First Systematic Population Survey of the Desert-adapted Lions, Northwest Namibia

Short Title: Population Survey of Desert-adapted Lions

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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 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 markers. A systematic whole count, identifying every adult individual (non-cub), 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 57-60 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. 36 female and 21 male lions were found during the survey, yielding a sex ratio of 1 ♀: 0.58 ♂. Results indicate lions are nearly twice as common in government-managed areas as they are within conservancy lands. While the population is considered stable and self-sustaining following recent declines, human-lion conflict (HLC) remains the primary cause of lion mortality and available prey declines are concerning. Caution is urged in managing the population: there remains little peer-reviewed scientific information about the behaviour and ecology of lions in northwest Namibia. Results serve as a baseline for future surveys, which will be an important part of monitoring this relatively small, widely-dispersed population.

Keywords

Panthera leo; desert-adapted lions; lions; local ecological knowledge; Namibia; Kunene; vibrissae; population survey

Introduction

The desert-adapted lion (*Panthera leo*) population of northwest Namibia's Kunene Region has been internationally recognized as an important part of maintaining the survival of free-ranging lions within Africa (Jacobson and Riggio 2018; IUCN 2018). The International Union for Conservation of Nature (IUCN) classifies the lion as 'Vulnerable,' meaning it faces a high risk of extinction in the wild. During the twenty-first century lion range has been reduced to approximately 10% of their historically-recorded range.

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). One notable exception to this overall trend has been the recovery of the desert-adapted lion population.

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 (Stander 2007, 2010, 2018; GRN 2017). 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 was previously undertaken. Furthermore, information on lions in this and other resource-limited areas, is generally lacking (but see: Funston 2011; Stander 2018).

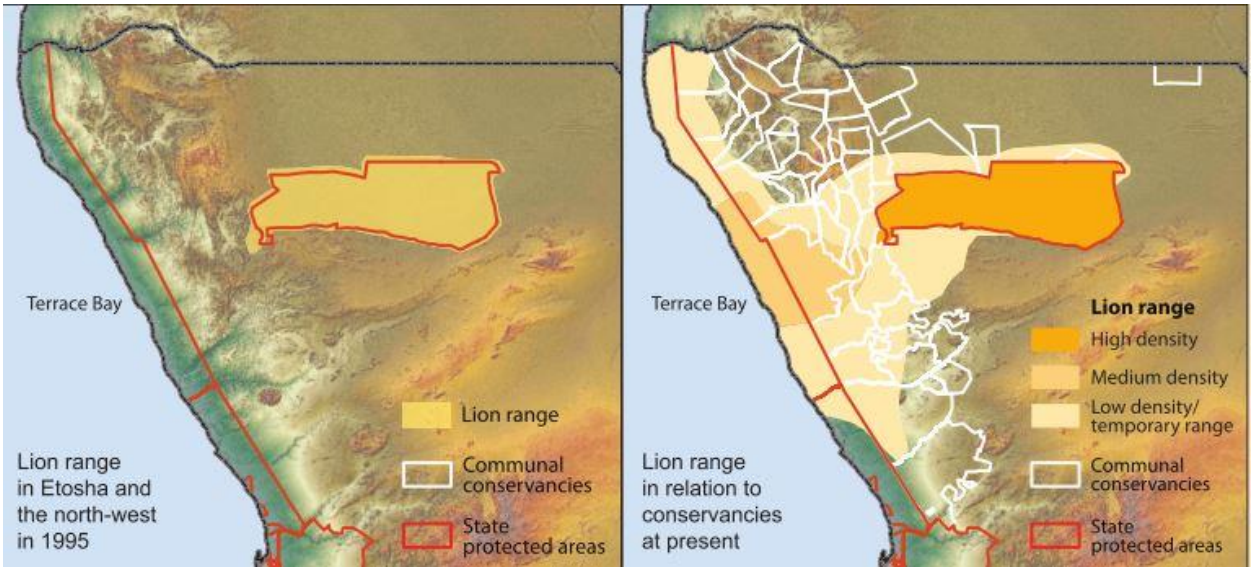

Figure 1: Lion range expansion in northwest Namibia's Kunene Region from 1995 to 2014 (NACSO 2016:40)

While the region's lion population evidently increased from 1997-2015, high levels of human-lion conflict (HLC) were also being recorded (GRN 2017), and these often resulted in lion mortalities from retaliatory killings. From 2005-2015, no fewer than 37 lion mortalities stemming from HLC were recorded in the desert-adapted lions' western range. Additionally, from 1975-2010, a mean-average of 29 lions per year were destroyed along Etosha's borders (Heydinger et al. 2022), the lions' eastern range. Such mortalities were particularly concerning because of the observed effect on the survival of males. By 2010, the sex ratio among a subset of the desert-adapted lions was estimated at 1 ♀: 0.18 ♂ (Stander 2010), well below the expected ratio for lions in other areas (Schaller 1972).

