TYPE Perspective
PUBLISHED 07 June 2024
DOI 10.3389/fcosc.2024.1402500

Check for updates

OPEN ACCESS

EDITED BY
Zaneta Kaszta,
University of Oxford, United Kingdom

REVIEWED BY
Ali T. Qashqaei,
Borderless Wildlife Conservation Society, Iran

*CORRESPONDENCE
Genevieve E. Finerty
genevieve.finerty@gmail.com
Natalia Borrego
nborrego@umn.edu

†These authors have contributed equally to this work and share first authorship

‡These authors share senior authorship

RECEIVED 17 March 2024
ACCEPTED 07 May 2024
PUBLISHED 07 June 2024

CITATION
Finerty GE, Borrego N, Alibhai SK, Jewell ZC, Tschanz P, Balone T, Gabaikanye T, Gana M, Monnaanoka S, Mamou M, Pudidaroma S, Tshiama M, Tshiama M, Araldi A, Crofoot MC, Henley S, Ithuteng PA and Schiess-Meier M (2024) The crossroads of tradition and modern technology: integrative approaches to studying carnivores in low density ecosystems.
Front. Conserv. Sci. 5:1402500.
doi: 10.3389/fcosc.2024.1402500

The crossroads of tradition and modern technology: integrative approaches to studying carnivores in low density ecosystems

Genevieve E. Finerty[1,2,3,4*†], Natalia Borrego[1,2,5*†], Sky K. Alibhai[6,7], Zoe C. Jewell[6,7], Philippe Tschanz[3,8,9], Trevor Balone[3], Tebelelo Gabaikanye[3], Moisapodi Gana[3], Supula Monnaanoka[3], Mosepele Mamou[3], Sokwa Pudidaroma[3], Meno Tshiama[3], Mpho Tshiama[3], Alessandro Araldi[3‡], Margaret C. Crofoot[1,2‡], Steve Henley[3‡], Pogiso 'Africa' Ithuteng[3‡] and Monika Schiess-Meier[3‡]

[1]Department of Biology, University of Konstanz, Konstanz, Germany, [2]Department for the Ecology of Animal Societies, Max Planck Institute for Animal Behavior, Konstanz, Germany, [3]Research Department, Leopard Ecology & Conservation, Gaborone, Botswana, [4]Wildlife Conservation Research Unit, Biology Department, University of Oxford, Oxford, United Kingdom, [5]The Lion Center, Department of Ecology and Evolution, University of Minnesota, St. Paul, MN, United States, [6]JMP Statistical Discovery LLC, Cary, NC, United States, [7]WildTrack, Nicholas School of the Environment, Duke University, Durham, NC, United States, [8]Agroscope, Agroecology and Environment, Zurich, Switzerland, [9]Department of Environmental Systems Science, Institute of Agricultural Sciences, ETH Zurich, Zurich, Switzerland

The study of large carnivores in semi-arid ecosystems presents inherent challenges due to their low densities, extensive home ranges, and elusive nature. We explore the potential for the synthesis of traditional knowledge (i.e. art of tracking) and modern technology to address challenges in conservation and wildlife research in these challenging environments. Our research focuses on the African lion (*Panthera leo*) in the Central Kalahari region of Botswana as a model system to demonstrate the potential of this integrative approach. Combining GPS tracking and traditional San trackers' expertise, we present two case studies: (1) the individual identification of lions via a combination of tracking and footprint analysis and (2) the monitoring of territorial behavior through a combination of GPS technology (i.e. GPS collars and handheld GPS devices) and non-invasive tracking. These approaches enhance our understanding of carnivore ecology as well as support conservation efforts by offering a non-invasive, cost-effective, and highly accurate means of monitoring populations. Our findings underscore the value of merging traditional tracking skills with contemporary analytical and technological developments to offer new insights into the ecology of carnivores in challenging environments. This approach not only improves data collection accuracy and efficiency but also fosters a deeper understanding of wildlife, ensuring the conservation and sustainable management of these species. Our work advocates for the inclusion of indigenous knowledge in conservation science, highlighting its relevance and applicability across various disciplines, thereby broadening the methodologies used to study wildlife, monitor populations, and inform conservation strategies.

KEYWORDS

carnivores, traditional knowledge, modern technology, behavior, African lion

1 Introduction

There are inherent challenges to studying large carnivores in semi-arid ecosystems where animals exist at low densities and exhibit some of the largest home ranges recorded (Ramsauer, 2007; Zehnder et al., 2018). For example, collecting individual-level data in these environments is complicated by animals' low density, elusiveness, and often poor visibility, which compounds the challenges of identifying individuals in species that lack distinctive features. Yet, the identification of individual animals is fundamental to wildlife research and monitoring, providing essential data for building longitudinal datasets and surveys vital for population biology and conservation efforts. Furthermore, despite considerable methodological advancement in e.g., animal tracking, in recent years, there remains a substantial challenge in observing behavioral processes in low-density ecosystems. However, behavioral data from these ecosystems is crucial to understand how wildlife populations may respond in the face of global change, with sub-Saharan Africa predicted to become increasingly arid over the next century (Gizaw and Gan, 2016; Engelbrecht et al., 2024).

Despite the challenges, studies providing insights from low density populations are critical to their conservation; large carnivores have experienced global population declines and range contraction, making them some of the most threatened species in the world (Ripple et al., 2014; Wolf and Ripple, 2017). African carnivore populations are declining at an alarming rate, making them a conservation priority (Bodasing, 2022), and semi-arid ecosystems include some of the last remaining strongholds for African carnivores, like lions (Riggio et al., 2012). Thus, understanding how species respond to and exist in these conditions will enable us to identify potentially vulnerable populations and develop conservation strategies. It is our perspective that the study of animals residing in these challenging environments requires outside-the-box approaches that allow researchers to integrate all the rich sources of information available in such landscapes.

