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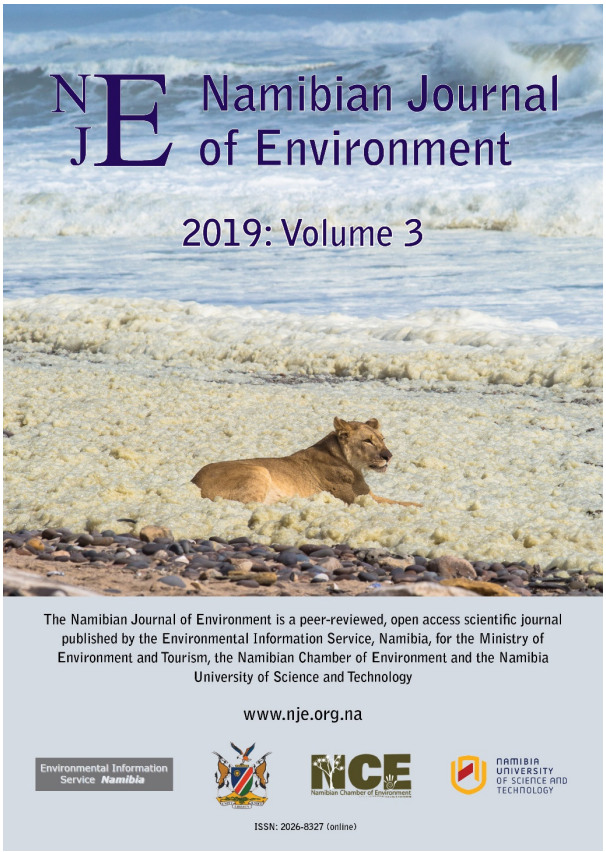

SECTION A: PEER-REVIEWED PAPERS

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Lions (*Panthera leo*) specialising on a marine diet in the Skeleton Coast National Park, Namibia

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ABSTRACT

The Skeleton Coast National Park in the northwest of Namibia supports a small population of African lions (*Panthera leo*) that are adapted to the harsh hyper-arid conditions. After a period of prolonged human-lion conflict during the 1980s lions disappeared from the Skeleton Coast for more than a decade. Due to favourable conditions, such as the development of communal conservancies and the growth of tourism in the area, lion populations started to recover along the Skeleton Coast in 2002. However, it took another 15 years for the lions to rediscover the rich marine food resources that their predecessors utilised in the 1980s. In 2017 two prides of lions started hunting cormorants (*Phalacrocorax* spp.) and Cape fur seals (*Arctocephalus pusillus*) on a regular basis. Over a period of 18 months, three young lioness of the Hoanib Floodplain pride killed two greater flamingos (*Phoenicopterus roseus*), 60 cormorants and 18 seals. The marine diet contributed to 79% of their food items and 86% of the biomass they consumed during this period. The marine resources along the intertidal zone of the Skeleton Coast provide an important source of energy and nutrients to lions that they could rely on when their terrestrial food resources are scarce.

Keywords: African lion; Cape fur seal; coastal habitat; cormorant; desert; marine diet; maritime mammal; Namibia; predation

INTRODUCTION

Predatory strategies are shaped by ecological constraints that may vary extensively between regions and habitats (Elliot & Cowen 1978, Sunquist & Sunquist 1989). The behaviour and ecological characteristics of predators are influenced by habitat and prey availability. More specifically, the density, distribution and richness of prey items in relation to habitat variations are key parameters that affect group size, home range size and behaviour of social predators (Macdonald 1983, Van Orsdol et al. 1985). Throughout its range the African lion (*Panthera leo*) is known to prey on a wide variety of species and the most abundant species generally form the mainstay of their diet (Hayward & Kerley 2005).

In the Namib Desert along the west coast of Namibia, lions have survived for centuries (Shortridge 1934, Ripple et al. 2014) and they have become uniquely adapted to the hyper-arid environment (Stander et al. 2018). The Skeleton Coast National Park (SCNP) was proclaimed by the Namibian authorities in 1971 to protect the unique habitat and its endemic animals and plants. Shortly thereafter officials reported evidence of lions living along the coastline that were feeding on seals and other marine-based food items. Bridgeford (1985) confirmed this during a short study and recorded 14 cases of lions feeding on Cape fur seals (*Arctocephalus pusillus*), as well as evidence of predation on white-breasted (*Phalacrocorax carbo*) and Cape cormorants (*P. capensis*). In 1985 an adult male lion was seen feeding on a beached pilot whale (*Globicephala melas*) (S Braine pers. com. 1986). These were the first records of lions living along the coast and feeding on marine organisms.

Terrestrial carnivores and other mammals are well known to utilise marine organisms at intertidal zones around the globe (Carlton & Hodder 2003). Termed 'maritime mammals' by Carlton & Hodder (2003), they play an important role in the flow of resources and energy between the land and the ocean. The utilisation of intertidal marine species by maritime mammals contribute to the transfer of energy between trophic levels, which is an important element of food webs (Polis et al. 1997). Four maritime mammals have been reported for the African coastline: chacma baboons (*Papio ursinus*) that feed on crustaceans and shellfish in South Africa (Avery & Siegfried 1980, McLachlan & Brown 1990), black-backed jackals (*Canis mesomelas*) that eat fish (*Mugil cephalus*) and mussels (*Bivalvia* spp.) along the Namibian coastline (Nel & Loutit 1986, Hiscocks & Perrin 1987), and brown hyaenas (*Hyaena brunnea*) have been recorded to eat crabs (*Brachyura* spp.; Stuart & Shaughnessy 1984) and to prey on Cape fur seal pups (Wiesel 2010).