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 subsequent lion killing in the Kunene Region. Social surveys at this time revealed lions were responsible for livestock losses averaging approximately N$55,000 (2023 value) per household during preceding 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 and declines coincided with an extended drought. By early 2021, researchers and government staff were concerned for 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. During the mid-to-late 2010s, several prides had also 'rediscovered' available prey along the Skeleton Coast, in the form of marine food items (Stander 2019). These related

[1] Free-ranging defined as lions inhabiting fenced areas > 1,000 km^2 or partially or unfenced areas > 500 km^2 (IUCN 2018).

issues – the effects of drought, diminished lion body condition in certain areas, and prides altering their diet – indicated the lion population may be undergoing a period of considerable strain, and likely population decline.

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. The objectives of this survey were to:

1) Individually identify all lions > one 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 monitoring going forward.

Survey results and an overview of methods are given here. Our discussion looks at the population numbers considering previously available estimates and contextualizes our findings relative to the prospects for the population considering HLC and a decreasing prey base. A longer report on the survey and the lion population is being released by MEFT (Heydinger and Muzuma, in press).

Material and Methods

Study Area

Since the 1990s, lions in northwest Namibia have occupied 51,380 km^2 (Stander 2007). Core lion range encompasses approximately 40,000 km^2, including eleven communal conservancies, three tourism concessions, and a portion of the Skeleton Coast National Park (SCNP) (Figure 2 & 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 where lions have repeatedly bred and occupied since the 1990s (Stander 2007, 2010; GRN 2017; Heydinger 2020).

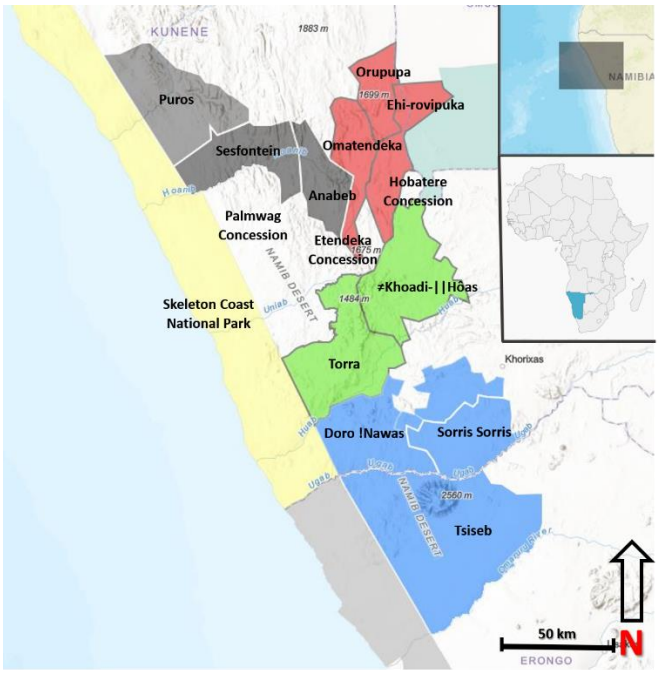

Figure 2: Core lion range with conservancy and government-managed area boundaries. Conservancies are coloured according to 'Lion Block' designations.

Conservancy	Human Population	Area (km²)
Anabeb	1402	1570
Puros	641	3562
Sesfontein	1491	2465
Ehi-rovipuka	1846	1980
Omatendeka	1985	1619
Orupupa	2024	1234
ǂKhoadi-ǁHoas	4308	3364
Torra	1064	3493
Doro ǃNawas	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*	0	8000

*Table 1: Surveyed communal conservancy and government-managed areas. *Skeleton Coast National Park encompasses 16,845 km²; the area surveyed within the park, from the Hoaruseb to the Huab rivers, encompasses approximately 8,000 km².*

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, localized 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 program 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 km² 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 (Owen-Smith 2010; NACSO 2020). 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).

