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RESEARCH ARTICLE

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First systematic population survey of the desert-adapted lions, Northwest Namibia

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Abstract

The desert-adapted lions (*Panthera leo*) of northwest Namibia inhabit arid and semi-arid habitats, primarily within communal conservancy lands, which they share with semi-nomadic pastoralists. Though of considerable conservation interest, no systematic population survey of these lions has previously been attempted. From 6 November 2022 to 6 January 2023, 45 trained surveyors covered approximately 40,000 km^2 of conservancy and government-managed lands, identifying individual lions by vibrissae (whisker-spot) patterns and other demographic indicators. A systematic whole count, identifying every adult individual, was used to estimate population size. This approach drew upon the local ecological knowledge (LEK) of the Lion Rangers, community conservationists responsible for identifying and monitoring lions in their respective communal conservancies, as well as Regional Services staff of Namibia's Ministry of Environment, Forestry and Tourism (MEFT). The population is estimated between 57 and 60 individual adult lions and 14 cubs; this represents an inferred decrease of 46–60% over the past five years. At 0.11–0.12 lions/100 km^2, this is the lowest recorded density for a free-ranging, self-sustaining lion population in Africa. Thirty-six female and 21 male lions were found during the survey, yielding a sex ratio of 1 ♀: 0.58 ♂. While the population is considered stable and self-sustaining despite recent declines, human-lion conflict (HLC) remains the primary cause of lion mortality and recent drops in available prey are also concerning. Results serve as a baseline for future surveys, which will be an important part of monitoring this relatively small, widely dispersed population.

KEYWORDS
communal conservancies, Kunene, Lion Rangers, local ecological knowledge, *Panthera leo*, vibrissae, whole count

Résumé

Les lions adaptés au désert (*Panthera leo*) du nord-ouest de la Namibie vivent dans des habitats arides et semi-arides, principalement sur des terres communales conservées, qu'ils partagent avec des éleveurs semi-nomades. Bien qu'ils présentent un intérêt considérable en termes de conservation, aucune étude systématique de la population

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de ces lions n'a été tentée jusqu'à présent. Du 6 novembre 2022 au 6 janvier 2023, 45 enquêteurs formés ont couvert environ 40,000 km^2 de terres conservées et gérées par le gouvernement, identifiant les lions individuels par des motifs de vibrisses (taches de fouet) et d'autres indicateurs démographiques. Un comptage systématique de l'ensemble, identifiant chaque individu adulte, a été utilisé pour estimer la taille de la population. Cette approche s'est appuyée sur les connaissances écologiques locales (LEK) des Lion Rangers, des conservateurs communautaires chargés d'identifier et de surveiller les lions dans leurs réserves communales respectives, ainsi que sur le personnel des services régionaux du ministère namibien de l'environnement, des forêts et du tourisme (MEFT). La population est estimée entre 57 et 60 lions adultes et 14 lionceaux; ceci représente une diminution de 46 à 60 % au cours des cinq dernières années. Avec 0.11–0.12 lion/100 km^2, il s'agit de la plus faible densité enregistrée pour une population de lions en liberté et autonome en Afrique. Trente-six femelles et 21 mâles ont été trouvés au cours de l'enquête, ce qui donne un sex-ratio de 1 ♀ : 0.58 ♂. Bien que la population soit considérée comme stable et autonome en dépit des déclins récents, les conflits entre l'homme et le lion (HLC) restent la principale cause de mortalité des lions et la diminution récente des proies disponibles est également préoccupante. Les résultats servent de référence pour les futures enquêtes, qui constitueront une partie importante du suivi de cette population relativement petite et largement dispersée.

1 | INTRODUCTION

Large-bodied, terrestrial carnivores help maintain biodiversity and ecosystem functions (Ray et al. 2005), yet most are facing population declines and shrinking ranges (Ripple et al. 2014). Accurate and precise counts are particularly important in managing large carnivores in low-productivity ecosystems, where populations can be more susceptible to stochastic effects from changing climatic patterns. Lions have been shown to alter their ranging patterns in response to rainfall and subsequent prey availability (Tuqa et al., 2014). In unfenced areas, this can bring lions into closer proximity to human settlements, leading to human-lion conflict (HLC) and subsequent population declines (Bauer et al. 2015; Hazzah et al., 2014; Stander, 2010).

The International Union for Conservation of Nature (IUCN) classifies the lion as 'Vulnerable', meaning the species faces a high risk of extinction in the wild. There are currently an estimated 20,000–30,000 free-ranging lions in Africa,[1] primarily within grassland ecosystems of eastern and southern Africa (IUCN, 2018). During the twenty-first century, lion range has been reduced to approximately 12% of their historically recorded range (IUCN, 2018). One notable exception to this overall trend of range reduction has been the recovery of the desert-adapted lions, west of Namibia's Etosha National Park.

The desert-adapted lion population of northwest Namibia's Kunene Region has been internationally recognised as an important part of maintaining the survival of free-ranging lions within Africa (IUCN, 2018; Jacobson & Riggio, 2018). Since the late 1990s, when it was estimated as low as 20 individuals (Stander, 2018), the population grew as high as an estimated 180 individuals in 2015 (GRN, 2017). During this time, lion range in the region greatly expanded (Figure 1). However, population estimates during this period were based primarily upon expert opinion (GRN, 2017; Stander, 2007, 2010, 2018). While intensive monitoring has taken place in the western reaches of the population's range since 1999 (Stander, 1999), no systematic survey of lions in northwest Namibia or any other low-productivity ecosystem has previously been undertaken (but see Funston, 2011; Stander, 2018).

While the region's lion population increased from 1997 to 2015 (NACSO, 2016), high levels of HLC were also recorded (GRN, 2017), and these often resulted in lion mortalities from retaliatory killings. From 2005 to 2015, no fewer than 37 lion mortalities stemming from HLC were recorded in the western part of these lions' range. Additionally, from 1975 to 2010, a mean average of 29 lions per year were destroyed along Etosha's borders (Heydinger et al., 2022), the lions' eastern range. These mortalities disproportionately involved males: by 2010, the sex ratio was estimated to be 1 ♀: 0.18 ♂ (Stander, 2010), well below ratios elsewhere (Barthold et al., 2016; Schaller, 1972; Stander, 1991).

In 2017, Namibia's Ministry of Environment, Forestry and Tourism (MEFT) released the *Human-Lion Conflict Management Plan for North West Namibia* (GRN, 2017) in response to high levels of HLC and concomitant lion killing in the Kunene Region. Social surveys at the time revealed that lions were responsible for livestock losses averaging approximately N$55,000 (2023 value) per

[1]Free-ranging defined as lions inhabiting fenced areas >1000 km^2 or partially or unfenced areas >500 km^2 (IUCN, 2018).

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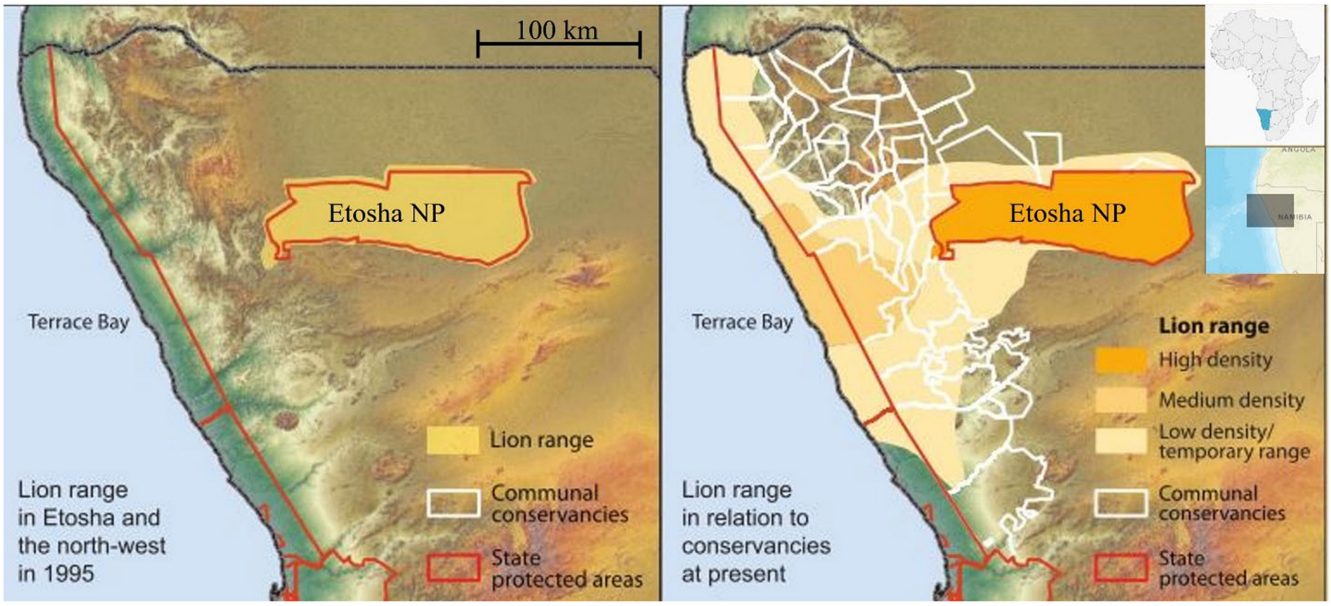

FIGURE 1 Lion range expansion in northwest Namibia's Kunene Region from 1995 to 2014 (reprinted from NACSO, 2016:40). Sources for this period estimate density from 1.6 to 2.67 lions/100 km^2 in Etosha, marked as 'high density' (Kilian & Moeller, 2015; Stander, 1991) and 0.49–0.71 lions/100 km^2 for 'medium density' western areas (Stander & Hanssen, 2003). Areas falling below these values are termed 'low density/temporary range' areas.

household during the preceding 3–5 years (Heydinger et al., 2019). Simultaneously, the lion population was thought to have declined by 22–37% from 2015 to 2017 (GRN, 2017; Stander, 2018). These losses coincided with an extended drought, and, by early 2021, Namibian authorities were concerned for the future of the region's lion population. In western areas, lions were appearing at farms in poor or critical body condition, resulting in certain individuals being destroyed, and, according to expert opinion, a reduced population. During the mid-to-late 2010s, several prides also 'rediscovered' available prey along the Skeleton Coast, in the form of marine food items (Stander, 2019). These related issues – the effects of drought, diminished lion body condition in certain areas, and prides altering their diet – indicated that the lion population may be at heightened risk.