A promising avenue, and the focus of our article, is for researchers to work alongside local communities to apply the traditional skill of animal tracking to study wildlife residing in these ecosystems. We aim to highlight the great potential for such collaborative efforts to address the above challenges. Although technological advances have greatly increased our capacity to study animals in the wild over time, each new advance has its own strengths and limitations. We outline here how the strengths of both old and new approaches can be melded to address some of the challenges researchers face. We use the African lion (*Panthera leo*) in a low-density habitat (Kalahari) as a model system.

2 Article scope and authors' perspective

In the Kalahari, with its expansive bed of sand, footprints left by animals form a narrative of their daily activities, with a continual flow of fresh data as the stage is refreshed by the elements. It is our perspective that the art of tracking is a promising approach to harness this information to address the challenges outlined above, especially where experts adept at interpreting such signs combine their knowledge with researchers pioneering advances in analytics and animal tracking technology. As authors, we recognize the clear opportunity new technological developments bring and welcome it. Local communities are also the custodians of a rich trove of knowledge about wildlife in their ecosystems. While not all local communities are expert trackers, these skills still exist in many southern African regions. These traditional skills and knowledge offer great opportunity to complement technological advances, and thereby, gain a more holistic understanding of high-conservation-priority populations.

The authors of this study are part of a diverse research team that includes local and international academics, applied researchers, and a highly skilled team of San trackers. We work together under the umbrella of the Leopard Ecology & Conservation (LEC) project to address open challenges in the conservation and research of leopard and lion populations in the Central Kalahari region of Botswana. For over 20 years, LEC has employed and worked alongside San trackers to collect data on wildlife populations. By employing San trackers for research, studies gather valuable data at a high level of detail while also building capacity and advocating for the value of traditional fieldcraft skills of indigenous people (Liebenberg et al., 2017).

Here, we present two case studies showcasing how integrating the art of tracking into formal research yields insights into the hidden lives of Kalahari lions. We open with the historical context of the art of tracking in the Kalahari region of southern Africa and its application to date in population monitoring and the study of behavior in African lions. We then frame our two case studies in the context of open challenges in (a) reliably monitoring low-density populations, and (b) studying animal behavior. We conclude by discussing synergies between these efforts and current advances in the two fields, highlighting exciting avenues for future studies. The case studies serve to demonstrate proof of concept and encourage readers to consider the value of both traditional and novel approaches in studying, managing, and conserving these critical wildlife populations.

3 The art of tracking in wildlife research

Eloff was among the first to document working alongside the bushman trackers as a formal research methodology to study lions in the Kalahari (Eloff, 1973, Eloff, 1984). With the aid of skilled trackers, Eloff was able to follow the nocturnal trails of lions in the Kalahari Gemsbok National Park, uncovering substantial differences in feeding ecology and daily activities between the Kalahari and other populations (Eloff, 1973, Eloff, 1984). Building on this work, Stander et al. (1997) first tested the reliability of tracking as a scientific approach to identify individual identity and the reconstruct complex nocturnal behaviors from the spoor of large African carnivores, including lions. Working with experienced Ju/'Hoan hunters in Namibia, Stander reported extraordinarily high levels of accuracy in identifying four large carnivore species from their spoor. Trackers were also able to identify sex in lions and successfully interpret behavioral activities including walking, stalking, and galloping.

Tracking has been successfully used to study the behavioral ecology of a number of carnivore species in southern Africa, predominantly focusing on foraging and/or hunting behaviors and daily travel distances, including caracals (*Caracal caracal*; Melville et al., 2004; Melville and Bothma, 2015), leopards (*Panthera pardus*; Bothma and Le Riche, 1984, Bothma and Le Riche, 1989, Bothma and Le Riche, 1993; Bothma, 1997; Melville et al., 2004; Stander et al., 2009), and wild dogs (*Lycaon pictus*; Romañach and Lindsey, 2008). Additionally, tracking has also been used to provide insight into territorial behaviors including rubbing and scratching (Bothma and Le Riche, 1995) and scent marking (Bothma and Coertze, 2004) by Kalahari leopards, something we build upon in our behavioral case study (subsection 4.2) on lions.

Despite the value in such studies on elusive, wide-ranging carnivores, recent use of tracking in behavioral ecology is limited. In contrast, tracking remains a popular tool for monitoring large African carnivores, providing a rapid and inexpensive way to survey populations across large spatial extents. Track surveys involve identifying animal tracks from the past 24 hours while driving at slow speeds, with a team of trackers positioned on the roof and, commonly, a seat attached to the front of a vehicle (e.g. Stander, 1998; Bauer et al., 2014; Midlane et al., 2015). Counts of tracks are then used to estimate population densities, often through an assumed linear relationship between observed track counts and true population density (Stander, 1998; Funston et al., 2010; Bauer et al., 2014, Bauer et al., 2015; Winterbach et al., 2016) or more recently, in Botswana, using the Formozov-Malyshev-Perelshin formula (Stephens et al., 2006; Keeping, 2014; Keeping et al., 2018; Ahlswede et al., 2019). In addition to their efficiency and speed, track-based surveys offer widespread benefits, including the ability to monitor multiple species concurrently and the potential for involving local communities in research. The latter of which offers the dual benefits of meeting conservation goals and offering employment opportunities.