Lion Blocks

Lion Blocks group neighbouring conservancies based on land use by lions, as inter-conservancy cooperation most accurately addresses challenges stemming from lions' landscape use. 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 program was an important motivating factor for the population survey so that conservation payments to conservancies could reflect actual 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.

Methods Review

Lions and other large carnivores are difficult to count and results are frequently affected by local conditions (IUCN 2018), including behaviour differences among individuals and spatial heterogeneity. Additionally, methods are constrained by time and resource availability. Methods considered included expert opinion, track surveys, call-in/playback surveys, spatially-explicit capture-recapture, and whole counts. Elliot et al. (2021) provide a thorough review of available methods for estimating lion abundance and density.

Previous lion population estimates for northwest Namibia relied primarily upon expert opinion (Stander 2007, 2010, 2018; GRN 2017). 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. Many of the assumptions of this method, including consistent ability to detect tracks, are not met for northwest Namibia, primarily due to rocky plains and mountainous areas that lions inhabit. 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 Elliot and Gopalaswamy 2017; Elliot et al. 2021; Roffler et al 2019); notably in a recently completed national lion population survey in Kenya (Elliot et al. 2021). While the Kenya survey was our inspiration, time and resource constraints, landscape topography, and repeatability challenges precluded us from adapting this approach. Additionally, inferred lion abundance and density within the Kunene Region called into immediate question whether an SECR approach was efficient, let alone feasible. The Kenya survey operation took place over 718 field days, across ten separate protected areas encompassing 42,994 km^2, making use of 45 vehicles, resulting in 2,634 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 approximately as large as the Kenya survey, 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 individual lions within a relatively limited timeframe, otherwise the population closure requirement is violated. The primary assumption is that all lions are counted. It may seem paradoxical to apply this approach to an area as massive, rugged, and remote as northwest Namibia. However, one consideration that has been largely overlooked in relevant literature and other, similar surveys, is the possible contribution of local ecological knowledge (LEK) to surveying large carnivore populations. 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 has been found to be most effective when knowledge holders are directly 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 employed by their conservancies and trained by conservation NGOs and government to monitor wildlife, including rare, dangerous, and cryptic species.

The success of these programs is interlinked with the successes of Namibia's community-based natural resource management (CBNRM) system (see: Stuart-Hill et al. 2005; Jacobsohn 2019).

The use of well-trained locals has been shown to be effective for acquiring high-quality knowledge of lion movements (Stander et al. 1997; Hazzah et al. 2014) while also helping reduce 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 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 our time and resource constraints, in combination with the LEK available from the Lion Rangers and MEFT Regional Services staff, we considered a whole count to be the best method available.

Lion Rangers

The Lion Rangers are community conservationists and livestock owners, selected by their communities to receive specialized training and equipment for lion monitoring and limiting HLC (lionrangers.org). Based-upon other successful CBNRM programs in Kunene (Hearn 2003; Jacobsohn and Owen-Smith 2003; Muntifering et al. 2017), as well as the Lion Guardians in Kenya and Tanzania (Hazzah et al. 2014; Dolrenry et al. 2016), the Lion Rangers' program goal is to support a sustainable lion population on communal lands in northwest Namibia. Objectives to reach this goal include limiting HLC to support local livelihoods and promoting the continued existence of the local lion population. There are currently 47 Lion Rangers across all 11 core lion range conservancies. Each Ranger monitors lion movements and provides timely information to farmers and conservancy personnel regarding lion presence, behaviour, and ecology, while supporting local livelihoods by helping keep farmers' livestock and families safe from HLC.

MEFT Regional Services staff are responsible for wildlife monitoring and wildlife-related law enforcement in Kunene. The knowledge and contributions of MEFT Regional Services staff were critical to the safe, efficient, and effective execution of this population survey. Regional Services staff 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).

Figure 3: Population survey field teams.

Data Collection

The survey was divided into three 3-week Sessions (A, B, and C), totalling 58 days (Figure 4). Survey personnel were divided into four teams. Each team surveyed a specific geographic area each Session, the boundaries of which overlapped to ensure landscape coverage. During Sessions A and B, all 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 south-north direction to the western boundary of Etosha National Park. (For a detailed survey schedule and workplan see: Heydinger and Muzuma, in-press). 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. When the other team members found lions, researchers were summoned to capture photographs for individual lion identification.