In early 2022, MEFT's Directorate of Scientific Services requested a comprehensive population survey of free-ranging lions inhabiting communal and government-managed lands in northwest Namibia's Kunene Region, west of Etosha National Park. The objectives of this survey were to:

1. Individually identify all lions >1 year old (non-cubs) within communal and government-managed lands and estimate their total numbers.
2. Use practical, repeatable and efficient methods to set a baseline for future lion population surveys in the region.
3. Centre the work of the Lion Rangers (see below) and other local experts to develop capacity for future monitoring.

We hypothesised that a total count based on individual identification would be possible, provided the existing methods were adapted to the landscape and drew upon the participation of highly skilled local conservationists with in-depth knowledge of the region's lion population. Given the low numbers and densities of lions thought to reside in this relatively remote and rugged region, we anticipated that spoor-based and capture-recapture-based approaches would be infeasible (see below). Provided proper planning and execution, we assumed that a dedicated, reasonably resourced team of community conservationists and government staff could effectively locate non-habituated lions while covering more than 40,000 km^2 of rugged desert and semi-desert in less than 2 months. From the outset, our focus was to set a baseline, to learn from our efforts and develop protocols for future surveys.

A longer report on the survey and the lion population was submitted to MEFT for endorsement in November 2023 (Muzuma & Heydinger, 2024).

2 | MATERIALS AND METHODS

2.1 | Study area

Since the 1990s, lions in northwest Namibia have occupied 51,380 km^2 (Stander, 2007), with a core range that encompasses approximately 40,000 km^2, including eleven communal conservancies, three tourism concessions and a portion of the Skeleton Coast National Park (SCNP) while excluding Etosha National Park (Figure 2 and Table 1). Based on monitoring and available GPS/satellite collar data, lions range freely within this landscape. Core lion ranges are defined as those areas consistently occupied by lions since the 1990s (GRN, 2017; Heydinger, 2020; Stander, 2007, 2010).

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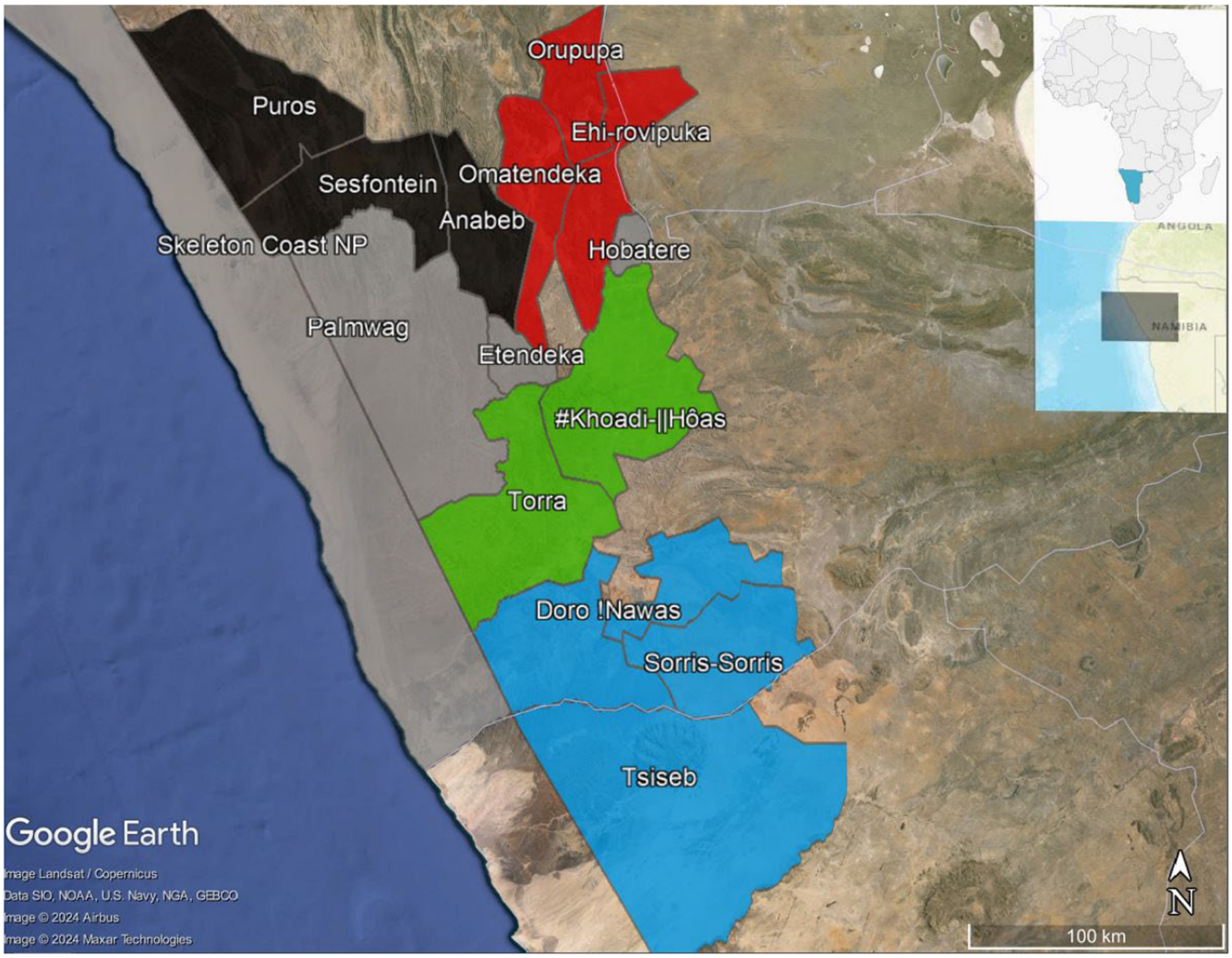

FIGURE 2 Core desert-adapted lion range conservancies and government-managed area boundaries. Conservancies are coloured according to 'Lion Blocks', which group neighbouring conservancies together based on lion pride movements (see below).

The survey area is dominated by the Namib Desert and includes Nama karoo along the western African escarpment, merging into highland savanna further east and bisected by east-to-west ephemeral riverbeds. The soil is typically basaltic, shallow, rocky and unproductive (Atlas of Namibia Team, 2022). Rainfall generally increases along a west-to-east gradient, though the entire area falls within the ≤200 mm isohyet and experiences ≥60% annual rainfall variability. During the wet season (January–May), rains fall in brief, localised downpours. Prey species, including gemsbok (*Oryx gazella*), springbok (*Antidorcas marsupialis*), mountain zebra (*Equus zebra*), giraffe (*Giraffa camelopardalis*) and kudu (*Tragelaphus strepsiceros*), respond to patchy rainfall and subsequent available grasses and browse. During the dry season (June–December), prey often congregate in riverbeds. Due to an intensive government borehole-drilling programme during the 1970s, much of the region is considered grazing-, not water-limited (Bollig, 2020). From 2000 to 2010, the region experienced a relatively wet period, resulting in wildlife and livestock increases. From 2011 to 2017, extensive drought caused the decline of indicator prey species (gemsbok, springbok and mountain zebra) by as much as 60% and livestock by as much as 67% (Heydinger et al., 2019). The entire Kunene Region is projected to experience a 2–3°C temperature increase by 2060 (Atlas of Namibia Team, 2022).

The 40,000 km^2 core lion range is home to approximately 19,800 rural residents, primarily Otjiherero- and Damara-speaking peoples, who enjoy qualified rights to manage and benefit from wildlife through Namibia's communal conservancy system (NACSO, 2020; Owen-Smith, 2010). Most are small-scale pastoralists for whom drought and predation represent significant threats to livelihoods. Lions alone account for approximately 20% of recorded livestock losses (Heydinger et al., 2019). Household incomes are generally low and insecure. By Namibian standards, 38% of residents in Kunene are considered impoverished while 24% are considered severely impoverished (NNPC, 2015); 63% of residents are unemployed (NNPC, 2018). Livelihoods have been further hampered by a downturn in tourism-based income stemming from the COVID-19 pandemic (Lendelvo et al., 2020).