There has been a recent renewal of interest by both academics and governments in integrating traditional local knowledge into the management and monitoring of wildlife (Elbroch et al., 2011; Thompson et al., 2020). Despite being one of the oldest skills developed in human culture (Liebenberg, 1990), tracking has only entered the scientific literature as a formal research method comparatively recently (Dorfman et al., 2023). There is, however, a growing acknowledgement from the scientific research community that tracking is a valuable resource in wildlife research and can complement modern techniques, reflected in a recent and timely review of tracking as a zoological research method (Dorfman et al., 2023). Below, we present two case studies from our work in the Central Kalahari that showcase how working with skilled local trackers can provide solutions to key challenges faced in monitoring and studying lions.

4 Case studies: the art of tracking as a solution to open challenges in wildlife research.

4.1 Case study 1: individual identification via footprints

Obtaining individual level data from wild animal populations is inherently challenging as it relies on locating individuals to sight (either directly or via remote tools such as camera traps) and the ability to determine individual identity from unique characteristics. This becomes particularly challenging when the focal species occur at low density, are elusive, or where visibility is poor. In response to this challenge, there are open opportunities for research into developments that facilitate new opportunities to capture information on individuals.

In addition to the low densities of lions in our study area, their home ranges (1131-4314 km^2) are among the largest recorded for lions (Zehnder et al., 2018) and we have faced persistent challenges in collecting sufficient information to make population-level inferences. In a search for innovative ways to augment our data collection, we encountered the Footprint Identification Technique (FIT): a robust, cost-effective, and non-invasive tool developed by WildTrack (www.wildtrack.org) for using tracking to monitor endangered species (Jewell, 2013; Jewell et al., 2016). To date, FIT has been applied to discriminate age, sex and individuals across a range of species in both captive and wild contexts, including white and black rhino (*Diceros bicornis*), lowland tapir (*Tapirus terrestris*), giant pandas (*Ailuropoda melanoleuca*), cheetah (*Acinonyx jubatus*), amur tigers (*Panthera tigris*), and pumas (*Puma concolor*) (Jewell et al., 2001; Alibhai et al., 2008; Law et al., 2013; Gu et al., 2014; Jewell et al., 2016; Law et al., 2018; Li et al., 2018; Moreira et al., 2018; Jewell et al., 2020; Kistner et al., 2022; Alibhai et al., 2023; Tucker et al., 2024).

The workflow for FIT (described in detail in Jewell et al., 2016) involves collecting images of footprints, followed by a cross-validated pairwise comparison of trails of prints using discriminant analysis of metrics extracted from the images (Figure 1). A user-friendly graphical user interface (GUI) provides clear interpretation of the results, making this a very accessible tool for practitioners and researchers. The method outputs a Ward's cluster dendrogram, providing information on the individual identity and the predicted number of lions with very high levels of accuracy (Figure 1). Inspired by the skills of indigenous trackers, strong tracking skills are very much central to the technique. Experienced trackers at LEC have excelled in locating and identifying high quality footprints, exemplifying the clear value of including these groups in wildlife research (Liebenberg et al., 2017; Ahlswede et al., 2019; Thompson et al., 2020).

FIT has great potential in both censusing populations and monitoring specific individuals. For example, the technique is showing promising results in discriminating between individual lions in our study area (Figure 1). Building the collaboration between WildTrack, LEC, trackers from the local community, and our research institutions has greatly expanded the scope and conservation impact of our research, something we hope will encourage other researchers to explore integrating traditional methods into their work.

