

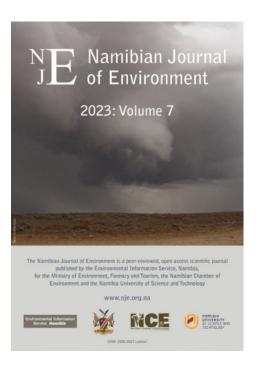
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SECTION B: RESEARCH REPORTS

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An evaluation of the simultaneous utilisation of the northern Namib coastline by desert-adapted lions (*Panthera leo*) and recreational shore anglers, during the 2022/2023 Torra Bay Campsite season, in the Skeleton Coast National Park

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Abstract

Since 2017 desert-adapted lions (*Panthera leo*) that occupy large sections of the Skeleton Coast National Park and the Northern Namib in Namibia have expanded their movements along the arid coastline and increased their use of marine food items in the inter-tidal zones. The annual opening of the Torra Bay Campsite during the December/January holiday period for offshore line fishing has raised increasing concerns of conflict between lions and anglers. During the 2022/2023 season the simultaneous use of the Torra Bay coastline by anglers and lions was evaluated. One lioness utilised the Torra Bay coastline for 34 days or 50% of the Torra Bay season. She adapted her activity patterns by hunting along the inter-tidal zones at night and retreated inland during the daytime and avoided interactions with anglers. Notwithstanding, the lioness continued to utilise the coastal habitat and prey on marine food items, particularly Cape fur seals (*Arctocephalus pusillus*) that contributed 78% of her biomass consumption. An awareness campaign with regular updates on five social media platforms in combination with the constant presence of conservation authorities may have contributed to public awareness, respectful behaviour from Torra Bay visitors and no incidents of conflict.

Keywords: African lion, angling, coastal habitat, Cape fur seal, human-lion conflict, marine diet, Namibia, Panthera leo

Introduction

For many decades the Namibian coastline has been renowned for its offshore line fishing opportunities (Kirchner *et al.* 2000). In recent years the northern section of the coastline that includes sections of the Skeleton National Coast Park (SCNP) has become particularly attractive to anglers. The seasonal access to the Torra Bay Campsite and the designated angling area, from December to January, has attracted large numbers of anglers that have unfettered access to almost 20 km of the coastline. It includes several ecologically sensitive areas, such as the Koigab Cape fur seal (*Arctocephalus pusillus*) breeding colony, the unique geological formations at the Uniab waterfall and the Holocene archeologic settlements scattered inside the Uniab Delta (Kinahan 2020).

Torra Bay has a colourful history that began in 1955 when livestock farmers from the Welwitschia area (now known as Khorixas) obtained permission from the Outjo Magistrate to establish a seasonal holiday location in the area of the Uniab River mouth (Bridgeford pers. com. 2023). During that period the area was still part of the Etosha Game Park that was only reduced to its current size by the Odendaal Commission in 1970 (Berry 1997). During those early years it is believed that farmers travelled to the area with livestock (sheep & chickens) and camped at various locations, such as James Bay (Paterson pers. com. 2023). The December to January seasonal camping at Torra Bay was formalised with the proclamation of the Skeleton National Coast Park in 1971 (Mendelsohn *et al.* 2002). A proposal during 1986/7 to keep Torra Bay Campsite open all year round was successfully blocked by the traditional Torra Bay visitors, who would book their campsite spots for the entire two months and travel regularly between their farms and Torra Bay (Paterson pers. com. 2023). This tradition still continues today, albeit at a much lower scale. The Torra Bay Campsite has since become a popular holiday destination for all Namibians and occasional visitors from abroad (Kazeurua 2018).

The historic presence of lions and other large carnivores utilising the coastal habitat along the SCNP, and in particular the Uniab Delta area, has been well documented (Bridgeford 1985, Shortridge 1934, Stander 2019). During the 1980s the combination of hyper-arid conditions and livestock farming along the borders of the SCNP (Carter 1990) led to excessive human-lion conflict, which resulted in the local extinction of free-ranging lions in the SCNP and surrounding areas (Stander *et al.* 2018).