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TABLE 1 Surveyed communal conservancy and government-managed areas.

Conservancy	Human population	Area (km^2)
Anabeb	1402	1570
Puros	641	3562
Sesfontein	1491	2465
Ehi-rovipuka	1846	1980
Omatendeka	1985	1619
Orupupa	2024	1234
ǂKhoadi-‖Hôas	4308	3364
Torra	1064	3493
Doro !Nawas	1242	3978
Sorris Sorris	950	2290
Tsiseb	2415	7913
Government area		
Etendeka Concession	0	633
Hobatere Concession	0	258
Palmwag Concession	0	5891
Skeleton Coast National Park[a]	0	8000

[a]Skeleton Coast National Park encompasses 16,845 km^2; the area surveyed within the park, from the Hoaruseb to the Huab rivers, encompasses approximately 8000 km^2. Color shading corresponds to 'Lion Block' designations.

2.2 | Lion Blocks

Lion Blocks group neighbouring conservancies based on pride ranging patterns, as well as communities of affiliated interest. Because lions do not recognise conservancy boundaries, grouping neighbouring conservancies more accurately reflects challenges stemming from lions' ranging patterns. The four blocks (Black, Red, Green, and Blue) were designated as part of the Kunene Lions Wildlife Credits program, whereby conservancies receive monetary benefits for living alongside lions (Conservation Namibia, 2023). This programme was a motivating factor for the population survey, so conservation payments to conservancies could reflect lion presence. Payment mechanisms are adapted from Heydinger et al. (2022). Because government-managed areas contain no permanent human residents, they are not part of any Lion Block.

2.3 | Methods review

Lions and other large carnivores are difficult to count, and results are frequently affected by spatial heterogeneity and individual behaviours (IUCN, 2018). Additionally, methods are constrained by time and resource availability. Elliot et al. (2021) provide a review of methods for estimating lion abundance and density. We considered counts based on expert opinion, track surveys, call-in/playback surveys, spatially-explicit capture-recapture and whole counts.

Previous lion population estimates for northwest Namibia relied primarily upon expert opinion (GRN, 2017; Stander, 2007, 2010, 2018). This approach is considered highly subjective, not yielding reliable abundance or density estimates or repeatable methods (Moqanaki et al., 2018). Track surveys rely upon a known relationship between track density and lion density, but many of the assumptions of this method, including consistent ability to detect tracks, are not met for northwest Namibia. Because call-in/playbacks are broadcast at night, individual identification is problematic and double counting is possible. In recent years, hierarchical models such as spatially explicit capture-recapture (SECR) are believed to increase the accuracy and precision of large carnivore population surveys (e.g. Braczkowski et al., 2020; Elliot et al., 2021; Elliot & Gopalaswamy, 2017; Roffler et al., 2019), notably in a recent national lion population survey in Kenya (Elliot et al., 2021). While the Kenya survey was our inspiration, time, resource and environmental constraints precluded us from adapting this approach. Additionally, inferred local lion abundance and density called into question whether an SECR approach was feasible. The Kenya survey took place over 718 field days, across ten separate protected areas encompassing 42,994 km^2, making use of 45 vehicles, resulting in 2634 lion 'captures' (detections). Results revealed lion densities ranging from 0 to 18.4 lions/100 km^2 (Elliot et al., 2021). Our survey sought to cover an area of approximately the same size, using ten vehicles or fewer, in less than one-tenth the time. Based on expert estimates, lion density within the landscape would nowhere exceed 3.0 lions/100 km^2.

Whole counts are based upon direct observation of individuals within a relatively limited timeframe; otherwise, the population closure requirement is violated. The primary assumption is that all individuals are counted; this technique has routinely been employed in other long-term lion studies, for example in the Serengeti and Ngorongoro Crater (Packer, 2023). It may seem paradoxical to apply this approach to an area as massive, rugged and remote as northwest Namibia. However, the important contributions that local ecological knowledge (LEK) can make to surveying large carnivore populations have been largely overlooked. We adopt Charnley et al.'s (2007: 15) definition of LEK, which is 'knowledge, practices, and beliefs regarding ecological relationships that are gained through extensive personal observation of and interaction with local ecosystems and shared among local resource users'. LEK is most effective when knowledge holders are engaged as active participants in biodiversity conservation (Charnley et al., 2007). In northwest Namibia, Lion Rangers, as well as Conservancy Game Guards and Rhino Rangers, are responsible for monitoring wildlife, including rare, dangerous and cryptic species. The success of these programmes is interlinked with the successes of Namibia's community-based natural resource management (CBNRM) system (see Jacobsohn, 2019; Stuart-Hill et al., 2005).

LEK has been shown to be effective for acquiring high-quality knowledge of lion movements (Hazzah et al., 2014; Stander et al., 1997) while also reducing lion mortalities stemming from HLC (Dolrenry et al., 2016). As noted by Dolrenry et al. (2016: 2), '[c]arnivore research is typically difficult due to rough terrain and the nocturnal habits, wide-ranging movements, and wariness of animals' – each of these describes

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part of the challenge of surveying lions in northwest Namibia. They continue, '[l]ocal human communities have generations of experience with lions due to their tradition of hunting them to protect livestock, and they know the region intimately because they move their herds seasonally over a very large area'. This too is the case within northwest Namibia's conservancies. Given existing time and resource constraints, a whole count, drawing on the LEK of the Lion Rangers and MEFT Regional Services staff, was deemed the best available method.

2.4 | Lion Rangers

The Lion Rangers are community conservationists and livestock owners, selected by their communities to receive specialised training and equipment for lion monitoring and limiting HLC (lionrangers.org). Based on other successful CBNRM and lion monitoring programmes in Kunene and elsewhere (Dolrenry et al., 2016; Hazzah et al., 2014; Hearn, 2003; Jacobsohn & Owen-Smith, 2003; Muntifering et al., 2015), the Lion Rangers' programme goal is a self-sustaining lion population on communal lands in northwest Namibia. There are currently 47 Lion Rangers across all 11 core lion range conservancies. Each Ranger monitors lion movements and informs farmers and conservation personnel of lion presence, as well as lion behaviour and ecology. All while supporting local livelihoods by limiting HLC.

MEFT Regional Services staff are responsible for wildlife monitoring and wildlife-related law enforcement. Regional Services staff contributed to the safe, efficient and effective execution of this survey. They also contributed high-quality LEK regarding numerous aspects of lion behaviour, movements and ecology. The contributions of these field teams were fundamental to making the whole count approach feasible (Figure 3).

2.5 | Data collection

The survey was divided into three three-week sessions (A, B and C), totalling 58 days, from 6 November 2022 to 6 January 2023 (Figure 4). Personnel were divided into four teams. Using a combination of foot- and vehicle-based patrols, as well as GPS/satellite collar response, each team surveyed a defined geographic area each Session, with overlapping boundaries to ensure landscape coverage. During sessions A and B, four teams moved in a coordinated north–south direction, covering the western extent of the lions' range, from the Hoaruseb river catchment in Puros to the Ugab river forming the Sorris-Sorris-Tsiseb border. During Session C, three teams covered the eastern area, moving in a coordinated southwest-northeast direction to the western boundary of Etosha National Park. (For a detailed survey schedule and workplan, see Muzuma & Heydinger, 2024).



FIGURE 3 Population survey field teams.

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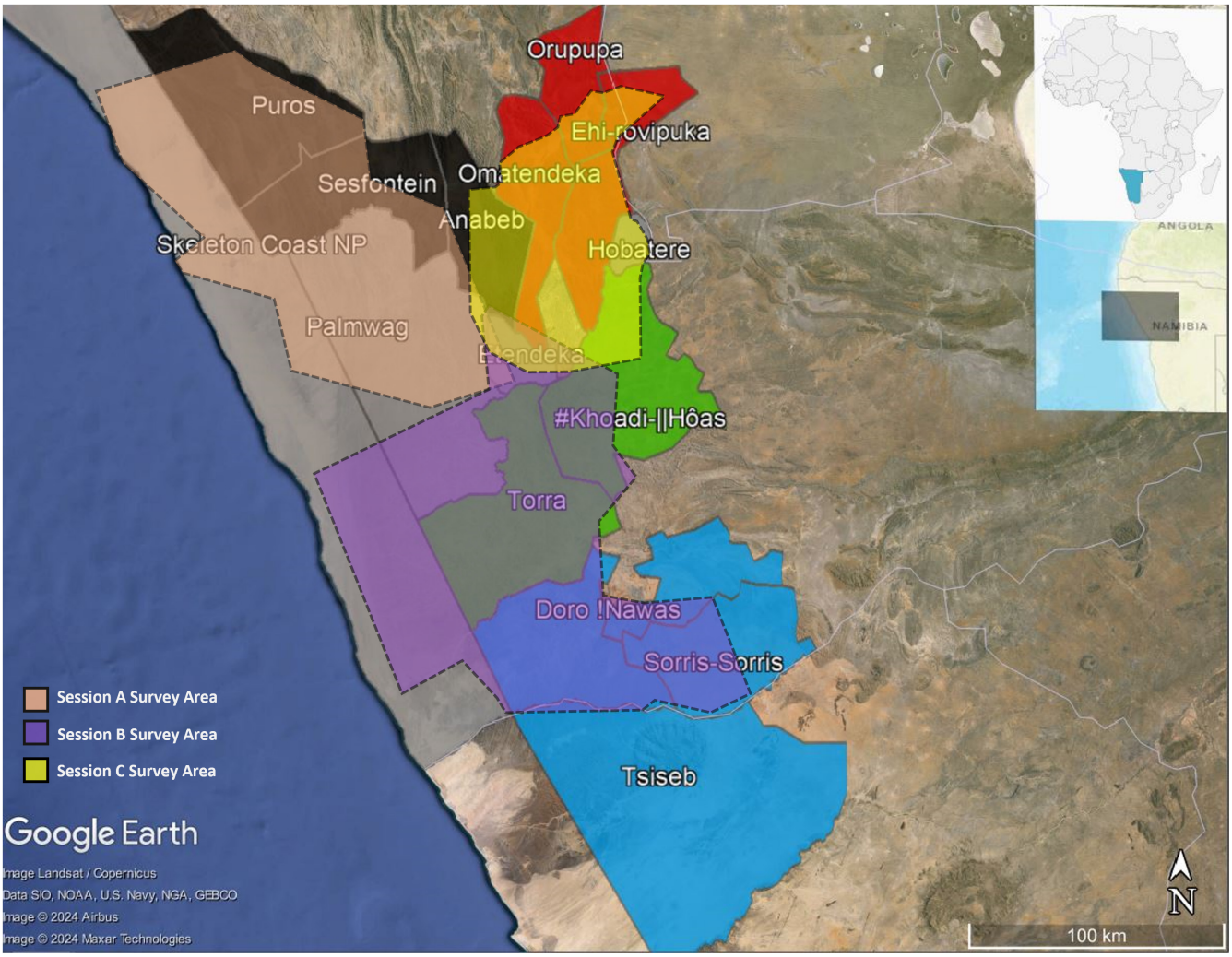