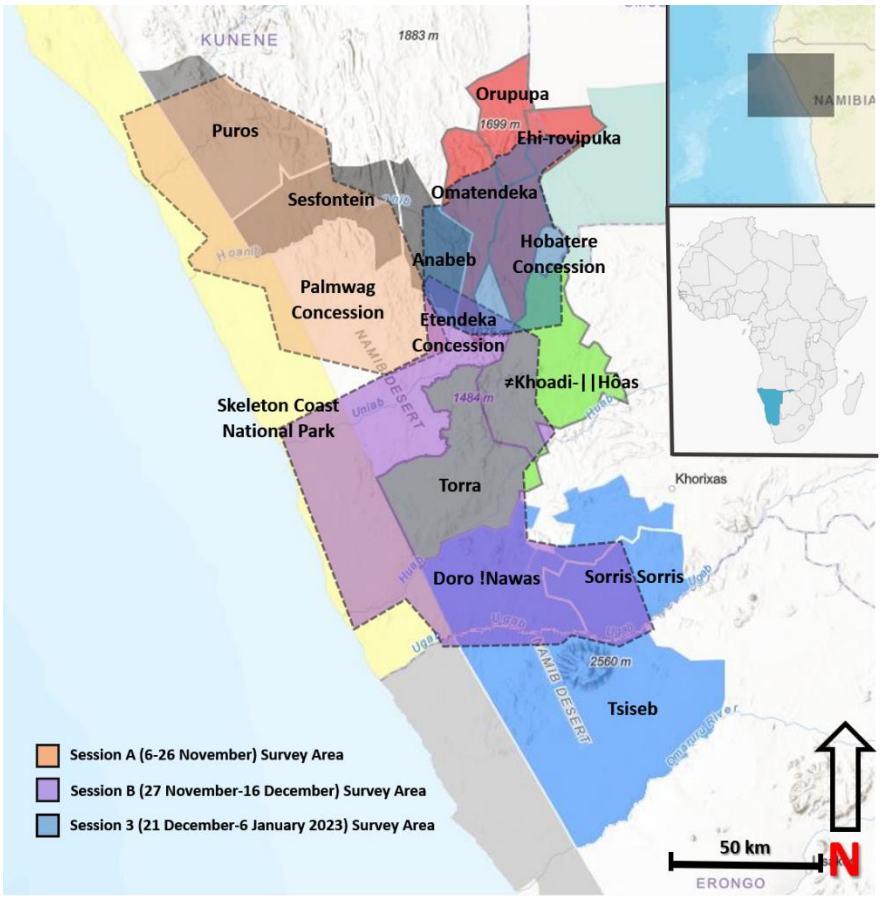

Figure 4: Population survey area with conservancy and government-managed boundaries with survey areas separated by session.

Within their respective geographic areas, each team was tasked with finding and identifying as many lions as possible, while covering all areas where lions were known to inhabit or visit, with a focus on maximizing landscape coverage. This was achieved using structured foot- and vehicle-based searches and/or GPS/satellite collar response.

Structured foot- and vehicle-based patrols

Teams systematically searched survey areas for lions, spoor, and fresh carcasses of prey species. Work typically began at daylight and continued through the day with adjacent teams coordinating the areas that would be covered by vehicles and which hard-to-reach areas would be covered on foot. Each day the goal was to effectively cover as much of the landscape as possible looking for lion spoor, excepting areas deemed inaccessible to lions (such as steep slopes or gorges). Local area Lion Rangers regularly advised teams about the areas that needed 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.'

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 approximately 70% of the population; 90% of social groups ("prides") having at least one collared individual.

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

Spatial Monitoring and Reporting Tool (SMART)

Teams recorded search effort for patrols and collar response via the Spatial Monitoring and Reporting Tool (SMART) mobile application (smartconservationtools.org), using a customized package developed for the Namibian survey and installed on all surveyors' GPS-enabled smartphones. Walking and driving effort were continuously 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 species of large mammals and waterhole locations.

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

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. 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 and Rudnai 1970). Because cubs are not included in many lion 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.

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 is well-maintained and healthy looking, 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 useful metric for assessing an individual's and pride's overall wellbeing. Body condition scores were noted by researchers during data analysis, which was confirmed by *in situ* impressions during the survey. It is recognized that lion's body condition can fluctuate widely throughout a year (Hanby et al. 1995); this especially being true in arid and semi-arid areas (Heydinger and Muzuma, pers obs).