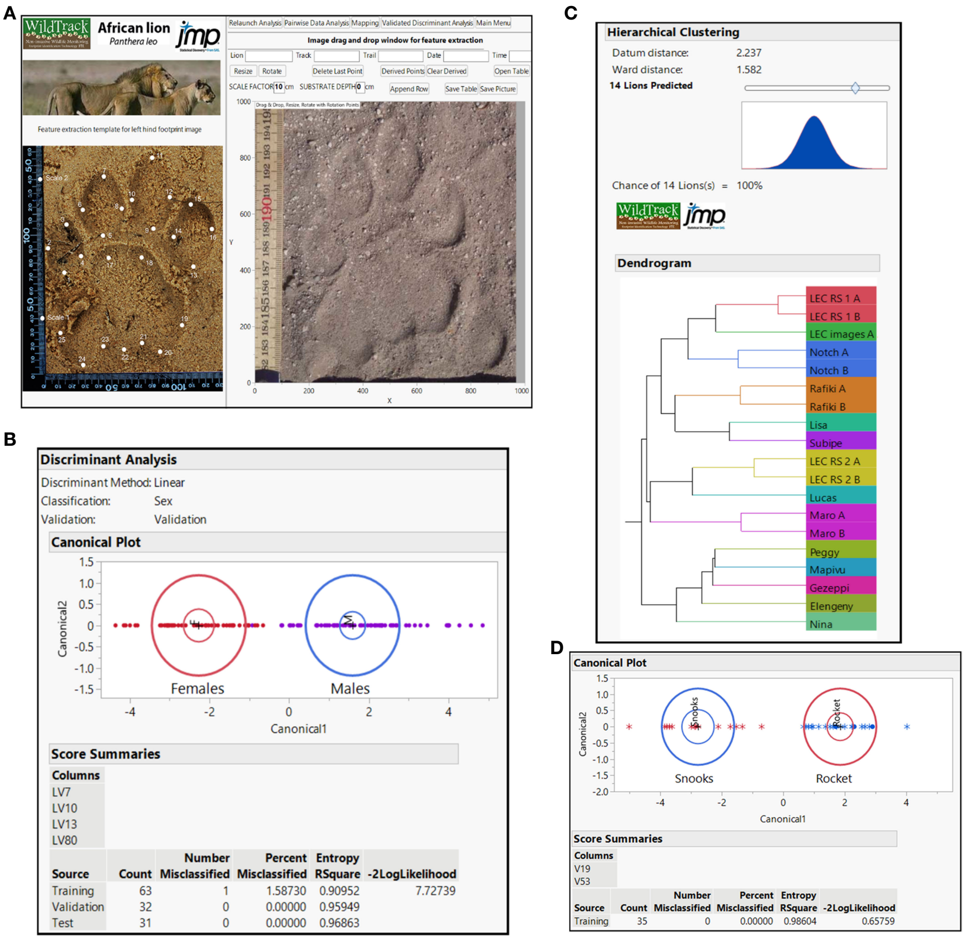

FIGURE 1
(A) shows the FIT feature extraction window in JMP software customised for the African lion. It allows image manipulation capabilities and once the landmark points have been placed, a script then generates over 100 variables in the form of distances, angles and areas. **(B)** shows the the sex discrimination output using Linear Discriminant Analysis (LDA) with 4 variables selected stepwise (in terms of their F-ratios). Partitioned data (Training = 0.5, Validation = 0.25, Test = 0.25) shows the very high levels of accuracy. **(C)** Shows the cluster dendrogram output using pairwise data analysis for individual identification with trails and sub-trails in FIT. Both the prediction for the number of lions and the classification of the trails and sub-trails was achieved with very high levels of accuracy. **(D)** shows classification of two related males using linear discriminant analysis with two variables selected stepwise based on F-ratios.

4.2 Case study 2: tracking territorial behavior

In low-density ecosystems, such as the Kalahari, where animals typically have large ranges and are highly mobile, behavioral observation is exceedingly challenging, particularly when these behaviors are temporally unpredictable and/or occur infrequently. Our second case study demonstrates how the art of tracking can be used to non-invasively study marking behavior in lions. Very little is known about territorial marking in lions beyond studies from the open plains of the Serengeti (e.g., Schaller, 1972). Given the extensive home ranges of lions in the Kalahari, it is likely that scent-marking behaviour may differ from that of lions living in more productive landscapes, like the Serengeti. For example, in more productive habitats, where small home ranges are typical, scent marks from hyenas are concentrated along their home range boundaries, but in less productive habitats, where hyaenas have larger home ranges, they are much more concentrated in central home range areas (Gorman and Mills, 1984).

Below we demonstrate that knowledge on scent-marking behavior in lions can be obtained non-invasively by combining the art of tracking with modern GPS technology. We use this data to test the hypothesis that, due to their large home ranges, Kalahari lions adopt a marking strategy that concentrates territorial marking within central home range areas.

We studied scent marking behavior in a coalition of two GPS-collared male lions for 15-days between April 13 to July 15, 2016. We used GPS fixes from the collars to locate known points along the lions' paths from the previous day. Alongside local San trackers, we used hand-held GPS devices to record a high-resolution path and reconstruct the lions' movement. While following the lions' trail, we also recorded and georeferenced all detectable marking behaviors, including rubbing against vegetation, urinating on the ground or vegetation, raking the ground or tree with their paws or claws, and defecating. To investigate how marking behavior varied within their home ranges, we estimated range utilization distributions (UDs) for the two lions from two years of collar GPS data and classified the UDs into 5 categories (0-20, 20-40, 40-60, 60-80, 80-100%). We summarized marking rates (defined as the total number of recorded marking behaviors per total distance tracked) for each of the UD classes and between two types of terrain we encountered while tracking the lions: along roads or in the bush 'off-road'. We found that lions adapted their scent-marking behaviour depending on location within their home range and the terrain they were moving through. Median marking rates were almost three times higher along roads compared to off-road. Preferentially marking along roads indicates a strategy that increases the likelihood of conspecifics encountering scent marks while minimizing the costs of producing them (Gosling and Roberts, 2001), as has been found in other carnivores (e.g., leopards, *Panthera pardus:* Rafiq et al. (2020) and Eurasian lynx, *Lynx lynx:* Krofel et al. (2017). They were also substantially higher towards the intermediate regions of their home range (40-60% UD class) compared to the inner core (0-20% UD class) and peripheral areas (80-100% UD class; Figure 2), thereby confirming our hypothesis of a more hinterland marking strategy as an adaptation to their large home ranges.

5 Discussion

The approaches detailed above open promising avenues for conservation science. For example, FIT holds the potential to convert tracks from records of animal presence to individually "marked" observations. These "captures" could be combined with other direct and indirect observations under extensions of classical mark-capture-recapture frameworks, e.g. Spatially Explicit Capture

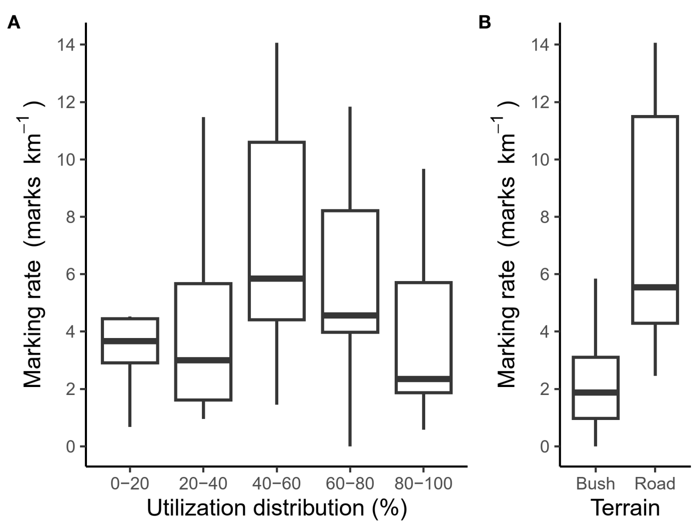

FIGURE 2
Comparison of marking rates with different utilization distribution categories **(A)** and between two terrains **(B)** in the study areas. To generate the range distributions, we used kernel density estimation with a fixed Gaussian kernel and an appropriate smoothing parameter, based on visual inspection of the output distributions. We used GIS layers for the study area, combined with field observations to assign marking behaviors to each of the two key terrains encountered while tracking.

