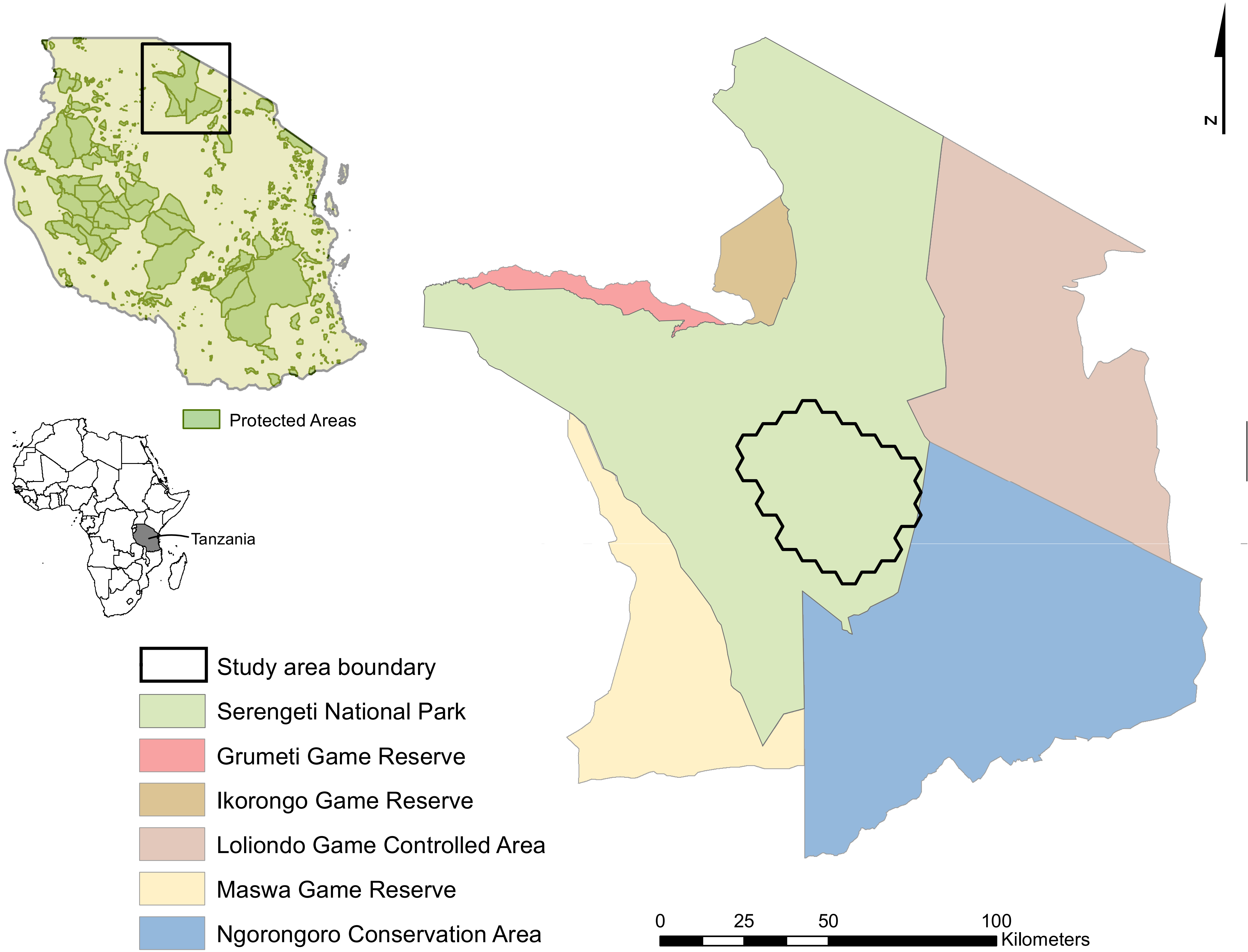
Fig. 1. Location of study area using track surveys to estimate lion abundance, Serengeti National Park, Tanzania, 2015–2016.