Marine mammals and birds that breed on land are extremely vulnerable to predation by terrestrial predators. As a result, they select small islands, the

Arctic or Antarctic to avoid predation by large carnivores. The Namib coastline is unique in that it is the only place where seals form colonies and breed on a continent inhabited by several large carnivore species, and where the humans have lived at low densities for millennia (Small et al. 2011). It is only in the Arctic where a large terrestrial carnivore, the polar bear (*Ursus maritimus*), preys on seals (Stirling & Archibald 1977).

The land-use practices bordering the SCNP, during the 1980s, were not conducive to wildlife. In an area with tremendously high tourism value, local communities living just outside the narrow SCNP were attempting to survive from uneconomical and unsustainable livestock farming (Carter 1990). Conflict between lions and the farmers was inevitable. Lions raided livestock and farmers retaliated (legally) by shooting or poisoning lions. By 1990 all the known lions that lived in the SCNP had been killed (Stander et al. 2018). Several years later, in 1997, a small remnant group of approximately 20 desert-adapted lions (hereafter referred to as the Desert lion population) was discovered in a mountainous region on the eastern edge of the Namib, and the Desert Lion Conservation research project (DLCP) was launched. Much had changed since the 1980s: several years of good rainfall saw an increase in wildlife numbers; the Namibian tourism industry was growing and providing value to wildlife; local people derived benefits from wildlife and tourism through the communal conservancies system (Naidoo et al. 2016); and the conditions were right for lions to find their way back to the Skeleton Coast and the rich marine food resources.

METHODS

Study Area

The area studied by the DLCP covers 51,500 km^2 of arid habitat that falls in the Etendeka Plateau landscape of the northern Namib Desert, with an annual rainfall of 0-100 mm (Mendelsohn et al. 2002). The area is dissected by a series of ephemeral drainage lines that provide food, water and shelter to most of the large mammal species, including elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), gemsbok (*Oryx gazella*), springbok (*Antidorcas marsupialis*) and lion, that live here. The area includes a protected area (the Skeleton Coast National Park), tourism concessions (Palmwag, Etendeka and Hobatere Concessions), and communal conservancies where people live and farm with livestock (Figure 1).

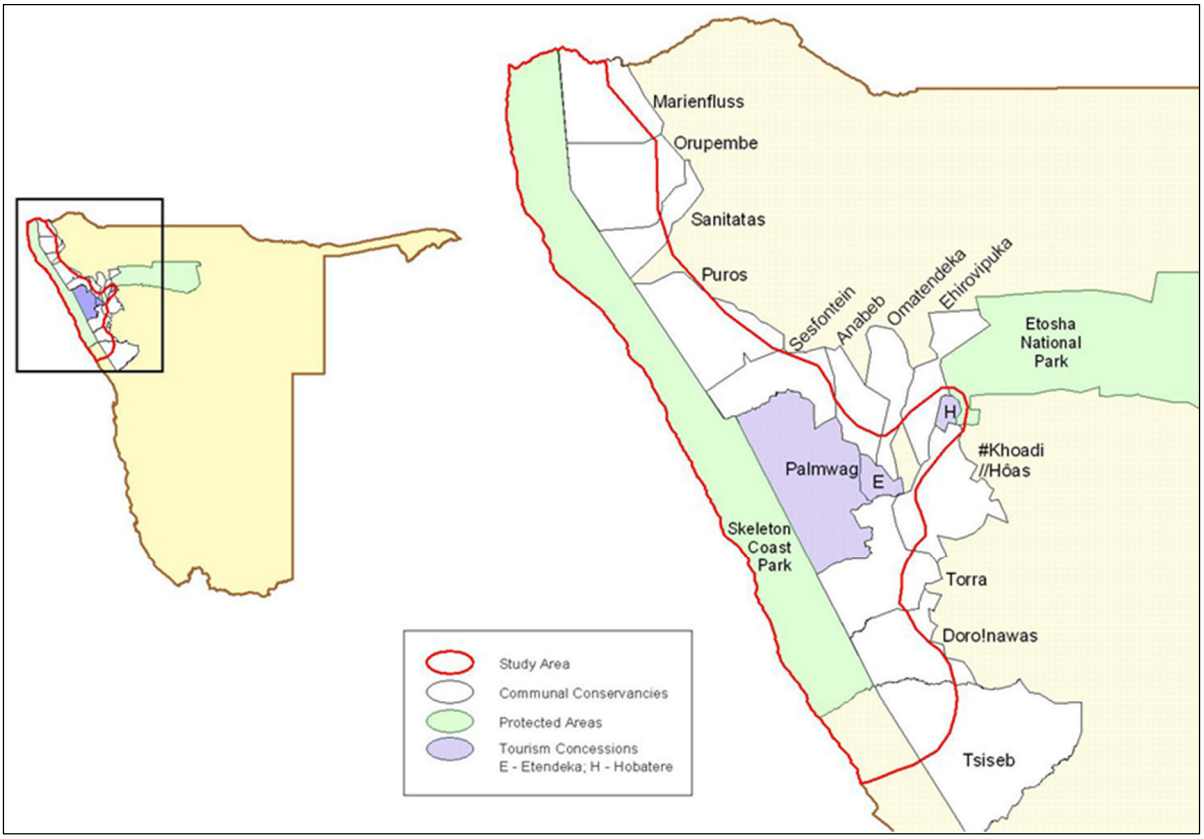

Figure 1: *The study area in the northwest of Namibia that includes the Skeleton Coast National Park, several tourism concessions and communal conservancies.*