Following the independence of Namibia in 1990, favourable conditions that included a stable political environment, the formation of communal conservancies, the growth of eco-tourism and increased rainfall patterns, resulted in the recovery of wildlife populations (Jones 1999, Owen-Smith 2011). By the end of 2002, the lion population had increased sufficiently to reoccupy sections of the SCNP, and by 2012 five prides occupied permanent home ranges in the SCNP that included

the coastal habitats (Stander 2019). The knowledge or "culture" of utilising the rich marine food resources along the intertidal zones had been lost during the population decline of the 1980s. It was only in 2017 that lionesses from two prides rediscovered the marine food resources and began utilising marine species such as Cape fur seals and cormorants (*Phalacrocorax* spp.) on a regular basis (Stander 2019).

The rediscovery of Cape fur seals and other marine food items by the desert-adapted lion population is a significant development from both a biological and conservation point of view. It is the only place on the African continent where a large apex carnivore species utilises marine food resources. Terrestrial carnivores that prey on marine species are referred to as maritime carnivores (Carlton & Holder 2011) because they, like some other mammal species, utilise food resources from two different trophic zones. The importance of maritime mammals to the global ecology has often been underappreciated (Carlton & Holder 2011); their reliance on marine food has benefits to the flow of nutrients between the zones and is important to global food webs (Polis *et al.* 1997).

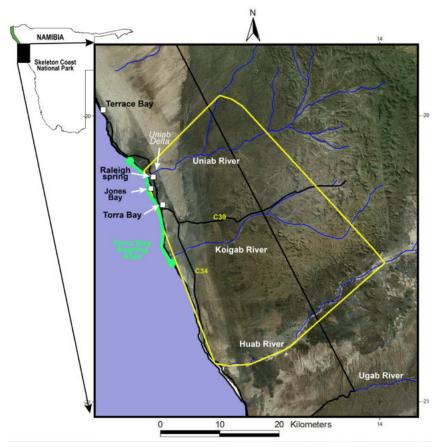
Desert-adapted lions have large home ranges to cope with the variability and low density of prey animals. In recent years this has resulted in all the major prides and groups of lions being involved in incidents of human-lion conflict (Stander *et al.* 2018). Those lions that have subsequently discovered the marine food resources, however, have not yet returned to the communal conservancy areas where people live with livestock. It is important for the conservation of the desert-adapted lion population and the mitigation of human-lion conflict that they can continue to utilise the marine food resources as an alternative to livestock (Stander 2019).

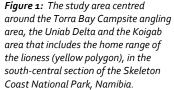
During the two-month period of the Torra Bay Campsite season (1 December 2022 to 31 January 2023), only one lioness utilised the area demarcated for recreation. The Ministry of Environment, Forestry & Tourism (MEFT) and Desert Lion Conservation (DLC) collaborated during the two-month period to monitor the movements and behaviour of the lioness, and to address any potential incidents of conflict.

Methods

Study area

The study area covered the central section of the SCNP and focussed on the entire area demarcated for Torra Bay Campsite visitors (Figure 1). Guided by the movements and home range of the lioness, the study area was expanded to also include the coastal zone west of the dune-belt; from Terrace Bay in the north to the Huab River in the south.





Observations, data capture and analysis

The lioness (Xpl-108) was one of a litter of three females born in mid 2013. Their mother, Xpl-45, exposed the three siblings to the Uniab Delta and passed on the knowledge of the marine food resources during mid-2017. The three young lionesses regularly returned to the Uniab Delta and utilised the marine foods at varying frequencies. Typical of lion fission-fusion grouping patterns (Schaller 1972), the lionesses often spent time together as well as extended periods apart that is a function of their large home ranges and low prey densities (Stander *et al.* 2018). At the age of 9 years, Xpl-108 was fitted with a satellite/VHF radio collar programmed to record hourly GPS positions and emit a constant motion-sensitive VHF signal. Observations started on 19 November 2022 (one week prior to the opening of Torra Bay) and continued until the end of January 2023. The movements and activities of the lioness were recorded over 24-hour cycles for a total of 70 days. For the periods that the lioness moved in the coastal zone and inland up to a distance of 15 km from the coastline, she was kept under 24-hour visual observation. Her movements further inland were monitored via satellite. Observation data were divided into seven consecutive 10-day periods to facilitate the calculation of fluctuations and changes in the movements and behaviour of the lion in relation to tourism and angling activities at Torra Bay Campsite.

A research vehicle was equipped with an array of night-vision and data recording systems. A built-in local area Wi-Fi network and server, which formed the backbone of the data recording process, recorded continuous video images from five infrared security cameras that were mounted on strategic points of the vehicle. With the addition of a thermal camera, linked to the directional VHF radio telemetry antenna, and a high resolution IR video camera, the research vehicle could be driven in total darkness and the lioness observed without disturbance.