FIGURE 4 Population survey area with conservancy and government-managed boundaries with survey areas separated by session. Session A (6–26 November 2022), Session B (27 November–16 December 2022), Session C (21 December 2022–6 January 2023).

Each team was composed of at least one government-approved lion researcher and Team Leader, two vehicles plus drivers and three to five Lion Rangers. Vehicles worked in tandem to cover their area by deploying Rangers for foot-based tracking, while also locating collared lions based on each day's workplan coordinated with adjacent teams. When other team members found lions, researchers were summoned to capture photographs for individual identification. Within their respective geographic areas, each team was tasked with finding and identifying as many lions as possible, with an emphasis on maximising landscape coverage and carefully searching areas lions were known to inhabit or visit.

2.6 | Structured foot- and vehicle-based patrols

Teams systematically searched survey areas for lions, spoor and fresh carcasses of prey. Work began at daylight and continued through the day. Adjacent teams coordinated which areas would be covered by vehicles and which hard-to-reach areas would be accessed on foot. Each day the goal was to effectively cover as much of the landscape as possible, excepting areas deemed inaccessible to lions (such as steep slopes or gorges). Lion Rangers regularly advised teams about areas needing additional attention. When spoor were located, the animals were tracked by Lion Rangers while other team members queried lion collar locations. Once found, lions were photographed for vibrissae (whisker-spot) patterns. If lions were known to already have been photographed, they were nevertheless tracked and identified, the adage being: 'the best way to find unknown lions is to find known lions'.

2.7 | GPS/satellite collar response

When the survey began, 43 active GPS/satellite collars were already deployed on lions; a further two were added during the survey. These 45 collars were conservatively estimated to cover 70% of the population, 90% of social groups ('prides') having at least one collared individual.

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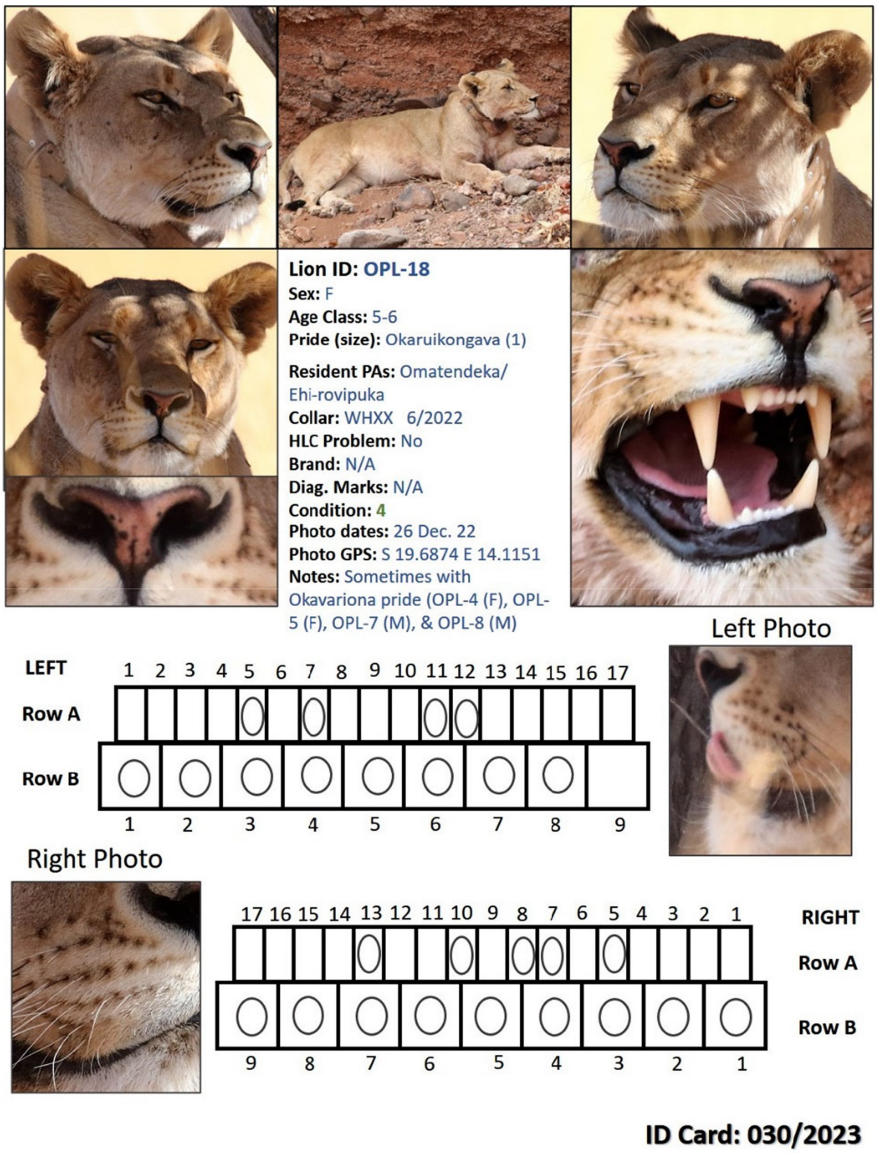

FIGURE 5 Lion ID card showing vibrissae patterns as well as other diagnostic information.

During each session, surveyors repeatedly visited all collared lions within their area, driving to GPS/satellite collar locations to capture identification photos. Numerous collared lions and their pride mates were photographed on multiple occasions, particularly when any pride member was thought to have been absent during previous visits. Collar locations also enabled surveyors to double-check for known lion presence. For example, when lion spoors were found, a GPS position was taken. This position was compared to collared lion movements within the area for the previous 2 weeks, enabling teams to focus on unknown, uncollared lions.

2.8 | Spatial Monitoring and Reporting Tool (SMART)

Teams recorded search effort via the Spatial Monitoring and Reporting Tool (SMART) mobile application (smartconservationtools.org), using a customised package developed for the survey and installed on all surveyors' GPS-enabled smartphones. Walking and driving effort were recorded by taking a GPS point every minute.

SMART data collection consisted of:

- Patrol effort (distance, location and duration), tracked using GPS software.
- Sighting records for lions, including tracks and other sign.
- Number of lions, including adults and cubs, along with body condition and other identifying characteristics.
- Supporting environmental information such as other large mammal sightings and waterhole locations.

Smartphone data were uploaded via cellular network or WIFI to a central server and database. Standardised reports were run of survey effort for each Ranger and each survey session.

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2.9 | Individual lion identification: Vibrissae

To identify individual lions, photos of vibrissae (whisker spots) were taken of both sides of each lions' face as described by Pennycuick and Rudnai (1970). Vibrissae are dark spots forming four to five parallel rows caudal to the mid-nose line located between the upper lip and nose, typically extending six to eight cm backwards (see Figure 5). Only the top two rows – row A and row B – are used for identification in combination with ear notches, dental wear, scarring, age and sex. When analysed as a composite (both sides of the face together), the number and location of vibrissae are unique within small- to medium-sized populations. No change in spots is evident once lions exceed one year old (Pennycuick & Rudnai, 1970). Because cubs are not included in population estimates due to high mortality rates, vibrissae were only recorded for individuals estimated to be over one year of age, even though all cubs were photographed. One pride could not be approached due to the presence of young cubs. Otherwise, both sides of all adults were photographed and analysed.