Data collection

The study area was covered systematically by tracking spoor and using sound playbacks to locate and observe individual lions. All lions, including small cubs, were photographed, using high-quality equipment, and individually identified using vibrissae spot patterns (Pennycuick & Rudnai 1970). Some adult and sub-adult lions were captured and individually marked by fitting VHF, GPS or satellite radio collars.

Individual lions selected for radio-collaring were immobilised following procedures described by Smuts et al. (1977) and Stander and Morkel (1991), and according to Namibian veterinary requirements. Attempts were made to mark and individually recognise 75% of the population and population estimates were calculated using mark-recapture models. Fitting of GPS and satellite collars and the selection of individuals were based on group structure and individual records collected over several years. Adults that associate regularly with the rest of the pride/group (using a Matrix of Association Index) with large calculated home ranges were favoured.

Radio-collared animals were located by vehicle, with the use of RFID radio loggers or with an aircraft. All visual observations of lions, including hunting and feeding behaviour were done from a specialised vehicle using low-light binoculars, thermal-image night vision goggles and Infrared equipment. Lions were habituated to the observation vehicles and the same vehicle was used for extended periods (5-10 years per vehicle, n=3) to ensure that observations on their behaviour were not influenced by the vehicle. During observations on hunting behaviour, the vehicle remained stationary at a safe distance and care was taken not to disturb the lions or the prey animals that they approached. When aspects of their hunting or feeding behaviour could not be observed visually, the information was obtained through spoor reconstructions following the methods described by Liebenberg (1990), Bothma & Le Riche (1993) and Stander et al. (1997).

Home range analyses were based on the daytime resting spots of lions with at least 24 hours between fixes to ensure independence. Home range size was calculated using the Minimum Convex Polygon (MCP, Harris et al. 1990). Sufficiency of sample size was tested by determining whether or not or not an asymptote of home range estimate was reached. Spatial analysis of home range data and mapping was done using ArcView 3.2 (Johnston 1998).

In addition to monitoring the movements of radio-collared lions to determine the frequency with which they visited the coast, the coastal habitat itself was surveyed every quarter for lion tracks and other signs of lions utilising the habitat. When the Hoanib Floodplain pride began utilising marine food items along the coast in May 2017, a concerted effort was made to record an unbiased sample of the food items killed and consumed. During an 18-month period, between May 2017 and November 2018, the lions were observed for periods of between 24 hours and seven continuous days to record their food intake.

RESULTS AND DISCUSSION

Home ranges and movement patterns

After the demise of the Desert lion population that occupied the coastal habitat and utilised marine food resources during the 1980s, there were no resident lions in the SCNP for more than a decade, between 1990 and 2001. As the population recovered from the decline and numbers increased, their distribution expanded and by mid-2001 several prides began utilising sections of the SCNP (Stander et al. 2018).

The first record of lions returning to the ocean came early in 2002, when three lionesses from the Hoaruseb Pride started exploring the coastline. Gradually more lions ventured into the SCNP and by 2012 a total of five prides (the Ugab, Huab, Uniab, Hoanib Floodplain & Hoaruseb prides) occupied home ranges that included the coastline (Figure 2). All five prides lived in large home ranges that extended ≥100 km inland from the ocean, which they maintained over many years (Table 1). The coastal

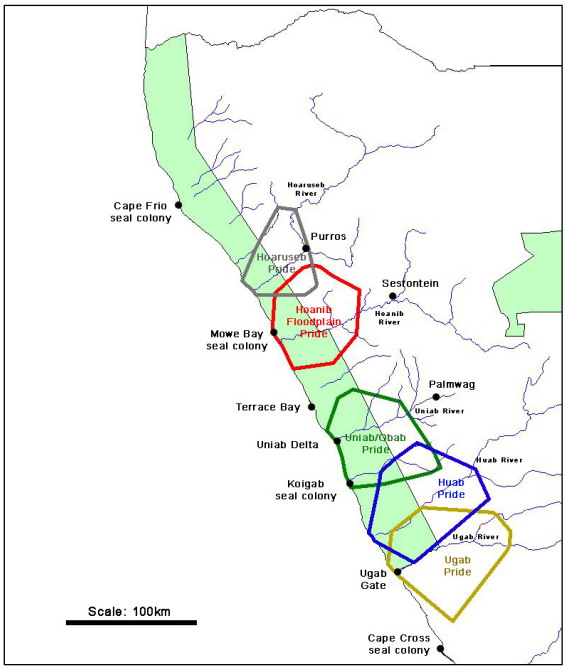

Figure 2: *The locations of four Cape fur seal colonies and the home ranges of five lion prides that utilised the coastal habitat in the Skeleton Coast National Park between 2002 and 2017*