Recapture (SECR) (Borchers and Efford, 2008; Royle et al., 2013) to counter the challenge of low capture probabilities. SECR has been adopted as the new standard for estimating spatial patterns of animal density (Dupont et al., 2021). However, such efforts require large investments in cost, labour and time. Additionally, once signs of presence are detected, the animal(s) must be tracked until the animal(s) is located and identified. If *individuals could be identified directly at this stage, from their prints*, it would significantly reduce the search effort needed to locate and photograph the animal(s), while also reducing the burden of off-road driving. Beyond surveys, tracking provides a 'window back in time' allowing for a broader and more detailed understanding of behaviors while removing potentially confounding observer effects. Furthermore, combining FIT with behavioral reconstruction via tracking provides a novel method to retrospectively observe individual behavior and inter-individual behavioral variation. This is particularly relevant within the wildlife management and conservation literature, where the role and extent of individual-level variation in behavior is far less understood, despite a clear link to population-level processes and ecological interactions that are key to research in this sphere (Merrick and Koprowski, 2017).

The case studies we presented showcase how taking an out-the-box approach—blending traditional skills with modern technology—can be used to effectively study large carnivores in challenging-to-study ecosystems. While we focus on lions, our approach could be easily applied to other species where suitable substrates (e.g., sand, mud, snow) and expertise to interpret animal signs exist. We believe that broadening the methodologies used to study wildlife —by incorporating a diverse range of expertise—holds great potential to enrich research, and ultimately better inform conservation. For example, our team is currently leveraging a unique blend of traditional tracking fieldcraft, sophisticated statistical analyses, and GPS data to explore decision-making in group hunts. By uniting distinct skills and perspectives from a diverse research team, this interdisciplinary collaboration is paving the way for the first detailed account of how lions cooperate to survive in the Kalahari. Recent discussions with the LEC trackers emphasize the dynamic nature of traditional tracking knowledge, which continues to evolve alongside technological advancements, highlighting its relevance and applicability to the field of research.

We'd like to note this paper's authors form a diverse team, including several San trackers. It is our view that tracking includes an intrinsic component of knowledge about animal behaviour and ecology, which when complemented by technology, can deepen our understanding of animals and ecosystems. Tools, like app-based data collection and handheld GPS devices, can improve data collection efficiency while also confirming trackers' field-generated perceptions through better visualization and quantification of observed phenomena. Trackers' skill levels are a critical factor in collecting reliable data (Gielen et al., 2024); by offering certification opportunities, research projects can build capacity and advocate for the value of traditional fieldcraft skills (Liebenberg et al., 2017), thereby working towards formal acknowledgement of these skills by the scientific community (Lawrence, 2020). Integrating local communities into research also provides an opportunity to engage the people whose livelihoods are directly impacted by wildlife with conservation science (e.g. Ransom et al., 2012). The involvement of local communities can play a substantial role in the success of conservation efforts (Nkansah-Dwamena, 2023). Both the level of acceptance for such efforts, and positive attitudes towards wildlife reserves are also closely linked to the perceived and realized benefits (Sekhar, 2003; Nkansah-Dwamena, 2023). Participatory research practices that involve local community members and offer research-based employment can significantly impact local livelihoods by 1) increasing economic stability, and 2) instilling a sense of pride and purpose in their cultural heritage and formal recognition of traditional skills. This highlights the great potential for community-based research projects to improve conservation outcomes and engage local communities with strategies to foster coexistence.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by AWERB, Zoology Department, University of Oxford and Ethical Review at Max Planck Institute of Animal Behavior. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

GF: Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. NB: Conceptualization, Funding acquisition, Investigation, Supervision, Writing – original draft, Writing – review & editing. SA: Data curation, Formal analysis, Methodology, Visualization, Writing – review & editing. ZJ: Data curation, Methodology, Writing – review & editing. PT: Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing. TB: Investigation, Writing – review & editing. TG: Investigation, Writing – review & editing. MG: Investigation, Writing – review & editing. SM: Investigation, Writing – review & editing. MM: Investigation, Writing – review & editing. SP: Investigation, Writing – review & editing. MeT: Investigation, Writing – review & editing. MpT: Investigation, Writing – review & editing. AA: Investigation, Project administration, Supervision, Writing – review & editing. MC: Funding acquisition, Writing – review & editing. SH: Methodology, Project administration, Supervision, Writing – review & editing. PI: Writing – review & editing, Investigation. MS-M: Funding acquisition, Writing – review & editing.

10.3389/fcosc.2024.1402500

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. Research costs for case study two were funded by the African Cats & Conservation Fund (ACACF) and author GF was supported by the U.K. Natural Environment Research Council (NERC) through the DTP in Environmental Research (Grant Number NE/L002612/1). Case study one was funded by the Alexander von Humboldt-Stiftung (Alexander von Humboldt Professorship endowed by the Federal Ministry of Education and Research and awarded to MC), Max Planck Institute of Animal Behavior, Department for the Ecology of Animal Societies and ACACF. Swiss Study Foundation and ETH Master Scholarship Programme.