2.10 | Body condition

Extended visual observation enabled surveyors to assign an overall body condition score to each lion. Body condition scores range from 1 (lowest/critical) to 5 (highest/excellent) (Heydinger, 2023) and are based on a lion's evident muscle tone, whether fur appears healthy and well-groomed, energy level, whether outlines of ribs, backbone and pelvic bones are visible and by reviewing collar movement data where available. These scores are subjective, though they provide a metric for assessing an individual's and pride's overall well-being. Body condition scores were confirmed by researchers and Lion Rangers based on in situ impressions and photographs. It is recognised that lion's body condition can fluctuate widely throughout a year (Hanby et al., 1995), especially in arid and semi-arid areas (Heydinger and Muzuma, pers obs).

2.11 | Estimated age

Lions' estimated ages were based upon available demographic markers such as manes (for males), tooth wear and colour, facial sacring, jowl slackness and nose pigmentation (Aging the African Lion, 2022; Heydinger, 2023; Miller et al., 2016). Age estimates were derived by examining photos in combination with known lion birth dates.

For every lion photographed, an individual ID card was created (Figure 5). In addition to vibrissae patterns, these cards record an individual's ID (alpha-numeric identifier), sex, age, pride name and size, home range area(s), collar ID number, whether the individual is known to cause HLC, brand ID, other identifying features, body condition, date(s) the photos were captured, GPS location of photo captures and other pertinent notes.

All photos were taken using Canon EOS 80D digital cameras with 150–600-mm zoom lenses.

All images were sorted into folders grouped according to survey session, survey week, date, researcher, lion group composition, location of sighting and name of group (if known). Following the survey, individual folders were created for each lion.

Data analyses were performed in Microsoft Excel and R Studio (R Studio Team, 2023).

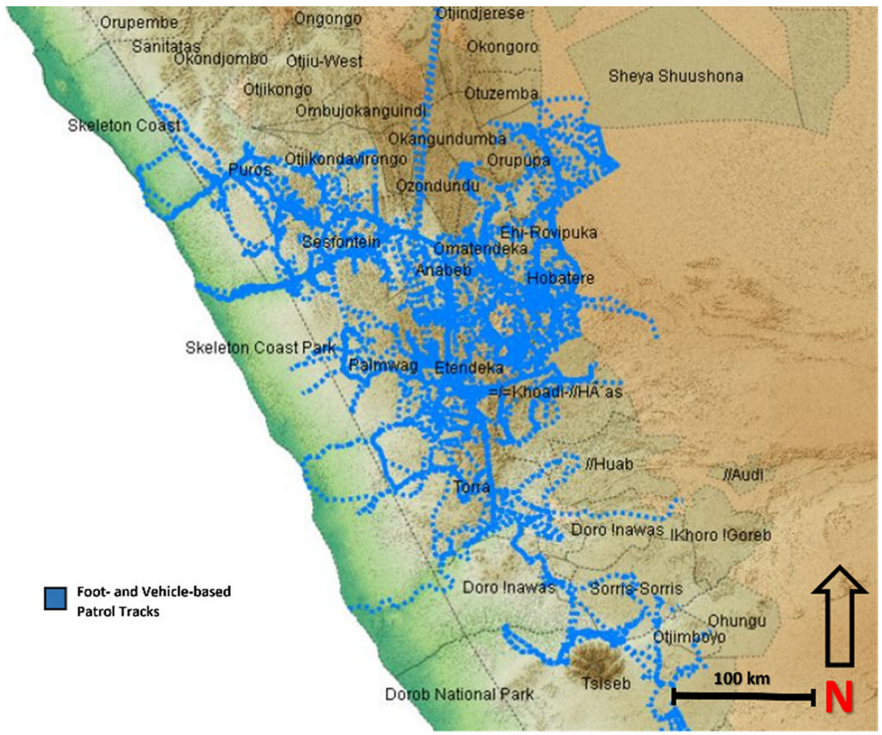

FIGURE 6 All Lion Ranger and MEFT Regional Services staff foot- and vehicle-based patrols that took place during the population survey, as generated by SMART patrol records.

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3 | RESULTS

3.1 | Abundance and density

Surveyors covered approximately 40,000 km^2, recording patrols totalling 10,155 km on foot and 83,290 by vehicle (Figure 6). Based upon approximately 6100 high-quality photos, complete bi-lateral vibrissae (left and right side analysed together) were available for 54 of 57 encountered adults. One pride consisting of three females could not be approached owing to the presence of small cubs; two of the three females were comprehensively photographed after the end of the survey. Bi-lateral vibrissae were found to be unique for all individuals. Lions were found during all survey Sessions at similar rates (Figure 7). Past anecdotal evidence suggests that a further three females may reside in the extreme south and west of the area, though no evidence was found during the survey or follow-up investigations. Our conservative population estimate is therefore 57–60 adult individuals (Table 2).

Of the identified lions, 36 were female and 21 were male, yielding an approximately normal sex ratio for adult lions of 1.0 ♀: 0.58 ♂ (Packer & Pusey, 1987; Schaller, 1972). The average estimated age of all (non-cub) males was 5.79 years ($\sigma = 1.87$). The average estimated age of all (non-cub) females was 6.72 ($\sigma = 1.58$).

Thirty-two lions (18 ♀ and 14 ♂) were found on conservancy lands, while 25 (17 ♀ and 8 ♂) were found within government-managed lands. This ratio (1: 0.78) belies the fact that conservancy lands encompass an area nearly 2.5 times that of government-managed lands (1: 0.42). Pearson's chi-square test reveals that lions are not equally distributed across the landscape (χ^2 (df 14) = 270.7, $p < 0.001$). However, neither the number of lions found (χ^2 (df 9) = 15, $p = 0.09$) nor lion density (χ^2 (df 11) = 15, $p = 0.18$) within conservancies versus government-managed areas differed significantly (Table S1). The average estimated age of males within conservancy lands ($n = 13$) was 5.04 years ($\sigma = 1.6$) while the average estimated age of males within government-managed lands ($n = 8$) was seven years; this difference was statistically significant ($p = 0.018$, two-tailed t-test). The average estimated age of females within conservancy lands ($n = 19$) was 6.24 years versus 7.26 years within government-managed lands ($n = 17$; $p = 0.053$).

Eighteen (12 ♀ and 6 ♂) lions were found in the Black Block with 14 of these in Anabeb Conservancy. Four lions (2 ♀ and 2 ♂) were found in the Red Block, all within Omatendeka Conservancy. Ten lions were found in the Green Block, seven (2 ♀ and 5 ♂) within ǂKhoadi-||Hôas and three (2 ♀ and 1 ♂) within Torra. No lions were found in the Blue Block (Table S1). Follow-up investigation in the Ugab River (boundary of Sorris-Sorris and Tsiseb conservancies) and surrounding landscape confirmed the absence of lions, though the area was previously inhabited by three adult females. No cubs were found in any of the conservancies.

Two females and two cubs were found within SCNP. Nine lions (6 ♀ and 3 ♂) and four cubs were found in Etendeka Concession. Six lions (4 ♀ and 2 ♂) and eight cubs were found in Hobatere Concession. Eight lions (5 ♀ and 3 ♂) and no cubs were found in the Palmwag Concession.

The recorded density for the whole survey area was 0.11 lions/100 km^2 (0.12 lions/100 km^2 if three lions indeed survive near the Ugab River). Density on all conservancy lands was 0.09 lions/100 km^2, ranging from zero (five conservancies) to 0.42 (Anabeb) lions/100 km^2. Density within the Black Block was 0.19 lions/100 km^2, 0.07 in the Red Block, and 0.15 in the Green Block. Within tourism concessions and SCNP, density ranged from 0.025 (SCNP) to 2.33 (Hobatere) lions/100 km^2. Density for all tourism concessions and SCNP was 0.17 lions/100 km^2.

3.2 | Pride sizes

The mean size for all prides was 3.2 adult individuals ($\sigma = 1.8$). Within conservancy lands, the mean pride size was 2.9 adults ($\sigma = 1.76$). Within government-managed lands, the mean pride size was 3.67

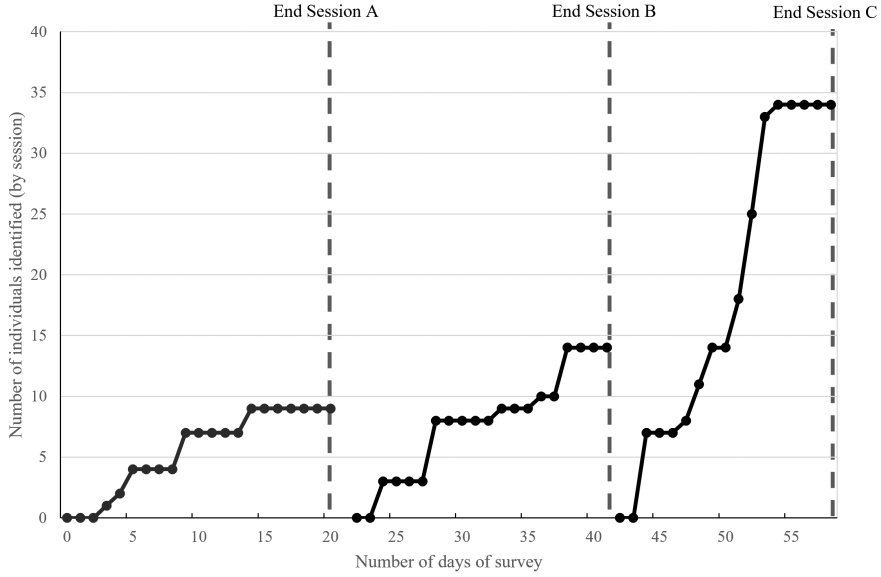

FIGURE 7 Number of individual lions found during each survey Session; number of days (x-axis) accounts for entire survey.