Table 1: *The home range sizes, the proportion of coastal habitat in each home range and the duration of monitoring of five lion prides in northwest Namibia.*

Pride	Home range size (km^2)[1]	Coastal habitat (%)[2]	Duration[3]	No. of fixes
Hoaruseb	2,850	1.5	4y 10m	1,761
Hoanib Floodplain	4,410	5.4	9y 5m	3,452
Uniab/Obab	4,730	6.9	8y 7m	3,120
Huab	5,770	1.5	4y 2m	1,531
Ugab	5,870	1.3	4y 10m	1,804
Mean	**4,726**	**3.3**	**6y 5m**	**2,334**
SD	**1,227**	**2.6**		**883**

[1] Home range size based on the Minimum Convex Polygon method.
[2] Coastal habitat area as a percentage of the pride's home range size.
[3] Duration in years and months of continuous monitoring with GPS or satellite collars.

habitat, however, only formed a small part (mean=3.3%) of their respective home ranges.

With an average size of 4,726 km^2, lions from the desert population in the northwest of Namibia have the largest recorded home ranges for the species (Celesia et al. 2010, Loveridge et al. 2009, Van Orsdol et al. 1985, Schaller 1972). This, however, is to be expected because ranging behaviour of animals is affected by a number of ecological factors (Gittleman & Harvey 1982, East 1984). Amongst social carnivores, home range size is influenced by the distribution and availability of food items (Macdonald 1983) where the scarcity of resources may lead to larger ranges (Mills & Knowlton 1991). This is especially relevant when the distribution of food resources is heterogeneous (Macdonald & Carr 1989). The arid environment of the Northern Namib supports low densities of suitable prey animals for lions that are also highly variable in their distribution. Lions have to be resourceful by hunting a range of different prey species in a wide variety of habitats in their home range, and by expanding their range when food is scarce.

Since the distribution of prey animals in the heterogeneous habitat of the Northern Namib is a function of patchy and unpredictable rainfall (Sharon 1981, Viljoen 1989, Lu et al. 2016), it is to be expected that the movement patterns of lions will not be uniform (Macdonald & Carr 1989). The behaviour of adult lions in the established prides suggested that they maintain a mental map of the food resources in their home ranges, and that they visit these food patches at particular intervals. Two of the prides (Hoanib Floodplain and Uniab/Obab), where the coastal habitat formed >5% of their respective home ranges, visited the coast at irregular intervals.

The Hoanib Floodplain pride visited the coast on eight occasions between August 2014 and November 2015 (Figure 3a & b). On average they spent 7.5 days (range: 4-14 days) along the coast, where they captured mainly gemsbok that are attracted to the fresh-water springs and green grass at the mouth of the Hoanib River. In between these visits the lions moved inland, up to 62 km from the mouth of the Hoanib River, for an average of 55.7 days (range: 12-156 days, n=7).

The Uniab/Obab pride visited the coastal habitat at the mouth of the Uniab River on six occasions between January and November 2015 (Figure 4a & b). They fed on gemsbok and ostrich (Struthio camelus) that are attracted to green grass and several small fresh-water springs at the Uniab Delta. The lions spent an average of 23.3 days (range: 7-60 days) in the coastal habitat at the Uniab Delta. In between these visits they moved inland, up to 38.9 km from the mouth of the Uniab River, for an average of 20 days (range: 5-41 days, n=5).

Predation and consumption of marine food items

The first confirmed evidence of lions utilising marine food items along the Skeleton Coast came in March 2006 when lionesses from the Hoaruseb pride were observed feeding on a Cape fur seal on a beach north of the Hoaruseb River. During the next ten years, lions were observed feeding on adult seals on a total of nine occasions. Similar to the findings by Bridgeford (1985) from the early 1980s, most of the incidents occurred in the vicinity of the Hoanib and Hoaruseb Rivers with two records from the Uniab River and one from the Huab River (Figure 2). At least three seals were killed by lions and since the cause of death of the remaining six seals was not confirmed, they may have been scavenged.

Up until the end of 2016 the killing and/or scavenging of seals by lions in the SCNP was opportunistic and sporadic. There are four Cape fur seal colonies situated within reach of where lions were distributed during that period (Figure 2). Based on the movements of radio-collared lions and spoor surveys along the coast, none of the lions visited the colonies, nor did they appear to be aware of the rich food resources on offer.

Early in 2017, when conditions for lions throughout the Desert population were difficult due to poor rainfall, the Hoanib Floodplain pride and the Uniab/Obab pride started using the rich marine food source along the coast. They were also the two prides with the largest proportion of coastal habitat in their respective home ranges (Table 1) and that visited the coastline most often.