Distances moved were calculated from hourly GPS locations and home range estimates were based on the minimum convex polygon method (MCP; Harris *et al.* 1990). Food intake and biomass consumed followed standard procedures using the average mass of an adult female (or adapted when the age and size of the prey animals were observed) minus 40% (for larger prey >50 kg) and 25% (smaller prey 5–50 kg) of inedible parts (Packer *et al.* 1990, Stander 1992). When predation and feeding behaviour could not be observed visually, due to fog or inaccessible terrain, the information was obtained the following day using spoor reconstruction and inspection of carcass remains (Liebenberg 1990, Stander *et al.* 1997).

During the daylight hours the lioness generally rested amongst vegetation or between hummocks. In an effort not to attract the attention of visitors, the research vehicle was parked on a high vantage point approximately 800 metres to 1 km away from the lioness. Surveillance cameras with powerful lenses or a spotting scope were used to monitor the lioness and the movements of visitors during the day. Motion detection events were set up on the surveillance cameras to assist with the monitoring and counting of tourist vehicles driving along the main road.

Social Media and Communications

Updates on the activities of the lioness and the Torra Bay visitors were made daily. A map of her movements, accompanied by photos of that day and short video clips (± 1 min) were edited and prepared from the research vehicle. Every second or third day this information was copied onto a memory flash-drive, packaged, and sent to Swakopmund via Namibia Wildlife Resorts (NWR) and visitors leaving the park.

In Swakopmund the information was edited and sent to the Netherlands where it was prepared for social media release. The DLC website (https://www.desertlion.info/) is the main communication platform, where the News section covers the current affairs. Sections of this information was then posted on other web platforms, like YouTube, Instagram & Facebook, with references back to the full report on the website.

The success of the monitoring exercise relied on dependable communication between the research vehicle and other involved parties, specifically DLC personnel both on site near Torra Bay and in Swakopmund, as well as the MEFT and NWR staff members at Torra Bay. It was also essential that the research vehicle and DLC personnel could at any stage retrieve the latest GPS position of the lion. As such, the research vehicle and DLC support vehicles were equipped with "Rover Units". These units were developed locally by Wide Horizons and DLC to communicate via satellite with a centralised server in Swakopmund, which then forwarded messages between the relevant parties. Messages were relayed either via SMS to a cell phone, or via satellite to other Rover units. The units were also used to retrieve the latest GPS position of lions fitted with satellite collars from the central server.

Results

Lion movements and behaviour ecology

During the 70-day period the lioness (Xpl-108) moved over a home-range area of 5,905 km² (Figure 2). She walked a total distance of 742 km at an average of 11.1 km/day (range: 0.2-43.3 km/day), and spent 34 days inside the Torra Bay Campsite area, as indicated by her movements and daily resting sites (Figures 3a, b & c). Apart from five days in the southern section (Figure 3a), near the Koigab seal colony, the lioness spent most of her time (n = 29 days) between Torra Bay and the mouth of the Uniab River, during two visits to the coastal habitat (Figure 3b, n = 20 days & Figure 3c, n = 9 days).

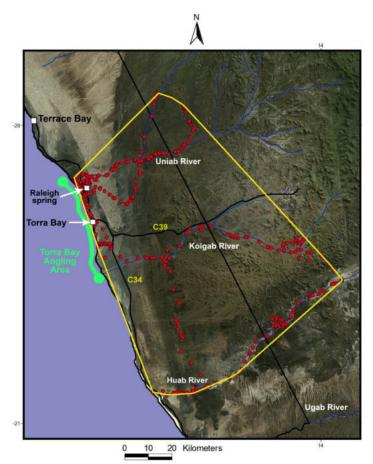


Figure 2: Movement patterns of lioness (Xpl-108) and estimated home range size (MCP) of 5,905 km² over a 70-day period.

During this period the lioness killed or scavenged a total of 30 prey animals, with the majority of her food consisting of Cape fur seals (Table 1). These food items amounted to a total estimate of 425 kg edible biomass and an average per capita food intake of 6.1 kg per day. This compares favourably with general food requirements for lions that varies between 5 kg and 8.5 kg/lioness/day (Packer *et al.* 1990, Stander 1992).

In total the lioness spent marginally more time in the coastal and beach habitats compared to the riverbeds, gravel plains and mountains of the inland habitat (Figure 4). The movement patterns and utilisation of the three main habitat types, however, varied substantially over the two months when the data were separated into seven consecutive ten-day periods (Figure 4).