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 (Miller et al. 2016; Aging the African Lion 2022; Heydinger 2023). All age estimates were performed 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 a lion's individual 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.

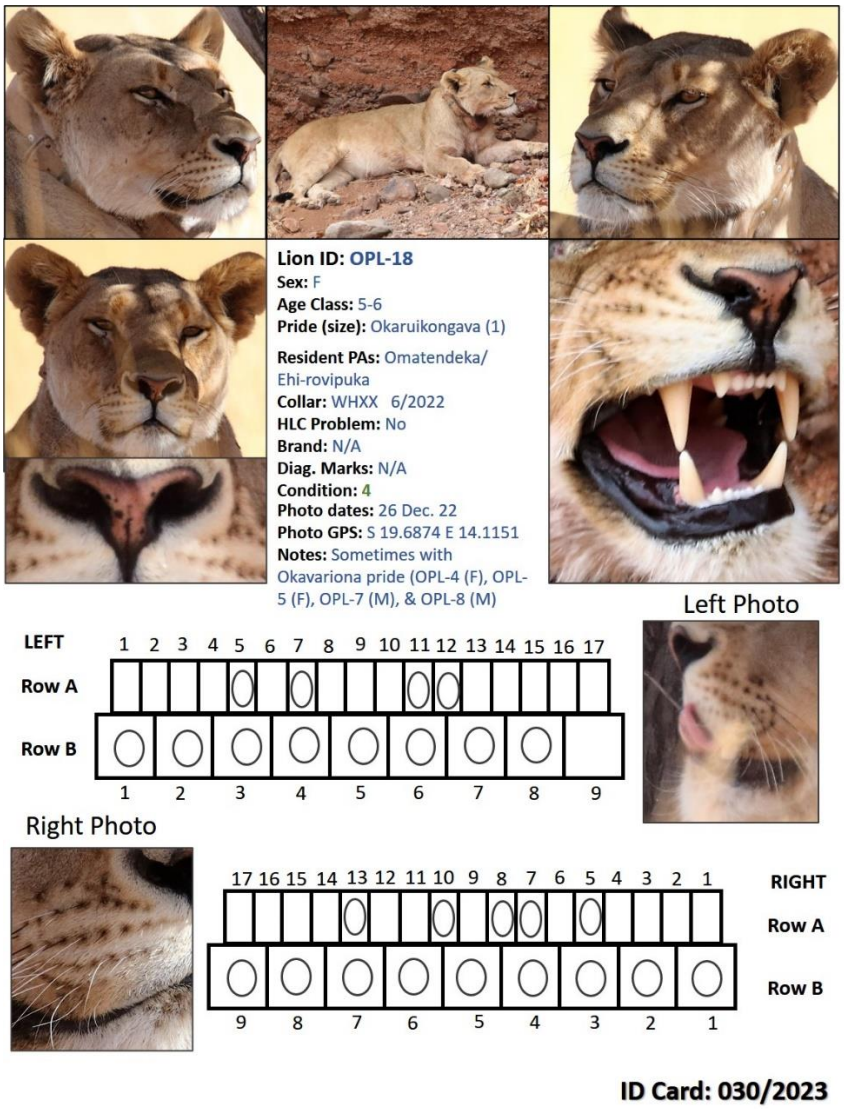

Figure 5: Lion ID card showing vibrissae pattern as well as other diagnostic and information unique to the individual.

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

Results

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 6,100 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; photos were taken, and 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. Past anecdotal evidence suggests 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 for these lions is therefore 57-60 adult individuals (Table 2).