Acknowledgments

We thank the Botswana Department of Wildlife and National Parks (DWNP) for permission to carry out the research (permit numbers: EWT 8/36/4 XXVIII (26) and ENT 8/36/4 XLVI (32)). This research would not have been possible without the work of all the Leopard Ecology & Conservation Project team, including previous coordinator Rosie Miles and her support in developing and permitting the projects. Our talented tracking team members are integral to our research, and we would like to acknowledge previous members and trackers involved in other LEC work: Duela Seganapofu, Xee Seganaphofu, Senxwai Mosololo, Mpeletsang Molefatholo, Phalatsa Nkadima, Tshomarelo Segootsane, and Oakantse Molapodi.

Conflict of interest

Authors SA and ZJ was employed by JMP Statistical Discovery LLC.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Ahlswede, S., Fabiano, E. C., Keeping, D., and Birkhofer, K. (2019). Using the Formozov–Malyshev–Pereleshin formula to convert mammal spoor counts into density estimates for long-term community-level monitoring. *Afr. J. Ecol.* 57, 177–189. doi: 10.1111/aje.12587

Alibhai, S. K., Gu, J., Jewell, Z. C., Morgan, J., Liu, D., and Jiang, G. (2023). 'I know the tiger by his paw': A non-invasive footprint identification technique for monitoring individual Amur tigers (Panthera tigris altaica) in snow. *Ecol. Inf.* 73, 101947. doi: 10.1016/j.ecoinf.2022.101947

Alibhai, S. K., Jewell, Z. C., and Law, P. R. (2008). A footprint technique to identify white rhino Ceratotherium simum at individual and species levels. *Endangered Species Res.* 4, 205–218. doi: 10.3354/esr00067

Bauer, D., Schiess-Meier, M., Mills, D. R., and Gusset, M. (2014). Using spoor and prey counts to determine temporal and spatial variation in lion (Panthera leo) density. *Can. J. Zoology* 92, 97–104. doi: 10.1139/cjz-2013-0176

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., et al. (2015). Lion (Panthera leo) populations are declining rapidly across Africa, except in intensively managed areas. *Proc. Natl. Acad. Sci.* 112, 14894–14899. doi: 10.1073/pnas.1500664112

Bodasing, T. (2022). The decline of large carnivores in Africa and opportunities for change. *Biol. Conserv.* 274, 109724. doi: 10.1016/j.biocon.2022.109724

Borchers, D. L., and Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64, 377–385. doi: 10.1111/j.1541-0420.2007.00927.x

Bothma, J. D. P. (1997). Multivariate analysis of the hunting tactics of Kalahari leopards (South Africa). *Koedoe - Afr. Protected Area Conserv. Sci.* 40, 41–56. doi: 10.4102/koedoe.v40i1.262

Bothma, J. D. P., and Coertze, R. J. (2004). Scent-marking frequency in southern Kalahari leopards. *South Afr. J. Wildlife Res.* 34, 163–169. Available at: https://hdl.handle.net/10520/EJC117190.

Bothma, J. D. P., and Le Riche, E. A. N. (1984). Aspects of the ecology and the behaviour of the leopard Panthera pardus in the Kalahari Desert. *Koedoe - Afr. Protected Area Conserv. Sci.* 27, 259–279. doi: 10.4102/koedoe.v27i2.585

Bothma, J. D. P., and Le Riche, E. A. N. (1989). Evidence of a new flexible hunting technique in Kalahari leopards. *South Afr. J. Wildlife Res.* 19, 57–60. Available at: https://hdl.handle.net/10520/AJA03794369_2693.

Bothma, J. D. P., and Le Riche, E. A. N. (1993). Disturbance bias when tracking Kalahari leopards Panthera pardus by spoor. *Koedoe - Afr. Protected Area Conserv. Sci.* 36, 109–112. doi: 10.4102/koedoe.v36i2.379

Bothma, J. D. P., and Le Riche, E. A. N. (1995). Evidence of the use of rubbing, scent-marking and scratching-posts by Kalahari leopards. *J. Arid Environ.* 29, 511–517. doi: 10.1016/S0140-1963(95)80023-9

Dorfman, A., Subach, A., and Scharf, I. (2023). Tracking spoor and field signs as a zoological research method. *Anim. Behav.* 203, 133–141. doi: 10.1016/j.anbehav.2023.07.006

Dupont, G., Royle, J. A., Nawaz, M. A., and Sutherland, C. (2021). Optimal sampling design for spatial capture-recapture. *Ecology* 102, e03262. doi: 10.1002/ecy.3262

Elbroch, M., Mwampamba, T. H., Santos, M. J., Zylberberg, M., Liebenberg, L., Minye, J., et al. (2011). The value, limitations, and challenges of employing local experts in conservation research. *Conserv. Biol.* 25, 1195–1202. doi: 10.1111/j.1523-1739.2011.01740.x

Eloff, F. C. (1973). Lion predation in the kalahari gemsbok national park. *South Afr. J. Wildlife Res.* 3, 59–63. Available: https://hdl.handle.net/10520/AJA03794369_2816.