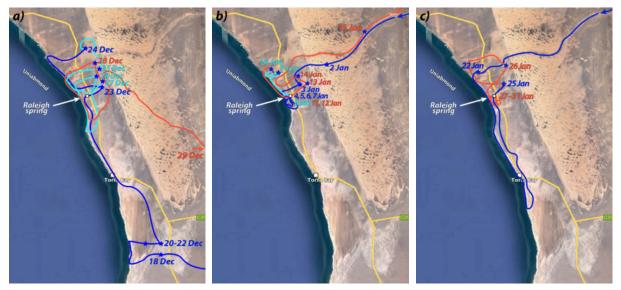


Figure 3: Daily movements of lioness (Xpl-108) in the Torra Bay Camping area during: a) December 2022, b) early-mid January 2023 and c) late January 2023. Blue stars indicate daytime resting spots with dates (except when lioness was at Raleigh spring) and coloured lines depict night-time movements.

The entire coastal habitat, which includes the dunes and the beaches, was significantly more productive for the lioness during the 70-day period (Table 2). During her inland visits the lioness walked longer distances (Student's t-test, t = 2.09, p < 0.05) and did not meet the minimum required food intake of 5 kg/day. The regular visits to the coast and the availability of marine food items, like Cape fur seals, enabled the lioness to increase her average daily food intake to 6.1 kg/day.

The importance of the coast and the marine food items is illustrated further when comparing energy expenditure, such as kilometres travelled per day, and food intake over the consecutive ten-day periods (Figure 5). During the third ten-day period (9–18 December 2022) the lioness walked 300 km at an average of 12.9 km/day without finding any food. Her return to the coast for the following 20 days, however, resulted in higher levels of food intake and substantially lower energy expenditure. A similar pattern of high energy output was evident during her third trip inland with an increase in food intake when she returned to the coastal habitat at the end of January 2023.

Interactions with tourist and anglers from Torra Bay Campsite

During the peak visitor period (20 December 2022 to 10 January 2023), when the lioness rested at Raleigh spring, between 68 and 193 vehicles drove past the spring along the main C34 road per day. Peak hours were during the morning (08hoo-11hoo) and the late afternoon (16hoo-18hoo) when between 14 and 32 vehicles were counted. The majority of vehicles (65%) simply drove past the spring without taking notice, whereas 15% slowed down or stopped briefly.

Table 1: Total number of prey animals captured or scavenged by lioness (Xpl-108) over the 70-day study period.

Prey species	Age	Number
Gemsbok (<i>Oryx gazella</i>)	Sub- adult	1
Springbok (Antidorcas marsupialis)	Sub- adult	2
Cape fur seal (Arctocephalus pusillus)	Adult	4
	Juvenile	8
	Pup	12
Egyptian goose (Alopochen aegyptiacus)	Adult	2
Copper shark (Carcharhinus brachyurus) ¹	Young adult	1
Total		30

¹ Copper (or Bronzy) shark scavenged and partially eaten.

A surprisingly large number of vehicles (20%) stopped, scanned the area and waited for an opportunity to view the lioness (Figure 6). It was pleasing to observe that none of the passengers of the vehicles that showed interest in the lion got out of their vehicles. On the few occasions that the lioness was visible from the main road, a total of eight vehicles spotted the lioness and observed her for up to two hours, whilst 34 vehicles drove past without looking.

During the 34 days that the lioness spent inside the Torra Bay Campsite area, she moved onto the beach at night on 25 occasions, only to return to Raleigh spring or other vegetation cover before daylight. When the lioness first arrived at the coast, after the opening of Torra Bay on 18 December 2022, she rested on a high lookout point for the entire day, where she observed all the vehicles and anglers moving up and down the coastline. That night she approached the beach with caution and after killing a large adult Cape fur seal during the early morning hours, she made an extraordinary effort to

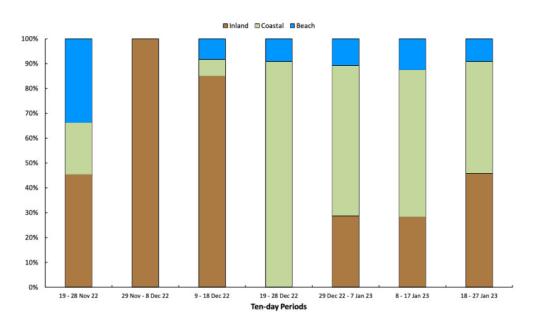


Figure 4: Proportion of time spent in three habitat types during seven consecutive ten-day periods by lioness (Xpl-108) over the 70-day study period (n = 1680).

drag the carcass 4.1 km inland, across a large salt pan and to the top of a high granite hill. She lay there for three days eating and watching the vehicle and people activities on the beaches. Showing remarkable awareness and adaptation to the new dynamics in her usual hunting grounds, the lioness changed her behaviour and refrained from spending any time on the beaches during the daytime (see Figure 4). During the ten-day period prior to the opening of Torra Bay, the lioness spent double the amount of time on the beach (Figure 7).