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adults ($\sigma = 1.9$; $p = 0.36$). When analysed separately from the three tourism concessions, the SCNP mean pride size was 1.33 adults ($\sigma = 0.47$) while the mean pride size for the tourism concessions was 3.75 ($\sigma = 1.6$). Because many prides move between conservancy and government-managed areas, these differences are reflective of lion locations during the survey but do not imply these individuals exclusively inhabit either conservancies or government-managed areas.

Concerning body condition, nearly all individuals were in good (4) condition ($\mu = 4.02$). The exceptions were three individuals in fine (3) and four in excellent (5) condition.

One male was known to have lost his mane following an HLC incident (poisoning) in October 2021. One female died during the survey due to HLC; she is not included in the total count.

4 | DISCUSSION

The desert-adapted lion population, estimated at 57–60 adult individuals, has likely declined in recent years – though this inference relies upon previous estimates using dissimilar methods. Despite this decline, however, the population appears to be stable and self-sustaining. Visual evidence indicates that nearly all adults (and cubs) are in good condition, the sex ratio is within normal bounds, and the number of cubs indicates active breeding. Areas of possible concern include: the declining prey base and negative perceptions of lions among locals; the extreme low density of the population and subsequent possibility for stochastic events related to changing climate and discrepancies in the apparent suitability for lions of conservancies versus government-managed areas.

TABLE 2 Overview of landscape-wide survey results.

Survey area	~40,000 km^2
Approx. area inhabited by lions	36,390 km^2
Lions found	57
Sex ratio	36♀:21♂ (1.0:0.58)
Cubs found	14
Lion density within conservancies	0.09/100 km^2
Lion density within government areas	0.17/100 km^2
Total lion density	0.11/100 km^2
Population estimate	57–60

4.1 | Lion deaths and HLC

We infer that the population has declined by 46–60% in the past 5 years (Table 3). During this same period, indicator prey species numbers have fallen by 53–85% (NACSO, 2023a). In comparison to population estimates from 2010, indicator prey species numbers have fallen by as much as 69–96%. In other desert habitats, prey abundance has been linked to large carnivore persistence and extent of ranging patterns (Khosravi et al., 2018). The decline in available prey may be the greatest threat to the population's persistence as this is considered among the leading drivers of HLC (GRN, 2017; NACSO, 2016). Furthermore, both wildlife and pastoralists follow available rains (Muzuma forthcoming), leading to increasing spatial overlap of humans, livestock and lions. Monitoring by the Lion Rangers and researchers is beginning to uncover the extent to which lions may struggle to secure adequate wild prey, particularly at certain times of year. While prey declines have been primarily attributed to the effects of periodic drought (NACSO, 2023b), it remains to be seen whether recent low levels of rainfall will continue.

Our findings represent the lowest population and lowest density estimates given for lions in northwest Namibia since the 1990s, when the first scientific records are available (Stander, 2000). We reiterate the need for caution when comparing population estimates based on dissimilar methods. Nevertheless, the recent inferred decline is concerning and highlights the need for heightened monitoring and research.

From 2000 to 2010, HLC incidents were responsible for 80% of lion (non-cub) mortalities (Stander, 2010); this trend continued through the 2010s (GRN, 2017) to the present. From 2021 through mid-2023, HLC has been responsible for at least 27 lions either being killed or permanently removed from northwest Namibia (Heydinger unpublished data). During this same period, lions have been responsible for at least 512 livestock deaths, including cattle, sheep, goats,

TABLE 3 Population estimates for indicator prey species and lions for 2010, 2015, and 2022.

Species	2010 population estimate	2015 population estimate	2017 population estimate	2022 population estimate
Gemsbok[a]	25,152	12,970 (↓ 48%)	6090 (↓ 53%)	899 (↓ 85%)
Springbok[a]	104,920	59,940 (↓ 43%)	70,420 (↑ 17%)	33,422 (↓ 53%)
Mountain Zebra[a]	20,460	17,910 (↓ 12%)	12,380 (↓ 31%)	5083 (↓ 59%)
Lions	*112–139*[b] (0.28–0.35 lions/100km^2)	*180*[c] (↑ 29–61%) (0.48–0.62 lions/100km^2)	*112–139*[d] (↓ 22–37%) (0.31–0.37 lions/100km^2)	57–60 (↓ 46–60%) (0.11–0.12 lions/100km^2)

Note: Population estimates for indicator prey species are for the entire Kunene Region. Percentage increase or decrease compare yearly estimate with previous estimate (e.g. 2015 compared to 2010). Italicised values are based on expert opinion. Sources footnoted below.

[a]NACSO (2023a).

[b]Stander (2010).

[c]GRN (2017).

[d]Stander (2018).

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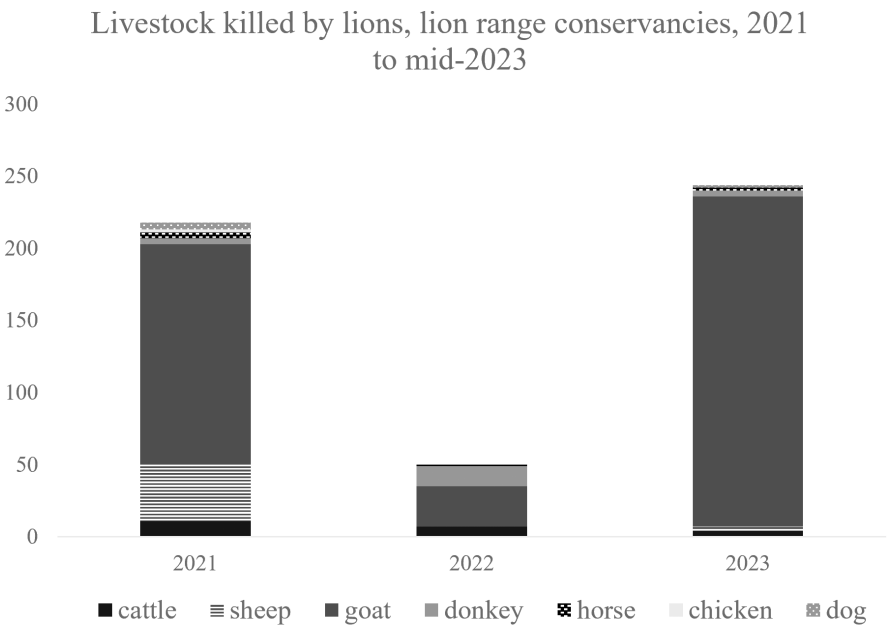

FIGURE 8 Livestock deaths to lions, all lion range conservancies, 2021 to mid-2023,
Source: Lion Rangers' field data.

donkeys and dogs (Figure 8). Since the conclusion of the population survey, at least six lions have been killed because of HLC.

Negative attitudes among conservancy residents towards lions may be contributing to HLC mortalities. Recently completed social surveys reveal 61% of conservancy farmers across the survey area have negative attitudes towards living with lions (Heydinger, 2022). HLC not only constrains pastoralists' livelihoods but also brings into question whether the only source of income available to most residents – livestock husbandry – is secure. The lion population's prospects may be greatly improved by further capacitating programs limiting HLC such as the Lion Rangers and tying lion presence to additional income for conservancy residents. One such programme being piloted is the Wildlife Credits programme (Conservation Namibia, 2023).

4.2 | Extreme low density

The density of the population is the lowest recorded for free-ranging, self-sustaining lion populations in Africa and the lowest comprehensive estimate given for the region. By comparison, density estimates for neighbouring Etosha National Park have ranged from 1.8 to 2.67 lions/100 km^2 (Goelst et al., 2018; Kilian & Moeller, 2015; Stander, 1991). In similarly arid areas in eastern Namibia, density estimates range from 0.2 to 1.72 lions/100 km^2 (Beukes et al., 2017; Funston, 2011).

Density is not uniform across the landscape (Table S1). Though lion density within government-managed areas (0.17 lions/100 km^2) is nearly double the density within communal areas (0.09–0.10 lions/100 km^2), these differences largely disappear when the Blue Block – where no lions were found – is removed, becoming (0.15 lions/100 km^2). Though we cannot definitively attribute the disappearance of lions from Blue Block conservancies to a specific cause, prey species declines have been exacerbated within these conservancies (NACSO, 2023a), seemingly stemming from poaching and insufficient wildlife monitoring.

Both the recent inferred population decline and subsequent extreme low density likely ultimately result from the low productivity of northwest Namibia's ecosystems. Limited prey availability also contributes to relatively small pride sizes and reduced population numbers, though further research is needed to assess this relationship in northwest Namibia (Funston, 2011; Mosser & Packer, 2009; Packer, 1986, 2023; Stander, 1992). Yet, lions in the region appear well-adapted to persist in these arid and semi-arid environments. Low density, and perhaps small pride sizes, may also buttress the population against deleterious processes such as disease, while making it more susceptible to stochastic events, including possible effects stemming from climate change (Atlas of Namibia Team, 2022). With the extensive and expanding GPS/satellite collar dataset, future publications will more fully examine desert-adapted lion ranging and grouping patterns.