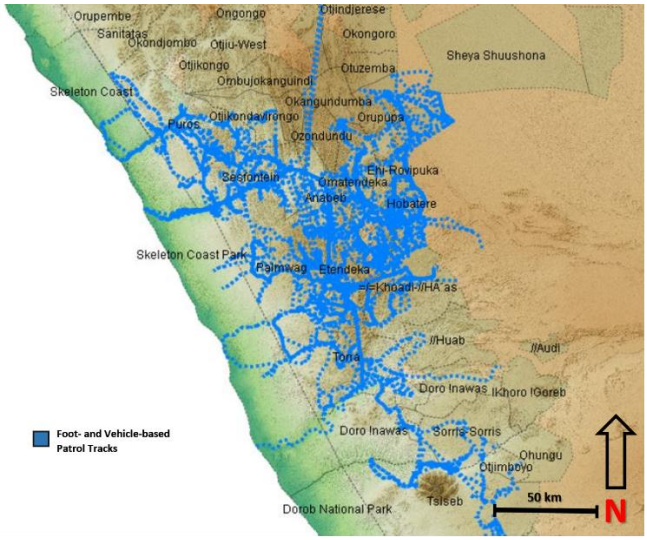

Figure 6: All Lion Ranger and MEFT Regional Services staff foot- and vehicle-based patrols which took place during the population survey, as generated by SMART patrol records.

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

Table 2: Overview of landscape-wide survey results.

Of the identified lions, 36 were female and 21 were male, yielding an approximately normal sex ratio, if not slightly female-biased, for adult lions of 1.0 ♀: 0.58 ♂ (Schaller 1972; Packer and Pusey 1987). The average estimated age of all (non-cub) males was 5.79 years. The average estimated age of all (non-cub) females was 6.72.

32 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). The average estimated age of males within conservancy lands (n = 13) was 5.04 years, 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 vs. 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-ǁHôas and three (2 ♀ and 1 ♂) within Torra. No lions were found in the Blue Block. 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.

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.

Pride Sizes

The mean size for all prides was 3.1 individuals. Within conservancy lands, mean pride size was 2.83 adult individuals. Within government-managed lands, mean pride size was 3.67 adult individuals ($P = 0.36$). When analysed separately from the three tourism concessions, SCNP mean pride size was 1.33 adult individuals, while mean pride size for the tourism concessions was 3.75 individuals. Because many prides move between conservancy and government-managed areas, these differences are illustrative.

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 a HLC incident (poisoning) in October 2021. One female died during the survey due to HLC, but she is not included in the total count.

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. Yet the population is likely self-sustaining. Visual evidence indicates 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 recent inferred population decline, likely stemming from HLC linked to a 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.

Lion Deaths and HLC

We infer that the population has declined by 46-60% in the past five years (Table 3). During this same period indicator prey species numbers have fallen by 53-85% (NACSO 2023). In comparison to indicator prey species population estimates from 2010, numbers of these species have fallen by as much as 69-96%. Lion survival has likely been affected by the dramatic decline in available prey, which may also be driving heightened levels of HLC.

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-upon dissimilar methods. Nevertheless, the recent inferred decline is concerning and highlights the need for heightened monitoring and research.

Species	2010 Population Estimate	2015 Population Estimate	2017 Population Estimate	2022 Population Estimate
Gemsbok[2]	25,152	12,970 (↓ 48%)	6,090 (↓ 53%)	899 (↓ 85%)
Springbok[2]	104,920	59,940 (↓ 43%)	70,420 (↑ 17%)	33,422 (↓ 53%)
Mountain Zebra[2]	20,460	17,910 (↓ 12%)	12,380 (↓ 31%)	5,083 (↓ 59%)
Lions	*112-139*[3] (0.28-0.35 lions/100km^2)	*180*[4] (↑ 29-61%) (0.48-0.62 lions/100 km^2)	*112-139*[5] (↓ 22-37%) (0.31-0.37 lions/100 km^2)	57-60 (↓ 46-60%) (0.11-0.12 lions/100 km^2)

Table 3: Population estimates for indicator prey species and lions for 2010, 2015, and 2022. Populations 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). Italicized values are based on expert opinion. Sources footnoted below. [2345]

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, donkeys, and dogs (Figure 7). Since the population survey, five lions have been killed because of HLC.