Most tourists were understanding and respectful of the presence of the lioness in the area. Many visitors expressed a keen interest in observing the uniquely desertadapted Skeleton Coast lions. On 13 occasions visitors attempted to drive offroad, which is illegal according to the permit conditions of the SCNP, to either approach the lioness or the research vehicle. A strong strobing flashlight was used to attract their attention and hand signals were used in an effort to ask vehicles not to approach. The method was successful, and people respected the requests. There were only two high-risk incidents and both involved the lioness approaching anglers that were still active and out of their vehicles after sunset. The flashing strobe light was again effective in alerting the tourists and preventing further escalations.

Communications, social media and information dissemination

The vehicle "Rover Units" and satellite communications via the centralised server in Swakopmund provided regular and reliable communications as well as hourly updates on the position of the lioness when it was needed. The process also ensured that the local authorities (MEFT & NWR office at Torra Bay) were kept up to date with the movements and activities of both the lioness and visitors, and that MEFT were alerted of potential conflict situations and illegal activities, such as off-road driving, by visitors.

The regular dissemination of digital information on social media, both in terms of quantity and quality, resulted in a substantial **Table 2:** Comparison between habitats, the distances travelled per day and the per capita food intake acquired by lioness (Xpl-108) over a consecutive 70-day period.

Behaviour ecology	Habitat type		Total
	Inland	Coastal	
	(East of the	(Dunes to the	
	dunes)	ocean)	
Average distance walked (km/day)	13.2 km	8.4 km	10.8 km
Standard error	± 1.52	± 0.56	
Range	0.2–43.3 km	0.6–38.4 km	0.2–43.3 km
n	35	35	70
Average food intake (kg/day) ¹	2.8 kg/day	10.2 kg/day	6.1 kg/day
Total biomass	96 kg	329 kg	372 kg
n	35	37	70

¹ Food intake is based on estimated eatable biomass consumed

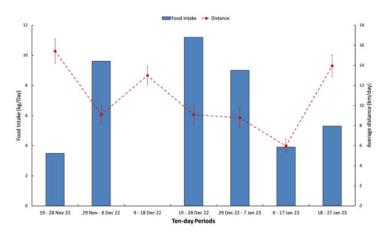
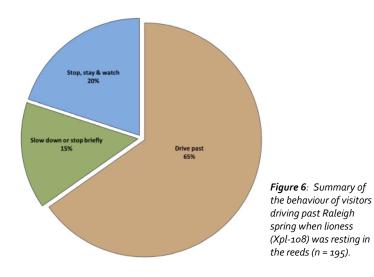


Figure 5: Daily food intake and average daily distances walked by lioness (Xpl-108) during seven consecutive ten-day periods over two months (n = 893).



increase in views of both new and returning visitors on all five social media platforms. Although the impact of the regular media updates cannot be directly quantified in terms of causality, it is our impression that it contributed to mostly favourable public awareness. The public awareness was not only evident amongst Torra Bay Campsite visitors, but was also noticeable from Namibia at large, as well as South Africa and abroad. The distribution of regular and current information in combination with the constant presence of both the MEFT and DLC research vehicle are believed to have contributed to public awareness and the prevention of potential conflict between anglers and the lioness.



Figure 7: The lioness (Xpl-108) spending the day on the beach inside of Torra Bay Campsite area one week before the opening of the 2022/2023 season.

Conclusion

During the two-month period between 1 December 2022 and 31 January 2023 the lioness spent 34 days inside the Torra Bay Campsite area and continued to utilise Cape fur seals as her main source of food. Notwithstanding, the lioness adapted her movements and behaviour to avoid interactions with the large number of vehicles and people moving along the beaches during the daytime. She hunted and searched for prey along the coastline at night and retreated inland to rest inside thick reed-beds or narrow gorges during the day. Her movements inland resulted in low food intake and high energy expenditure levels. As a result, she returned to the coast regularly where the availability of marine food items significantly increased her daily per capita food intake whilst moving shorter distances per day and expending less energy.