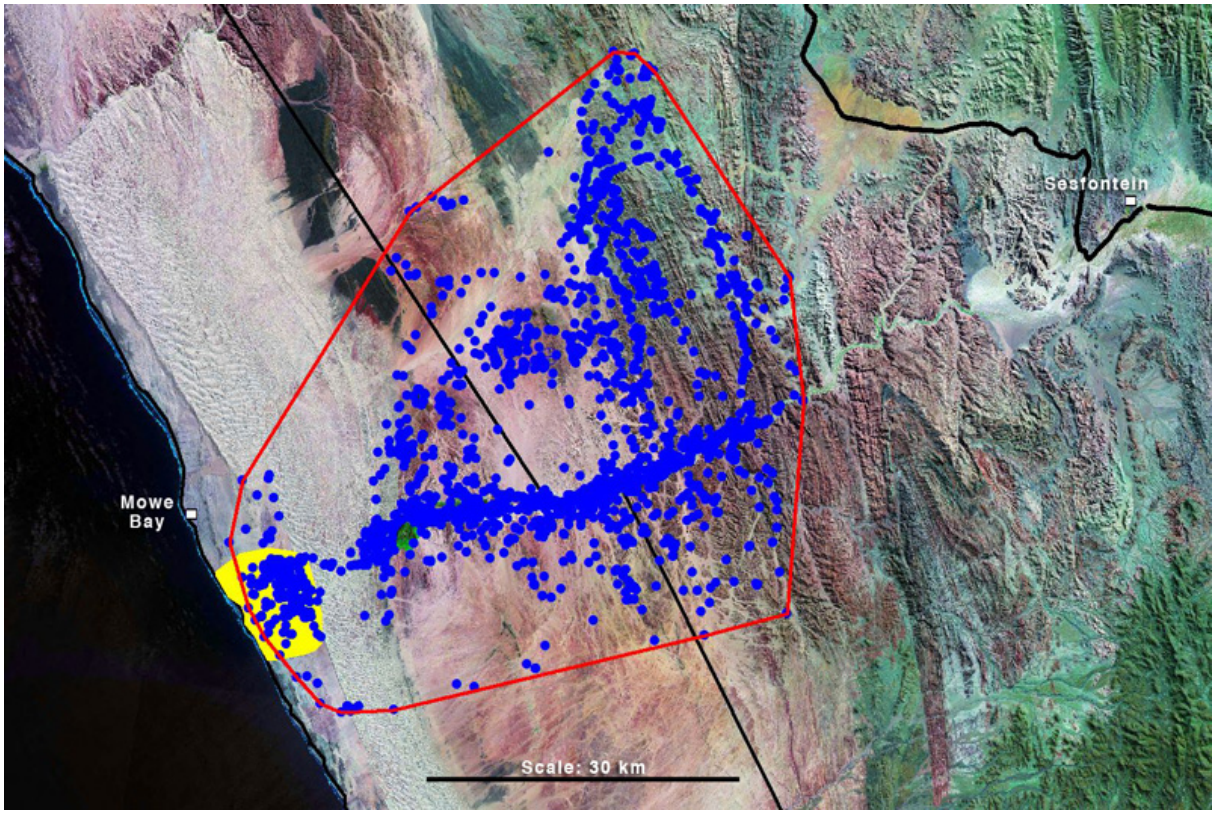

Figure 3a: *The home range area and movements of the Hoanib Floodplain pride in relation to the coastal habitat around the mouth of the Hoanib River (yellow area) between August 2014 and November 2015 (See Figure 3b).*