Though we did not take biological samples during the survey, prior and subsequent post-mortems have not indicated disease is prevalent within the population, possibly due to the population's low density and arid and semi-arid environmental conditions. Studies on population genetics and how these may affect resistance to disease are ongoing (Dasch et al., 2021).

4.3 | Contextualising male numbers

Of the 21 males, ten (47%) are subadults yet to disperse from their natal prides. The probability of male lion mortality in northwest Namibia is highest for subadults between the ages of three and six ($p = 0.2–0.25$ per year, Stander, 2010). Because of relatively high levels of mortality between the ages of three and six, many of these

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young males may not survive to breed. Additionally, since the survey was completed, three males above five years of age were killed following HLC incidents within conservancy lands. Relative to population viability, the limited number of adult males, coupled with a relatively high probability of subadult male mortality, is concerning. The significantly lower average age of males within conservancy lands ($\mu = 5.04$ years) compared to within government-managed lands ($\mu = 7$ years) is noteworthy. The cause of the discrepancy in male ages between conservancy and government-managed lands is unknown, though mortalities due to HLC are strongly suspected as a driving force.

4.4 | Lions in government-managed areas

Lions inhabiting government-managed areas, where human settlement is prohibited, are less likely to cause HLC incidents, and therefore may be less likely to be killed in retaliation. This may contribute to the significantly higher average estimated age of all lions (non-cubs) in government-managed lands ($\mu = 7.18$ years) compared to within conservancies ($\mu = 5.75$ years). It is worth noting that though we found a relatively high proportion of the population within government-managed areas, individuals and prides range widely. Many desert-adapted lion prides regularly cross between conservancy and government-managed areas (Heydinger et al., 2022; Stander & Hanssen, 2003), and lions have been shown to alter ranging patterns in response to changing rainfall and subsequent prey dispersal (e.g. Tuqa et al., 2014). As Loveridge et al. (2017) have shown, lions may avoid areas of high anthropogenic risk, particularly in landscapes where HLC is the primary cause of lion mortalities. Within northwest Namibia, we infer that lions are similarly responding to anthropogenic risks, particularly when cubs are present. It is also worth noting that ranging patterns are likely affected by HLC interventions when lions are chased away from farming areas.

The presence of cubs within government-managed lands, and their complete absence on conservancy lands, underscores the difference between these land designations. Because the Etendeka, Hobatere and Palmwag Concessions and SCNP together encompass a range of environments broadly representative of the survey area, ecological factors such as rainfall or landscape features are unlikely to explain discrepancies in lion presence or pride structure. Further research is needed to interrogate whether different management approaches between conservancies and government-managed lands are affecting lion presence, social structures and survival. Anecdotally, government-managed areas appear to act as a refuge: they may be more desirable for lions than conservancy lands. Whether this is driven by an absence of HLC is unknown.

While obtaining total counts of large carnivores is considered 'all but impossible' (Elliot et al., 2021: vii), and lions are 'notoriously difficult to count' (IUCN, 2018: 17), we believe a nearly complete count has been achieved here. We re-emphasise that this survey employed a repeatable methodology so as to serve as a baseline for future surveys. Since its conclusion, no previously unknown adult lions have been found. As of February 2024, Lion Rangers have performed an additional 5860 foot- and vehicle-based patrols, covering 92,642 km across the survey area (Lion Rangers unpublished data). During this period, 95 motion-activated trail cameras have been deployed for 1997 'camera nights'. These have recorded 3505 images of medium- and large-bodied mammals (Williams et al., 2021), including 100 photos of lions (Heydinger unpublished data). Despite being deployed specifically within areas where lions may have been missed during the survey, no unknown lions have been encountered, either by Lion Rangers or on trail cameras.

5 | SUMMARY

Regarding the survey objectives:

1. All known lions (non-cubs) inhabiting communal and government-managed lands west of Etosha National Park were identified, along with a further 14 cubs. High-quality vibrissae photos were captured of 54 of 57 individuals. The population is estimated at 57–60 individuals.
2. Drawing on the expertise of lion researchers, the Lion Rangers, and MEFT staff, practical, repeatable and efficient methods set a baseline for future northwest lion population surveys. Combining LEK with technical remote sensing equipment in the form of GPS/satellite collars and camera traps, diverse and complimentary methods enabled survey teams to cover desert-adapted lion range efficiently and effectively. All lions tracked or seen during the survey were identified and all spoor were attributed to specific individuals.
3. From the planning to implementation and follow-up phases, the Lion Rangers and MEFT staff took centre stage. Methods were inclusive, drawing upon local expertise. The survey itself served as capacity development and further training for the Lion Rangers and MEFT staff. Greater capacity development in the form of technical knowledge is needed to continue empowering the Lion Rangers as custodians of lions and lion conservation within communal lands.

The LEK of the Lion Rangers and MEFT Regional Services staff are critical to monitoring lions and limiting HLC in northwest Namibia. By further developing their capacities as both conservation practitioners and leaders, this survey forms a baseline for future surveys. It also can serve as a model to be adapted for monitoring and surveying other large, wide-ranging carnivores outside of fenced protected areas.

FUNDING INFORMATION

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CONFLICT OF INTEREST STATEMENT

No conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Aging the African Lion. (2022). Retrieved October 10, 2022, from https://agingtheafricanlion.com/.

Atlas of Namibia Team. (2022). *Atlas of Namibia: Its land, water, and life*. Namibia Nature Foundation.

Barthold, J. A., Loveridge, A. J., Macdonald, D. W., Packer, C., & Colchero, F. (2016). Bayesian estimates of male and female African lion mortality for future use in population management. *Journal of Applied Ecology*, *53*, 295–304.

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. P., Macdonald, D. W., & 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.

Beukes, B. O., Radloff, F., & Ferreira, S. (2017). Estimating African lion abundance in the southwestern Kgalagadi Transfrontier Park. *African Journal of Wildlife Research*, *47*(1), 10–23.

Bollig, M. (2020). *Shaping the African Savannah: From capitalist frontier to arid Eden in Namibia*. Cambridge University Press.

Braczkowski, A., Gopalaswamy, A. M., Elliot, N. B., Possingham, H. P., Bezzina, A., Maron, M., Biggs, D., & Allan, J. R. (2020). Restoring Africa's lions: Start with good counts. *Frontiers in Ecology and Evolution*, *8*, 138.

Charnley, S., Fischer, A. P., & Jones, E. T. (2007). Integrating traditional and local ecological knowledge into forest biodiversity conservation in the Pacific northwest. *Forest Ecology and Management*, *246*, 14–28.

Conservation Namibia. (2023). Wildlife credits: Innovation in conservation by and for Namibians. https://communityconservationnamibia.com/support-to-conservation/livelihoods/specialist-articles/diversifying-income-with-wildlife-credits

Dasch, N., Versfeld, W., Uiseb, K., Hoth, T., Stander, P., Hartmann, A., Beytell, P., Hanssen, L., & Kuhn, R. (2021). *Genetic constitution and genetic structure of lions populations in northern Namibia*. Ongava Research Center. https://www.orc.eco/post/genetic-constitution-and-genetic-structure-of-lion-populations-in-northern-namibia

Dolrenry, S., Hazzah, L., & Frank, L. G. (2016). Conservation and monitoring of a persecuted African lion population by Maasai warriors. *Conservation Biology*, *30*, 467–475.

Elliot, N. B., Broekhuis, F., Omondi, P., Ngene, S., Kariuki, L., Sankan, K., Chege, M., Wato, Y., Amoke, I., Dolrenry, S., & Gopalaswamy, A. M. (2021). *Report on the application of novel estimating methodologies to monitor lion abundance within source populations and large carnivore occupancy at a national scale*. Wildlife Research and Training Institute and Kenya Wildlife Service.

Elliot, N. B., & Gopalaswamy, A. M. (2017). Toward accurate and precise estimates of lion density. *Conservation Biology*, *31*, 934–943.

Funston, P. J. (2011). Population characteristics of lions (Panthera leo) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, *41*, 1–10.

Goelst, C., Moeller, M., & Kilian, W. (2018). Etosha National Park Carnivore Monitoring Project Update, unofficial report Re: Lion GPS-satellite monitoring, 2018 lion population call-up survey. Unpublished Report.

GRN. (2017). *Human-lion conflict management plan for north West Namibia*. MET.

Hanby, J. P., Bygott, J. D., & Packer, C. (1995). Ecology, demography, and behavior of lions in two contrasting habitats: Ngorongoro crater and the Serengeti Plains. In A. R. E. Sinclair & P. Arcese (Eds.), *Serengeti II: Dynamics, management, and conservation of an ecosystem* (pp. 315–331). University of Chicago Press.

Hazzah, L. N., Dolrenry, S., Naughton-Treves, L., Edwards, C. T., Mwebi, O., Kearney, F., & Frank, L. (2014). Efficacy of two lion conservation programs in Maasailand, Kenya. *Conservation Biology*, *28*, 851–860.

Hearn, M. (2003). Assessment of biological and human factors limiting the West Kunene rhino population. Report for the SADC Regional Programme for Rhino Conservation.

Heydinger, J. (2020). *Humans, livestock, and lions in Northwest Namibia* (PhD thesis). Macquarie/University of Minnesota.