The regular posting of current information on the activities and whereabouts of the lioness on a range of social media platforms, appeared to have increased awareness amongst the public and visitors to Torra Bay Campsite. There were no incidents of conflict between the Torra Bay visitors and the lioness. This may also be due to the constant presence of the DLC research vehicle when the lioness was inside the Torra Bay Campsite area. On eight occasions the lioness was observed by visitors that where patient and waited inside their vehicles for an opportunity to view her. The number of vehicles that attempted to drive off-road towards the lioness, however, is alarming, and without the presence of the research vehicle and the MEFT, these events may have escalated and resulted in conflict.

The presence of large maritime carnivores, and in particular an apex predator such as the lion, along the African coastline and moving onto beaches is unique to Namibia. The potential tourism value of seeing a free-ranging lion on a beach in the SCNP is arguably enormous. Future tourism developments in the SCNP would be wise to consider the value of this unusual phenomenon and to develop ecologically sensitive tourism concessions that focus on the distinctive ecological, geological and archaeological characteristics of the region, rather than continuing with a 70-year old tradition of relatively uncontrolled off-shore line fishing.

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References

- Berry HH (1997) Historical review of the Etosha Region and its subsequent administration as a National Park. *Madoqua* 20: 3-12.
- Bridgeford PA (1985) Unusual diet of the lion *Panthera leo* in the Skeleton Coast Park. *Madoqua* 14: 187-188.
- Carlton JT, Hodder J (2003) Maritime mammals: Terrestrial mammals as consumers in marine intertidal communities. *Marine Ecology Progress Series* 256: 271-286.
- Carter LA (1990) The wildlife survey of Skeleton Coast Park, Damaraland, Kaokoland, north-west Namibia May/June 1990. Report to the Commission of the European Communities, Windhoek, Namibia.
- Harris S, Cresswell WJ, Forde PG, Trewhella WJ, Woollard T, Wray S (1990) Home-range analysis using radio-tracking data a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 20: 97-123.
- Jones BTB (1999) Policy lessons from the evolution of a community-based approach to wildlife management, Kunene Region, Namibia. *Journal of International Development* 11: (2) 295-304.
- Kazeurua J (2018) Evaluating stakeholder perceptions concerning the free-roaming desert-adapted lions in the Skeleton Coast National Park in Namibia. University of the Free State. http://hdl.handle.net/11660/11567
- Kinahan J (2020) Namib: The archaeology of an African desert. https://www.jstor.org/stable/j.ctv24tr7nf
- Kirchner CH, Sakko AL, Barnes JI (2000) An economic valuation of the Namibian recreational shore-angling fishery. *African Journal of Marine Science* 22: 17-25

- Liebenberg L (1990) *The Art of Tracking: The Origin of Science*. David Philip. Cape Town, South Africa.
- Mendelsohn J, Jarvis A, Roberts C, Robertson T (2002) Atlas of Namibia: A Portrait of the Land and its People. David Philip Publishers, Cape Town, South Africa.
- Owen-Smith G (2011) An arid Eden; a personal account of conservation in the Kaokoveld. Jonathan Ball Publishers.
- Packer C, Scheel D, Pusey AE (1990) Why lions form groups: food is not enough. *American Naturalist*. 136: 1-19.

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28: 289–316.

- Schaller GB (1972) *The Serengeti Lion*. Chicago, University of Chicago Press.
- Shortridge GC (1934) The Mammals of South West Africa. William Heinemann Ltd., London, UK.
- Stander P, Steenkamp W, Steenkamp L (2018) Vanishing Kings Lions of the Namib Desert. HPH Publishing, Johannesburg, South Africa.
- Stander PE, Ghau //, Tsisaba D, #oma //, |ui | (1997) Tracking and the interpretation of spoor: a scientifically sound method in ecology. *Journal of Zoology, London* 242: 329-341.
- Stander PE (1992) Foraging dynamics of lions in a semi-arid environment. *Canadian Journal of Zoology* 70: 8-21.
- Stander PE (2019) Lions (*Panthera leo*) specialising on a marine diet in the Skeleton Coast National Park, Namibia. *Namibian Journal of Environment*. 3: 1-10.



The lioness Xpl-108 looking over Jones Bay after sundown when all the anglers were back at the Torra Bay Campsite.