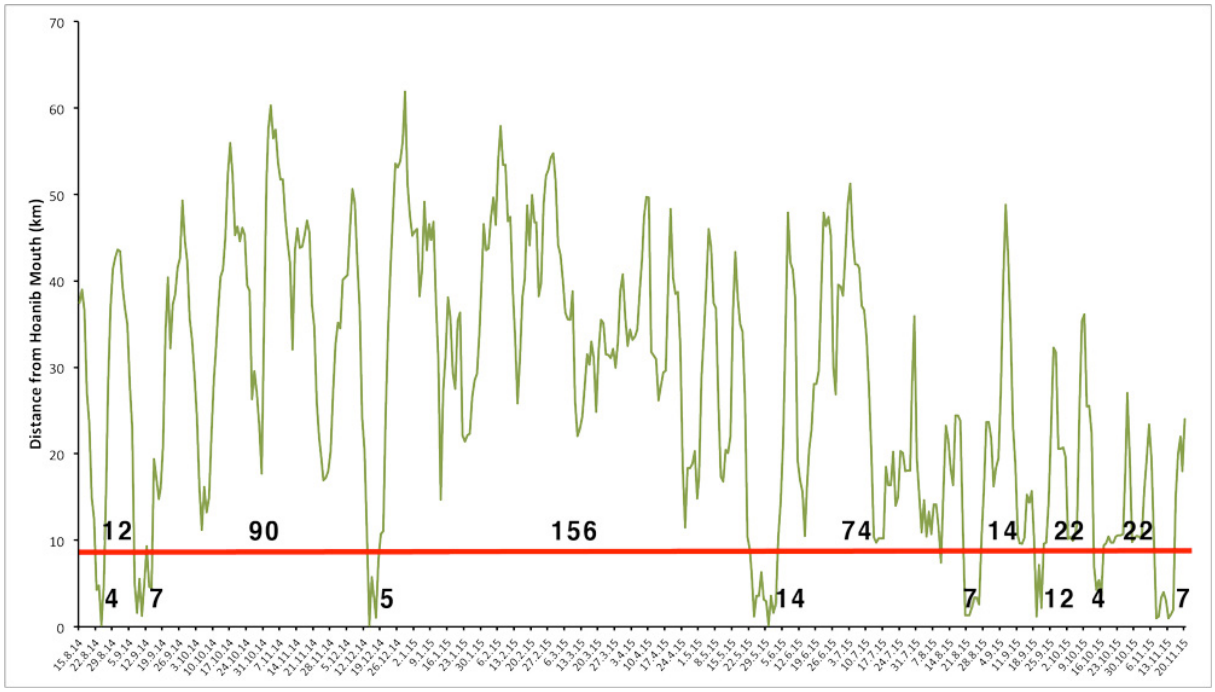

Figure 3b: *The movements of the Hoanib Floodplain pride displayed as sequential distances from the coastal habitat around the mouth of the Hoanib River between August 2014 and November 2015. The yellow area on the map (see Figure 3a) and the area below the red line on the graph denote the coastal habitat at the mouth of the Hoanib River. The numbers of days that the Hoanib Floodplain pride spent at the coast are indicated by the numbers below the red line and the number of days further inland by the numbers above the red line.*

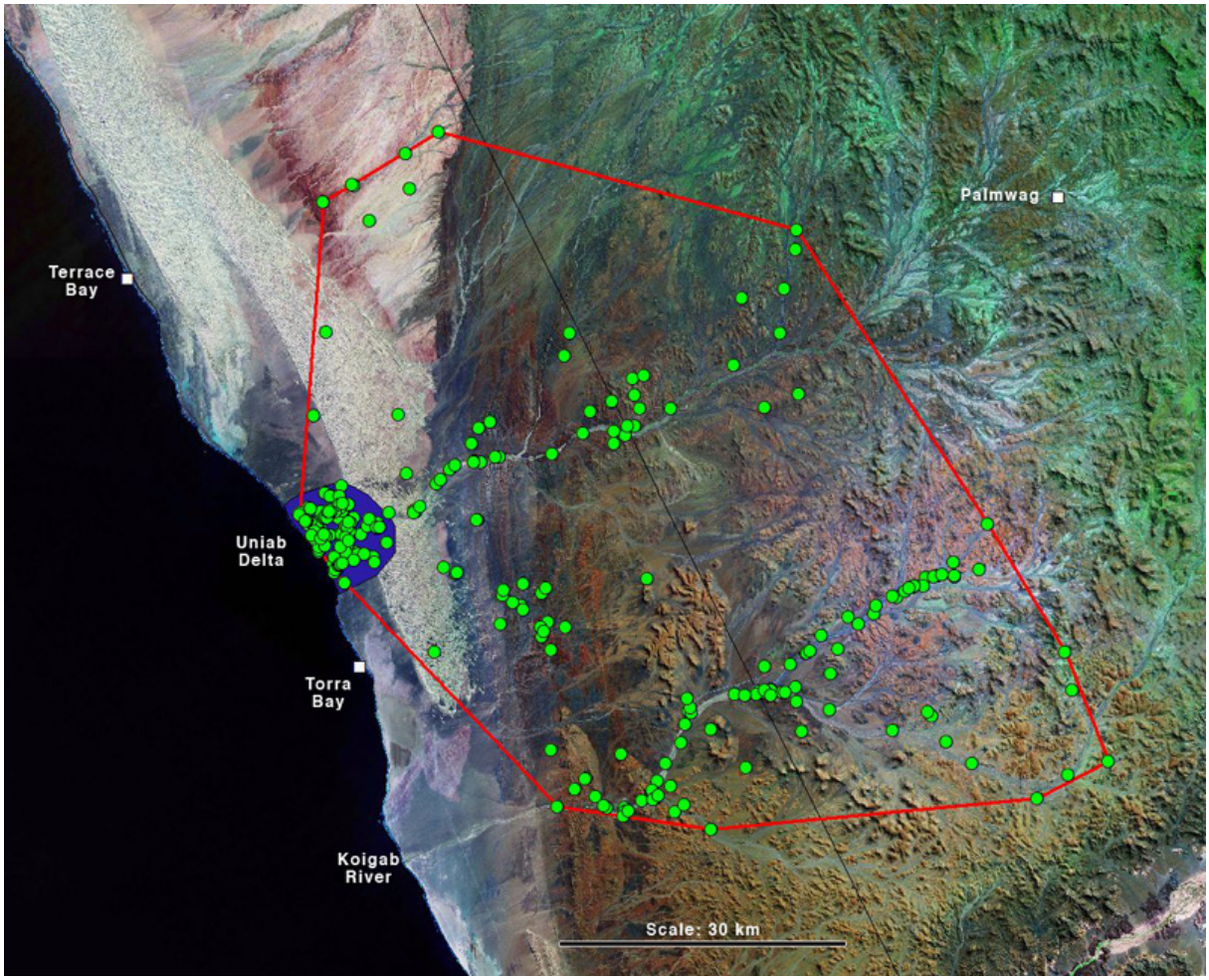

Figure 4a: *The home range area and movements of the Uniab/Obab pride in relation to the coastal habitat at the Uniab Delta (yellow area) between January and November 2015 (See Figure 4b).*