Heydinger, J. (2022). *Human-lion conflict farmer surveys: Mitigation and impacts*. Lion Rangers Program. http://lionrangers.org/wp-content/uploads/2023/10/Human-Lion-Conflict-Survey-Report.pdf

Heydinger, J. (2023). Lion ranger training and operations manual. Prepared for the Community Conservation Fund of Namibia; Windhoek, Namibia. http://lionrangers.org/wp-content/uploads/2023/10/Upadted-Print-VersionLion-Ranger-Manual.pdf

Heydinger, J., Diggle, R., Stuart-Hill, G., Dierkes, K., & Packer, C. (2022). Differentiated payments for ecosystem services based on estimated prey consumption by lions within communal conservancies in northwest Namibia. *Ecosystem Services*, *53*, 101403.

Heydinger, J., Packer, C., & Tsaneb, J. (2019). Desert-adapted lions on communal land: Surveying the costs incurred by, and perspectives of, communal-area livestock owners in northwest Namibia. *Biological Conservation*, *236*, 496–504.

IUCN SSC Cat Specialist Group. (2018). Guidelines for the Conservation of Lions in Africa, Version 1.0 - December 2018. Muri/Bern, Switzerland.

Jacobsohn, M. (2019). *Life is like a kudu horn: A conservation memoir*. Jacana.

Jacobsohn, M., & Owen-Smith, G. (2003). Integrating conservation and development: A Namibian case study. *Nomadic Peoples*, *7*, 92–109.

Jacobson, A., & Riggio, J. (2018). Big cats in Africa: Status update on the African lion, cheetah and leopard, with recommendations for effective big cat conservation funding. Report prepared for National Geographic Society.

Khosravi, R., Hemami, M. R., & Cushman, S. A. (2018). Multispecies assessment of core areas and connectivity of desert carnivores in central Iran. *Diversity and Distributions*, *24*, 193–207. https://doi.org/10.1111/ddi.12672

Kilian, W., & Moeller, C.-H. (2015). *Etosha National Park lion (Panthera leo) survey report*. Ministry of Environment and Tourism, Namibia. Unpublished Report.

Lendelvo, S., Pinto, M., & Sullivan, S. (2020). A perfect storm? COVID-19 and community-based conservation in Namibia. *Namibian Journal of Environment*, *4*, 1–15.

Loveridge, A., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: How African lions respond to spatial variation in risk. *Journal of Applied Ecology*, *54*(3), 815–825.

Miller, J. R. B., Balme, G., Lindsey, P. A., Loveridge, A. J., Becker, M. S., Begg, C., Brink, H., Dolrenry, S., Hunt, J. E., Jansson, I., Macdonald, D. W., Mandisodza-Chikerema, R. L., Cotterill, A. O., Packer, C., Rosengren, D., Stratford, K., Trinkel, M., White, P. A., Winterbach, C., … Funston, P. J. (2016). Aging traits and sustainable trophy hunting of African lions. *Biological Conservation*, *201*, 160–168.

Moqanaki, E. M., Jiménez, J., Bensch, S., & López-Bao, J. V. (2018). Counting bears in the Iranian Caucasus: Remarkable mismatch between scientifically-sound population estimates and perceptions. *Biological Conservation*, *220*, 182–191.

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

Muntifering, J. R., Linklater, W. L., Clark, S. G., Uri-Khob, S., Kasaona, J. K., Uiseb, K., Du Preez, P., Kasaona, K., Beytell, P., Ketji, J., Hambo, B., Brown, M. A., Thouless, C., Jacobs, S., & Knight, A. T. (2015).

13652028, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/aje.13266, Wiley Online Library on [17/04/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Harnessing values to save the rhinoceros: Insights from Namibia. *Oryx*, *51*, 98–105.
Muzuma, U., & Heydinger, J. (2024). Report on the Population Survey of Free-ranging Lions of Northwest Namibia, with Results and Recommendations 2022. Namibia ministry of environment, Forestry and Tourism. Windhoek, Namibia.
Namibia Association of CBNRM Support Organizations (NACSO). (2016). *The state of community conservation in Namibia – A review of communal conservancies, community forests and other CBNRM initiatives (2016 Annual Report)*. NACSO. https://www.nacso.org.na/sites/default/files/State%20of%20Community%20Conservation%20book%202016%20web.pdf
NACSO. (2020). *The state of community conservation in Namibia (Annual Report 2018)*. NACSO. https://www.nacso.org.na/sites/default/files/State%20of%20Community%20Conservation%20book%202018%20web.pdf
NACSO. (2023a). Game counts in north-West Namibia. https://www.nacso.org.na/sites/default/files/North%20West%20Game%20Count-Regional%202022%20final.pdf
NACSO. (2023b). *The state of community conservation in Namibia (annual report 2022)*. NACSO. https://www.nacso.org.na/sites/default/files/2022SOCCAnnualReport_p7.pdf
Namibia National Planning Commission (NNPC). (2015). *Namibia poverty mapping*. Namibia National Planning Commission.
NNPC. (2018). *Status of the Namibian economy*. NNPC.
Owen-Smith, G. (2010). *An arid Eden: A personal account of conservation in the Kaokoveld*. Jonathan Ball.
Packer, C. (1986). The ecology of sociality in felids. In D. I. Rubinstein & R. W. Wrangham (Eds.), *Birds and mammals* (pp. 429–451). Princeton University Press.
Packer, C. (2023). *The lion: Behavior, ecology and conservation of an iconic species*. Princeton University Press.
Packer, C., & Pusey, A. E. (1987). Intrasexual cooperation and the sex ratio in African lions. *American Naturalist*, *130*, 636–642.
Pennycuick, C. J., & Rudnai, J. (1970). A method of identifying individual lion with an analysis of the reliability of identification. *Journal of Zoology*, *160*, 497–508.
Ray, J. C., Redford, K., Steneck, R., & Berger, J. (2005). *Large carnivores and the conservation of biodiversity*. Island Press.
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 large carnivores. *Science*, *343*, 1241481.
Roffler, G. H., Waite, J. N., Pilgrim, K. L., Zarn, K. E., & Schwartz, M. K. (2019). Estimating abundance of a cryptic social carnivore using spatially explicit capture–recapture. *Wildlife Society Bulletin*, *43*, 31–41.
RStudio Team. (2023). *RStudio: Integrated development environment for R*. RStudio. https://www.rstudio.com/
Schaller, G. B. (1972). *The Serengeti lion: A study in predator-prey relations*. University of Chicago Press.
Stander, P. E. (1991). Demography of lions in the Etosha National Park. *Madoqua*, *18*(1), 1–9.
Stander, P. E. (1992). Cooperative hunting in lions: The role of the individual. *Behavioral Ecology and Sociobiology*, *29*, 445–454.
Stander, P. E. (1999). Conservation of lions and other large carnivores in Etosha National Park and Khorixas District, Namibia (Prepared for Namibia Ministry of Environment and Tourism).
Stander, P. E. (2000). *Conservation of lions and other large carnivores in the Kunene region, Namibia: Population ecology and long term monitoring of free-ranging populations in a marginal and arid environment*. Report of the National Carnivore Monitoring Project.
Stander, P. E. (2007). Behaviour-ecology and conservation of desert-adapted lions; 2007 Progress report of the Kunene lion project, Namibia (Prepared for Namibia Ministry of Environment and Tourism).
Stander, P. E. (2010). The impact of male-biased mortality on the population structure of desert-adapted lions in Namibia (prepared for Namibia Ministry of Environment and tourism).
Stander, P. E. (2018). *Vanishing kings: Lions of the Namib Desert*. HPH Publishing.
Stander, P. E. (2019). Lions (*Panthera leo*) specialising on a marine diet in the Skeleton Coast National Park, Namibia. *Namibian Journal of Environment*, *3*, 1–10.
Stander, P. E., Ghau, I. I., Tsisaba, D., Oma, I. I., & Vi. (1997). Tracking and the interpretation of spoor: A scientifically sound method in ecology. *Journal of Zoology*, *242*, 329–341.
Stander, P. E., & Hanssen, L. (2003). *Population ecology of desert-adapted lions in the Kunene region, Namibia*. Report for Namibia Ministry of Environment and Tourism. http://www.the-eis.com/viewfile.php?pth=data/literature/Populationecologyofdesert_adaptedlionsintheKuneneRegion.pdf
Stuart-Hill, G., Diggle, R., Munali, B., Tagg, J., & Ward, D. (2005). The event book system: A community-based natural resource monitoring system from Namibia. *Biodiversity and Conservation*, *14*, 2611–2631.
Tuqa, J., Funston, P., Musyoki, C., Ojwang, G. O., Gichuki, N. N., Bauer, H., Tamis, W., Dolrenry, S., Van't Zelfde, M., de Snoo, G. R., & de Iongh, H. H. (2014). Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation*, *2*, 1–10.
Williams, K. S., Pitman, R. T., Mann, G. K. H., Whittington-Jones, G., Comley, J., Williams, S. T., Hill, R. A., Balme, G. A., & Parker, D. M. (2021). Utilizing bycatch camera-trap data for broad-scale occupancy and conservation: A case study of the brown hyaena Parahyaena brunnea. *Oryx*, *55*, 216–226.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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