Eloff, F. C. (1984). Food ecology of the Kalahari lion Panthera leo vernayi. *Koedoe - Afr. Protected Area Conserv. Sci.* 27, 249–258. doi: 10.4102/koedoe.v27i2.584

Engelbrecht, F. A., Steinkopf, J., Padavatan, J., and Midgley, G. F. (2024). "Projections of future climate change in Southern Africa and the potential for regional tipping points," in *Sustainability of Southern African Ecosystems under Global Change*. Eds. G. P. von Maltiz, G. F. Midgley, J. Veitch, C. Brümmer, R. P. Rötter, F. A. Viehberg and M. Veste (Cham, Springer), 169–190.

Funston, P. J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D. M., et al. (2010). Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *J. Zoology* 281, 56–65. doi: 10.1111/j.1469-7998.2009.00682.x

Gielen, M.-C., Johannes, X., Kashe, N., Khumo, G., Zoronxhogo, Z., and Schtickzelle, N. (2024). Monitoring wildlife abundance through track surveys: A capture-mark-recapture inspired approach to assess track detection by certified trackers in the Kalahari, Botswana. *Global Ecol. Conserv.* 51, 156–169. doi: 10.1016/j.gecco.2024.e02924

Gizaw, M. S., and Gan, T. Y. (2016). Impact of climate change and El Niño episodes on droughts in sub-Saharan Africa. *Climate Dynamics* 49, 665–682. doi: 10.1007/s00382-016-3366-2

Gorman, M. L., and Mills, M. G. L. (1984). Scent marking strategies in hyaenas (Mammalia). *J. zoology* 202, 535–547. doi: 10.1111/j.1469-7998.1984.tb05050.x

Gosling, L. M., and Roberts, S. C. (2001). "Scent-marking by male mammals: cheat-proof signals to competitors and mates," in *Advances in the Study of Behavior* (Academic Press), 169–217. doi: 10.1016/S0065-3454(01)80007-3

Gu, J., Alibhai, S. K., Jewell, Z. C., Jiang, G., and Ma, J. (2014). Sex determination of Amur tigers (Panthera tigris altaica) from footprints in snow. *Wildlife Soc. Bull.* 38, 495–502. doi: 10.1002/wsb.432

Jewell, Z. C. (2013). Effect of monitoring technique on quality of conservation science. *Conserv. Biol.* 27, 501–508. doi: 10.1111/cobi.12066

Jewell, Z. C., Alibhai, S. K., and Law, P. R. (2001). Censusing and monitoring black rhino (Diceros bicornis) using an objective spoor (footprint) identification technique. *J. Zoology* 254, 1–16. doi: 10.1017/S0952836901000516

Jewell, Z. C., Alibhai, S. K., Law, P. R., Uiseb, K., and Lee, S. (2020). Monitoring rhinoceroses in Namibia's private custodianship properties. *PeerJ* 8, e9670. doi: 10.7717/peerj.9670

Jewell, Z. C., Alibhai, S. K., Weise, F., Munro, S., Van Vuuren, M., and Van Vuuren, R. (2016). Spotting cheetahs: identifying individuals by their footprints. *J. Vis. Exp.* 111, 54034. doi: 10.3791/54034-v

Keeping, D. (2014). Rapid assessment of wildlife abundance: Estimating animal density with track counts using body mass-day range scaling rules. *Anim. Conserv.* 17, 486–497. doi: 10.1111/acv.12113

Keeping, D., Burger, J. H., Keitsile, A. O., Gielen, M. C., Mudongo, E., Wallgren, M., et al. (2018). Can trackers count free-ranging wildlife as effectively and efficiently as conventional aerial survey and distance sampling? Implications for citizen science in the Kalahari, Botswana. *Biol. Conserv.* 223, 156–169. doi: 10.1016/j.biocon.2018.04.027

Kistner, F., Slaney, L., Jewell, Z. C., Ben-David, A., and Alibhai, S. K. (2022). It's otterly confusing - distinguishing between footprints of three of the four sympatric Asian otter species using morphometrics and machine learning. *OTTER J. Int. Otter Survival Fund*, 108–125.

Krofel, M., Hočevar, L., and Allen, M. L. (2017). Does human infrastructure shape scent marking in a solitary felid? *Mamm. Biol.* 87, 36–39. doi: 10.1016/j.mambio.2017.05.003

Law, P. R., Jewell, Z., and Alibhai, S. (2013). Using shape and size to quantify variation in footprints for individual identification: Case study with white rhinoceros (Ceratotherium simum). *Wildlife Soc. Bull.* 37, 433–438. doi: 10.1002/wsb.250

Law, P. R., Jewell, Z. C., and Alibhai, S. K. (2018). Disassociation between black rhinoceros (Diceros bicornis) mothers and their calves. *Afr. J. Ecol.* 57, 268–269. doi: 10.1111/aje.12582

Lawrence, K. (2020). What Can We Learn from CyberTracking: Applications of an International Tracker Evaluation System for Professional and Citizen Science, and the Theory of Original Wisdom. Connecticut: University of Connecticut.

Li, B. V., Alibhai, S., Jewell, Z., Li, D., and Zhang, H. (2018). Using footprints to identify and sex giant pandas. *Biol. Conserv.* 218, 83–90. doi: 10.1016/j.biocon.2017.11.029

Liebenberg, L. (1990). *The art of tracking The origin of science* (South Africa: Claremont).

Liebenberg, L., Steventon, J., Brahman, N., Benadie, K., Minye, J., Langwane, H., et al. (2017). Smartphone Icon User Interface design for non-literate trackers and its implications for an inclusive citizen science. *Biol. Conserv.* 208, 155–162. doi: 10.1016/j.biocon.2016.04.033

Melville, H. I. A. S., and Bothma, J. D. P. (2015). Possible optimal foraging for Brants's whistling rats by caracals in the Kgalagadi Transfrontier Park. *Afr. Zoology* 41, 134–136. doi: 10.1080/15627020.2006.11407344

Melville, H. I. A. S., Bothma, J. D. P., and Mills, M. G. L. (2004). Prey selection by caracal in Kgalagadi Transfrontier Park. *South Afr. J. Wildlife Res.* 34, 67–75.