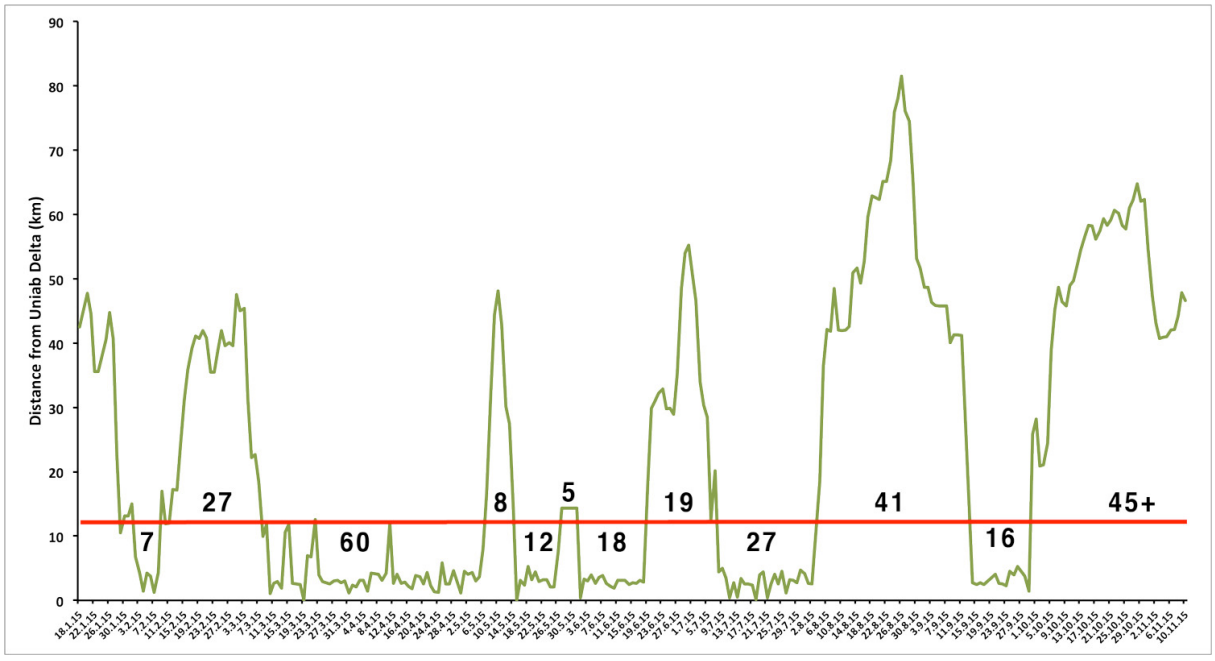

Figure 4b: *The movements of the Uniab/Obab pride displayed as sequential distances from the coastal habitat at the Uniab Delta between January and November 2015. The yellow area on the map (see Figure 4a) and the area below the red line on the graph denote the coastal habitat at the Uniab Delta. The number of days that the Uniab/Obab pride spent at the coast are indicated by the numbers below the red line and the number of days further inland by the numbers above the red line.*

Lions from the Uniab/Obab pride have been visiting the Uniab Delta on a regular basis since 2014. They moved along the coastal zone between Torra Bay and Terrace Bay and fed primarily on gemsbok and ostriches. In April 2017 one lioness that was in poor condition started killing cormorants at Torra Bay. During a two-day period, she was observed catching and consuming six white-breasted cormorants, four Cape cormorants and one adult brown hyaena. The lioness then moved further south along the coast and started to prey on Cape fur seals from the Koigab colony. Over a period of four weeks she killed and consumed a minimum of eight adult seals.

At the mouth of the Hoanib River three young lionesses from the Hoanib Floodplain pride began depending on a marine diet in March 2017. Their mother died of natural causes when the lionesses were barely a year old. Driven by hunger and desperation, the young lionesses found their way over the dunes and swam onto an island at a fresh-water spring near the coast. Here they started killing cormorants that roost on the island at night (Figure 5a). They became skilled in hunting a wider range of wetland birds, including flamingos and red-billed teals (*Anas erythrorhyncha*). The large numbers of resident Cape and white-breasted cormorants provided them with a nutritious and reliable marine diet. The lionesses began following the large flocks of cormorants and hunting them at night on the mud-flats and along the coastline (Figure 5b). This brought them into contact with Cape fur seals from the Möwe Bay colony that rest on the beaches. At first the lions scavenged seal carcasses that they found along the beaches (n=5), and then they expropriated seal carcasses from brown hyaenas (n=2). Early in 2018 the lionesses started killing seals themselves. Initially they took only juveniles of less than a year old, but as they became more experienced they selected larger seals of >50kg, including a few adult females (Figure 5c & d).

During visual observations on 62 days and supplemented by spoor reconstructions in the coastal habitat between May 2017 and November 2018, the lionesses killed and consumed a total 89 animals of eight different species (Table 2). The majority of their food items were cormorants (n=60) and seals (n=13). The 89 food items provided an estimated 701 kg of edible biomass that the lionesses consumed. Marine species (seals, cormorants and flamingos combined) contributed 79% of the food items and 86% of the biomass that the lionesses consumed during the observation periods. On numerous occasions the lionesses were observed exploring the intertidal zone and investigating items in shallow water (Figure 5c). But it was not possible to determine whether or not they utilised any other marine organisms.