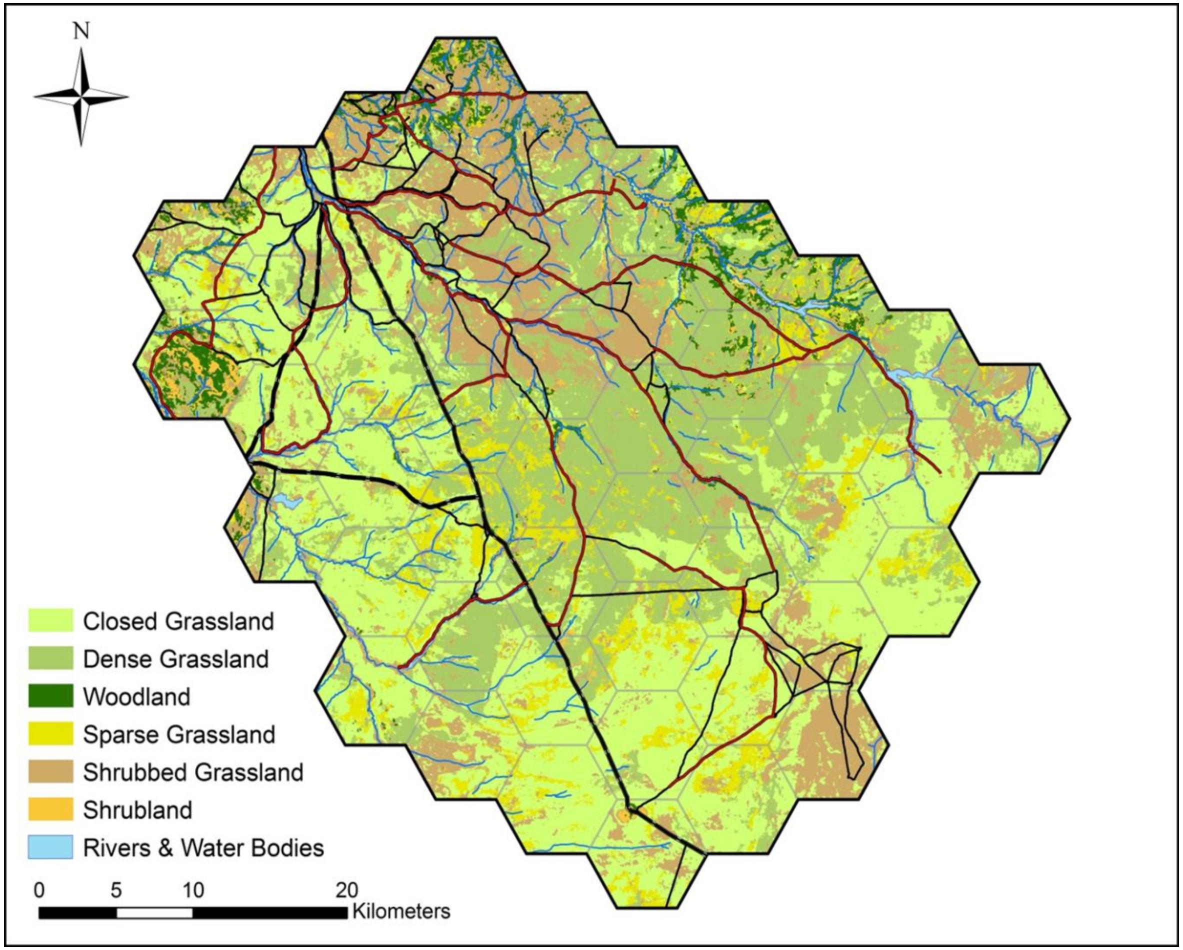
Fig. 2. Location of routes (red lines) used to detect tracks to estimate lion abundance, Serengeti National Park, Tanzania, 2015–2016.

Fig. 3. Weekly estimated abundance of lions (with 95% confidence limits) using track surveys following Winterbach et al. (2016), Serengeti National Park, Tanzania, 2015–2016.


90
80
70
60
50
40
30
20
10
0
Lions/100 km²
1
2
3
4
5
6
7
Week


90
80
70
60
50
40
30
20
10
0
Lions/100 km²
1
2
3
4
5
6
Week


Protected Areas
Tanzania
N
Study area boundary
Serengeti National Park
Grumeti Game Reserve
Ikorongo Game Reserve
Loliondo Game Controlled Area
Maswa Game Reserve
Ngorongoro Conservation Area
0
25
50
100
Kilometers


N
Closed Grassland
Dense Grassland
Woodland
Sparse Grassland
Shrubbed Grassland
Shrubland
Rivers & Water Bodies
0
5
10
20
Kilometers