Merrick, M. J., and Koprowski, J. L. (2017). Should we consider individual behavior differences in applied wildlife conservation studies? *Biol. Conserv.* 209, 34–44. doi: 10.1016/j.biocon.2017.01.021

Midlane, N., Justin O'Riain, M., Balme, G. A., and 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 Conserv.* 24, 1311–1327. doi: 10.1007/s10531-015-0858-z

Moreira, D. O., Alibhai, S. K., Jewell, Z. C., da Cunha, C. J., Seibert, J. B., and Gatti, A. (2018). Determining the numbers of a landscape architect species (Tapirus terrestris), using footprints. *PeerJ* 6, e4591. doi: 10.7717/peerj.4591

Nkansah-Dwamena, E. (2023). Lessons learned from community engagement and participation in fostering coexistence and minimizing human-wildlife conflict in Ghana. *Trees Forests People* 14, 100430. doi: 10.1016/j.tfp.2023.100430

Rafiq, K., Jordan, N. R., Meloro, C., Wilson, A. M., Hayward, M. W., Wich, S. A., et al. (2020). Scent-marking strategies of a solitary carnivore: boundary and road scent marking in the leopard. *Anim. Behav.* 161, 115–126. doi: 10.1016/j.anbehav.2019.12.016

Ramsauer, S. (2007). *Living at low density: a study of within and between pride dynamics in Kalahari lions*. Verlag Dr. Hut.

Ransom, J. I., Kaczensky, P., Lubow, B. C., Ganbaatar, O., and Altansukh, N. (2012). A collaborative approach for estimating terrestrial wildlife abundance. *Biol. Conserv.* 153, 219–226. doi: 10.1016/j.biocon.2012.05.006

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., et al. (2012). The size of savannah Africa: a lion's (Panthera leo) view. *Biodiversity Conserv.* 22, 17–35. doi: 10.1007/s10531-012-0381-4

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., et al. (2014). Status and ecological effects of the world's largest carnivores. *Science* 343, 1241484. doi: 10.1126/science.1241484

Romañach, S. S., and Lindsey, P. A. (2008). Conservation implications of prey responses to wild dogs Lycaon pictus during the denning season on wildlife ranches. *Anim. Conserv.* 11, 111–117. doi: 10.1111/j.1469-1795.2007.00156.x

Royle, J. A., Chandler, R. B., Sollman, R., and Gardner, B. (2013). *Spatial capture-recapture* (Academic press). doi: 10.1016/B978-0-12-405939-9.00005-0

Schaller, G. B. (1972). *The Serengeti lion: a study of predator-prey relations* (Chicago: University of Chicago Press).

Sekhar, N. U. (2003). Local people's attitudes towards conservation and wildlife tourism around Sariska Tiger Reserve, India. *J. Environ. Manage* 69, 339–347. doi: 10.1016/j.jenvman.2003.09.002

Stander, P. E. (1998). Spoor counts as indices of large carnivore populations; the relationship between spoor frequency, sampling effort and true density. *J. Appl. Ecol.* 35, 378–385. doi: 10.1046/j.1365-2664.1998.00313.x

Stander, P. E., Ghau, I. I., Tsisaba, D. O., and Oma, I. I. (1997). Tracking and the interpretation of spoor: a scientifcally sound method in ecology. *J. zoology* 24.2, 329–341. doi: 10.1111/j.1469-7998.1997.tb05805.x

Stander, P. E., Haden, P. J., Kaqece, I. I., and Ghau, I. I. (2009). The ecology of asociality in Namibian leopards. *J. Zoology* 242, 343–364. doi: 10.1111/j.1469-7998.1997.tb05806.x

Stephens, P. A., Zaumyslova, O. Y., Miquelle, D. G., Myslenkov, A. I., and Hayward, G. D. (2006). Estimating population density from indirect sign: Track counts and the Formozov-Malyshev-Pereleshin formula. *Anim. Conserv.* 9, 339–348. doi: 10.1111/j.1469-1795.2006.00044.x

Thompson, K.-L., Lantz, T. C., and Ban, N. C. (2020). A review of Indigenous knowledge and participation in environmental monitoring. *Ecol. Soc.* 25. doi: 10.5751/ES-11503-250210

Tucker, J. M., King, C., Lekivetz, R., Murdoch, R., Jewell, Z. C., and Alibhai, S. K. (2024). Development of a non-invasive method for species and sex identification of rare forest carnivores using footprint identification technology. *Ecol. Inf.* 79, 102431. doi: 10.1016/j.ecoinf.2023.102431

Winterbach, C. W., Ferreira, S. M., Funston, P. J., and Somers, M. J. (2016). Simplified large African carnivore density estimators from track indices. *PeerJ* 2016, e2662. doi: 10.7717/peerj.2662

Wolf, C., and Ripple, W. J. (2017). Range contractions of the world's large carnivores. *R. Soc. Open Sci.* 4, 1170052. doi: 10.1098/rsos.170052

Zehnder, A., Henley, S., and Weibel, R. (2018). Home ranges of lions in the Kalahari, Botswana exhibit vast sizes and high temporal variability. *Zoology (Jena)* 128, 46–54. doi: 10.1016/j.zool.2018.04.001