Figure 5: *Lionesses foraging along the Namibian coastline: (a) catching cormorants on a small island, (b) hunting cormorants at the Hoanib Lagoon, (c) foraging along the intertidal zone, and (d) feeding on a Cape fur seal.*

Table 2: *The number of recorded prey species killed and the estimated biomass consumed by the Hoanib Floodplain pride in the Skeleton Coast National Park, between May 2017 and November 2018.*

Species	Number	Biomass (kg)[1]
Gemsbok *Oryx gazella*	1	65
Porcupine *Hystrix africaeaustralis*	2	19
Black-backed jackal *Canis mesomelas*	4	12
Cape fur seal *Arctocephalus pusillus*: Juvenile (<1 year) Sub-adult & adult (>50 kg)	 13 5	 273 240
Cape cormorant *Phalacrocorax capensis*	47	61
White-breasted cormorant *Phalacrocorax carbo*	13	26
Red-billed teal *Anas erythrorhyncha*	2	1
Greater flamingo *Phoenicopterus roseus*	2	4
Total	**89**	**701**

[1] Edible biomass was calculated by subtracting the percentage inedible biomass from the mass of the prey animal or the known mass of an adult female of the species.

The use of marine food resources by lions in the SCNP is an adaptation to the constraints imposed by their environment. Apart from the information presented by Bridgeford (1985) for lions from the same area during the 1980s, there is no evidence of lions utilising marine species anywhere else throughout their range (Carlton & Hodder 2003, Hayward & Kerley 2005). There are also currently no free-ranging lions that utilise or are resident in coastal habitats (Riggio et al. 2013, Ripple et al 2014). Specialising on unusual prey species, however, is not uncommon and in some areas lion prey on porcupines (Eloff 1984), rhinoceroses (Brain et al. 1999, Matipano 2004) and elephants (Ruggiero 1991).

The role of maritime mammal predation on marine intertidal communities in the transfer of energy between trophic levels is generally poorly understood, but recent studies have demonstrated the importance of landward flow of energy between the sea and the land (Polis et al. 1997). Furthermore, marine resources are an important source of energy and nutrients to many maritime mammal populations (Stapp et al. 1999). When lions identified the value and availability of marine foods along the Namibian coastline in May 2017, they began utilising the resource. The Hoanib Floodplain pride, in particular, currently derive a substantial proportion of their food items and biomass from marine resources. In other arid areas and ecosystems with high seasonal fluctuations in food availability many coastal carnivore populations rely on a marine diet when their terrestrial food items are scarce (Suraci et al. 2006), such as coyotes (*Canis latrans*) in the arid areas of Baja California that feed on a range of marine species, including mammals, sea turtles and birds (Rose & Polis 1998), Arctic foxes (*Alopex lagopus*) at the Bering sea (Fay & Stephenson 1989) and many examples of bears (*Ursus* spp.) in British Columbia, Canada & Alaska (Carlton & Hodder 2003).

The marine resources along the Skeleton Coast are potentially a valuable and reliable source of nutrients and energy to the Desert lion population. When the Skeleton Coast lions of the 1980s were killed, their knowledge of the marine food resources along the coast was lost as well. Once conditions changed and became favourable again in 1997, the population recovered within four years and repopulated several of their former ranges in the SCNP. For the next 15 years, lions moved to the ocean occasionally and inspected the coastline, but they did not forage along the intertidal zones, as their predecessors of the 1980s did. The knowledge of the rich marine food resource was only regained in 2017. The importance of marine resources to the survival of many terrestrial mammals, including the Skeleton Coast lions, may have been overlooked (Stapp et al. 1999). In the arid environment of the Northern Namib, with its variable rainfall patterns and unpredictable distribution of food items, the rich marine resources along its coastline can provide an important and reliable source of food to the lion population.

CONCLUSION

After an absence of more than 35 years, lions have returned to the coastal habitat of the SCNP to prey on marine organisms. As a species, lions are now on the list of maritime mammals, as the largest of the coastal carnivores, that prey on marine organisms.

Conflict between livestock farmers and lions during the 1980s resulted in a considerable decline in the population and lions were absent from the SCNP for more than ten years. Once conditions had improved by 1997, the Desert lion population recovered and repopulated the SCNP within four years. Five distinct prides utilised sections of the coastline. Due to the constraints imposed by the hyper-arid environment they occupied large home ranges – the largest yet recorded for the species. The coastal habitat formed a small proportion of their large home ranges, but data from two prides revealed that the lions visited the coast regularly.

Following the recovery of the population and the return of lions to the coast, the incidents of predation or scavenging on Cape fur seals appeared

opportunistic and occurred sporadically for more than a decade. In 2017, lions from two prides began to forage along the coastal habitat and the intertidal zone, where they mainly preyed on cormorants and Cape fur seals. The lions had found a rich and reliable marine resource that can provide then with an important source of energy. Preliminary observations of lions investigating and foraging along the intertidal zones suggest that they may learn to prey on other marine organisms, like shellfish, crabs or sea turtles. The intertidal zones along the Skeleton Coast provide a rich source of energy that the Desert lion population could rely on when their traditional terrestrial food resources are low.

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