[2] NACSO 2023
[3] Stander 2010
[4] GRN 2017
[5] Stander 2018

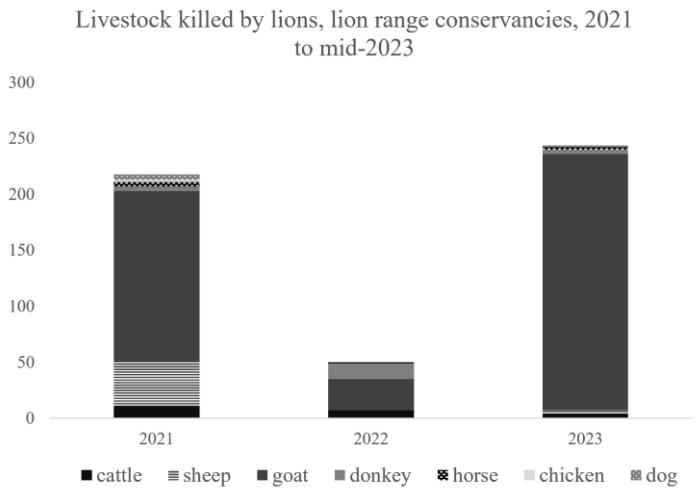

Figure 7: Livestock deaths to lions, all lion range conservancies, 2021 to mid-2023, source: Lion Rangers' field data.

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 program being piloted is the Wildlife Credits program (Conservation Namibia 2023).

Extreme Low Density

The extreme low density of the population (0.11-0.12 lions/100 km^2) is the lowest recorded for free-ranging, self-sustaining lion populations in Africa and the lowest given for the region. Density is not uniform across the landscape. Within government-managed areas lion density (0.17 lions/100 km^2) is nearly double that of density within communal areas (0.09-0.10 lions/100 km^2). However, when the Blue Block conservancies are removed, lion density within communal conservancies (0.15 lions/100 km^2) is similar to density within government-managed areas.

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 (Packer 1986; Stander 1992; Mosser and Packer 2009; Funston 2011; Packer 2023). 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).

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 extreme low density and arid and semi-arid conditions.

Contextualizing Male Numbers

Of the 21 males, ten (47%) are subadults yet to disperse from their natal pride. 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, from: Stander 2010). Because of relatively high levels of mortality between the ages of three and six,

many of these 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 (μ = 5.04 years) compared to within government-managed lands (μ = 7 years) is noteworthy. The cause for 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. Further research is needed to better understand male ranging patterns, behaviour, and survival.

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 (μ = 7.18 years) compared to within conservancies (μ = 5.75 years). The higher relative density of lions within government-managed areas indicates improved survival prospects. 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. Further research is needed to interrogate whether different management approaches between conservancies and government-managed lands are affecting lion presence, social structures, and survival. It appears that government-managed areas 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), we believe a nearly complete count has been achieved here. Lions were found during all survey Sessions at similar rates (Figure 8) and no previously unknown adult lions have been found since the survey was completed. During the intervening months, Lion Rangers have performed 5,860 foot- and vehicle-based patrols, covering 92,642 km across the survey area (Lion Rangers unpublished data). Additionally, 95 motion-activated trail cameras have been deployed for 1,903 ‘camera nights’ since the survey was completed. These have recorded 3,505 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 recorded, either by the Rangers or on trail cameras. Both during the survey and since, the LEK of the Lion Rangers and MEFT Regional Services staff are critical to monitoring lions and limiting HLC in northwest Namibia. This survey and the Lion Rangers ongoing efforts form a baseline for future surveys, which should be repeated every three to five years as an important part of conserving and managing the desert-adapted lion population.

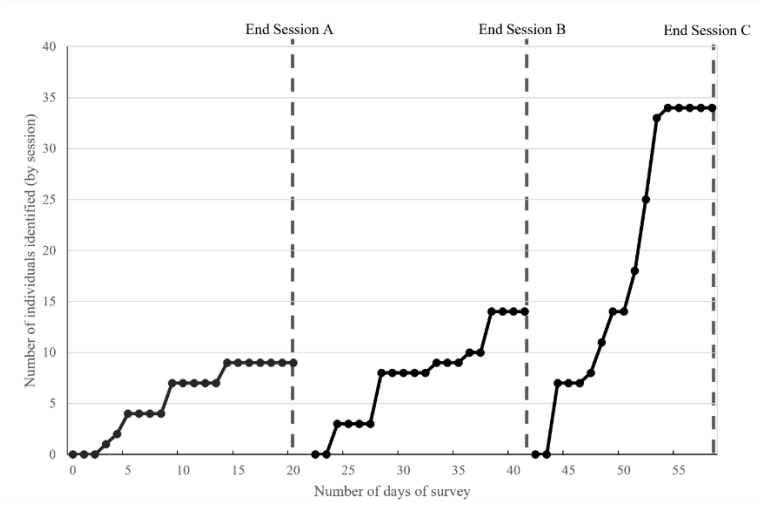

Figure 8: Number of lions found during the survey, divided by each Session.

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